Tobias Naaf

# Floristic homogenization and impoverishment – herb layer changes over two decades in deciduous forest patches of the Weser-Elbe region (NW Germany)

Ph.D.-Thesis

Institut für Biochemie und Biologie, Universität Potsdam
Leibniz-Zentrum für Agrarlandschaftsforschung, Müncheberg

# Floristic homogenization and impoverishment – herb layer changes over two decades in deciduous forest patches of the Weser-Elbe region (NW Germany)

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Tobias Naaf

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# Table of Contents

# General Introduction

Humans have altered their environment all over the planet, most intensively during the last centuries. Substantial environmental alterations include land transformations, alterations of the biogeochemical cycles and the transportation of species across biogeographic barriers (Vitousek et al. 1997). Conversions from native ecosystems to agricultural and urban lands have led to a loss of natural habitats and to habitat fragmentation (Andrén 1994; Vellend 2003). The release of $CO_2$ and other greenhouse gases to the atmosphere has altered the global climate (IPCC 2007). The addition of fixed N to terrestrial ecosystems has caused eutrophication and acidification (Bobbink et al. 2010). These and other alterations have been occurring more rapidly than any natural environmental changes in the Earth's history and are expected to accelerate in the future (Tilman & Lehman 2001). As a result, we observe a worldwide loss of species that are not able to survive in a human-modified environment (Chapin et al. 2000; Dirzo & Raven 2003). At the same time, human-induced invasions of exotic species cause a mixing of once disparate floras and faunas (McKinney & Lockwood 1999). These changes occur across all taxonomic groups (Lockwood & McKinney 2001) and across spatial scales (e.g., Rooney et al. 2004; Qian & Ricklefs 2006; Smart et al. 2006).

Despite our awareness of these abiotic and biotic changes, we still have a limited understanding of how particular environmental changes affect particular biological communities. This understanding, however, is necessary to be able to reduce or prevent further biotic impoverishment. Although extinctions and invasions occur at a rate of several magnitudes higher than before humanity's dominance on Earth, shifts in species composition are difficult to verify and analyze in a scientific manner, because verifiable changes take place over time periods that are long in relation to the grant duration of ordinary research projects (Franklin 1989). Also, changes are often latent. For instance, many invasive species outlast with a few individuals for several decades or even centuries after their introduction before they start to spread rapidly (Kowarik 2003). Long-living organisms, such as many forest herbs, respond slowly or delayed to environmental changes (Vellend et al. 2006; Kuusaari et al. 2009). To be able to quantify shifts in species composition and diversity and to relate these shifts to environmental changes, long-term studies are essential (Franklin 1989; Bakker et al. 1996). In vegetation science, the resurvey of (semi-)permanent plots represents the most reliable approach to study vegetation dynamics and the underlying mechanisms (Pickett 1989; Bakker et al. 1996; Faliński 2003).

With this study, I took advantage of the rare situation, that plot locations in a large number of forest stands in the Weser-Elbe region in NW Germany were accurately documented at the time of a first survey more than 20 years ago. Moreover, with the help of the researcher who established the plots (the supervisor of this thesis), it was possible to relocate and resurvey a substantial number of plots (*n* = 175) using the original methods.

## Why another resurvey study in temperate forests?

There are numerous studies on long-term changes in forest vegetation both in Europe and other temperate regions (Appendix I). However, most of these studies suffer from one or several of the following drawbacks. Often the studies are confined to one single forest or few stands located close to each other (Kwiatkowska 1994; Lameire et al. 2000; von Oheimb & Brunet 2007). While these studies provide interesting insight into the local processes involved in vegetation dynamics, the responsible drivers are often specific for that location, and results cannot be generalized to larger spatial scales. Studies on a regional scale are often not based on (semi-)permanent plots, but rely on "comparable" plots (i.e., in "close" proximity) for the resurvey (Hédl 2004; Kirby et al. 2005; Wiegmann & Waller 2006) or compare phytosociological relevés of a certain type taken in intervals (without relocation; Bürger 1991; Diekmann & Dupré 1997; Haveman & Schaminee 2005). These studies may reveal general trends in species shifts in response to large-scale environmental changes, especially when based on large datasets. However, for particular species, the risk of bias due to misplacement errors or an uneven distribution of relevés over space, time and authorship (Haveman & Janssen 2008) may be substantial. Furthermore, many resurvey studies in forests focus on changes in response to one or few specific environmental drivers (Appendix I). However, when the species composition is determined by several environmental constraints, simultaneous responses to several environmental alterations are likely (Tilman & Lehman 2001). Quantitative estimations of the relative importance of potential environmental drivers are still missing. Moreover, the identification of changes in species composition is often restricted to a taxonomic level or the use of Ellenberg indicator values. These restrictions make a comparison to results from regions with a different flora difficult and are of limited value for the identification of the underlying mechanisms. More recent concepts, such as functional diversity or beta diversity (see below), have been neglected so far.

With this study, I tried to extent the existing knowledge with a comprehensive analysis of different aspects of species compositional and diversity changes. The 175 plots are distributed across a 7600 km² region and could be relocated with an error of 1-2 m. Eight kinds of environmental alterations acting on various spatial scales (local to global) were considered as potential drivers of vegetation changes.

## Facets of plant species diversity

In the present study, the changes in species composition and diversity are viewed at the level of plant communities. Plant communities can be analyzed at three levels of abstraction, the taxonomic, functional and phylogenetic level (Webb et al. 2002; McGill et al. 2006; Prinzing et al. 2008). This study focuses on taxonomic and functional composition and diversity (Fig. I). While changes at the taxonomic level might be most relevant for conservation purposes, they are of limited value for the comparison with other studies and for our understanding of the processes involved. Assessing species-compositional changes in terms of functional traits does not only allow for generalizations by comparisons with studies from other biogeographic regions but also for a deeper insight into the underlying mechanisms (McGill et al. 2006). The performance of species in a community in response to environmental changes is determined by their traits (Lavorel & Garnier 2002). The importance of functional diversity, i.e., the extent of functional trait differences among the species in a community (Tilman 2001), rather than species richness per se for aspects of ecosystem functioning, such as primary production or nutrient cycling, has often been stressed (Tilman et al. 1997; Díaz & Cabido 2001; Hooper et al. 2005). Functional diversity is also related to the mechanisms that drive the assembly of species from a regional pool into local communities (Hooper et al. 2005; de Bello et al. 2009; Thompson et al. 2010). On the one hand, competition among species sets a lower limit to the trait similarity among coexisting species, resulting in large trait differences within communities (MacArthur & Levins 1967; Weiher & Keddy 1995; Wilson 2007). On the other hand, environmental filters select for those traits that enable species to cope with environmental adversity, thus limiting the range of possible trait values (Keddy 1992; Díaz et al. 1998; Cornwell et al. 2006). The analysis of functional diversity can therefore help to understand the coexistence and diversity of species in communities. Aspects of functional diversity and community assembly have rarely been considered in studies on long-term changes in forest vegetation so far. In this study, I analyzed functional diversity patterns to reveal assembly mechanisms in forest plant communities and their changes over time (Fig. I).

Plant species diversity can be partitioned into its spatial components, i.e. the within-community (α) diversity and the between-community (β) diversity (Whittaker 1972; Lande 1996; Jost 2007). Until recently, resurvey studies focused on changes in α diversity only (e.g., Brunet et al. 1996; Lameire et al. 2000; Taverna et al. 2005). At the turn of the century, the loss of biotic distinctiveness in communities or whole floras and faunas (termed biotic homogenization) has been recognized as an important form of biotic impoverishment (McKinney & Lockwood 1999; Lockwood & McKinney 2001; Rooney et al. 2004). Since then, changes in β diversity in response to environmental changes have been receiving increasing attention (e.g., Smith et al. 2006; Jurasinski & Kreyling 2007; Rogers et al. 2008). In temperate Europe, studies on long-term changes in forest vegetation have only very recently started to consider changes in β diversity (van Calster et al. 2007; Vellend et al. 2007; Keith et al. 2009; but see Persson 1980). It is still unclear whether biotic homogenization is a global phenomenon that occurs across biogeographic regions and across habitat types (Olden 2006; Castro & Jaksic 2008). Also, the relationship between changes in α and β diversity, i.e., the question under which circumstances a change in β diversity is more associated with species losses or species invasions, remains elusive (e.g., Rooney et al. 2004; Smith et al. 2006; Jurasinski & Kreyling 2007). The quantification of the degree of biotic homogenization (or differentiation) and associated changes in α diversity was a primary objective of this study (Fig. I). I took into account both the taxonomic and the functional level.

## What makes herb layer communities in temperate deciduous forests an interesting research object?

The forests in the European lowlands are strongly fragmented. In the study area, forest patches cover c. 9.8% of the landscape. At the time of maximum deforestation (around 1770) forest cover was even lower (c. 4.6%). The forested area was fragmented into several hundred patches with an average size of 20-30 ha (Kelm 1994). Forest fragmentation is considered a major threat to forest plant species diversity (Honnay et al. 2005) because it affects the viability of plant populations in several ways (Lienert 2004; Honney et al. 2005). Small, isolated populations encounter a higher risk of losing genetic variability through genetic drift, increased inbreeding and reduced gene flow between populations (Lienert 2004; Honnay et al. 2007). A lower genetic diversity may lead to a reduced reproductive success (Jacquemyn et al. 2002; Kolb 2005; Kolb & Lindhorst 2006) and a reduced evolutionary capacity to adapt to a changing environment (Lienert 2004). Indirectly, small populations suffer from fragmentation because they are less efficient in attracting pollinators. A reduced pollinator abundance and diversity results in a reduced reproductive success (Tomimatsu & Ohara 2002; Kolb 2008). Furthermore, fragmentation enhances the edge effect due to a larger perimeter-to-area ratio in small patches (Lienert 2004). Near the edge, forest species may suffer from an unfavorable microclimate, nutrient inputs from the surrounding agricultural landscape and increased competition by non-forest species (Honnay et al. 2005).

Typical forest species represent a group of plant species that are particularly affected by fragmentation (Kolb & Diekmann 2005). They exhibit a suite of traits that reflects their adaptation to continuous, relatively stable forest ecosystems characterized by infrequent small-scale disturbance (Honnay et al. 2005). These traits include high longevity, the ability to reproduce vegetatively, the production of few and heavy seeds, which are not persistent in the soil, and a lack of specific adaptations to long-distance dispersal (Bierzychudek 1982; Graae & Sunde 2000; Bossuyt et al. 2002; Whigham 2004; Kolb & Diekmann 2005). This combination of attributes can be summarized as a low dispersability or colonization capacity (Ehrlén & van Groenendahl 1998; Verheyen et al. 2003). Migration rates of typical forest species are often low (<2 m yr$^{-1}$; Brunet & von Oheimb 1998; Bossuyt et al. 1999; Dzwonko 2001; Orczewska 2009). Slow-colonizing forest species are known as ancient forest species, because they are restricted to forest patches with a habitat continuity of several centuries (Peterken & Game 1984; Wulf 1997; Hermy et al. 1999). Post-agricultural forests may have a lower species richness of these forest plants than ancient forests even after several 100 years (Vellend 2003). Thus, ancient forest species are considered most sensitive to environmental alterations and their survival will largely depend on their environmental tolerance (Honnay et al. 2002).

Although there is evidence for a lower reproductive success of forest plants in small, isolated populations (Jacquemyn et al. 2002; Tomimatsu & Ohara 2002; Kolb & Lindhorst 2006), and for negative effects of reduced patch area and patch connectivity on the occurrence of some forest species (Dupré & Ehrlén 2002;

Jacquemyn et al. 2003; Kolb & Diekmann 2004), there is little evidence that forest fragmentation has led to large-scale extinctions of forest plant populations so far (Honnay et al. 2005; but see Vellend et al. 2006). Rather, even small forest patches may sustain a high richness of forest plant species for a long time (Honnay et al. 1999). This delayed response to fragmentation is due to the specific life history of typical forest plant species. Many forest plants have life spans of several decades and are able to persist during periods of unfavorable conditions via prolonged clonal growth (Inghe & Tamm 1985; Ehrlén & Lehtilä 2002). This makes them less vulnerable to genetic impoverishment and pollen limitation (Honnay et al. 2005). Thus, in regions, in which fragmentation took place not more than a few centuries ago, the time period since then may be not long enough to allow the observation of substantial extinctions (Dupré & Ehrlén 2002; Honnay et al. 2005). The forest fragments are therefore said to have an “extinction debt” (Tilman et al. 1994; Vellend et al. 2006). This implies that we may expect a gradual decline of forest plant species in response to fragmentation even without further environmental changes.

The high level of habitat fragmentation and the special characteristics of many forest plant species make forest plant communities in NW Germany an interesting research object for the study of long-term changes. All data used in the analyses of this study were collected in mature, deciduous forest stands with a habitat continuity of more than 200 years (Wulf 1997). Many of these ancient forest patches are assumed to represent remnants of larger forested areas that existed at least since the Neolithic (Kelm 1994). Despite an extensive exploitation during the last millennium, these forests still represent some of the most near-natural and most species-rich terrestrial ecosystems in NW Germany. Several of the typical forest species are listed as endangered species on the regional Red List (Garve 2004). Thus, any changes in plant species composition and diversity that would include losses of typical forest species would be unacceptable from a conservational point of view (Wulf & Kelm 1994). The quantification of these changes and the identification of the underlying mechanisms are therefore considered essential for conservation purposes.

## General objectives

The general objectives of this study can be summarized as follows (Fig. I):

(i) I aimed to quantify changes in plant species diversity at the taxonomic and functional level for all spatial components.

(ii) I intended to determine shifts in species composition in terms of species’ niche breadth and functional traits. Thereby, I tried to assess the degree of biotic impoverishment and to reveal changes in community assembly mechanisms.

(iii) I aimed at finding indications on the most likely environmental drivers for the observed changes.

## Outline of the study

This thesis consists of four chapters (Fig. I). These represent self-contained research papers that have been published or have been submitted for publication in international, peer-reviewed journals. They can be read independently and thus contain some redundant information, particularly on study area and methods. While their main intention was to pursue the general objectives mentioned above, their specific research questions sometimes go beyond these general objectives, particularly in Chapters 2 and 3.

All chapters were written by myself and are based on my own data analyses. I also collected the field data for the present-day situation and assembled the trait data. During the publication processes, I corresponded to editors and referees. All chapters were co-authored by Prof. Dr. Monika Wulf who contributed to the manuscripts in several ways. She set the stage for this study by having the general idea and securing the funding. Most importantly, she provided the historical plant community data and assisted me in relocating the original plots and calibrating my cover-abundance estimates. While Chapters 1 and 4 are the result of ideas that developed from our fruitful discussions, Chapters 2 and 3 are based on my own ideas that emerged from my literature research. M. Wulf reviewed all chapters and her comments helped to improve the manuscripts. Given her co-authorship, I will use the first person plural in the following.

**Chapter 1:** “Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale”

This chapter is dedicated mainly to the first and partly to the second objective. We quantified the changes in α and β diversity at the taxonomic level. The focus is on the question whether biotic homogenization occurs among the forest plant communities of the Weser-Elbe region and whether this homogenization is more associated with a decline in habitat specialists (i.e., a decrease in α diversity) or the invasion of habitat generalists (i.e., an increase in α diversity). Additionally, we explore the effect of applying three different β diversity measures on the outcome of our investigations.

**Chapter 2:** “Multiplicative functional diversity partitioning gives insight into assembly mechanisms in temperate forest plant communities”

The main purpose of this paper was to assess the benefit of a recently introduced method for the study of community assembly mechanisms and to demonstrate some general patterns in community assembly. Although this methodological focus is clearly beyond the objectives outlined above, the paper yielded some valuable results with respect to the first two objectives. The changes in α and β diversity in the forest plant communities of the Weser-Elbe region are quantified at the functional level and compared to those at the taxonomic level. We also assess, whether the community assembly mechanisms revealed by the diversity partitioning approach remained stable over time.

**Chapter 3:** “Community assembly mechanisms in temperate forest plant communities along gradients of soil fertility and disturbance and over time”

In this chapter, we studied the assembly mechanisms in the forest plant communities more thoroughly, taking into account the differences along the main environmental gradients. With regard to the second objective, we compared the distribution patterns of traits related to competition and reproduction between sampling periods to find out whether and where along the gradients community assembly mechanisms had changed.

**Chapter 4:** “Traits of winner and loser species indicate drivers of herb layer changes over two decades in forests of NW Germany”

This chapter is mostly dedicated to the third objective, but the second objective is inherently pursued as well. In the absence of plot-based data on the environmental conditions 20 years ago, we relied on a trait-based approach to find indications on the relative importance of the most likely environmental drives for the observed herb layer changes. Thereby, substantial species shifts as reflected by a high number of identified winner and loser species become evident.

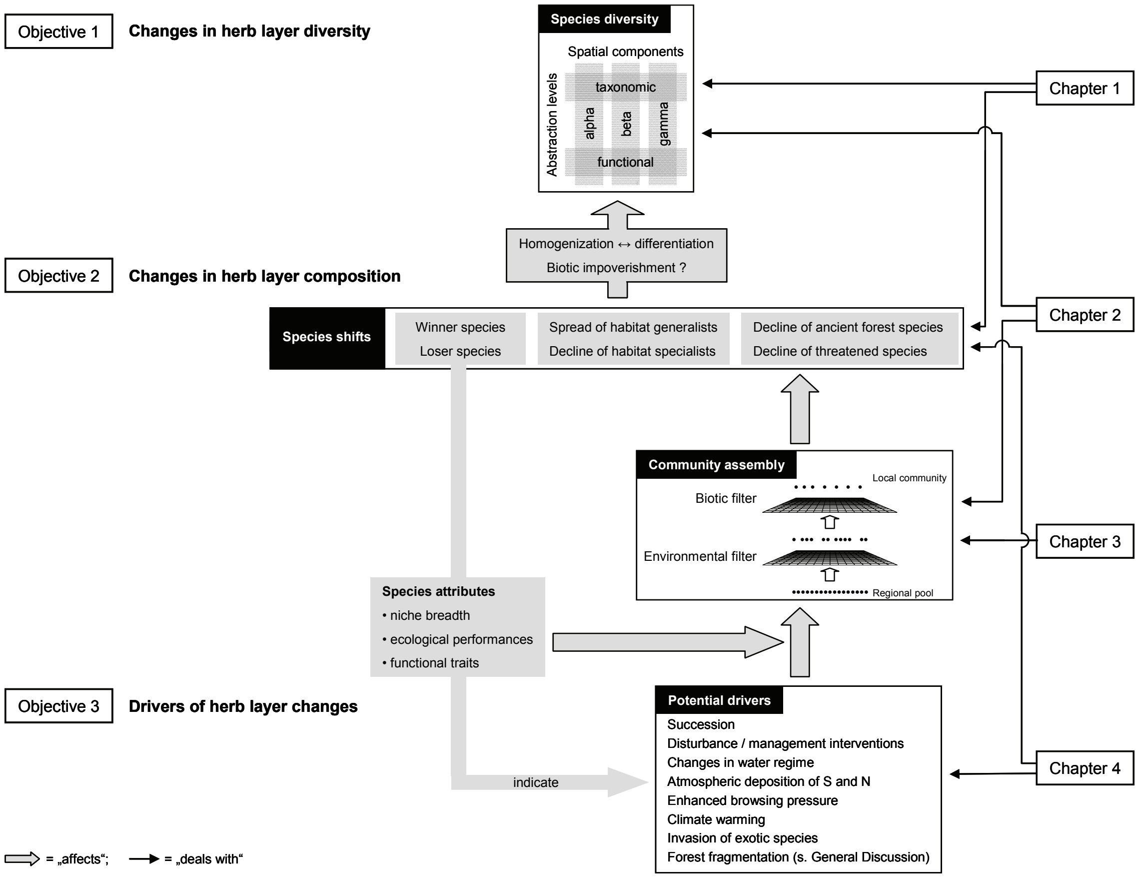

**Fig. I.** Structural relationship between the objectives, the main topics and the four chapters of this thesis.

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# Chapter 1

TOBIAS NAAF & MONIKA WULF

# Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale

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## 1.1 Abstract

In European temperate forests, changes in the compositional similarity among local plant communities (beta diversity) have rarely been studied due to the lack of adequate baseline data. Several studies, however, report the spread of common, generalist species or a decline in specialized, rare species. Both processes may lead to increased similarity among communities, i.e. biotic homogenization. To quantify changes in beta diversity, we resampled the herb layer composition of ancient broadleaf forests at 175 semi-permanent plots distributed across the Weser-Elbe region in NW Germany 20 years after first sampling. We hypothesized that beta diversity would have decreased on average as a result of a spread of habitat generalists and a decline in habitat specialists. After two decades, the forest communities did not yet exhibit severe biotic impoverishment, although there was a broad trend towards homogenization. The actual magnitude of change depended on which beta diversity measure was applied. The downward trend was primarily the result of the spread of native species that are able to tolerate broad pH and moisture ranges. A distinction between forest specialists (closely tied to forest habitats) and generalists (also found in open habitats) did not help explain changes in beta diversity. The study shows that on the regional scale and in habitats not yet threatened by the invasion of alien species, shifts in native species can promote biotic homogenization.

## 1.2 Introduction

A gradual increase in compositional similarity among formerly distinct biological communities is called biotic homogenization (Olden & Rooney 2006). This process has received much attention during the last decade (McKinney & Lockwood 1999; Olden & Rooney 2006). Biotic homogenization has been observed across an array of different taxonomic groups and at various spatial scales (Lockwood & McKinney 2001; Olden et al. 2004). Most previous studies on biotic homogenization have been conducted at a biogeographic level, i.e., they compared extant and historical species lists among sampling units that aggregated environmental heterogeneity (e.g., cities, counties or states) and were distributed across bioregional boundaries (e.g., states, countries or continents; Castro et al. 2007; McKinney 2004; Qian et al. 2008; Schwartz et al. 2006). These studies focused on the homogenizing or differentiating effects of alien species.

However, there are very few studies that have quantified changes in compositional similarity among local communities at a regional or landscape scale (Rogers et al. 2008; Rooney et al. 2004; Smart et al. 2006). Such studies are most relevant for conservation goals because conservation planning is often implemented at that scale (Ferrier 2002; Margules & Pressey 2000). They provide insight into ecological mechanisms, as species are observed within their habitats and in arrangement with competing species (Huston 1999). The lack of studies comparing local communities at the regional scale is probably due to the absence of adequate historical baseline data. Exact relocation and resurvey of locations that were surveyed in the past represent the only method for an exact quantification of changes in community differentiation for an explicit time interval (Olden & Rooney 2006). In the present study, we were able to use a broad historical dataset from 1986-88 comprising local forest plant communities from 175 semi-permanent plots in the Weser-Elbe region in NW Germany.

There are numerous long-term studies on changes in forest vegetation in temperate Europe, but hardly any of these studies address changes in compositional similarity or they do so only at the local scale (Persson 1980; van Calster et al. 2007). There are, however, studies that observed the spread of common, generalist species or the decline of more specialized, rare species, which are key processes that may result in community homogenization (McKinney & Lockwood 1999; Olden & Poff 2003). For instance, studies on the impact of atmospheric depositions and forest management on herb layer vegetation observed an increase in 'weedy' species, including ruderal, nitrophilous or non-forest species (Falkengren-Grerup 1995; Thimonier et al. 1992; van Calster et al. 2007). Others found a loss of specialized forest herbs that require high pH (Hédl 2004; Falkengren-Grerup & Tyler 1991; Tyler et al. 2002). A comparison of ancient (continuously forested for several centuries) and recent (on former agricultural fields) forests in several regions in Europe and NE North America found a reduced degree of community differentiation among recent forests (Vellend et al. 2007). However, to our knowledge, there has been no comparison of historical data with present-day data at a regional scale in order to determine if ancient forests in Europe are also subject to biotic homogenization. All forests surveyed in the present study were ancient.

Biotic homogenization does not always lead to biotic impoverishment. A decrease in beta diversity may be accompanied by an increase (e.g., Jurasinski et al. 2007; Smart et al. 2006) or a decrease in alpha diversity (e.g., Kwiatkowska 1994; Rogers et al. 2008). To assess conservation relevance, we not only have to determine the net shift in alpha and beta diversity, but also the quantity and identity of gained and lost species (Rooney et al. 2007). Therefore, we quantified shifts in the numbers of species of different groups of habitat specialists and generalists and related these numbers to the observed changes in beta diversity.

An increase in the compositional similarity among communities is equivalent to a decrease in beta diversity, i.e., the extent of differentiation of communities along environmental gradients (Whittaker 1972; Olden & Rooney 2006). Beta diversity is most often quantified with similarity or dissimilarity metrics (Jurasinski et al. 2009) and among the many available metrics (Koleff et al. 2003; Wolda 1981), Jaccard's index (Table 1) has been the most frequently used in studies on biotic homogenization (Olden & Rooney 2006). However, Jaccard's index has been criticized for being sensitive to differences in species richness among sites (Koleff et al. 2003). A simple metric that may be more appropriate in measuring real turnover in the sense that species are both gained and lost (beta diversity sensu Whittaker 1972) is Lennon's index (Koleff et al. 2003; a modification of Simpson's asymmetric index (Simpson 1943); Table 1). It was recently applied in several studies on the beta diversity of plant assemblages (e.g., Kühn & Klotz 2006; La Sorte et al. 2008). Both Jaccard's and Lennon's index rely on presence/absence data and cannot reveal smaller changes in community differentiation that are caused by shifts in species abundances. The Bray-Curtis dissimilarity index (Table 1) accounts for species abundances and is recommended for quantifying biotic homogenization (Olden & Rooney 2006). Like Jaccard's index, it is influenced by differences in species richness among sites (Wolda 1981). Although it is known that the observed magnitude of similarity or dissimilarity varies among different metrics, a comparison of the different outcomes for biotic homogenization when applied to local plant communities is still due.

**Table 1.** Dissimilarity indices used to quantify beta diversity.

| Reference | Formula | Legend |
|---|---|---|
| Jaccard 1912 | $J = 1 - \frac{a}{a+b+c} = \frac{b+c}{a+b+c}$ | *a* is the number of species common to both sites; *b* and *c* are the numbers of species only present in one of the sites; min(*b*,*c*) refers to the smaller value of *b* and *c* |
| Lennon et al. 2001 | $L = 1 - \frac{a}{\min(b,c) + a} = \frac{\min(b,c)}{\min(b,c) + a}$ | |
| Bray & Curtis 1957 | $BC = \frac{\Sigma \lvert x_{ij} - x_{ik} \rvert}{\Sigma \left( x_{ij} + x_{ik} \right)}$ | $x_{ij}$ and $x_{ik}$ are the abundances of species *i* at sites *j* and *k*, respectively |

The main objectives of this study were (i) to quantify the degree of homogenization or differentiation of forest plant communities at the regional scale, (ii) to determine the contribution of shifts in the numbers of habitat specialists and generalists, and (iii) to compare the outcomes when using three different dissimilarity indices to measure beta diversity. We hypothesized an average decrease in beta diversity associated with a decrease in habitat specialists on the one hand and an increase in habitat generalists on the other. Due to considerable differences in species richness among sites, we expected marked differences in outcomes when using Jaccard's vs. Lennon's index. We also expected the Bray-Curtis index to indicate stronger changes in community differentiation than the qualitative indices.

## 1.3 Methods

### Historical data set and resampling

In order to quantify changes in beta diversity, we resurveyed the herb layer communities of 175 deciduous forest stands distributed across the 7 600 km² Weser-Elbe region in the lowlands of NW Germany (Fig. 1). The climate is suboceanic with a mean annual precipitation ranging from 713 mm (Bremen) to 796 mm (Hamburg; data available at http://www.dwd.de). The investigated forests grow on loamy ground moraines with varying proportions of sand and clay. Soil types range from eutric cambisols to stagnosols and (histic) gleysols (Wulf 1992).

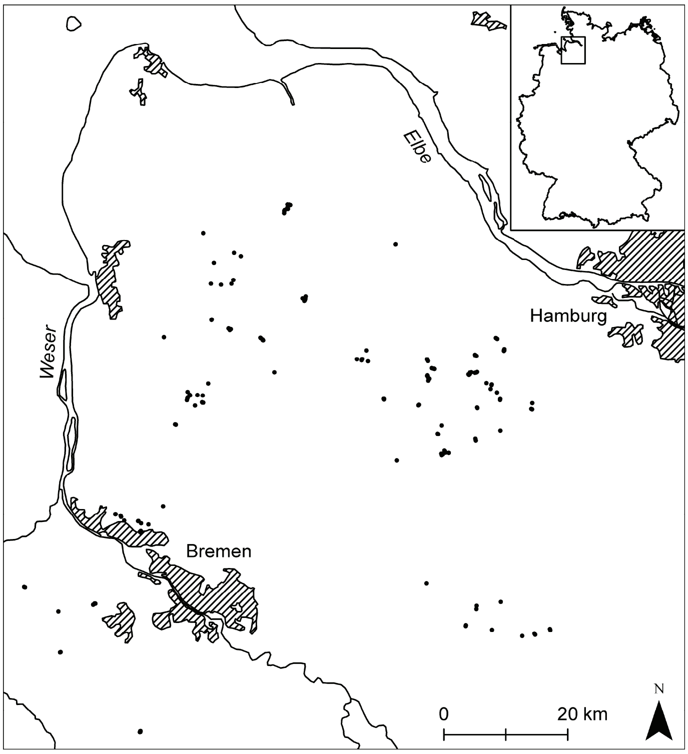

**Fig. 1.** Distribution of the 175 study sites (black dots) across the Weser-Elbe region in NW Germany.

About 9.8% of the region is covered by forest, of which 25% is ancient (Kelm 1994). The forests are strongly fragmented and embedded in an intensely cultivated agricultural landscape. Deciduous broadleaf forests constitute less than 25% of the forested area (Wulf & Kelm 1994).

The forests were initially surveyed by the co-author from 1986 to 1988 (hereafter 1988) with the main aims being to provide a phytosociological classification of lowland forests on mineral soils (alliances Alno-Ulmion and Carpinion) and to relate community types to nutritional status and groundwater level. The site conditions cover a soil acidity and a moisture gradient. The overstory is dominated by alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) on wet and moist sites, by oak (*Quercus robur*) and hornbeam (*Carpinus betulus*) on moderately moist sites and by European beech (*Fagus sylvatica*) on slightly moist sites (Wulf 1992). All stands were mature in 1988 and located in ancient forests (habitat continuity > 200 years; Wulf 1997). Plots were placed in undisturbed sites with an evenly closed canopy and a homogenous herb layer composition. Plot size ranged from 100 to 400 m². We do not believe the variation in plot size was problematic because we did not find a significant species-area relationship (extra variance explained by plot size in a linear regression model ($R^2 = 0.290$; $P \leq 0.001$) including also light availability, pH and moisture as predictors: 1.2% with $P = 0.094$).

Of the original 415 plots, 92% could be exactly (with an error of 1 to 2 m) relocated in 2008. Two types of documents were used for relocation: coordinates drawn from maps at a scale of 1 : 25 000 (with an error < 100 m) and sketches of each plot showing the tree trunks and other structures, like stumps or large stones along the plot margins. Unfortunately, many plots were situated close to each other in the same stand and thus represented pseudoreplicates. Of these, we selected only the plot that was least disturbed by forest management activities for our resurvey. Since the original plots were all placed in undisturbed sites, including more disturbed plots in the dataset would result in an overestimation of changes due to management activities. Some of the plots (23 across 15 sites) had been too strongly altered by management practices and as a consequence were excluded. In the remaining 175 sites, management activities during the last two decades ranged from no disturbance at all to single trees logged or wind-thrown to several trees removed causing soil disturbance (driving tracks) and larger canopy gaps.

This biased set of plots was used to resurvey the herb layer composition in 2008/09 (hereafter 2008) with the original method used by Wulf (1992). The abundance of all vascular plant species in the herb layer (≤ 1 m height; tree seedlings and saplings excluded) was recorded in spring and summer using a combined cover-abundance scale (Table 2; Barkman et al. 1964). To ensure consistent estimation of cover-abundance degrees between sampling periods, the estimates made by the researcher in 2008 were calibrated with those of the original researcher on several plots until no further deviations occurred. After matching the species lists, the combined species list contained 158 taxa (154 species and 4 superspecies).

**Table 2.** Cover-abundance scale used for plant species recording.

| BDS scale [a] | # Individuals | Cover [%] | Numeric scale [b] |
|---|---|---|---|
| +r | 1 – 2 | < 1 | 1 |
| +p | 3 – 20 | < 1 | 2 |
| +a | 3 – 20 | 1 – 2 | |
| +b | 3 – 20 | 2 – 5 | |
| 1p | 20 – 100 | < 1 | 3 |
| 1a | 20 – 100 | 1 – 2 | |
| 1b | 20 – 100 | 2 – 5 | |
| 2m | > 100 | < 5.0 | 4 |
| 2a | any | 5.0 – 12.5 | 5 |
| 2b | any | 12.5 – 25.0 | 6 |
| 3a | any | 25.0 – 37.5 | 6.5 |
| 3b | any | 37.5 – 50.0 | 7 |
| 4a | any | 50.0 – 62.5 | 7.5 |
| 4b | any | 62.5 – 75.0 | 8 |
| 5a | any | 75.0 – 87.5 | 8.5 |
| 5b | any | 87.5 – 100 | 9 |

[a] according to Barkman, Doing & Segal (1964)

[b] numeric transformation according to van der Maarel (1979)

## Data analysis

*Changes in beta diversity*

We aimed to relate beta diversity and its changes to site-specific variables including species numbers of certain species groups. Therefore, we defined beta diversity as a site's degree of community differentiation. This value was calculated by taking the average pairwise dissimilarity of a site compared to all other sites (Lennon et al. 2001; Vellend et al. 2007). We used the three aforementioned dissimilarity metrics (Table 1) to calculate three different beta diversity measures, $\beta_J$, $\beta_L$, and $\beta_{BC}$, for the beta diversity calculated with Jaccard's, Lennon's and the Bray-Curtis index, respectively. We calculated beta diversity for each site and each sampling period. All three measures were multiplied by 100 to bring them into the range of zero (identical species composition) to 100 (no shared species).

Because there are $n(n\text{-}1)/2$ elements in a dissimilarity matrix calculated from $n$ sites, using $n(n\text{-}1)/2\text{-}1$ as the degrees of freedom in a paired $T$-test would increase the rate of type I error. Therefore, we tested the mean changes in beta diversity between sampling periods ($\Delta\beta$) with a paired-samples randomization test (Manly 2007). The null hypothesis for this test is that the mean $\Delta\beta$ across sites is zero. To test differences between sampling periods for consistency across the dataset (i.e., across the region), we used Fisher's sign test, for which the null hypothesis is that decreases or increases in beta diversity are equally likely.

We also determined the number of sites where there was a significant decrease or increase in beta diversity. For this purpose, we tested the beta diversity of each site individually for differences between sampling periods with a paired-samples randomization test. To account for the large number of tests ($n$ = 175), a difference between sampling periods was regarded as significant if $P \leq 0.01$.

To compare the different beta diversity measures, we tested $\beta_J$, $\beta_L$, and $\beta_{BC}$ for correlation with each other using Pearson's correlation coefficient as the test statistic in a randomization test (Manly 2007). We also regressed $\Delta\beta_{BC}$ on $\Delta\beta_J$. The slope of the regression line was tested against the value 1.0 using a two-sided randomization test (Manly 2007). A slope > 1.0 for $\Delta\beta_{BC}$ would support our hypothesis that $\beta_{BC}$ is more sensitive to changes in community differentiation than $\beta_J$.

*Defining habitat specialists and generalists*

Biotic homogenization may be the result of a decrease in habitat specialists, an increase in habitat generalists or both (Olden & Poff 2003; Rooney et al. 2004). However, what exactly are the habitat specialists and generalists in our case? In studies on forest vegetation in Central Europe, habitat generalists are often understood to be the opposite of true forest species, such that generalists are species that are able to exist (or even perform better) in open habitats, in contrast to those species that are restricted to forest habitats (Decocq et al. 2005; Naaf & Wulf 2007; van Oheimb & Härdtle 2009). Therefore, we counted the number of true forest species (hereafter forest specialists, $N_{\mathrm{S.forest}}$) and the number of forest generalists ($N_{\mathrm{G.forest}}$) in each site according to the German reference list of Schmidt et al. (2003).

Species are not only more or less specialized to the forest habitat but also to soil conditions. The two main factors determining differences in species composition among the studied sites in the Weser-Elbe region have been reported to be soil pH and soil moisture (Wulf 1992). This was confirmed by regressing both factors on the three dimensions produced by a non-metric multidimensional scaling (McCune & Grace 2002) of the 2008 data (stress = 18.5; no environmental data was available for 1988), which yielded an $R^2$-value of 30.1% for soil pH and 27.1% for soil moisture.

The range of studied sites (pH from 3.1 to 6.7 and soil moisture from slightly moist to wet) represented the upper half of the total gradient present in the region excluding forests on dry and acidic soils. Thus, the gradients covered by our dataset had only one “extreme” end. We expected, therefore, that the species most susceptible to environmental changes would be those that were restricted to the higher end of the range. We defined species with their optimum (i.e., the abundance-weighted average of pH or moisture values) in the upper third of the range of all optima as habitat specialists. Species were treated as habitat generalists if they (a) had an optimum in the intermediate third of the optima range and (b) occupied at least two thirds of the whole pH or moisture gradient.

For measurements of soil pH, ten subsamples (0-10 cm depth) per 400 m² were taken by systematic random sampling in each plot, then pooled into one sample, air-dried and sieved (2 mm). After extracting 10 g of soil with 25 ml 0.01M $CaCl_2$ ($\geq$ 1 h), the pH was measured with an electrometric pH meter. Soil moisture was measured as the volumetric water content in the topsoil (0 – 10 cm) using an EasyTest Time-Domain Reflectometry field probe (Institute of Agrophysics, Polish Academy of Sciences, Lublin, Poland). Measurements were taken in two subsequent years (2008/09) during five days at the end of March (assumed moisture maximum). In each plot, five measurements per 100 m² were taken using systematic random sampling.

For each site, we counted the number of pH specialists ($N_{\mathrm{S.pH}}$) and pH generalists ($N_{\mathrm{G.pH}}$) as well as the number of moisture specialists ($N_{\mathrm{S.moisture}}$) and moisture generalists ($N_{\mathrm{G.moisture}}$). We also determined the overall species richness per site as a measure of alpha diversity. Changes in species numbers ($\Delta N$) between sampling periods were tested with a paired-samples randomization test and a Fisher’s sign test for consistency across the region.

*Relating changes in beta diversity and species numbers*

A main objective of our study was to find out if a decrease or an increase in beta diversity is more closely associated with a decrease or an increase in habitat specialists or generalists. As a first step, we tested $\Delta N$ for the six species groups and alpha diversity for correlations with $\Delta\beta_{\mathrm{J}}$, $\Delta\beta_{\mathrm{L}}$ and $\Delta\beta_{\mathrm{BC}}$. Significance was assessed with randomization tests using Pearson’s correlation coefficient as the test statistic (Manly 2007). Because some of the species groups were confounded (e.g., many of the pH specialists were also forest specialists and many of the forest generalists were also pH generalists), we conducted multivariate tests as a second step. For each beta diversity measure, we fitted a linear regression model to see which set of species groups best explained the change in beta diversity. The minimal adequate model was found with a stepwise backwards elimination approach starting with a model that included the $\Delta N$'s for all six species groups. The explanatory variables were then tested for their individual contribution to the explained variance using the partial $F$ ratio as the test statistic. Significance was determined by comparing the observed partial $F$ ratio to the distribution obtained by random permutations of the observations of the explanatory variable being tested. The variables were eliminated until all variables were significant at $P \leq 0.05$. The final model was tested for significance by comparing the overall $F$ ratio to the distribution obtained by random permutations of the observations of the response variable (Manly 2007).

All analyses were computed with R 2.9.1 (R Development Core Team 2009).

## 1.4 Results

### Changes in beta diversity over two decades

The three beta diversity measures differed mainly in their absolute position within the potential range between 0 and 100 (Fig. 2, Table 3). $\beta_L$ was lower than $\beta_J$ and strongly correlated with $\beta_J$ in 1988 ($r = 0.80$, $P < 0.001$) but less strongly so in 2008 ($r = 0.62$, $P < 0.001$). $\beta_{BC}$ was also generally lower than $\beta_J$ (although less pronounced than $\beta_L$, Fig. 2) and the two measures were highly correlated for both sampling periods ($r = 0.92$ and 0.95 in 1988 and 2008, respectively, $P < 0.001$).

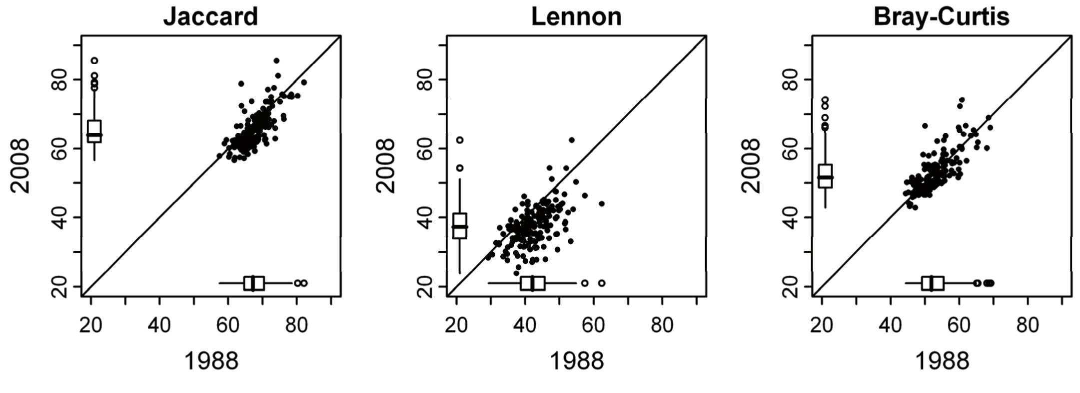

**Fig. 2.** Changes in beta diversity over two decades at the 175 sites for the three dissimilarity indices (Table 1). Line slope is 1.0. Boxplots are standard boxplots. For statistical significance see Table 3.

The observed $\Delta\beta$ differed depending on the beta diversity measure applied. The two measures relying on presence/absence data ($\beta_J$ and $\beta_L$) indicated average decreases in beta diversity of 3.4% and 11.7%, respectively (Table 3). The Fisher's sign tests proved that these changes were consistent across the region (column 6 in Table 3). In contrast, $\beta_{BC}$ did not change significantly on average. With all three beta diversity measures, the number of sites with a significant decrease in beta diversity exceeded the number of sites with a significant increase, particularly with regard to $\beta_J$ and $\beta_L$ (Table 3).

**Table 3.** Mean beta diversity and its change ($\Delta\beta$) between sampling periods ($n = 175$) and number of sites with a significant ($P \leq 0.01$) change in beta diversity as tested by paired-samples randomization tests for the three dissimilarity indices.

| Dissimilarity index | Mean β | | Mean Δβ | $P$ [a] | $P$ [b] | # Sites with | | |
|---|---|---|---|---|---|---|---|---|
| | 1988 | 2008 | | | | decrease | increase | no change |
| Jaccard | 67.6 | 65.3 | -2.3 | < 0.001 | < 0.001 | 111 | 19 | 45 |
| Lennon | 42.5 | 37.5 | -5.0 | < 0.001 | < 0.001 | 121 | 11 | 43 |
| Bray-Curtis | 52.9 | 52.9 | 0.0 | 0.947 | 0.225 | 67 | 50 | 58 |

[a] Paired-samples randomization test

[b] Fisher's sign test

Despite the more or less strong correlations between $\beta_J$ and $\beta_L$ in both sampling periods, their corresponding changes ($\Delta\beta_J$ and $\Delta\beta_L$) showed only a moderate correlation (Fig. 3a). Sites tended to have a stronger decrease in $\beta_L$ than in $\beta_J$ (sites below the bisector line). At many of these sites, the average difference in species number compared to all other sites increased, which led to a decline in $\beta_L$ even where $\beta_J$ had increased (lower right quadrant in Fig. 3a).

The changes of $\beta_J$ and $\beta_{BC}$ between sampling periods were highly correlated (Fig. 3b). While there were several sites that showed both a decrease in $\beta_J$ and an increase in $\beta_{BC}$ (upper left quadrant in Fig. 3b), there were almost no sites that showed both a decrease in $\beta_{BC}$ and an increase in $\beta_J$ (lower right quadrant in Fig. 3b). The slope of the linear regression line was less than 1.0, indicating that $\Delta\beta_{BC}$ in either direction was not consistently larger than $\Delta\beta_J$.

### Changes in species numbers

Over the two decades, alpha diversity consistently increased by almost four species on average (Table 4), which was a result of increases in the number of forest specialists ($N_{S.forest}$) and in the numbers of all three generalist groups ($N_{G.forest}$, $N_{G.pH}$ and $N_{G.moisture}$), each of which had consistently added several species. In contrast, the number of the other specialist species slightly decreased ($N_{S.pH}$) or did not change significantly ($N_{S.moisture}$) on average. For these two groups, the number of sites with a decrease exceeded those with an increase, while for all other groups, the number of sites with an increase in species number was far higher. Note that the sign of the mean change in species number was the same for forest-related specialists and

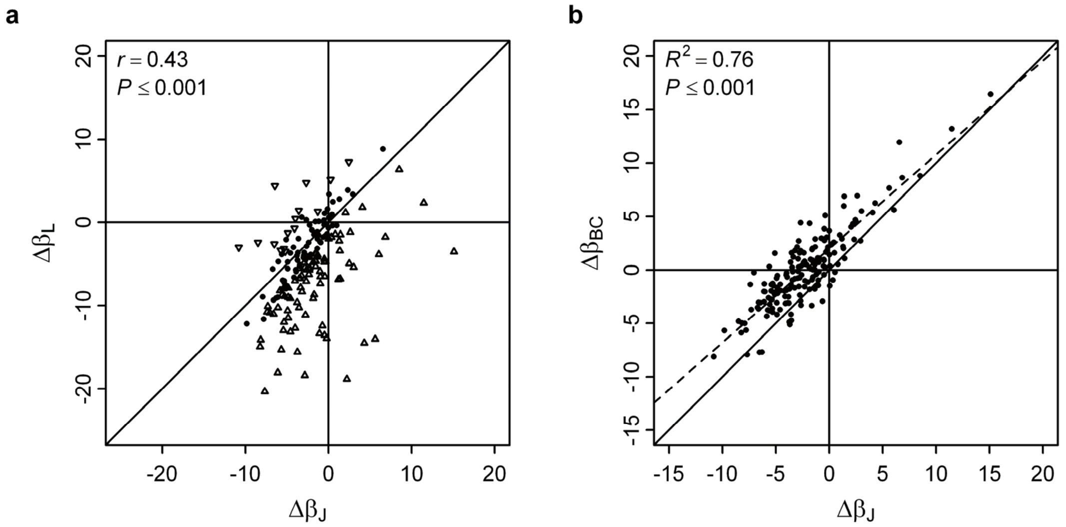

**Fig. 3.** Correlation between changes in beta diversity calculated with Jaccard's dissimilarity index ($\Delta\beta_J$) and the one calculated with (a) Lennon's dissimilarity index ($\Delta\beta_L$) and (b) the Bray-Curtis dissimilarity index ($\Delta\beta_{BC}$). Slope of the solid line is 1.0. Symbols in (a): Δ increase in the average pairwise difference in species number between the given site and all other sites (δ) over two decades, ∇ decrease in δ, ● no essential change ($-2 \leq \delta \leq 2$). The dashed line in (b) represents the regression line with a slope of 0.88, which is significantly different from 1.0 (two-sided randomization test: $P = 0.002$).

generalists, while it was the opposite for soil-related specialists and generalists (Table 4).

**Table 4.** Mean species numbers (*N*) and changes (Δ*N*) between sampling periods ($n$ = 175) and number of sites with a decrease, increase and no change in *N*.

| Species group | | Mean *N* | | Δ*N* | $P^a$ | $P^b$ | # Sites with | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1988 | 2008 | | | | decrease | increase | no change |
| Alpha diversity | | 28.0 | 31.7 | 3.7 | < 0.001 | < 0.001 | 47 | 117 | 11 |
| Specialists | forest | 16.1 | 18.1 | 2.0 | < 0.001 | < 0.001 | 46 | 113 | 16 |
| | pH | 5.2 | 4.9 | -0.3 | 0.037 | 0.013 | 76 | 50 | 49 |
| | moisture | 1.4 | 1.2 | -0.2 | 0.150 | 0.151 | 43 | 33 | 99 |
| Generalists | forest | 11.9 | 13.5 | 1.6 | < 0.001 | < 0.001 | 55 | 97 | 23 |
| | pH | 20.0 | 23.3 | 3.3 | < 0.001 | < 0.001 | 32 | 128 | 15 |
| | moisture | 24.4 | 27.9 | 3.5 | < 0.001 | < 0.001 | 42 | 117 | 16 |

[a] Paired-samples randomization test
[b] Fisher's sign test

### Associations between changes in beta diversity and changes in species numbers

In general, correlations between changes in beta diversity and changes in species numbers pointed in the same direction for the three beta diversity measures, but differed in strength and significance (Table 5). Correlations with $\Delta\beta_J$ were generally stronger and more significant than correlations with $\Delta\beta_L$. Correlations with $\Delta\beta_{BC}$ took an intermediate position. Generally, changes in beta diversity were negatively correlated with changes in alpha diversity (for $\Delta\beta_L$ only with minor significance) indicating that a lower degree of community differentiation is associated with a higher species richness. Correlations were also negative between changes in beta diversity and the $\Delta N$'s of habitat generalists (with less or no significance for forest generalists). Correlations with $\Delta N$'s of habitat specialists were less consistent. While $\Delta\beta_J$ and $\Delta\beta_{BC}$ showed a highly significant negative correlation with the $\Delta N$ of forest specialists, all other correlations with $\Delta N$'s of habitat specialists (except for pH specialists) were not significant.

**Table 5.** Correlation between changes in species numbers ($\Delta N$) for all species groups and changes in beta diversity ($\Delta\beta$) for the three beta diversity measures (Table 1). Significance: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, $^{(*)}$ $P \leq 0.1$.

| $\Delta N$ Species group | | $\Delta\beta_J$ | $\Delta\beta_L$ | $\Delta\beta_{BC}$ |
|---|---|---|---|---|
| Alpha diversity | | -0.41 *** | -0.14 $^{(*)}$ | -0.30 *** |
| Specialists | forest | -0.50 *** | -0.12 | -0.45 *** |
| | pH | -0.17 * | -0.04 | -0.11 |
| | moisture | 0.10 | -0.08 | 0.12 |
| Generalists | forest | -0.24 ** | -0.13 $^{(*)}$ | -0.11 |
| | pH | -0.55 *** | -0.19 * | -0.42 *** |
| | moisture | -0.55 *** | -0.19 * | -0.41 *** |

The minimal adequate regression models of changes in beta diversity against changes in species numbers were very similar for $\Delta\beta_J$ and $\Delta\beta_{BC}$ (Table 6). They explained almost 60 and 40% of the variance in $\Delta\beta_J$ and $\Delta\beta_{BC}$, respectively. In both models, the $\Delta N$'s of pH and moisture generalists showed a negative effect on $\Delta\beta$, while the $\Delta N$'s of both forest specialists and generalists showed a positive effect on $\Delta\beta$. This positive effect is in contrast to the negative association found when the $\Delta N$'s of forest specialists and generalists were tested individually for correlation with $\Delta\beta$ (Table 5). The $\Delta N$'s of the soil-related habitat specialists did not significantly contribute to explaining changes in beta diversity. For $\Delta\beta_L$, the final regression model contained the $\Delta N$ of moisture generalists as the only explanatory variable. It explained only 4% of the variance in $\Delta\beta_L$.

**Table 6.** Linear regression models of changes in beta diversity ($\Delta\beta$) against changes in species numbers ($\Delta N$) for the three beta diversity measures (Table 1).

| Explanatory variables | Partial regression coefficient in the final model | % Explained variance when added last to the model | $P^a$ | $R^2$ | $P^b$ |
|---|---|---|---|---|---|
| Jaccard | | | | | |
| $\Delta N$ forest specialists | 0.78 | 10.3 | < 0.001 | 0.58 | < 0.001 |
| $\Delta N$ forest generalists | 0.96 | 26.4 | < 0.001 | | |
| $\Delta N$ pH generalists | -0.67 | 8.7 | < 0.001 | | |
| $\Delta N$ moisture generalists | -0.89 | 14.8 | < 0.001 | | |
| Lennon | | | | | |
| $\Delta N$ moisture generalists | -0.17 | 3.7 | 0.011 | 0.04 | 0.010 |
| Bray-Curtis | | | | | |
| $\Delta N$ forest specialists | 0.38 | 2.3 | 0.013 | 0.39 | < 0.001 |
| $\Delta N$ forest generalists | 0.81 | 18.3 | < 0.001 | | |
| $\Delta N$ pH generalists | -0.56 | 5.9 | < 0.001 | | |
| $\Delta N$ moisture generalists | -0.56 | 5.7 | < 0.001 | | |

[a] partial F randomization test
[b] overall F randomization test

## 1.5 Discussion

### Homogenization and differentiation with different beta diversity measures

Despite differences among different beta diversity measures, we see a clear trend toward a decrease in beta diversity and a homogenization of forest plant communities after two decades. The average rate of homogenization (change per year) found in the Weser-Elbe region over a 20 year period when using the Bray-Curtis index was lower (0%) than that found among hardwood forest communities in southern and northern Wisconsin over a 50 year period (-0.044% and -0.054%; Rogers et al. 2008; Rooney et al. 2004). However, rates of homogenization calculated with Jaccard's and Lennon's index in the Weser-Elbe region were higher (-0.115% and -0.250%). There are also a few studies on forest vegetation changes in temperate Europe that report a convergence among different herb layer communities, but these studies were restricted to single forests (Persson 1980; van Calster et al. 2007). Our results show that biotic homogenization is underway on the regional scale.

The three measures used to quantify beta diversity were strongly correlated with each other, yet the difference in outcome for the degree of homogenization was considerable (Table 3). The observed differences among beta diversity measures reflect two changes in community composition. First, the stronger decrease in $\beta_L$ than in $\beta_J$ (Table 3) indicates an increased difference in species richness among sites. Consider the following example: If the number of unique species gained at site A is greater than the number of unique species lost at site B, Jaccard's dissimilarity will increase, whereas Lennon's dissimilarity will decrease. This discrepancy occurs because the real turnover (i.e., the number of gains and losses from one site compared to the other) becomes lower, while at the same time the difference in species richness between sites becomes larger. These changes occurred at several sites in our study (lower right quadrant in Fig. 3b). Indeed, the range in species richness per site increased from 12 to 47 species in 1988 to 10 to 56 species in 2008. The mean difference in species richness among sites increased by 2.4 species.

Second, the balance in $\Delta\beta_{BC}$ compared to the significant decrease in $\beta_J$ reflects a greater importance of colonizations and extinctions of low abundance species than changes in abundant species. Losses or gains of species may have little effect on $\Delta\beta_{BC}$ if their cover-abundance is low. For instance, a change in cover-abundance from 0 to 2 (a gain) has a lower effect than a change from 7 to 4. It seems that the effects of colonizations that led to a decrease in $\beta_J$ were masked by changes in cover-abundance when using $\beta_{BC}$. Our hypothesis that $\Delta\beta_{BC}$ (in either direction) should be consistently larger than $\Delta\beta_J$ was not supported (Fig. 3a). In a study on changes in similarity among avian assemblages in North America, La Sorte & McKinney (2007) found the decrease in beta diversity was more pronounced when accounting for species abundances. They concluded that minor increases in similarity based on species gains can mask more substantial increases in similarity based on local abundance. Thus, omission of abundance data could lead to an underestimation of the actual magnitude of homogenization and its impact on ecosystems. However, in our study, either the gained species did not yet have high local abundances at the time of the resurvey or the lost species did not have high abundances at the time of the initial survey, so these gains and losses had a limited effect on $\beta_{BC}$. Still, these changes indicate a process of decreasing dissimilarity among communities.

### Which habitat specialists and generalists drive changes in community differentiation?

Many previous studies on biotic homogenization have emphasized the invasion of alien species as a cause of homogenization (e.g., McKinney 2004; Olden & Poff 2003; Schwarz et al. 2006). The only conspicuous alien species in our dataset was *Impatiens parviflora*, whose occupancy increased from 1% to 11% and which thus had a differentiating rather than homogenizing effect. However, our study is an example of the frequently observed pattern that a decline in beta diversity occurs alongside an increase in local alpha diversity (e.g., Jurasinski et al. 2007; Smart et al. 2006; van Calster et al. 2007). Our results suggest that 'native invaders' from the regional pool were responsible for the decrease in community differentiation. Besides the spread of habitat generalists (all types), we also observed an increase in the number of forest specialists but no significant change in the number of soil-related specialists (Table 4). The correlation and regression analyses revealed that decreases in beta diversity (as at least indicated by the qualitative beta diversity measures) were largely the result of an increase in the number of soil-related generalists (Tables 5 and 6). There was hardly any evidence that changes in the numbers of soil-related specialists influenced changes in beta diversity. In forests in Wisconsin, species with a broad habitat range also increased and were mainly responsible for the increased similarity among plant communities (Rogers et al. 2008; Rooney et al. 2004). However, this was accompanied by a considerable decline in mean local alpha diversity due to the loss of uncommon specialists (Wiegmann & Waller 2006). In the Weser-Elbe region, the average loss of soil-related habitat specialists was not yet significant (Table 4), indicating a lower degree of biotic impoverishment after two decades than after 50 years in Wisconsin.

Our findings for the species groups of forest specialists and generalists were unexpected for two reasons: (a) The signs for the correlation and partial regression coefficients were the same in both species groups (Tables 5 and 6). Thus, the underlying mechanisms did not differentiate between these two species groups, and a distinction between them does not help explain changes in beta diversity. This was unexpected, since previous studies have shown that a distinction between these groups can be quite useful in explaining differences in species composition and diversity (e.g., Decocq et al. 2005; Naaf & Wulf 2007; von Oheimb & Härdtle 2009). (b) As a result of multivariate testing, the sign changed in both species groups indicating a positive effect on changes in beta diversity in the regression models (Table 6). The likely reason is that both forest specialists and generalists were often also pH or moisture generalists. Their numbers and, thus their changes, were highly correlated ($r > 0.8$ for $\Delta N$'s). $\Delta N_{\mathrm{S.forest}}$ and $\Delta N_{\mathrm{G.forest}}$ explained a unique proportion of variance in the regression model in addition to the proportion already explained by $\Delta N_{\mathrm{G.pH}}$ and $\Delta N_{\mathrm{G.moisture}}$. This proportion was likely due to other species among the forest specialists or generalists, e.g., moisture specialists. This was confirmed when forest specialists and generalists were excluded from the regression analyses. Then, the final models for $\Delta\beta_{\mathrm{J}}$ and $\Delta\beta_{\mathrm{BC}}$ contained $\Delta N$ for moisture specialists which had a highly significant partial regression coefficient of 1.03 and 0.95, respectively, and explained a unique variance proportion of 11.0 and 9.1%, respectively. Thus, losses and gains of moisture specialists were also responsible for decreases and increases in beta diversity, respectively.

The low extent to which $\Delta\beta_{\mathrm{L}}$ could be explained by changes in the numbers of habitat specialists and generalists was surprising, particularly because changes in $\beta_{\mathrm{L}}$ were more pronounced than changes in $\beta_{\mathrm{J}}$ and $\beta_{\mathrm{BC}}$. It seems that the compositional changes reflected by changes in $\beta_{\mathrm{L}}$ were more complex than simple increases or decreases in habitat specialists or generalists. At this stage, we cannot offer a solution to the question of which kind of species would better explain the decrease in $\beta_{\mathrm{L}}$.

## 1.6 Conclusions

After two decades, the forest communities in the Weser-Elbe region have not yet been subjected to severe biotic impoverishment, although there is a broad trend towards homogenization. Our study shows that, even *within* biogeographical regions with a homogeneous species pool and in habitats not yet threatened by the invasion of alien species, shifts in native species with different habitat ranges can cause changes in beta diversity. Distinguishing several groups of habitat specialists and generalists revealed that the habitat range referring to soil-related factors (pH and moisture) is relevant for the homogenizing or differentiating effect of species. A distinction of species confined to forest habitats and those able to occupy open habitats does not help to explain patterns of diversity changes in the Weser-Elbe region.

Our study shows that the choice of dissimilarity metric not only determines the magnitude of dissimilarity computed among communities, but also the magnitude of change in community differentiation. We do not recommend one of the three beta diversity measures as the best, but conclude that using them alongside one another should be common practice as it deepens the insight into compositional changes.

Comparisons with forests in Wisconsin suggest that biotic impoverishment might become more severe over the next few decades, if the ‘native invaders’ become locally more abundant and if the losses of habitat specialists become significant. Therefore, we believe that further observation of compositional changes in the forests of the Weser-Elbe region is necessary. The drivers of compositional changes should be identified before biotic impoverishment becomes more severe. The analyses performed in this paper do not provide evidence of which environmental alterations are responsible for the ongoing changes in community differentiation. To elucidate the underlying mechanisms, future analyses should examine how habitat quality has changed over the last decades and which functional traits of the winner and loser species act as filters for species selection.

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# Chapter 2

TOBIAS NAAF & MONIKA WULF

# Multiplicative functional diversity partitioning gives insight into assembly mechanisms in temperate forest plant communities

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This chapter is in revision.

## 2.1 Abstract

A main objective of functional diversity (FD) analyses is to provide insights into the mechanisms that drive the assembly of communities from a regional species pool. Recently, the partitioning of FD into within-community (α) and among-community (β) components has been introduced as a useful method for this purpose. However, the insights gained were based on a single trait and an unreliable measure of functional β diversity that was derived from additive partitioning of Rao's quadratic entropy. In this study, we used a multiplicative approach to partition the FD of temperate forest plant communities in NW Germany, producing a more reliable measure of functional β diversity. Our aims were to confirm and generalize the previously found patterns for three major trait axes and to assess their stability over a time period of two decades. Across all traits, functional α diversity was almost as high as the regional FD, demonstrating the necessity of functional differentiation among coexisting species. The low functional turnover contrasted with a high species turnover, indicating functional redundancy among taxonomically distinct communities. Trait convergence and divergence patterns revealed by null model tests differed across traits and were not significant for multidimensional FD. The FD partitions and most null model tests were similar in both time periods. Our study demonstrates that multiplicative FD partitioning is able to reveal simultaneous effects of limiting similarity mechanisms and environmental filtering on community assembly. It shows that basic assembly patterns (high functional differentiation within communities, functional redundancy among communities), occur across habitat types and trait axes, and remain stable over time.

## 2.2 Introduction

The quantification and analysis of functional diversity (FD) in biological communities has become a major topic in ecological studies over the last decade (Díaz & Cabido 2001; Hooper et al. 2005; Villéger et al. 2008). One aim is to derive patterns and mechanisms by which animal and plant communities assemble from a regional species pool (Mayfield et al. 2005; Petchey et al. 2007; Thompson et al. 2010). Two assembly mechanisms have received particular attention: competitive filtering, which limits trait similarity among coexisting species (Weiher & Keddy 1995; Stubbs & Wilson 2004), and environmental filtering, which permits only those traits that enable species to cope with environmental adversity (Díaz et al. 1998; Cornwell et al. 2006). However, debate remains about the most appropriate methods to demonstrate the existence of these assembly mechanisms in particular sets of communities (e.g., Pillar et al. 2009; Podani 2009; Thompson et al. 2010).

Recently, de Bello et al. (2009) have demonstrated that the partitioning of FD into spatial components can be used to gain insight into the processes of species assembly and coexistence. They partitioned the regional (γ) FD into within-community (α) FD and among-community (β) FD using an additive approach, as proposed by Pavoine & Dolédec (2005). Using Rao's quadratic entropy (*Q*; Botta-Dukát 2005) as an FD measure, they found that β FD was remarkably low compared to α FD. Thus, trait differences among species within habitats were almost as great as trait differences across the full range of environmental conditions. The authors interpreted this finding as an indication that species coexistence is associated with functional differentiation among species, as predicted by limiting similarity theory (MacArthur & Levins 1967; Weiher & Keddy 1995). In another key result, they found that low β FD contrasted with high β species diversity. They interpreted this finding as an indication that plant communities might be ecologically redundant in the sense that a high level of replacement of species along environmental gradients results in stable functional assemblages (de Bello et al. 2009).

The problem with the chosen approach, as demonstrated by Jost (2007) and Ricotta & Szeidl (2009), is that the β component of Rao's $Q$ calculated from additive partitioning approaches zero when α FD is high, even if the communities considered are completely distinct (taxonomically and functionally). Thus, it is unclear whether a low β FD value is actually the result of a low level of functional turnover or merely the mathematical consequence of additive partitioning. One solution to this problem would be to use "numbers equivalents" instead of the original $Q$ values and to apply multiplicative FD partitioning (Ricotta & Szeidl 2009). Furthermore, de Bello et al. (2009) based their analysis on community data from pastures in NE Spain and used only a single trait (specific leaf area). To assess whether the observed patterns can be generalized for communities with other habitat types and for different traits, more research is needed.

In this study, our aim is to reveal mechanisms of community assembly using a multiplicative FD partitioning approach. We used data on temperate forest plant communities in NW Germany, which were available for two sampling periods with a time lag of 20 years (Naaf & Wulf 2010). Previous analyses of these data have indicated marked changes in species composition as a result of environmental changes, including disturbance by forest management activities, enhanced browsing pressure, acidification and climate warming (Naaf & Wulf in press). We were therefore interested in three main questions: (i) whether the findings of de Bello et al. (2009) could be confirmed for forest communities using multiplicative FD partitioning; (ii) whether these findings could be generalized for major trait axes other than that represented by specific leaf area and (iii) whether the identified mechanisms of community assembly would be stable over time, even in the face of environmental changes.

## 2.3 Methods

### Study system

We used species data from 175 herb layer communities in ancient forest patches that are distributed across the 7600 km² Weser-Elbe region in NW Germany (N52.90° - N53.66°; E8.40° - E9.66°). The sites vary in their soil pH (3.1-6.7), soil moisture (slightly moist to wet) and level of disturbance over the last two decades. While the stands were originally in a mature and largely undisturbed state (i.e., a homogeneous herb layer and closed canopy) at the time of first sampling in 1986-88 (hereafter 1988), the level of disturbance in 2008-2009 (hereafter 2008) ranged from undisturbed to substantially disturbed by forest management activities or natural tree fall, resulting in a canopy closure of < 50% and heavy soil damage (Naaf & Wulf in press). The dominant tree species in both sampling periods were *Alnus glutinosa*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior* and *Quercus robur*. The herbaceous plant species composition was sampled in both sampling periods using a nine-degree combined cover-abundance scale (Naaf & Wulf 2010). Plot size ranged from 100 to 400 m², but we found no significant species-area relationship after accounting for the environmental variability (Naaf & Wulf 2010). Species with less than three occurrences in at least one of the sampling periods were excluded from data analyses.

## Quantifying functional diversity

In addition to specific leaf area (SLA), we used canopy height (CH) and diaspore weight (DW) as functional traits. These three traits are considered to represent largely independent fundamental plant strategies (Westoby 1998; Díaz et al. 2004; Laughlin et al. 2010). We took most trait values from the LEDA traitbase (Kleyer et al. 2008). For 34 species, we measured SLA ourselves according to the standards defined in Kleyer et al. (2008). Canopy height and DW were $\log_e$-transformed. We calculated FD as Rao's $Q$ using each trait individually as well as all three traits combined. As distance measures, we used the Euclidean distance for single traits and Gower's distance for the multiple trait set. Gower's distance was used because it can cope with missing values (Pavoine et al. 2009); one SLA value was missing from the data set. All distance matrices were transformed into ultrametric distances (Pavoine et al. 2005) using least-squares fitting (with the function *ls_fit_ultrametric* in the R package *clue*; Hornik 2010) to ensure that all species would be needed to maximize $Q$ (Pavoine et al. 2005). The ultrametric distances were squared to ensure concavity of $Q$ (Champely & Chessel 2002) and then normalized to the range [0, 1] to ensure that $Q$ would also fall within [0, 1] and that $Q \leq D$, where $D$ is the Gini-Simpson diversity (Ricotta & Szeidl 2009).

## Multiplicative diversity partitioning

Recently, Jost (2007) has demonstrated that diversity indices of the Gini-Simpson family (including Rao's $Q$; Ricotta & Szeidl 2009) do not satisfy the replication principle; i.e., the Gini-Simpson diversity of a pool of two completely distinct assemblages with equal diversity is not twice the diversity of each single assemblage. As a consequence, the β diversity calculated from additive partitioning approaches zero when α diversity is high, even if the communities are completely distinct. To solve this problem, we used "numbers equivalents" instead of the original diversity indices (Jost 2007). The equivalent species number $\hat{Q}$ of Rao's $Q$ is defined as the number of equally likely and maximally dissimilar species needed to produce the given value of $Q$ (with $\hat{Q}=1/(1-Q)$; Ricotta & Szeidl 2009). After conversion of the average α FD ($\bar{\alpha}_Q$) and the regional γ FD ($\gamma_Q$) into their numbers equivalents $\hat{\alpha}_Q$ and $\hat{\gamma}_Q$, a natural measure for β FD resulting from the replication principle is $\hat{\beta}_Q=\hat{\gamma}_Q/\hat{\alpha}_Q$. This measure represents the number of equally large, equally diverse and completely distinct (taxonomically and functionally) communities in the region needed to produce $\hat{\gamma}_Q$. Rao's $Q$ for the regional pool was calculated by treating the pool as a single community, where the abundance of each species was given by the sum of its relative abundances over all communities divided by the number of communities. So that we could compare functional diversity and turnover with species diversity and turnover, we also partitioned the Gini-Simpson diversity (GSD; using numbers equivalents) and species richness (SR).

A null model was used to test for deviations of the observed FD components from those expected at random. Significant deviations would indicate the presence of community assembly mechanisms, such as limiting similarity or environmental filtering (de Bello et al. 2009). For the null model, we simulated 1000 random communities using the *commsimulator* function with the *quasiswap* method in the R package *vegan* (Oksanen et al. 2010). This method keeps the original frequencies and species numbers per site constant. Maintaining the original frequencies during randomization is essential to avoid inflation of FD in random communities due to high occurrences of species that are rare and functionally unusual in the observed communities (Thompson et al. 2010). After randomization, the original abundances for each species were randomly distributed across their occurrences so that the total abundance of each species was also maintained. We calculated the *P*-values for the two-tailed tests with the formula $P=\min[2S/(1001);2L/(1001)]$, where $S$ and $L$ refer to the number of randomized $\hat{Q}$ values less than or equal to and greater than or equal to the observed $\hat{Q}$, respectively (Manly 2007).

All diversity components were calculated for both sampling periods. To test for significant differences between years, we used an additional randomization test. Under the null assumption that the test statistics did not differ between sampling periods, the communities were randomly assigned to one of sampling periods 1000 times (while maintaining paired observations at each sampling site). The *P*-values for the two-tailed tests were calculated as explained above. All data analyses and calculations were conducted with R 2.10.1 (R Development Core Team 2010).

## 2.4 Results

### Multiplicative diversity partitioning

The relationships between the FD components (Table 1) and the deviations between their observed and expected values according to the null model (Fig. 1) were very similar in the two sampling periods. Across all single traits and the multiple trait set, α FD was only slightly lower than γ FD, resulting in a β FD value that was marginally greater than 1 (Table 1). This low functional turnover contrasts with a considerable amount of species turnover. Approximately four completely distinct communities were needed to build the regional pool (according to SR). Turnover decreased markedly when species abundances were taken into account (according to GSD).

For SLA and CH, α FD was higher than expected, whereas for DW, α FD was lower than expected (in 1988 only with $P < 0.1$; Fig. 1). The α FD calculated for the multiple trait set was within the expected range. For all single traits (except DW in 1988) and the multiple trait set, β FD was higher than expected.

**Table 1.** Functional and species diversity components as a result of multiplicative diversity partitioning for both sampling periods and differences between sampling periods.

| | 1988 | | | 2008 | | | Difference between sampling periods | | |
|---|---|---|---|---|---|---|---|---|---|
| | α | β | γ | α | β | γ | α | β | γ |
| Functional diversity for | | | | | | | | | |
| Specific leaf area | 1.24 | 1.006 | 1.25 | 1.22 | 1.005 | 1.23 | -0.02 ** | -0.001 | -0.02 ** |
| Canopy height | 1.70 | 1.019 | 1.74 | 1.66 | 1.016 | 1.69 | -0.04 ** | -0.004 ** | -0.05 ** |
| Diaspore weight | 1.15 | 1.004 | 1.15 | 1.17 | 1.005 | 1.17 | 0.02 ** | 0.001 ** | 0.02 ** |
| Multiple trait set | 1.57 | 1.015 | 1.59 | 1.59 | 1.015 | 1.61 | 0.02 | 0.000 | 0.02 |
| Species richness | 24.6 | 4.141 | 102 | 27.0 | 3.886 | 105 | 2.4 ** | -0.254 ** | 3 ** |
| Gini-Simpson diversity | 18.5 | 1.761 | 32.7 | 19.7 | 1.778 | 35.0 | 1.1 | 0.017 | 2.3 ** |

** $P \leq 0.01$

### Changes over time

Differences between sampling periods were not consistent across traits (Table 1). While both α FD and γ FD significantly decreased over time for SLA and CH, they increased for DW. Beta FD did not change for SLA, decreased for CH and increased for DW. None of the FD components changed significantly when calculated from the multiple trait set.

Species diversity in terms of SR increased within communities and in the pool but decreased between communities (Table 1). In terms of GSD, only the γ component increased, while α and β diversity did not change significantly.

## 2.5 Discussion

### Community assembly mechanisms

Multiplicative diversity partitioning provided evidence for both types of community assembly mechanisms (limiting similarity and environmental filtering). First, the FD of the whole region was almost completely represented by a single average community (Table 1). Therefore, trait differences among species within habitats can

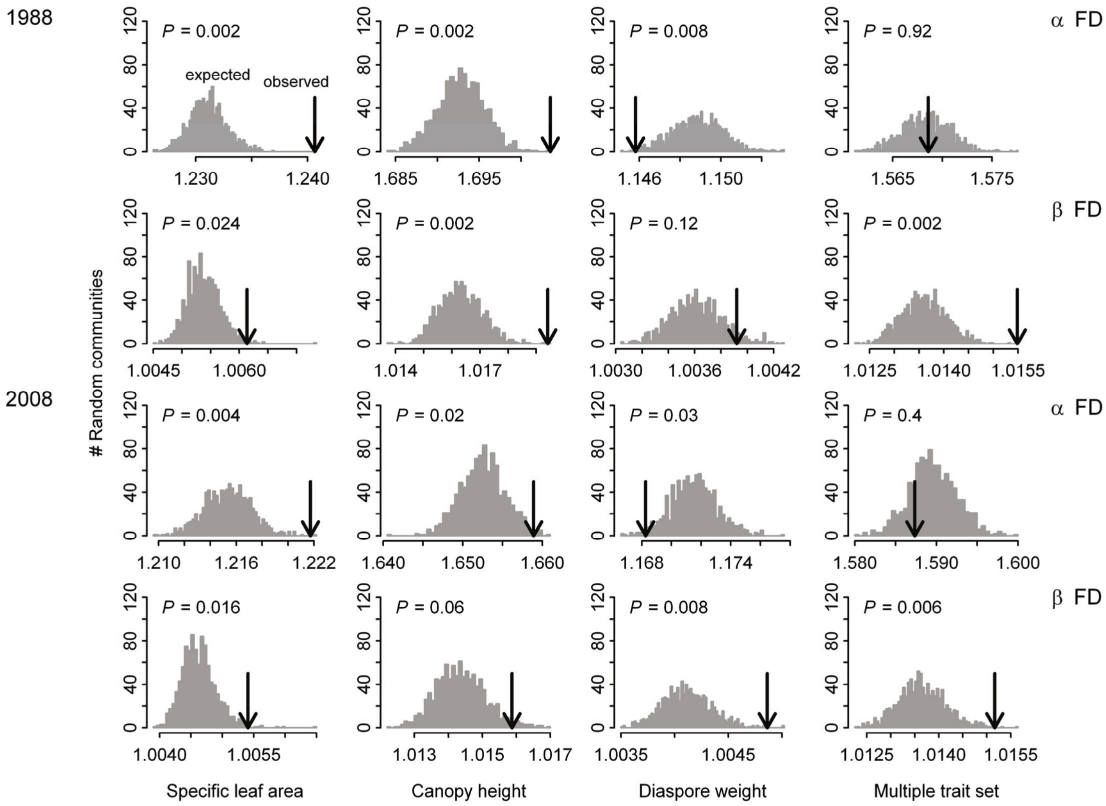

**Fig. 1.** Observed functional alpha diversity (α FD) and beta diversity (β FD) in both sampling periods compared to the expected distributions calculated from 1000 random communities. Functional diversity was assessed for each of three single traits (specific leaf area, canopy height and diaspore weight) and for the multiple-trait set. Functional diversity is expressed in numbers equivalents (see text). The *P*-values indicate significant deviations of the observed values from the expected values according to a two-tailed test (see text).

be as great as trait differences across the whole range of environmental conditions. This pattern contradicts the idea that environmental constraints simply determine what traits are permitted (Díaz et al. 1998; Cornwell et al. 2006). In agreement with limiting similarity theory, this finding indicates that species coexistence is generally associated with functional differentiation among species (MacArthur & Levins 1967; Stubbs & Wilson 2004). Large trait differences among coexisting species in comparison to differences among communities have also been observed by de Bello et al. (2009) for SLA. Here, however, this pattern is shown to be consistent across three major trait axes as well as the multiple trait set.

It could be argued that α and γ FD values were close together simply because the environmental gradient represented by our data set is too narrow. However, the low functional turnover among communities was accompanied by a considerable degree of species turnover (Table 1). A remarkable difference between β SR and β FD has also been observed by Pavoine & Dolédec (2005) and de Bello et al. (2009). However, because they based their FD partitioning on the original values of Rao's *Q* (not numbers equivalents), it is not clear whether their β FD values were low due to a real lack of functional turnover or due to the inability of $\beta_Q$ to reflect functional turnover (Ricotta & Szeidl 2009). It might also be argued that having a lower β GSD compared to β SR indicates that the consideration of abundances might be partly responsible for the much lower β FD. However, calculating α and γ FD with equal abundances for all species would still result in β FD values < 1.02. Thus, by using numbers equivalents, our study shows that a markedly lower level of functional turnover than species turnover is a general pattern that is consistent across traits (Fukami et al. 2005; Kahmen & Poschlod 2008). This finding supports the existence of functional redundancy among communities and indicates that the replacement of species along environmental gradients results in stable functional assemblages (de Bello et al. 2009).

The null model tests provide evidence for environmental filtering, although this pattern is not consistent across traits. For DW, α FD was lower and β FD was higher than would be expected at random. This type of trait convergence pattern has been interpreted as an indication that environmental filters are operating (Cornwell et al. 2006; Petchey et al. 2007; de Bello et al. 2009). In this case, the environment selects for species with particular reproduction and dispersal strategies, as reflected by their DW (Westoby et al. 2002). Most other studies have found indications of environmental filtering for vegetative, non-regenerative traits (e.g., Weiher et al. 1998; Cornwell & Ackerly 2009). In our data set, the FD of the vegetative traits (SLA and CH) only partly indicated environmental filtering; β FD was higher than expected at random, as one would predict if habitat differences determined the functional composition of the communities. However, α FD was also higher than expected at random, arguing against a strong impact of environmental filters.

Note that this independent behavior of α and β FD is possible only because of the multiplicative partitioning approach (cf. Baselga 2010). Under the additive approach applied by de Bello et al. (2009), α and β FD were coupled: α FD was always lower and β FD always higher than expected at random. Independent of the partitioning approach, de Bello et al. (2009) found a convergence pattern for SLA in pastures in NE Spain (i.e., an α FD lower than expected), while we found a divergence pattern for SLA in temperate forest communities (i.e., an α FD higher than expected). These results demonstrate that trait distribution patterns may differ depending on the habitat or community type examined (Weiher & Keddy 1995).

### FD and community assembly over time

The patterns of trait convergence and divergence changed little over the two decades (Fig. 1). Thus, multiplicative FD partitioning does not indicate marked changes in community assembly mechanisms. The only appreciable difference was found in the β FD calculated for DW, which was not higher than expected in 1988 but was in 2008 (Fig. 1). This higher functional differentiation among communities with respect to DW (Table 1) might result from the higher variation in the level of disturbance found at the sites in 2008 compared to 1988 (Naaf & Wulf in press). Soil damage from harvesting activities in combination with increased light availability enables species with particular reproductive traits (e.g., small, easily dispersible or long-living seeds) to establish (Hodkinson et al. 1998; Degen et al. 2005; Eycott et al. 2006). In our data set, this phenomenon resulted not only in an increase in α FD (cf. Degen et al. 2005; Biswas & Mallik 2010) but also in an increase in β FD (Table 1).

The comparison of species diversity components between sampling periods indicated that α SR increased over the last 20 years (Table 1), whereas β SR decreased. This pattern was not found for GSD. These observations are consistent with the findings of a previous study in which we used other numerical methods (Naaf & Wulf 2010). We interpreted our results as the beginning of taxonomical homogenization, which was less pronounced when species abundances were taken into account (Naaf & Wulf 2010). Here, we see that the decrease in species turnover has not yet resulted in functional homogenization (Table 1). We found a slight decrease in β FD for CH only. The high functional redundancy that already exists among communities (see above) will prevent rapid functional homogenization of communities even if species compositions continue to converge.

## 2.6 Conclusions

Relying on a multiplicative diversity partitioning approach, this study demonstrates the simultaneous effects of limiting similarity mechanisms and environmental filtering on community assembly. It therefore confirms the essential results of de Bello et al. (2009), but is based on reliable FD components. In particular, a within-community FD that is almost as high as the regional FD (demonstrating functional differentiation within communities) and a high level of species turnover accompanied by a low level of functional turnover (demonstrating functional redundancy among communities) seem to be general patterns that occur across community types and across traits. However, using data on forest herb layer communities, we found no environmental filtering effect (i.e., a trait convergence pattern) for SLA, as was found by de Bello et al. (2009). Instead, we found such an effect for DW. Thus, trait divergence and convergence patterns are consistent across neither community types nor across traits. In particular, vegetative and reproductive traits might show different responses to competitive and environmental adversity (cf. Weiher & Keddy 1995; Grime 2006).

Moreover, null model tests were not significant when α FD was calculated from multidimensional trait distances, although they were when α FD was calculated for each single trait. This result casts doubt upon the use of multidimensional FD indices (as proposed by, e.g., Villéger et al. 2008 and applied by, e.g., Mouillot et al. 2007 and Thompson et al. 2010) when the objective is to obtain insight into mechanisms of community assembly. Simultaneous effects of competitive and environmental filtering might be obscured (cf. Weiher et al. 1998; Stubbs & Wilson 2004). Finally, the general patterns of high FD within communities and functional redundancy among communities in different habitats were observed equally in both sampling periods, demonstrating that basic mechanisms of community assembly remain stable even in the face of environmental changes.

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# Chapter 3

TOBIAS NAAF & MONIKA WULF

# Community assembly mechanisms in temperate forest plant communities along gradients of soil fertility and disturbance and over time

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This chapter is in revision.

## 3.1 Abstract

Plant community assembly from a regional pool is largely driven by two mechanisms: environmental filtering and niche partitioning, which result in trait convergence or divergence, respectively. Although empirical evidence for both assembly mechanisms exists, the environmental conditions and traits where each of the two assembly patterns is prevalent remain unclear. We studied community assembly mechanisms in herb layer communities of temperate forest patches in NW Germany, looking at distributions of competitive and reproductive traits along gradients of soil fertility and disturbance. We also examined how community assembly patterns changed over a time span of two decades. Canopy height tended to converge toward taller species with increasing soil fertility and increasing light availability. Most reproductive traits tended to diverge with an increasing degree of disturbance and with increasing fertility. Comparisons over time indicated that disturbance events induced the coexistence of species with different reproductive strategies and also selected for tall species as a result of enhanced competitive adversity. Our study demonstrates that in accordance with existing hypotheses, competitive traits (e.g., canopy height) can be convergent under environmental favorability. However, this convergence is associated with a divergence of traits related to other challenges (e.g., reproduction), indicating that true functional redundancy within communities does not exist. Moreover, our study shows that the expected divergence of reproductive traits at disturbed sites can be accompanied by a convergence of other traits (e.g., canopy height), indicating that several assembly mechanisms can operate simultaneously.

## 3.2 Introduction

There is increasing evidence that biological communities are not random assemblages from a regional species pool, but the result of two main assembly mechanisms: (1) environmental filtering that permits the transmission of only those traits that enable species to cope with environmental adversity and therefore leads to trait convergence (Díaz et al. 1998; Cornwell et al. 2006) and (2) niche partitioning as a result of interspecific competition that sets a limit to the similarity of coexisting species and therefore leads to trait divergence (MacArthur & Levins 1967; Weiher & Keddy 1995; Stubbs & Wilson 2004). It is generally accepted that both trait convergence and trait divergence occur for certain traits in plant communities under specific environmental conditions (Weiher & Keddy 1995; Wilson 2007; Cornwell & Ackerly 2009). However, there is still a debate about the circumstances (environmental conditions and traits) under which either of the two assembly patterns is prevalent (Grime 2006; Navas & Violle 2009). Studying community assembly patterns and how these patterns are related to environmental conditions is essential for understanding how environmental changes affect our biosphere (McGill et al. 2006). Weiher & Keddy (1995) predicted that under environmental favorability, i.e., in communities characterized by competitive adversity, traits associated with competition will be divergent (trait differences will be greater than expected by chance). In contrast, Grime (2006) challenged that competition is the mainspring of trait variation within communities. He suggested that strong competition in productive communities leads to an exclusion of certain species and trait values (trait convergence). Instead, he advocated disturbance as a main source of trait divergence, particularly in traits related to reproduction. Navas & Violle (2009) aimed to reconcile these views in terms of functional diversity (FD). They hypothesized a unimodal behavior of FD along a gradient from extremely severe environments to productive sites with strong competitive adversity. While FD is reduced at both ends of the gradient due to convergence of traits related to either stress tolerance or competition, competition-related traits are expected to be the most divergent when the impact of competition is balanced by other environmental factors. All these hypotheses have not been sufficiently tested yet and the empirical evidence so far is ambiguous. For instance, Weiher et al. (1998) observed increasing trait divergence with increasing soil fertility in wetland plant communities, whereas Schamp et al. (2008) found neither trait divergence nor convergence of competitive traits in an old field, i.e., an undisturbed, productive site. In temperate forests of southern Ontario, Schamp & Aarssen (2009) observed no relationship between the trait distribution among species and the degree of disturbance (contrary to Grime's (2006) predictions), but they did not include reproductive traits.

In this study, we sought evidence for community assembly mechanisms in temperate, deciduous forest plant communities in NW Germany. Temperate forests are underrepresented in studies of community assembly, and there are two reasons why our data were most suitable to study patterns of community assembly. First, the environmental conditions represented by the data comprised both a gradient of soil fertility (assumed to be related to competition; Weiher et al. 1998) and a gradient of disturbance. Second, species compositional data were available for two time periods with a time lag of two decades. Only few studies have surveyed community assembly over time. Thompson et al. (2010) analyzed trait distribution patterns in a roadside plant community over five decades, but found no marked changes in assembly mechanisms. It is thus unclear how fast assembly mechanisms can change over time. We know from previous analyses of our data that the species composition in these forests has considerably changed during the past two decades (Naaf & Wulf 2010). The local opening of the canopy by single-tree harvesting or natural tree fall in combination with soil damage from harvesting activities is considered one of the most important drivers (Naaf & Wulf in press). We expected, therefore, to observe marked changes in trait distribution patterns, particularly in the context of Grime's (2006) perception that disturbance promotes trait divergence.

We addressed three main questions: (1) Are competitive traits divergent with increasing site fertility as hypothesized by Weiher & Keddy (1995) or convergent as predicted by Grime (2006) and Navas & Violle (2009)? (2) Is an enhanced degree of disturbance associated with trait divergence as hypothesized by Grime (2006)? (3) Did community assembly patterns change over two decades?

## 3.3 Methods

### Study system

We used species data on 175 herb layer communities in ancient forest patches that are distributed across the 7600 km² Weser-Elbe region in NW Germany. The tree layer is dominated by *Alnus glutinosa*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior* and *Quercus robur*. The site conditions comprise two main gradients that are related to soil fertility and disturbance by forest management activities or natural tree falls (Fig. 1).

The herbaceous plant species composition was first sampled in 1986-1988 (hereafter 1988) and again in 2008/2009 (hereafter 2008) using 100 to 400 m² plots. Plot size explained an additional 1.8% ($P = 0.031$) of the variation in species richness, after accounting for the effects of soil fertility and disturbance (Fig. 1). Species abundance was assessed using a nine-degree combined cover-abundance scale (Barkman et al. 1964). The stands were in a mature state and undisturbed in 1988 (i.e., without larger canopy gaps and with a homogeneous herb layer; Wulf 1992).

In 2008, we measured four environmental variables and determined the degree of disturbance. Soil pH was measured as pH($CaCl_2$) in soil samples (0-10 cm depth). As a measure of base supply, the sum of plant-available concentrations of Ca, K and Mg (S-value) was used. Soil moisture was measured as the volumetric water content in the topsoil (0-10 cm) using field probes for time-domain reflectometry. For the assessment of light availability, we analyzed hemispherical photographs of the tree canopy and calculated the canopy openness (the proportion of visible sky in the sky region above a zenith angle of 60°). The degree of disturbance experienced by a plot during the last two decades was assessed on a five-degree scale:

$D_0$: undisturbed since first observation ($n = 45$),
$D_1$: light canopy thinning with one or several trees removed or thrown by wind; canopy still almost closed; light or no traces of driving tracks ($n = 80$),
$D_2$: intermediate canopy thinning with several trees removed or thrown by wind; smaller gaps in the canopy; driving tracks usually found; small heaps of slash may occur ($n = 41$),
$D_3$: moderate canopy thinning with several trees removed or thrown by wind; large gaps in the canopy; obvious driving tracks and soil damages ($n = 6$),
$D_4$: heavy canopy thinning with more than half of the trees removed or thrown by wind; canopy rather open; deep driving damages are common; quantities of slash remaining, often in large heaps ($n = 3$).

For additional details on the study area, plant species recording and measurements of environmental variables, please refer to Naaf & Wulf (2010).

We derived independent gradients of fertility and disturbance as the first two principal components of a principle component analysis of the environmental variables (Fig. 1). The first principle component (fertility gradient) explained 44.5% of the variation among sites and had the highest loadings for moisture, pH and S-value. Moisture and base richness are largely coupled in the study area because base cations (particularly Ca) that are released from marl stone or clay layers in a depth accessible to tree roots can be most effectively taken up and delivered to the top soil via tree leaf litter at moist sites where *Fraxinus excelsior* is dominant (Wulf 1992). The second principle component (disturbance gradient) explained 29.6% of the variation among sites and had the highest loadings for the degree of disturbance and light availability (Fig. 1).

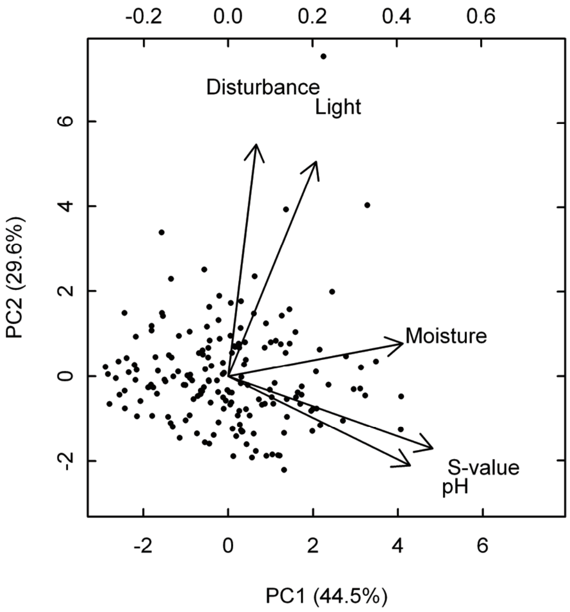

**Fig. 1.** Biplot of a principle component analysis of the environmental variables. Eigenvalues of the principle components are given in parentheses. Label centers correspond to loadings. Left and bottom axes are scaled in score units of observations; top and right axes are scaled in loading units of environmental variables. Loadings for disturbance, light availability, moisture, pH and S-value for the first principle component are 0.08, 0.26, 0.52, 0.54 and 0.61, respectively, and for the second principle component 0.69, 0.64, 0.10, -0.26 and -0.21, respectively.

## Assessing trait distributions along environmental gradients

We included three traits related to competitive ability and five traits related to reproductive strategy in our analyses (Table 1). Besides maximum canopy height (CH), which is frequently used as an indicator of competitive ability (e.g., Weiher et al. 1998; Schamp & Aarssen 2009), we considered lateral spread (LS) and specific leaf area (SLA) as traits related to competition. Lateral spread indicates a species' potential to occupy space in horizontal directions and thus complements CH as a measure of vertical growth potential (Hodgson et al. 1999; Gross et al. 2007). Specific leaf area was used as a proxy for potential relative growth rate (Westoby et al. 2002). Species in resource-rich environments tend to have a larger SLA than species in resource-limited environments (Fonseca et al. 2000; Westoby et al. 2002). Under the assumption that competition increases with resource availability, we expected SLA to reflect competitive ability. For traits related to reproduction (Díaz & Cabido 1997; Kolb et al. 2006), we used the onset and end of flowering period

**Table 1.** Functional traits used to measure functional diversity. CLOPLA1 is the database of Klimeš et al. 1997 and the numbers refer to clonal growth types defined in the database; data sources: 1 Kleyer et al. 2008, 2 Klimeš et al. 1997, 3 Klimešová and Klimeš 2008, 4 Klotz et al. 2002, 5 Own measurements, 6 Rothmaler 2005, 7 Thompson et al. 1997.

| | Description | Source | # Missing values |
|---|---|---|---|
| Competitive traits | | | |
| Canopy height (CH) | Maximum canopy height (m); log-transformed | 1, 6 | 0 |
| Lateral spread (LS) | 0: Non-clonal<br>1: <10 cm yr$^{-1}$ (CLOPLA 1: 1,2,4,6,7,9,12,13,15-20)<br>2: 10-25 cm yr$^{-1}$ (CLOPLA 1: 3,5,8,10,11,14)<br>3: >25 cm yr$^{-1}$ (CLOPLA 3) | 2, 3 | 0 |
| Specific leaf area (SLA) | mm² mg$^{-1}$ | 1, 5 | 1 (1.0%) |
| Reproductive traits | | | |
| Onset of flowering period (FP$_{onset}$) | Month | 6, 4 | 0 |
| End of flowering period (FP$_{end}$) | Month | 6, 4 | 0 |
| Pollination mode (PM) | Respective frequency of pollination by insects, pollination by wind and self-pollination on a scale from 0 to 4 | 4 | 8 (7.6%) |
| Dispersule weight (DW) | Generative dispersule weight (mg); log-transformed | 1, 4 | 0 |
| Seed longevity index (LI) | according to Thompson et al. (1998) | 7 | 13 (12.4%) |

(FP$_{onset}$, FP$_{end}$), pollination mode (PM), dispersule weight (DW) and seed longevity index (LI; Table 1).

As a measure of trait variation within a community, we used functional diversity (FD; Mayfield et al. 2005; Petchey et al. 2007; Thompson et al. 2010). We assessed FD using each trait individually as well as two multiple trait sets: competitive traits and reproductive traits. Among the many FD measures, we chose Rao's quadratic entropy $Q = \sum_{i,j}^{S} d_{ij} p_i p_j$ , where $S$ is the species richness, $d_{ij}$ is the distance in trait space between species $i$ and $j$, and $p_i$ and $p_j$ are the relative abundances of species $i$ and $j$ (Botta-Dukát 2005). Recently, this measure has been frequently applied (e.g., de Bello et al. 2009; Thompson et al. 2010) because it has several advantages: it takes species abundances into account, it can be applied to single and multiple traits and it is concave (i.e., $Q$ cannot decrease when mixing several assemblages, $\gamma_Q \geq \overline{\alpha}_Q$) as long as the matrix $[\sqrt{d_{ij}}]$ is Euclidean (Champely & Chessel 2002). We used the Euclidean distance as a distance measure for the single traits except for PM, which is a fuzzy variable (Table 1). For this trait, we used the extended version of Gower's distance supplied by Pavoine et al. (2009). Gower's distance can be used for data sets with missing values (Pavoine et al. 2009) and it was therefore also used to run principal coordinates analyses on the multiple trait sets. The first two axes (87.2% of the variation) and three axes (72.0% of the variation) were used to calculate Euclidean distances for the competitive and reproductive trait sets, respectively, to avoid overweighting of correlated traits (Lepš et al. 2006). All distance matrices were transformed into ultrametric distances (Pavoine et al. 2005) using least-squares fitting (with the function *ls_fit_ultrametric* in the R package *clue*; Hornik 2010) to ensure that all species would be needed to maximize $Q$ (Pavoine et al. 2005). The distances were then squared to ensure concavity of $Q$ (Champely & Chessel 2002).

A null model was used to quantify the degree to which FD in a community was higher or lower than expected at random, i.e., to measure the degree of trait divergence and convergence, respectively. We simulated 1000 random communities using the *commsimulator* function with the *quasiswap* method in the R package *vegan* (Oksanen et al. 2010). This method maintains row and column totals of the site-by-species matrix, thereby keeping the number of occurrences of a species and the number of species per site constant. Maintenance of the original frequencies of species during randomization is essential to avoid inflation of FD in random communities due to high occurrences of species that are rare and functionally unusual in observed communities (Thompson et al. 2010). After randomization, the original abundances for each species were randomly distributed across its occurrences so that the total abundance of each species was also maintained. We calculated $z$-scores calculated as $z = (O - E)/sd$, where $O$ is the observed $Q$, $E$ is the expected $Q$ (i.e., the mean across the 1001 null communities, including the original one) and $sd$ is the standard deviation across the null communities (Schamp & Aarssen 2009). For each community, the $z$-score was tested for significance with a two-tailed test. The p-values were calculated with the formula $P = \min[2S/(1001); 2L/(1001)]$, where $S$ and $L$ refer to the number of randomized $\hat{Q}$'s less than or equal to and greater than or equal to the observed $\hat{Q}$, respectively (Manly 2007). Positive $z$-scores indicate trait divergence and negative $z$-scores indicate trait convergence. The $z$-scores were also tested for significant deviations from zero across sites with Wilcoxon signed rank tests.

To assess trait distributions along the two environmental gradients, we tested mean trait values, Rao's $Q$ and $z$-scores for correlation with the gradients using the 2008 data. For PM, mean trait values were calculated for each level. The trait distribution statistics were also calculated for the 1988 data. We correlated the differences between sampling periods with the two environmental gradients to determine the circumstances under which trait distribution patterns had changed most. Changes over time were tested for significance across sites with Wilcoxon signed rank tests. All data analyses and calculations were conducted with R 2.10.1 (R Development Core Team 2010).

## 3.4 Results

### Trait distributions along environmental gradients

The $z$-scores of all but one trait were more or less evenly distributed around zero and not significantly lower or higher than zero when tested across sites. The mean $z$-score for $FP_{end}$ was significantly lower than zero (Wilcoxon signed rank test: $P < 0.001$). For all other traits and trait sets, positive correlations of $z$-scores with an environmental gradient imply trait divergence at the upper end and trait convergence at the lower end of the gradient. The reverse is true for negative correlations (Fig. 2).

Two of the competitive traits (CH and SLA) tended to converge at more fertile sites (Table 2, Fig. 2a). Their FD was increasingly lower than expected at random when fertility increased. Correlations between mean trait values and the fertility gradient showed that fertility tended to select for taller species and species with a lower SLA. Canopy height tended also to converge toward taller species with an increasing degree of disturbance (Table 3).

The FD of most reproductive traits (except $FP_{onset}$) tended to be higher at more disturbed sites (Table 3). Pollination mode, LI and the whole reproductive trait set showed an increasingly higher FD than expected at random when the degree of disturbance increased (Table 3, Fig. 2b). In spite of this divergence pattern, most mean trait values were correlated with the disturbance gradient. Species tended to start and finish their flowering period later, to be pollinated more by wind and less by insects and to have lighter and longer-living seeds at more disturbed sites. Three of the reproductive traits ($FP_{end}$, DW and LI) also tended to have a higher FD value with increasing fertility, i.e., under assumed enhanced competitive adversity (Table 2).

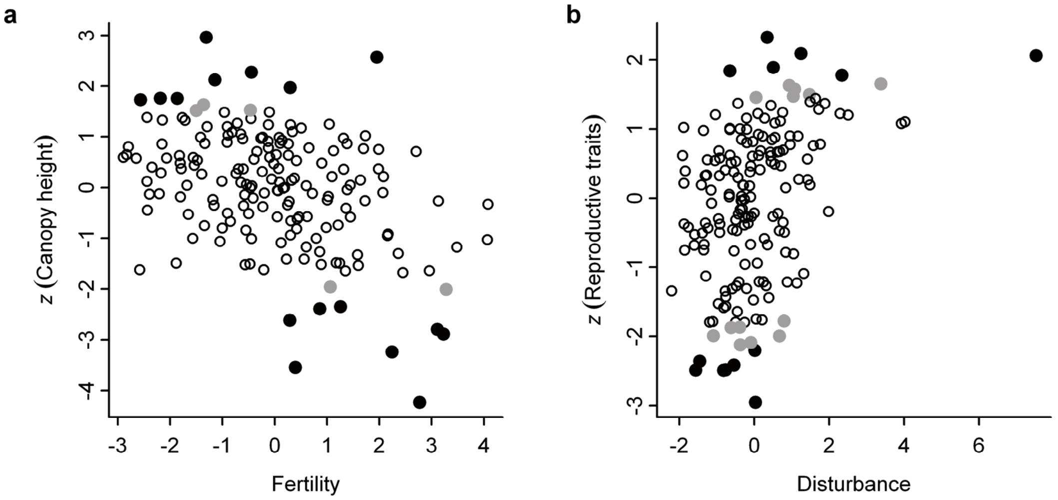

**Fig. 2.** $z$-scores of (a) canopy height and (b) the reproductive trait set along gradients of fertility and disturbance, respectively. Filled dots represent sites with a significant trait divergence (positive $z$-scores) or trait convergence (negative $z$-scores) at a significance level of 0.05 (black) and 0.1 (grey).

**Table 2.** Correlations between trait distribution statistics and the fertility gradient (PC1 in Fig. 1). See Table 1 for explanations of trait name abbreviations. Functional diversity (FD) was calculated as Rao's *Q*. *z*-scores are observed minus expected FD divided by the standard deviation across null communities (see text). Significance of correlations: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Significant correlations are printed in bold face.

| Trait / trait set | | Mean | FD | *z*-score |
|---|---|---|---|---|
| Competitive trait set | | | -0.04 | **-0.27** *** |
| CH | | **0.39** *** | **-0.49** *** | **-0.41** *** |
| LS | | -0.12 | 0.11 | -0.13 |
| SLA | | **-0.40** *** | **-0.24** ** | **-0.30** *** |
| Reproductive trait set | | | 0.12 | -0.05 |
| $\mathrm{FP}_{\mathrm{onset}}$ | | **0.36** *** | -0.01 | -0.04 |
| $\mathrm{FP}_{\mathrm{end}}$ | | **0.38** *** | **0.30** *** | 0.05 |
| | Insects | 0.13 | | |
| PM | Wind | -0.05 | 0.00 | -0.11 |
| | Self | -0.08 | | |
| DW | | **-0.42** *** | **0.22** ** | 0.09 |
| LI | | **0.40** *** | **0.41** *** | **0.27** *** |

**Table 3.** Correlations between trait distribution statistics and the disturbance gradient (PC2 in Fig. 1). See Table 1 for explanations of trait name abbreviations. Functional diversity (FD) was calculated as Rao's *Q*. *z*-scores are observed minus expected FD divided by the standard deviation across null communities (see text). Significance of correlations: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Significant correlations are printed in bold face.

| Trait / trait set | | Mean | FD | *z*-score |
|---|---|---|---|---|
| Competitive trait set | | | 0.10 | 0.05 |
| CH | | **0.47** *** | **-0.33** *** | **-0.36** *** |
| LS | | 0.03 | **0.19** * | 0.14 |
| SLA | | -0.14 | **0.22** ** | **0.19** * |
| Reproductive trait set | | | **0.43** *** | **0.39** *** |
| $\mathrm{FP}_{\mathrm{onset}}$ | | **0.49** *** | **-0.24** ** | **-0.23** ** |
| $\mathrm{FP}_{\mathrm{end}}$ | | **0.41** *** | **0.15** * | 0.05 |
| | Insects | **-0.36** *** | | |
| PM | Wind | **0.30** *** | **0.36** *** | **0.33** *** |
| | Self | 0.14 | | |
| DW | | **-0.31** *** | **0.15** * | 0.09 |
| LI | | **0.39** *** | **0.34** *** | **0.36** *** |

## Changes in trait distribution patterns over time

Changes in trait distributions between the sampling periods did not vary much along the fertility gradient (Appendix), but along the disturbance gradient. At sites that experienced significant disturbance during the last decades, trait composition had shifted toward taller species, species with later onset and end of flowering, species pollinated more by wind and less by insects and species with lighter and longer-living seeds (Table 4). The FD and the degree of trait divergence (as measured by the *z*-score) had increased at more disturbed sites for PM, DW, LI and the whole reproductive trait set. However, canopy height tended to have converged at more disturbed sites.

**Table 4.** Correlations of differences in trait distribution statistics between sampling periods with the disturbance gradient (PC2 in Fig. 1). See Table 1 for explanations of trait name abbreviations. Functional diversity (FD) was calculated as Rao's *Q*. *z*-scores are observed minus expected FD divided by the standard deviation across null communities (see text). Arrows indicate a significant ($P \leq 0.05$) positive (↑) or negative (↓) change of the corresponding statistic over time as tested by a Wilcoxon signed rank test across sites. Significance of correlations: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Significant correlations are printed in bold face.

| Trait / Trait set | | Difference between sampling periods in | | |
|---|---|---|---|---|
| | | Mean | FD | *z*-score |
| Competitive trait set | | | 0.03 | -0.01 |
| CH | | ↑ **0.48** *** | ↓ **-0.26** *** | **-0.28** *** |
| SLA | | **-0.18** * | 0.14 | 0.10 |
| LS | | ↑ 0.03 | 0.10 | 0.05 |
| Reproductive trait set | | | ↑ **0.38** *** | **0.37** *** |
| $\mathrm{FP}_{\mathrm{onset}}$ | | **0.45** *** | -0.14 | -0.12 |
| $\mathrm{FP}_{\mathrm{end}}$ | | ↑ **0.33** *** | ↑ 0.10 | 0.03 |
| | Insects | ↓ **-0.28** *** | | |
| PM | Wind | ↑ **0.36** *** | ↑ **0.34** *** | **0.32** *** |
| | Self | -0.08 | | |
| DW | | ↓ **-0.37** *** | ↑ **0.23** ** | **0.17** * |
| LI | | ↑ **0.31** *** | ↑ **0.30** *** | **0.27** *** |

# 3.5 Discussion

## Community assembly along the fertility gradient

The trait distribution patterns found along the fertility gradient mainly support the hypotheses of Grime (2006) and Navas & Violle (2009) while they partly contradict the hypothesis of Weiher & Keddy (1995). Two of the competitive traits (CH and SLA) tended to be convergent at more fertile sites (Table 2), as predicted by Grime (2006). The enhanced competitive adversity tended to select for taller species. Similarly, Schamp & Aarssen (2009) observed that species in temperate forests in Ontario were increasingly taller than expected with increasing productivity at the site. However, they could not find a height range smaller than that expected by chance (i.e., no trait convergence pattern). Instead, they observed that most species were relatively small (right-skewed distribution), which they interpreted as an indication of only a limited size-advantage, i.e., that other traits (related to survival and reproduction) must also contribute to competitive ability. In agreement with this assumption, we found that three reproductive traits ($\mathrm{FP}_{\mathrm{end}}$, DW and LI) showed a higher FD with increasing fertility (i.e., under conditions assumed to be more competitive; Table 2). For LI, FD was even higher than expected at random (Table 2). This might simply be the result of the higher species richness at more fertile sites (correlation between SR and fertility: $r = 0.52$, $P < 0.001$) but may also indicate that differences in reproduction strategy may allow species to coexist under competitive conditions when competitive traits are convergent.

In contrast to these findings from forest vegetation, Weiher et al. (1998) found different patterns in riverine wetlands along the Ottawa River. They observed an increasing dispersion for several size-related traits (measured as nearest-neighbor distance in multivariate trait space) with increasing fertility (as predicted by Weiher & Keddy 1995). These contradictory observations suggest that the assembly mechanisms under competitive conditions at fertile sites might differ between community types.

While the mean CH increased with increasing fertility, SLA decreased (Table 2). However, as an indicator of competitive ability, SLA was expected to be higher and not lower at more fertile sites (Westoby et al. 2002). This unexpected result might be explained by differences in light availability along the fertility gradient (note the positive loading of light availability on the first principle component; Fig. 1). Even at the less fertile sites, the soil was not really poor in nutrients, but light availability was low due to strongly shading tree species like *Carpinus betulus* or *Fagus sylvatica*. Forest plants specialized to these habitats may have a very large SLA (Westoby et al. 2002; Janse-ten Klooster et al. 2007). This is not necessary at more fertile sites, where tree species with a less dense canopy, e.g., *Fraxinus excelsior* and *Alnus glutinosa*, dominate (correlation between mean SLA and light availability: $r = -0.29$, $P < 0.001$). Thus, we believe that although SLA is related to fertility, it does not reflect competitive ability in these communities. Rather, SLA may reflect shade tolerance (Janse-ten Klooster et al. 2007).

Trait distribution statistics of LS were not correlated with the fertility gradient (Table 2); thus, either LS does not reflect competitive ability in these communities or the reflected component of competitive ability (horizontal space acquisition) does not follow the suggested principle of trait convergence and divergence (Grime 2006; Navas & Violle 2009). A lack of response of LS to fertility might also be a result of the suboptimal scaling of the variable on a four-degree scale (Table 1).

### Community assembly along the disturbance gradient

For the majority of reproductive traits, we observed a higher FD at more disturbed sites. Pollination mode, LI and the whole reproductive trait set tended to be more divergent when the degree of disturbance was higher (Table 3, Fig. 2b). Thus, the observed patterns are largely consistent with Grime's (2006) hypothesis that disturbance causes differentiation in reproductive traits. Indications that the FD, particularly of reproductive traits, can be higher in disturbed forests stands have been found previously, but without reference to a null model (e.g., Degen et al. 2005;

Biswas & Mallik 2010). Our results demonstrate that trait divergence is not always a result of (past) competition among species (Weiher & Keddy 1995), but can be caused by external factors that create new niches (Grime 2006). However, a trait divergence pattern with respect to disturbance was not observed for all reproduction-related traits. The $\mathrm{FP}_{\mathrm{onset}}$ tended to be convergent at more disturbed sites (Table 3), indicating that disturbance selects for plant species that begin flowering later. This is likely because most of the early flowering species are small (correlation between $\mathrm{FP}_{\mathrm{onset}}$ and CH: $r = 0.68$, $P \leq 0.001$) and are therefore at a competitive disadvantage under increased light availability. This observation supports the results of studies in other temperate forests, where stands disturbed by single-tree harvesting hold a higher proportion of summer-flowering species and undisturbed stands hold a higher proportion of spring-flowering species (Decocq et al. 2004; Aubin et al. 2007). These distinct behaviors of different reproductive traits are a good example for that it is important to evaluate FD not only in a multidimensional trait space (e.g., Mouillot et al. 2007; Thompson et al. 2010) but to consider traits individually. Otherwise, important assembly mechanisms might be masked (Weiher et al. 1998; Stubbs & Wilson 2004).

Canopy height tended to converge toward taller species also with an increasing degree of disturbance (Table 3). According to Weiher & Keddy (1995), an increased degree of disturbance should reduce the importance of competition for community assembly. In our communities, however, a higher degree of disturbance was always associated with more favorable light conditions (Fig. 1). According to Navas & Violle (2009), the enhanced competition under higher resource availability should promote fast-growing and taller species. Schamp & Aarssen (2009) did not find any relationship between the distribution of plant height in communities and the degree of disturbance. However, they did not take species abundance into account and suggested that their disturbance gradient might have been too short.

### Community assembly patterns over time

Changes over time could be observed mainly at sites that experienced considerable disturbance over the last two decades. Here, trait divergence for some reproductive traits had increased (Table 4), supporting the validity of Grime's (2006) hypotheses. The disturbance events that occurred between sampling periods created niches that were then occupied by species with different reproduction strategies (e.g., species able to germinate from a persistent seed bank or species pollinated by wind). The increased light availability also enhanced the competitive adversity that selected for taller species (Navas & Violle 2009), as indicated by the increased convergence of CH (Table 4). These results demonstrate that changes in environmental conditions alter the operative community assembly mechanisms quickly, leading to an adjusted species composition already after two decades. Previously, we found that the forest communities in the Weser-Elbe region are subject to moderate taxonomic homogenization (Naaf & Wulf 2010). Here, our results indicate that disturbance promoted the establishment of species with distinct functional attributes, thus causing functional differentiation.

## 3.6 Conclusions

Our study shows that the community assembly mechanisms at the upper and lower end of the fertility and disturbance gradients may differ greatly from each other. This observation agrees with previous findings (Weiher et al. 1998; Cornwell & Ackerly 2009; Schamp & Aarssen 2009). Studies in which trait distribution statistics are averaged across habitats (e.g., Stubbs & Wilson 2004; Mayfield et al. 2005; de Bello et al. 2009) should therefore be regarded with caution. The observed relationships between trait distribution patterns and environmental gradients indicate that previous hypotheses of Grime (2006) and Navas & Violle (2009) are correct in principle: with environmental favorability (e.g., higher fertility or increased light availability after disturbance) competitive traits (e.g., CH) are convergent. Also, both the comparison of trait distribution patterns along the disturbance gradient and over time confirmed that disturbance causes trait divergence and enables the coexistence of species with different reproduction strategies (Grime 2006). In addition, however, our results suggest that a trait convergence under competitive adversity is associated with a divergence of traits related to other challenges (e.g., reproduction). Thus, in agreement with the limiting similarity theory, our findings indicate that true functional redundancy within communities does not exist (Loreau 2004). Inversely, our results suggest that a divergence of reproductive traits caused by disturbance is accompanied by a convergence of other traits (e.g., CH), stressing once more that several assembly mechanisms can operate simultaneously (Weiher & Keddy 1995).

## 3.7 Acknowledgements

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## 3.9 Appendix

Correlations of differences in trait distribution statistics between sampling periods with the fertility gradient (PC1 in Fig. 1). See Table 1 for explanations of trait name abbreviations. Functional diversity (FD) was calculated as Rao's *Q*. *z*-scores are observed minus expected FD divided by the standard deviation across null communities (see text). Arrows indicate a significant ($P \leq 0.05$) positive (↑) or negative (↓) change of the corresponding statistic over time as tested by a Wilcoxon signed rank test across sites. Significance of correlations: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Significant correlations are printed in bold face.

| Trait / Trait set | | | Difference between sampling periods in | | | |
|---|---|---|---|---|---|---|
| | | | Mean | | FD | *z*-score |
| Competitive trait set | | | | | 0.07 | -0.03 |
| CH | | ↑ | -0.15 | ↓ | 0.09 | 0.09 |
| SLA | | | 0.04 | | 0.00 | -0.03 |
| LS | | ↑ | -0.01 | | 0.06 | -0.05 |
| Reproductive trait set | | | | ↑ | -0.08 | -0.12 |
| $\mathrm{FP}_{onset}$ | | | -0.08 | | **0.16 *** | **0.19 *** |
| $\mathrm{FP}_{end}$ | | ↑ | -0.04 | ↑ | 0.07 | 0.06 |
| | Insects | ↓ | **0.17 *** | | | |
| PM | Wind | ↑ | **-0.22 **** | ↑ | -0.14 | **-0.16 *** |
| | Self | | 0.12 | | | |
| DW | | ↓ | -0.08 | ↑ | 0.08 | 0.05 |
| LI | | ↑ | 0.02 | ↑ | 0.01 | -0.05 |

# Chapter 4

TOBIAS NAAF & MONIKA WULF

# Traits of winner and loser species indicate drivers of herb layer changes over two decades in forests of NW Germany

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This chapter is accepted for publication in the *Journal of Vegetation Science*.

## 4.1 Abstract

**Question:** What are the most likely environmental drivers for compositional herb layer changes as indicated by trait differences between winner and loser species?
**Location:** Weser-Elbe region (NW Germany)
**Methods:** We resurveyed the herb layer communities of ancient forest patches on base-rich sites relying on 175 semi-permanent plots. Species traits were tested for their ability to discriminate between winner and loser species using logistic regression analyses and deviance partitioning.
**Results:** Of 115 species tested, 31 were identified as winner species and 30 as loser species. Winner species had higher seed longevity, flowered later in the season and had more often an oceanic distribution compared to loser species. Loser species tended to have a higher specific leaf area, to be more susceptible to deer browsing and to have a performance optimum at higher soil pH values compared to winner species. The loser species also represented several ancient forest and threatened species. Deviance partitioning indicated that local drivers (i.e., disturbance due to forest management) were primarily responsible for the species shifts, while regional drivers (i.e., browsing pressure and acidification from atmospheric deposition) and global drivers (i.e., climate warming) had moderate effects. There was no evidence that canopy closure, drainage or eutrophication contributed to herb layer changes.
**Conclusions:** The relative importance of the different drivers indicated by the winner and loser species differs from that found in previous long-term studies. Relating species traits to species performance is a valuable tool that provides insight into the environmental drivers that are most likely responsible for herb layer changes.

**Nomenclature:** Wisskirchen & Haeupler (1998)

## 4.2 Introduction

Human activities have caused a worldwide loss of biodiversity, and the rate of species loss has increased during the last centuries (Dirzo & Raven 2003). Environmental alterations act as a non-random filter selecting for species best able to survive in a human-modified landscape (“winners”). Species adapted to specific habitat conditions and sensitive to environmental changes are likely to become extinct (“losers”) (McKinney & Lockwood 1999). Sessile organisms with limited dispersal abilities are particularly threatened by environmental changes, especially when these species live in small isolated populations, like many forest herbs in the strongly fragmented forest remnants in the west European lowlands (Hermy et al. 1999; Verheyen et al. 2003; Kolb & Diekmann 2005). Numerous long-term studies in temperate Europe have documented shifts in herb layer composition. They have attributed the observed changes to the following main environmental drivers: atmospheric deposition of acidifying and eutrophying substances, changes in the forest management regime and changes in the soil water balance (e.g., Thimonier et al. 1994; Brunet et al. 1997; Lameire et al. 2000). Winner species are often comparably nitrogen-demanding while at the same time acid-tolerant (e.g., Thimonier et al. 1994; Diekmann et al. 1999; Kirby et al. 2005). In response to canopy opening and substrate disturbance, winner species are mostly “weedy” species typically found in forest clearings, fringes or other non-forest habitats (e.g., Falkengren-Grerup & Tyler 1991; Brunet et al. 1996; van Calster et al. 2007). Particularly on acidic soils, acid-tolerant species are among the winner species (e.g., Wittig et al. 1985; Thimonier et al. 1994; Hédl 2004). In contrast, loser species are mostly acid-intolerant (e.g., Wittig et al. 1985; Thimonier et al. 1994; Baeten et al. 2009) and specialized to closed forests (e.g., Falkengren-Grerup & Tyler 1991; Brunet et al. 1997; Kirby et al. 2005). In formerly oak-rich and often grazed forests, thermophilic and light-demanding species are most prominent among the loser species as a result of shifts in tree species dominance and increased canopy density (e.g., von Oheimb & Brunet 2007; Baeten et al. 2009; Keith et al. 2009). In some studies, drainage was the main factor that caused the loss of moisture-indicating species (e.g., Fischer 1993; Lameire et al. 2000).

Although the studies cited above appear to give a clear picture of species shifts in European temperate forests and the corresponding environmental drivers, there are some shortcomings and questions that remain unanswered. First, the representativeness of many studies is limited. Resurveys often comprise only a single forest or a few forests located close to each other (e.g., Thimonier et al. 1994; Lameire et al. 2000; Baeten et al. 2009). Others do not rely on (semi-)permanent plots (e.g., Diekmann & Dupré 1997; Kirby et al. 2005). The few studies that resurveyed (semi-)permanent plots and at the same time covered an entire region were mainly confined to southern Sweden (e.g., Falkengren-Grerup & Tyler 1991; Brunet et al. 1997; Diekmann & Falkengren-Grerup 2002). In this study, we could rely on a large data set ($n$ = 175) comprising semi-permanent plots that could be relocated within an error of 1 to 2 m and that are distributed across a 7600 km$^2$ region.

Second, the relative importance of the potential environmental drivers is still unclear. Most of the studies mentioned above focus on one or two factors while neglecting others. It is likely that shifts in species composition are the result of a complex of different drivers. These drivers can act on different spatial scales, i.e., on the local scale (e.g., changes in canopy cover; Dahlgren et al. 2006; Baeten et al. 2009), on the regional scale (e.g., atmospheric deposition; Diekmann & Falkengren-Grerup 2002; Keith et al. 2009) or on the global scale (e.g., climate warming; Skov & Svenning 2004; van der Veken et al. 2004). A quantification of the relative contribution of these different drivers is essential if we want to discuss the priority of any conservation measures. In this study, we considered drivers covering all spatial scales.

Third, many long-term studies in Europe rely almost exclusively on Ellenberg indicator values (Ellenberg et al. 2001) to conclude from species performances on changes in habitat quality (e.g., Lameire et al. 2000; Hédl 2004; Baeten et al. 2009; Keith et al. 2009). However, there is additional knowledge on the ecological performance of species and on how morphological and life-history traits are related to environmental conditions. This knowledge can be used to relate species performances to drivers other than those represented by Ellenberg values. For instance, Wiegmann & Waller (2006) used growth form and pollination mode to explain compositional changes over five decades in hardwood forests of northern Wisconsin. They observed declines in biotically pollinated herbs with conspicuous flowers alongside an increase in graminoids. They suggested herbivory by deer as a main driver.

In our study, we used a comprehensive list of species traits to find indications of the most likely drivers responsible for herb layer changes in forest patches of NW Germany. We had three main objectives. First, we aimed to identify winner and loser species by comparing species' abundances between the sampling periods 1986 to 1988 and 2008/2009. Because we found a net increase in species richness in previous analyses (Naaf & Wulf 2010), we expected to find a greater number of winner species compared to loser species. Second, we aimed to test the hypothesis that winner and loser species differ in their trait attributes. If this hypothesis were to be true, the discriminating traits would allow us to deduce the most likely environmental drivers. Third, we aimed to quantify the relative importance of local, regional and global drivers.

## 4.3 Materials and methods

### Study region

The investigated forest stands are distributed across the Weser-Elbe region in the lowlands of NW Germany (Fig. 1). The climate is sub-oceanic with mean temperatures of 1.6 and 17.7 °C in January and July, respectively. Mean annual precipitation ranges from 700 mm (Bremen) to 715 mm (Hamburg; values are averages over three decades from 1979 to 2008; data available at http://www.dwd.de). Forest patches constitute 9.8% of the area, and 25% of these patches are ancient (Kelm 1994). Forests are embedded in an intensively cultivated agricultural landscape. Deciduous broadleaf stands constitute less than 25% of the forested area (Wulf & Kelm 1994). The study is restricted to sites in the upper half of the whole fertility and moisture gradient present in the region, excluding forests on dry and extremely acidic soils. The investigated forests grow on loamy ground moraines with varying proportions of sand and clay. Soil types range from eutric cambisols to stagnosols and (histic) gleysols. Soil pH (0-10 cm) varies between 3.1 and 6.7, soil moisture from slightly moist to wet. The overstory is dominated by *Alnus glutinosa* and *Fraxinus excelsior* on wet and moist sites, by *Carpinus betulus* and *Quercus robur* on moderately moist sites and by *Fagus sylvatica* on slightly moist sites (Wulf 1992).

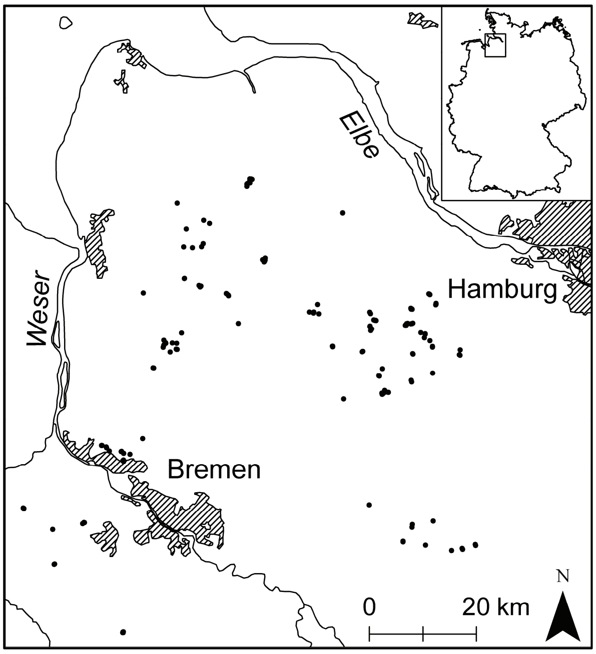

**Fig. 1.** Distribution of the 175 study sites (black dots) across the 7600 km² Weser-Elbe region in NW Germany.

## Potential environmental drivers

We considered eight potential environmental drivers that may have contributed to changes in forest vegetation in the Weser-Elbe region. These drivers operate over three different spatial scales (Table 1). On the local scale, natural succession may lead to (1) changes in canopy cover. Canopy cover may increase in the absence of any disturbance or decrease as a result of natural tree fall; in either case, the light availability for the herb layer is altered. (2) Disturbance by forest management activities or natural wind throw not only changes the light environment but also causes soil disturbance. Management practices (i.e., harvesting of a single or a few trees less than once per ten years) have generally not changed over the last few decades, but single cutting events still may have affected ground vegetation (see below). As another driver on the local scale, we considered (3) changes in soil moisture as a result of an altered groundwater table. The agricultural landscape surrounding forest patches contains many drainage ditches and watercourses. These were built or enlarged mainly during the 1950s and 1960s to prevent agricultural fields from flooding (Seedorf & Meyer 1992). Some groundwater-measuring stations in the region have documented a decreasing trend during the last few decades, while others indicate no change or even a rising trend (unpublished data from the regional hydrological service). On the regional scale, atmospheric deposition of (4) acidifying and (5) eutrophying substances (see Fig. S1 in Supplementary Information) may have affected herb layer composition (Bobbink et al. 2010). Sulfur deposition in the region has strongly decreased over the last few decades but was still high in 1990 (c. 30 kg S ha$^{-1}$ yr$^{-1}$). In contrast, nitrogen (N) deposition, of which about two-thirds are in the form of $NH_4^+$, is still rather high, amounting to around 20 kg $ha^{-1}$ $yr^{-1}$ in 2005 (figures estimated from the EMEP database at http://www.emep.int). We also considered (6) enhanced browsing pressure as a driver on the regional scale. There are two deer species in the Weser-Elbe region whose foraging may affect herb layer composition: roe deer (*Capreolus capreolus* L.) and fallow deer (*Dama dama* L.). The true abundances of these species are not known, but their trends can be estimated from the number of culled individuals per year. While the number of culled roe deer individuals per 1000 ha per year fluctuated between 25 and 30 since 1986 (averaged across the region), the number of culled fallow deer individuals per 1000 ha per year increased from 2.7 to 4.9 between 1986 and 2008 (unpublished data from the municipal hunting authorities). As a driver on the global scale, we included (7) climate warming. Meteorological data indicate that the length of the growing season (number of days with an average temperature of ≥5 °C) has on average increased by 1 day per year from 1979 to 2008 (Fig. S2). This was mainly due to increasing temperatures in the winter; the mean temperature of the coldest month (January) increased by about 4 °C on average since 1979 (figures are for Bremen and were estimated from data available at http://www.dwd.de). Finally, the transportation and (8) invasion of exotic species into the region were considered as drivers on the global scale (Lambdon et al. 2008).

### Resampling of the herb layer composition

The forests were initially surveyed by the co-author from 1986 to 1988 (hereafter 1988; Wulf 1992). All stands were mature in 1988 and located in ancient forests (habitat continuity > 200 years; Wulf 1997). For plant species recording, 415 plots were placed in undisturbed sites with an evenly closed canopy and a homogenous herb layer composition. Plot size varied between 100 and 400 m², but we did not find a significant species-area relationship. In a linear regression model (data from 2008/2009) including plot size, pH, base supply, moisture, light availability and disturbance as predictors ($R^2 = 0.29$, $F_{6,168} = 11.7$, $P < 0.001$), extra variance explained by plot size was 1.5% (partial $F_{1,168} = 3.5$, $P = 0.061$). In the present study, we focused on differences in species abundances between sampling periods, thus, any differences in species richness among plots due to different plot sizes should not affect our results. The abundances of all vascular plant species in the herb layer (≤ 1 m height) were recorded in spring and summer using the nine-degree combined cover-abundance scale of Barkman et al. (1964; see Naaf & Wulf 2010 for details). Tree species (i.e., species whose adult individuals occur in the tree layer in the study area, but not woody species in general) were excluded for two reasons: (a) their occurrence is less determined by environmental conditions but depends mostly on the occurrence of mother trees in the vicinity, which, in turn, is strongly dependent on forest management; and (b) their abundance varies considerably between years in dependence of the seed output of the surrounding trees. For our resurvey in 2008/2009 (hereafter, 2008), we used 175 plots that could be relocated within an error of 1 to 2 m. Relocation was possible with the aid of coordinates drawn from maps at a scale of 1 : 25 000 (with an error <100 m) and sketches of each plot, showing important structures, such as tree trunks, stumps or large stones, along the plot margins. Pseudoreplicates (i.e., plots within the same stand, defined as a part of a forest patch with a uniform structure and tree species composition) and plots too heavily altered by forest management (i.e., clear-cut or afforested) were excluded. Plant species were recorded using the original method and the same plot sizes as in 1988. To reduce systematic errors due to personal cover-abundance estimation, the estimates made by the researcher in 2008 (first author) were calibrated with those of the original researcher (co-author) on several plots until no further deviations occurred.

## Measurements of environmental conditions

In 2008, we measured the main environmental factors responsible for differences in species composition among forest stands in NW Germany (Wulf 1992; Härdtle et al. 2003). Soil pH was measured as pH($CaCl_2$) in soil samples taken at a depth of 0-10 cm. The soil samples were also used to measure the plant-available concentrations of Ca, K and Mg, which were then summed to form a single measure of base supply (S-value). Soil moisture was measured as the volumetric water content in the topsoil (0-10 cm) using time-domain reflectometry field probes. As a measure of light availability, we derived the canopy openness (proportion of visible sky) from hemispherical photographs. For a more detailed description of the measurements, see Appendix S1. We also assessed the degree of disturbance experienced by a plot during the last two decades using a five-degree scale according to Falkengren-Grerup & Tyler (1991) and Brunet et al. (1997):

$D_0$: undisturbed since first observation ($n$ = 45)
$D_1$: light canopy thinning with one or several trees removed or thrown by wind; canopy still almost closed; no traces of driving tracks or light driving tracks ($n$ = 80)
$D_2$: intermediate canopy thinning with several trees removed or thrown by wind; smaller gaps in the canopy; driving tracks usually found; small heaps of slash may occur ($n$ = 41)
$D_3$: moderate canopy thinning with several trees removed or thrown by wind; large gaps in the canopy; obvious driving tracks and soil damage ($n$ = 6)
$D_4$: heavy canopy thinning with more than half of the trees removed or thrown by wind; canopy rather open; deep driving damage common; quantities of slash remaining, often in large heaps ($n$ = 3)

## Plant species traits

To gain insights into the likely environmental drivers, we used 16 plant species traits to characterize the winner and loser species (Table 1). This trait set comprised both ecological performances and functional response traits. While the former are by definition related to an environmental driver (Violle et al. 2007), the latter were assessed as responsive to an environmental driver on the basis of current knowledge from the literature (Appendix S2). For each of the five environmental variables

**Table 1.** Plant species traits related to environmental drivers.

| Drivers | Related traits | Trait description | Reference[a] | Source[b] | Missing values |
|---|---|---|---|---|---|
| **Local drivers** | | | | | |
| Canopy cover changes | Light optimum | Abundance-weighted average of light availability (%) | | 8 | - |
| | SLA | Specific leaf area (mm$^2$ mg$^{-1}$) | 4, 15, 28, 29 | 6, 8 | - |
| | Flowering phenology | Onset and end of flowering in month | 1, 5, 12, 13 | 7, 9 | 11 (18%) |
| Disturbance | Disturbance optimum | Abundance-weighted average of the degree of disturbance | | 8 | - |
| | Long-distance dispersal | 0 Not adapted to long-distance dispersal<br>1 Adapted to dispersal by wind or animals (except ants) | 7, 11, 20 | 1, 9 | - |
| | Seed longevity | Seed longevity index according to Thompson et al. (1998) | 6, 7, 10, 11, 20 | 10 | 6 (10%) |
| Soil moisture changes | Moisture optimum | Abundance-weighted average of soil moisture content (%) | | 8 | - |
| **Regional drivers** | | | | | |
| Acid deposition | pH optimum | Abundance-weighted average of soil pH | | 8 | - |
| | S-value optimum | Abundance-weighted average of the base supply (mmol$_c$ (100 g)$^{-1}$) | | 8 | - |
| N deposition | Ellenberg N | Nitrogen indicator value | 2, 3, 19, 21, 25 | 4 | 11 (18%) |
| | $N_{dev}$ | Index indicating if a species is favored (positive values) or inhibited (negative values) by eutrophication | 8 | 2 | 24 (39%) |
| Browsing pressure | Browsing attractiveness | 0 never or rarely browsed by roe deer<br>1 sometimes slightly browsed<br>2 frequently moderately browsed<br>3 seasonally strongly browsed or moderately throughout the year<br>4 frequently strongly browsed | 9, 17 | 3 | |
| | Graminoid | 0 Other growth form<br>1 Grass, sedge or rush | 14, 16, 22, 27 | 9 | |
| **Global drivers** | | | | | |
| Climate warming | Latitudinal distribution | 0 Distributed throughout (northerly distribution edge in boreal or arctic zone)<br>1 Southern distribution (northerly distribution edge in temperate zone) | 23, 24, 26 | 9 | 1 (1.6%) |
| | Oceanity | 0 Non-oceanic distribution (max. continentality > 4)<br>1 Oceanic distribution (min. continentality 1 AND max. continentality $\leq$ 4) | 23, 26 | 9 | 1 (1.6%) |
| Invasion of alien species | Native/Exotic status | 0 Native<br>1 Exotic | 18 | 5 | |

[a] References providing evidence for the relationships between species traits and the corresponding drivers: 1 Aubin et al. 2007; 2 Borchsenius et al 2004; 3 Brunet et al. 1998; 4 Dahlgren et al. 2006; 5 Decocq et al. 2004a; 6 Decocq et al. 2004b; 7 Degen et al. 2005; 8 Diekmann & Falkengren-Grerup 2002; 9 Ellenberg Jun. 1988; 10 Eriksson 1995; 11 Eycott et al. 2006; 12 Falk et al. 2008; 13 Heinrich 1976; 14 Horsley et al. 2003; 15 Janse-ten Klooster et al. 2007; 16 Kirby 2001; 17 Klötzli 1965; 18 Lambdon et al. 2008; 19 Lameire et al. 2000; 20 Naaf & Wulf 2007; 21 Pitcairn et al. 1998; 22 Rooney & Waller 2003; 23 Skov & Svenning 2004; 24 Thuiller et al. 2005; 25 van Calster et al. 2007; 26 van der Veken et al. 2004; 27 von Oheimb et al. 2003; 28 Westoby et al. 2002; 29 Wilson et al. 1999. For bibliographic details, see Appendix S2.

[b] Data sources for the trait values: 1 Bundesamt für Naturschutz 2003; 2 Diekmann & Falkengren-Grerup 2002; 3 Ellenberg Jun. 1988; 4 Ellenberg et al. 2001; 5 Garve 2004; 6 Kleyer et al. 2008; 7 Klotz et al. 2002; 8 Own measurements; 9 Rothmaler 2005; 10 Thompson et al. 1997. For bibliographic details, see Appendix S3.

measured for each plot (see above), we calculated species optima as abundance-weighted averages. Most of remaining trait data were taken from the literature (Table 1).

## Data analysis

To identify plant species that have consistently increased or decreased in abundance, we subtracted the abundance matrices of the two sampling periods. We used Fisher's sign tests to determine whether the abundance changes of each species significantly deviated from zero. This test uses only the sign rather than the actual values of the abundance changes, thus a significant result means that the abundance of the corresponding species has consistently changed across the region. Plots where a species was absent in both sampling periods are disregarded by the test. Only species with at least five occurrences in either of the sampling periods were considered. We defined a species with a significant ($P \leq 0.05$) positive average change in abundance as a "winner" and a species with a significant negative average change as a "loser". We judged missing a possibly indicative winner or loser species by committing a type II error worse than keeping an in fact non-indicative species in the analyses by committing a type I error (Moran 2003). Therefore, we decided not to adjust *P*-values for multiple testing.

The characterization of winner and loser species by traits related to environmental changes was achieved following two steps. First, we applied univariate tests to evaluate whether winner and loser species differed in their trait attributes. We used the $\chi^2$-statistic for categorical variables and the *T*-statistic for numeric variables. The statistics for all trait variables were simultaneously tested for significance by comparing them to random distributions based on 10 000 samples obtained by randomly allocating the species to the two groups. We adjusted *P*-values by controlling the false discovery rate (Benjamini & Hochberg 1995), i.e., the adjusted *P*-values represent the expected proportion of significant results that are considered to be truly null cases (false discoveries) when the threshold for $H_0$ rejection is set to the original *P*-value. In a second step, we used multivariate tests, because (a) several traits were correlated with each other (Table S3) and (b) traits may have competing effects on species performance that result in non-significant univariate effects. Therefore, we included all traits as potential predictors in a multiple logistic regression model. Species performance (coded as 1 for winners and 0 for losers) was used as binary response variable. The best subset of traits to explain species performance (minimal adequate model) was found by fitting models for all possible subsets. The model with the lowest Akaike Information Criterion was chosen from among the models that were not overfitted and in which all predictors contributed significantly ($P \leq 0.1$) to the reduction of deviance. The significance of each predictor was tested using a partial $\chi^2$-test based on 10 000 random permutations of the observations of the tested predictor variable. As a measure of the ability of the significant trait combinations to discriminate between winner and loser species, we calculated the area under the receiver operating characteristic (ROC) curve (*AUC*;

Fielding & Bell 1997). In addition to the minimal adequate model, we used a deviance partitioning approach with the aim of assessing the relative importance of local, regional and global drivers. Analogous to variation partitioning (Legendre & Legendre 1998), the deviance explained in the full logistic regression model was partitioned into the unique and shared proportions explained by traits related to local, regional or global drivers (Table 1). We will refer to the sum of the unique and shared proportion of deviance explained by a particular trait group as the total contribution of that trait group. All calculations were done with R (version 2.10.1, R Foundation for Statistical Computing, Vienna, Austria).

## 4.4 Results

### Winner and loser species

Fisher's sign test was applied to 115 species and identified 31 species as winners and 30 species as losers (significantly more than the 2.9 winner and the 2.9 loser species expected by chance at a significance level of $P \leq 0.05$; Table S1). Average abundance changes among winner and loser species ranged from -2.5 (*Myosotis scorpioides*) to +2.9 (*Holcus mollis*). Five of the winner species were not present in 1988 (*Frangula alnus*, *Holcus mollis*, *Hypericum maculatum*, *Lythrum salicaria* and *Prunus serotina*). All loser species were still present in the region in 2008, but some had five or fewer occurrences (*Angelica sylvestris*, *Mycelis muralis* and *Myosotis scorpioides* agg.). The group of winner species was rather heterogeneous and was comprised of 11 woody species, 11 forbs, 7 graminoids and 2 pteridophytes. The group of loser species was much more homogenous and was comprised of 24 forbs, 3 graminoids and 3 pteridophytes. A list of all winner and loser species with their trait attributes is provided in Table S2.

### Discriminating species traits

Only two of the 61 species were exotic (*Impatiens parviflora* and *Prunus serotina*, both winner species). The native/exotic status was therefore excluded from statistical analyses. The univariate tests revealed that winner and loser species differed significantly in four of the remaining 16 traits (Table 2, Fig. 2). Winner species stopped flowering on average about one month later (Fig. 2a) and tended to build a persistent seed bank in contrast to loser species (Fig. 2c). Loser species had on average a higher pH optimum (Fig. 2d). Among the winner species, there were significantly more species with an oceanic distribution (Fig. 2f). Winner species also tended to perform better in disturbed sites than loser species (Fig. 2b), and loser species tended to have a higher S-value optimum than winner species (Fig. 2e). However, these last two differences barely missed significance (Table 2).

Some species with missing values or some traits with missing values had to be excluded to conduct the logistic regression analyses. Analyses of several variants indicated that a minimum of information was lost when the traits flowering

**Table 2.** Trait differences between winner and loser species as tested by *T* (numerical traits) and $\chi^2$ (categorical traits) randomization tests. *P*-values were adjusted to control the false discovery rate (Benjamini & Hochberg 1995).

| | # Winner | # Loser | Mean winner | Mean loser | Proportion winner (%) | Proportion loser (%) | *T* | $\chi^2$ | *P* |
|---|---|---|---|---|---|---|---|---|---|
| Light optimum | 31 | 30 | 0.124 | 0.119 | | | 1.03 | | 0.431 |
| SLA | 31 | 30 | 31.1 | 36.2 | | | -1.10 | | 0.417 |
| Onset of flowering | 20 | 30 | 5.55 | 4.97 | | | 1.59 | | 0.205 |
| End of flowering | 20 | 30 | 7.80 | 6.70 | | | 2.62 | | 0.043 |
| Disturbance optimum | 31 | 30 | 1.30 | 1.14 | | | 2.10 | | 0.078 |
| Long-distance dispersal | 31 | 30 | | | 90.3 | 70.0 | | 3.98 | 0.142 |
| Seed longevity | 28 | 27 | 0.351 | 0.115 | | | 3.72 | | 0.006 |
| Moisture optimum | 31 | 30 | 43.4 | 44.0 | | | -0.44 | | 0.757 |
| pH optimum | 31 | 30 | 5.26 | 5.45 | | | -2.96 | | 0.018 |
| S-value optimum | 31 | 30 | 11.3 | 12.8 | | | -2.32 | | 0.070 |
| Ellenberg N | 24 | 26 | 5.29 | 5.65 | | | -0.86 | | 0.486 |
| $N_{dev}$ | 17 | 20 | 1.04 | 1.37 | | | -0.15 | | 0.943 |
| Browsing attractiveness | 25 | 27 | 1.76 | 1.78 | | | -0.05 | | 0.943 |
| Graminoid | 31 | 30 | | | 22.6 | 10.0 | | 1.76 | 0.417 |
| Latitudinal distribution | 30 | 30 | | | 53.3 | 30.0 | | 3.36 | 0.178 |
| Oceanity | 30 | 30 | | | 40.0 | 3.3 | | 11.88 | 0.006 |

phenology, Ellenberg N and $N_{dev}$ (all with several missing values) were excluded. When included, these did not enter into the final model. We will therefore focus on the variant without these traits. The minimal adequate model contained five of the potential 12 predictor variables considered (Table 3; Pseudo-$R^2$ = 0.47, $P < 0.001$, $AUC = 0.91$). Three of these (seed longevity, oceanity and long-distance dispersal) had a positive sign, indicating that winner species tended to have a persistent seed bank, to have an oceanic distribution and to be able to disperse over long distances. Specific leaf area and browsing attractiveness had negative signs, indicating that loser species tended to have a higher SLA and to be more susceptible to deer browsing than winner species. Three of the predictors (SLA, browsing attractiveness and long-distance dispersal) did not show a significant difference between winner and loser species in the univariate tests.

Deviance partitioning showed that traits related to local drivers constituted the largest proportion (total contribution c. 27%) of the differences between winner and loser species (Fig. 3). The total contributions of traits related to regional and global drivers were less than half as large (each around 10%). The unique contributions of the individual trait groups were generally larger than the corresponding total contributions. This resulted in negative shared effects. The unique contribution of traits related to regional drivers was clearly larger (c. 29%) than that of traits related to global drivers (c. 16.5%).

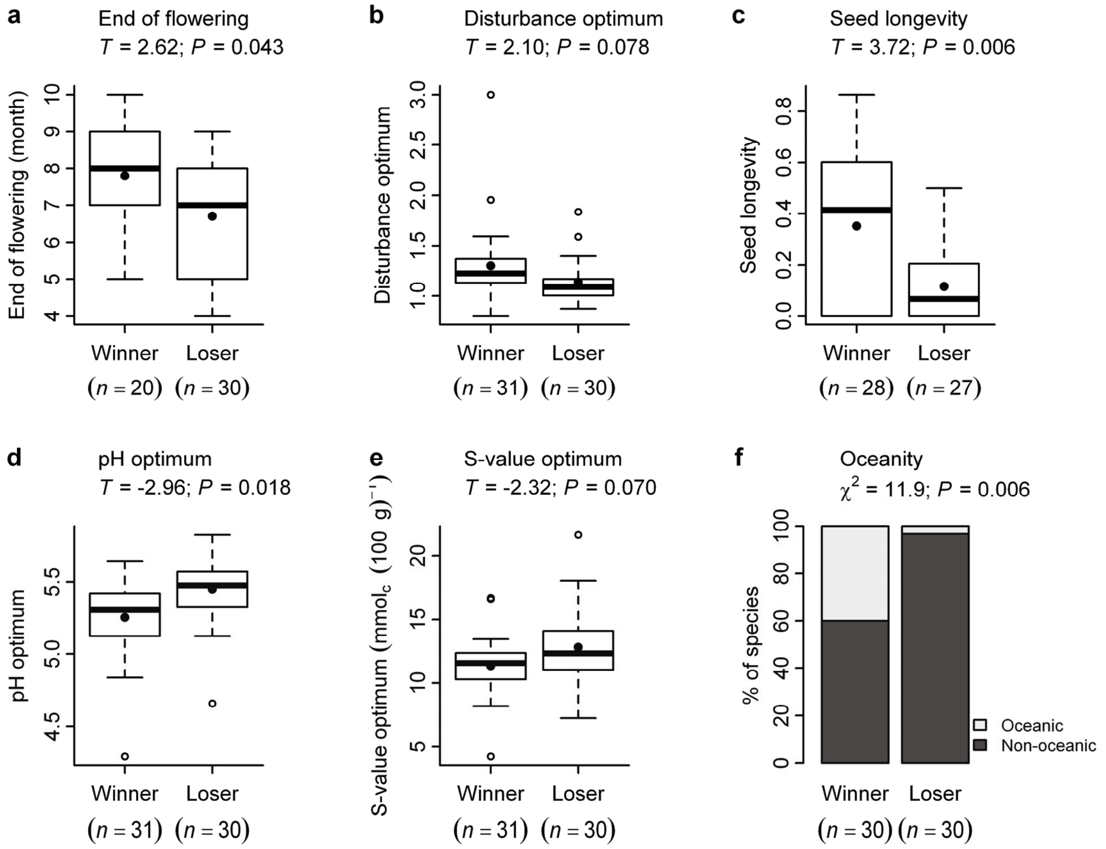

**Fig. 2.** Differences between winner and loser species in their trait values. Box plots are standard box plots.

## 4.5 Discussion

### Identity of winner and loser species

The identification of winner and loser species showed that significant shifts in species composition have taken place during the last two decades. More than half of the species tested (53%) have consistently increased or decreased in abundance (Table S1). Contrary to our expectations, the number of loser species was almost as high as the number of winner species. Most other studies that tested individual species for significant changes in abundance (or frequency) found either disproportionately more winners (e.g., Falkengren-Grerup & Tyler 1991; Thimonier et al. 1994; Brunet et al. 1997) or more losers (e.g., Lameire et al. 2000; Taverna et al. 2005; von Oheimb & Brunet 2007). The observed decline in the abundance of loser species may be of conservation relevance. Twelve of the loser species (compared to three winner species) are tied to ancient forests (Wulf 1997), e.g., *Adoxa moschatellina*, *Galium odoratum* and *Mercurialis perennis*. Seven loser species are listed on the Red List of endangered plant species in Lower Saxony (Garve 2004), e.g., *Paris quadrifolia*, *Phyteuma nigrum* and *Pulmonaria obscura*.

**Table 3.** Minimum adequate logistic regression model[a] for the discrimination between winner ($n = 22$) and loser ($n = 24$) species. The proportion of deviance explained by the model is 47.4% ($P < 0.001$). The area under the receiver operating characteristic curve (*AUC*) is 0.91.

| Significant predictors | Sign | Unique proportion of deviance explained (%) | $P$ [b] |
|---|---|---|---|
| SLA | − | 17.9 | 0.002 |
| Seed longevity | + | 17.3 | 0.002 |
| Oceanity | + | 13.6 | 0.009 |
| Browsing attractiveness | − | 9.9 | 0.027 |
| Long-distance dispersal | + | 7.6 | 0.052 |

[a] To obtain the best trade-off between the exclusion of species with missing values and the exclusion of traits with missing values, the traits onset and end of flowering, Ellenberg N and $N_{dev}$ (all with several missing values) had to be excluded. These traits did not enter the minimum adequate model when considered as potential predictors.

[b] Partial $\chi^2$ randomization test

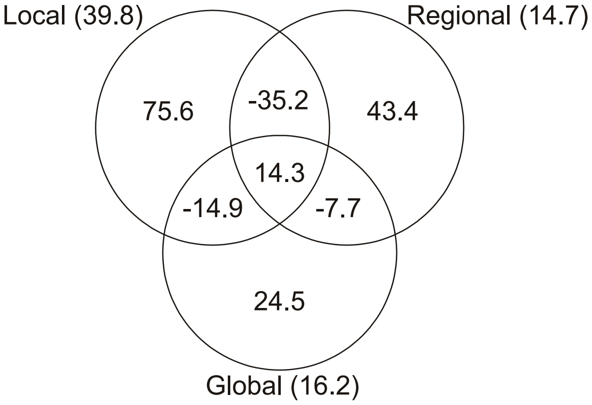

**Fig. 3.** Unique and shared proportions (%) of explained deviance in the full logistic regression model. The total amount of explained deviance in the model (67.3%) was set to 100%. Included traits were light optimum, SLA, disturbance optimum, long-distance dispersal, seed longevity and moisture optimum as traits related to local drivers; pH optimum, S-value optimum, browsing attractiveness and graminoid as traits related to regional drivers; and latitudinal distribution and oceanity as traits related to global drivers.

## Environmental drivers indicated by species traits

The traits discriminating between winner and loser species indicate that three environmental factors are most likely to drive herb layer changes: disturbance, climate warming and browsing by deer. The two most important traits for discriminating between winner and loser species were SLA and seed longevity (Table 3, Fig. 2c). Winner species with a lower SLA, i.e., with leaves that have greater physical strength (e.g., *Juncus effusus*, *Lonicera periclymenum* and *Rubus fruticosus* agg.), are able to tolerate the higher radiation and lower humidity beneath a more open canopy (Westoby et al. 2002; Dahlgren et al. 2006). Loser species with a high SLA (e.g., *Galium odoratum*, *Impatiens noli-tangere* and *Oxalis acetosella*) are well adapted to the low-light environment beneath a closed forest canopy (Wilson et al. 1999). In addition, winner species with long-living seeds (e.g., *Cardamine flexuosa*, *Carex remota* and *Rumex sanguineus*) can re-establish from a persistent seed bank when forest management activities damage the soil surface and create favorable light conditions (Eriksson 1995; Brunet et al. 1996; Decocq et al. 2004b). We suggest, therefore, that disturbance by forest management activities is most likely to be responsible for the high performance of species with a lower SLA and greater seed longevity, as well as the low performance of species with a high SLA. There were also some species with a high SLA among winner species (e.g., the grasses *Agrostis capillaris*, *Holcus lanatus* and *H. mollis*) or with a low SLA among loser species (e.g., *Angelica sylvestris* and *Filipendula ulmaria*). This inconsistency explains why winner and loser species did not differ in their SLA according to the univariate test (Table 2). We think that the former were probably favored due to their high seed longevity or tolerance to browsing, and the latter were inhibited because of their attractiveness to deer (Table S2). As another trait related to disturbance, long-distance dispersal contributed to the discrimination between winner and loser species (Table 3). However, the ability to disperse over long distances was probably of minor importance for the good performance of winner species because many of the loser species were capable of long-distance dispersal as well (Table S2), resulting in non-significant differences between winner and loser species in the univariate test (Table 2). Further trait differences between winner and loser species support the view that disturbance is an important environmental driver. Winner species flowered later in the season than loser species (Fig. 2a), which is typical for species growing beneath an open canopy (Heinrich 1976; Decocq et al. 2004a; Aubin et al. 2007). Winner species also tended to have a higher affinity to disturbed sites than loser species (Fig. 2b). However, these traits failed to be significant when SLA, seed longevity and long-distance dispersal were included in the logistic regression model (Table 3). In contrast to our results, several other long-term studies across central Europe document a trend toward more shady conditions and the decline of species adapted to more open canopies (e.g., Diekmann et al. 1999; Dahlgren et al. 2006; Baeten et al. 2009; Keith et al. 2009). In these studies, natural succession after the abandonment of cattle grazing or regular management interventions has led to a gradual canopy closure. In our study system, however, the original plots were located in mature stands with a rather closed canopy and selected 20 years ago with the goal of describing and classifying the herb layer communities of undisturbed forests (Wulf 1992). Thus, the observed changes in species composition partly document the effects of disturbance by forest management.

Another important trait for discriminating between winner and loser species was oceanity (Table 3). The proportion of species with an oceanic distribution was significantly larger in winner species (Fig. 2f). There was no evidence that species with a southern distribution were more common among winner than among loser species (Table 2). Still, we interpret the high performance of species with an oceanic distribution (e.g., *Chrysosplenium oppositifolium*, *Hedera helix*, *Ilex aquifolium*, *Lonicera periclymenum* and *Veronica montana*) as a response to the increasingly warmer winters. One might argue this effect could also be due to more “oceanic” microclimatic conditions within stands (reduced temperature amplitude, increased air humidity) as a result of succession toward increased canopy closure. However, as discussed above, there is a trend toward more open canopies as a result of thinnings or natural tree fall rather than toward a gradual canopy closure. Furthermore, shifts in species abundances that eventually result in range shifts are predicted by species distribution models (Skov & Svenning 2004; van der Veken et al. 2004). Few empirical studies so far have observed shifts in local abundances of temperate forest plants in response to climate change. In a resurvey of 103 British woods after 30 years, Kirby et al. (2005) observed changes in mean cover that were related to an increase in the duration of the growing season for 17 species. However, decreases or increases in cover were not associated with a northern, southern, continental or oceanic distribution of the species (Kirby et al. 2005). Our study suggests that species with certain distributions may already show responses to climate warming over a short time period of two decades.

Although only playing a minor role, browsing attractiveness contributed to the discrimination between winner and loser species. The univariate test for differences in browsing attractiveness between winner and loser species was not significant, indicating that browsing pressure was competing with other drivers. The negative impact of deer browsing on some more attractive winner species may have been compensated for by positive effects of disturbance (e.g., *Carex sylvatica* and *Rubus fruticosus* agg.) or warmer winters (e.g., *Hedera helix* and *Ribes rubrum*). On the other hand, loser species not susceptible to deer browsing may have been negatively affected by other drivers, for instance increased radiation (e.g., *Oxalis acetosella*) or acidification (e.g., *Equisetum arvense*, *Myosotis scorpioides* agg. and *Pulmonaria obscura*; see below).

Evidence for other environmental drivers was rather limited. We found no indication that an increased canopy cover or changes in soil moisture were responsible for herb layer changes (Table 2). This does not mean that these factors might not have influenced species composition in single plots, but across the region their effects were not significant. The pH and S-value optimum were slightly higher in loser than in winner species, suggesting that loser species might have been negatively affected by soil acidification. However, the effect was not large enough to result in significant contributions of pH or S-value optimum in the minimal adequate model. These results argue against the hypothesis that ongoing soil acidification as a result of atmospheric deposition is a major driver of herb layer changes in the surveyed forests. But then it is not obvious why some species with a high pH or S-value optimum (e.g., *Equisetum sylvaticum*, *Hepatica nobilis*, *Pulmonaria obscura*) should have decreased in abundance. Several other long-term studies from central Europe found more convincing evidence for herb layer responses to soil acidification (e.g., Falkengren-Grerup 1986; Thimonier et al. 1994; Diekmann et al. 1999; Baeten et al. 2009). Many studies also identified eutrophication due to N deposition as a major driver of compositional changes in deciduous forests (e.g., Falkengren-Grerup & Eriksson 1990; Thimonier et al. 1994; Lameire et al. 2000; Kirby et al. 2005). In contrast, the two traits related to eutrophication in our study failed to discriminate between winner and loser species (Table 2). The reason why our analyses provide only weak or no evidence for the drivers of acidification and eutrophication, respectively, may be the limited soil acidity gradient covered by our data set. The selected sites represent the most naturally base-rich sites in the region. Relatively high soil pH values combined with a high water availability result in a high N supply from mineralization. The results would probably look different if less fertile sites had been included (Falkengren-Grerup & Eriksson 1990; Thimonier et al. 1994; Baeten et al. 2009).

There was also little evidence that invasions by exotic species were of major importance for the observed herb layer changes. The invasion of exotic species is generally seen as a major threat to native plant communities (Ohlemüller et al. 2006; Lambdon et al. 2008). In our forests, the two exotic winner species attained only low abundances and frequencies in 2008 (Table S1). A reason for this might be the low invasibility of broad-leaved deciduous forests compared to other habitats (Chytrý et al. 2008). However, several studies document that *Impatiens parviflora* (Obidzinski & Symonides 2000; Chmura & Sierka 2007) and *Prunus serotina* (Closset-Kopp et al. 2007; Chabrerie et al. 2010) can be much more successful invaders in temperate European forests and are promoted by disturbance. It remains to be seen whether these two species become more frequent and dominant over the next few decades.

### Relative importance of local, regional and global drivers

Deviance partitioning clearly indicated that drivers on the local scale, here mainly disturbance by forest management activities, were most responsible for species shifts (Fig. 3). This was expected because local drivers act more immediately on the local habitat than large-scale drivers. The relative importance of regional and global drivers is difficult to assess. When all traits are taken into account, the relative importance of regional drivers (here browsing pressure and acidification) must be assessed at a higher level than that of global drivers (here climate warming) as indicated by the clearly larger unique effect of traits related to regional drivers (Fig. 3). However, in the minimum adequate model, oceanity had a higher unique effect than browsing attractiveness, while pH and S-value optimum did not contribute significantly to the reduction of deviance (Table 3). The relatively large negative contributions shared between trait groups (Fig. 3) indicate that all trait groups taken together explain species performance better than the sum of the total contributions of these groups. This is the result of the competing, opposing effects (see examples above) of the different trait groups (Legendre & Legendre 1998). These results demonstrate the importance of multivariate analyses in combination with univariate tests for a comprehensive understanding of species performance in response to environmental changes.

## 4.6 Conclusions

Our study demonstrates that it is possible to use ecological performances and functional traits to provide insight into those environmental drivers that are most likely causing changes in herb layer communities. According to our analyses, the drivers were disturbance by forest management activities, climate warming and deer browsing. Little evidence was found for acidification, and no evidence was found for a gradual canopy closure, soil moisture changes or eutrophication from N deposition. Certainly, more research is needed to see whether the relative importance of the considered drivers can be generalized for other regions. Future long-term studies should include plot-based environmental data for both of the compared time periods to provide higher certainty assessments of the responsible environmental changes.

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## 4.9 Supplementary Material

### Appendix S1. Measurements of environmental conditions in 2008

For measurements of soil pH and basic cations available to plants, ten subsamples (0-10 cm depth) per 400 m² (i.e., proportionally less in smaller plots) were collected by systematic random sampling in each plot, then pooled into one sample, air-dried and sieved (2 mm). After extracting 10 g of soil with 25 ml 0.01M $CaCl_2$ ($\geq$ 1 h), the pH was measured with an electrometric pH meter. Plant-available concentrations of Ca, K and Mg were measured with an atom-absorption spectrometer (Ca and Mg) and a spectral photometer (K) after extracting 5 g of soil with 100 ml of an ammonium-acetate solution (9.01 g hydrolyzed lactic acid plus 18.75 g acetic acid plus 7.70 g ammonium-acetate, filled up with distilled water to 1 l solution). The concentrations of Ca, K and Mg were summed to form a single measure of base supply (S-value) for analyses.

Soil moisture was measured as the volumetric water content in the topsoil (0-10 cm) using an EasyTest Time-Domain Reflectometry field probe (Institute of Agrophysics, Polish Academy of Sciences, Lublin, Poland). Measurements were taken in two subsequent years (2008/09) during five days at the end of March (assumed moisture maximum) and at the beginning of September (assumed moisture minimum). In each plot, five measurements per 100 m² were taken using systematic random sampling. Preliminary analyses showed that the soil moisture in March averaged over the two years provided a better explanation for differences in species composition among plots than soil moisture in September or any combined set of moisture variables (as measured by matrix correlations between a Bray-Curtis distance matrix calculated from the species abundance matrix and Euclidean distance matrices calculated from moisture variables). We used, therefore, the measurements in March as the moisture variable in our analyses.

We assessed light availability with hemispherical photographs of the canopy. Photographs were taken under uniform sky conditions during the time of full foliation (June and July) using a 180° fisheye lens mounted on a digital camera (HemiView System by Delta-T Devices, Cambridge, UK). Depending on plot size, one to four photographs per plot (i.e. one per 100 m²) were taken. As a measure of light availability, we calculated the average canopy openness (proportion of visible sky in the sky region above a zenith angle of 60°) per plot using HemiView Canopy Analysis Software (version 2.1, Delta-T Devices Ltd., Cambridge, UK).

## Appendix S2. Plant species traits related to potential environmental drivers

We used seven traits to indicate responses to local drivers. As traits related to changes in canopy cover, we chose the light optimum (derived from our own measurements), specific leaf area (SLA) and onset and end of the flowering period. SLA is positively correlated with shade-tolerance in herbaceous species and woody saplings (Wilson et al. 1999; Westoby et al. 2002; Janse-ten Klooster et al. 2007) and was found to be a good predictor of plant frequency changes following gradual canopy closure (Dahlgren et al. 2006). SLA is also related to precipitation and nutrient availability (Fonseca et al. 2000; Wright et al. 2001); however, the corresponding gradients in our data were assumed to be short. For 45 species, the databases did not provide information on SLA. For these species, we measured SLA according to the standards defined by Kleyer et al. (2008). Flowering phenology is known to be associated with shade avoidance. Species that occur beneath open canopies can afford to flower longer or later in the season, whereas species of closed forests usually flower early in the season to avoid the deep shade beneath dense foliage (Heinrich 1976; Decocq et al. 2004a; Aubin et al. 2007; Falk et al. 2008). Shrub species occur as non-flowering juveniles in the herb layer; therefore, we assigned missing values to shrubs for the onset and end of the flowering period. As traits related to disturbance (comprising enhanced light availability and soil damages), we included the disturbance optimum (derived from our own assessments), long-distance dispersal ability and seed longevity. Dispersal through space or time enables species not able to survive beneath a closed canopy to establish when a disturbance event suddenly uncovers bare soil and creates favorable light conditions (Eriksson 1995; Brunet et al. 1996; Decocq et al. 2004b; Degen et al.

2005; Eycott et al. 2006; Naaf & Wulf 2007). Pteridophytes received missing values for seed longevity. We used the moisture optimum (derived from our own measurements) as a trait related to soil moisture changes.

Six traits were used to indicate responses to regional drivers. The pH and S-value optimum (both derived from our own measurements) were used to indicate effects of atmospheric acid deposition. For N deposition, we used (a) N indicator values from Ellenberg et al. (2001) and (b) $N_{dev}$-values published by Diekmann & Falkengren-Grerup (2002). While the former has been frequently used in central Europe to link herb layer composition to N availability (e.g., Diekmann & Dupré 1997; Brunet et al. 1998; Pitcairn et al. 1998; Lameire et al. 2000; Borchsenius et al. 2004; van Calster et al. 2007), the latter has rarely been applied. The $N_{dev}$-values were derived from species optima with respect to soil pH and nitrification ratio and were explicitly developed to predict species responses to atmospheric N deposition. Species with a positive $N_{dev}$-value will be favored by N deposition, while species with a negative $N_{dev}$-value will be inhibited. Although the $N_{dev}$-values were derived from sites in southern Sweden, species responses from central European permanent plot studies were well predicted by these $N_{dev}$-values (Diekmann & Falkengren-Grerup 2002). The response to browsing pressure was represented by (a) a semiquantitative browsing attractiveness score and (b) growth form. Browsing attractiveness is an estimate on a five-degree scale of how attractive plant species are as browse for roe deer. The browsing attractiveness score was developed by Klötzli (1965) for Switzerland and adapted and tested by Ellenberg Jun. (1988) for northern Germany. There is also plenty of evidence indicating that grasses and other graminoids are favored by a higher browsing pressure, whereas forbs and woody species are mostly negatively affected (e.g., Kirby 2001; Horsley et al. 2003; Rooney & Waller 2003; von Oheimb et al. 2003). Graminoids were therefore used as an additional indicator for changes in browsing pressure.

Three traits were used to indicate responses to global drivers. To derive ecological performances that correspond to climatic conditions, we used (a) the latitudinal range distribution of species and (b) the occupied range in the continentality gradient from western to eastern Europe (data from Rothmaler 2005). For plant species in temperate Europe, climatic envelope models and similar approaches predict strong northward range shifts and less pronounced eastward range shifts (Skov & Svenning 2004; van der Veken et al. 2004; Thuiller et al. 2005). Range shifts should become obvious by changes in local species abundances due to altered competitive abilities. With respect to the latitudinal distribution, we distinguished between species whose distributions are limited to the southern part of Europe with their northerly distribution edge in the temperate zone and species that are distributed throughout the floristic zones with their northerly distribution edge in the boreal or arctic zone (Table 1). With respect to oceanity, we distinguished between species whose distribution can be described as oceanic and those that occur also or mainly in the more continental parts of Europe (Table 1). We assumed that species with a southern distribution would be favored by a prolonged growing season and that species with an oceanic distribution would benefit from warmer temperatures in the winter.

Finally, we distinguished between native and exotic species to assess how herb layer composition is influenced by the invasion of exotic species (Lambdon et al. 2008).

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## Appendix S3. Bibliographic details for data sources in Table 1

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**Table S1.** Mean abundance change[a] of winner and loser species.

| | Abundance | | Change in abundance | $P$[b] |
|---|---|---|---|---|
| | 1988 | 2008 | | |
| Winner species: | | | | |
| *Agrostis capillaris* | 0.7 | 3.5 | 2.8 | 0.001 |
| *Cardamine flexuosa* | 1.1 | 1.7 | 0.7 | 0.002 |
| *Carex remota* | 1.6 | 2.8 | 1.2 | < 0.001 |
| *Carex sylvatica* | 2.6 | 3.5 | 0.8 | < 0.001 |
| *Chrysosplenium oppositifolium* | 0.6 | 3.2 | 2.6 | < 0.001 |
| *Corylus avellana* | 1.3 | 1.8 | 0.5 | 0.001 |
| *Crataegus laevigata* s.l. | 1.2 | 1.5 | 0.3 | 0.008 |
| *Dryopteris carthusiana* | 0.5 | 1.6 | 1.2 | < 0.001 |
| *Dryopteris dilatata* | 0.8 | 1.5 | 0.7 | < 0.001 |
| *Frangula alnus* | 0.0 | 1.4 | 1.4 | < 0.001 |
| *Galium aparine* | 1.9 | 2.3 | 0.3 | 0.046 |
| *Glechoma hederacea* | 2.0 | 3.3 | 1.3 | < 0.001 |
| *Hedera helix* | 1.5 | 2.9 | 1.4 | < 0.001 |
| *Holcus lanatus* | 0.3 | 2.7 | 2.4 | 0.010 |
| *Holcus mollis* | 0.0 | 2.9 | 2.9 | < 0.001 |
| *Hypericum maculatum* s.l. | 0.0 | 1.6 | 1.6 | < 0.001 |
| *Ilex aquifolium* | 0.8 | 1.9 | 1.2 | < 0.001 |
| *Impatiens parviflora* | 0.3 | 3.0 | 2.7 | < 0.001 |
| *Juncus effusus* | 0.6 | 1.8 | 1.2 | < 0.001 |
| *Lonicera periclymenum* | 1.8 | 2.1 | 0.3 | 0.015 |
| *Luzula pilosa* | 1.3 | 1.9 | 0.6 | 0.039 |
| *Lythrum salicaria* | 0.0 | 1.4 | 1.4 | < 0.001 |
| *Prunus serotina* | 0.0 | 1.4 | 1.4 | < 0.001 |
| *Ribes rubrum* | 0.8 | 1.8 | 1.0 | < 0.001 |
| *Rubus fruticosus* agg. | 1.5 | 2.1 | 0.6 | 0.003 |
| *Rumex sanguineus* | 0.6 | 1.5 | 0.9 | 0.002 |
| *Sambucus nigra* | 0.5 | 1.4 | 0.9 | < 0.001 |
| *Scutellaria galericulata* | 0.8 | 1.9 | 1.1 | 0.008 |
| *Sorbus aucuparia* | 1.0 | 1.1 | 0.2 | 0.036 |
| *Taraxacum* sect. *Ruderalia* | 0.6 | 1.1 | 0.5 | 0.001 |
| *Veronica montana* | 2.1 | 3.4 | 1.3 | < 0.001 |
| Loser species: | | | | |
| *Adoxa moschatellina* | 3.5 | 2.8 | -0.7 | < 0.001 |
| *Anemone nemorosa* | 6.9 | 5.9 | -1.1 | < 0.001 |
| *Angelica sylvestris* | 1.8 | 0.2 | -1.6 | < 0.001 |
| *Brachypodium sylvaticum* | 2.9 | 2.0 | -0.9 | < 0.001 |
| *Circaea lutetiana* | 3.6 | 3.4 | -0.2 | 0.027 |
| *Crepis paludosa* | 3.2 | 2.2 | -0.9 | < 0.001 |
| *Equisetum arvense* | 1.6 | 1.4 | -0.3 | 0.049 |
| *Equisetum hyemale* | 3.0 | 2.3 | -0.7 | 0.015 |
| *Equisetum sylvaticum* | 2.3 | 1.6 | -0.7 | 0.018 |
| *Festuca gigantea* | 2.4 | 1.1 | -1.3 | < 0.001 |
| *Filipendula ulmaria* | 2.7 | 2.1 | -0.6 | < 0.001 |
| *Galium odoratum* | 5.1 | 3.7 | -1.5 | < 0.001 |
| *Geum rivale* | 3.2 | 2.4 | -0.7 | < 0.001 |
| *Hepatica nobilis* | 2.9 | 2.2 | -0.7 | 0.010 |
| *Impatiens noli-tangere* | 3.3 | 1.7 | -1.6 | < 0.001 |
| *Lamium galeobdolon* s.str. | 4.9 | 4.5 | -0.4 | 0.007 |
| *Lysimachia vulgaris* | 2.0 | 0.9 | -1.1 | 0.001 |
| *Mercurialis perennis* | 7.3 | 5.6 | -1.7 | < 0.001 |
| *Milium effusum* | 3.5 | 3.3 | -0.2 | < 0.001 |
| *Mycelis muralis* | 1.7 | 0.5 | -1.2 | 0.019 |
| *Myosotis scorpioides* agg. | 3.2 | 0.6 | -2.5 | < 0.001 |
| *Oxalis acetosella* | 4.7 | 3.4 | -1.3 | < 0.001 |
| *Paris quadrifolia* | 3.1 | 2.8 | -0.3 | 0.021 |
| *Phyteuma nigrum* | 2.6 | 1.9 | -0.7 | 0.032 |
| *Pulmonaria obscura* | 3.5 | 2.3 | -1.2 | < 0.001 |
| *Ranunculus auricomus* agg. | 2.8 | 2.6 | -0.3 | 0.004 |
| *Ranunculus ficaria* | 5.8 | 5.4 | -0.4 | < 0.001 |
| *Sanicula europaea* | 3.1 | 2.2 | -1.0 | < 0.001 |
| *Stachys sylvatica* | 2.9 | 2.5 | -0.4 | < 0.001 |
| *Valeriana officinalis* agg. | 2.5 | 1.2 | -1.3 | 0.004 |

[a] Mean abundance change refers to only those plots where the species was not absent in both sampling periods

[b] Fisher's sign test

**Table S2a.** Functional traits of winner species. For trait definitions see Table 1.

| | Light optimum (%) | SLA (mm$^2$ mg$^{-1}$) | Flowering | | Disturbance optimum | Long-distance dispersal | Seed longevity | Moisture optimum (vol %) | pH optimum | S-value optimum (mmol$_c$ (100g)$^{-1}$) | Ellenberg N | N$_{dev}$ | Browsing attractiveness | Graminoid | Latitudinal distribution | Oceanity | Exotic |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | onset | end | | | | | | | | | | | | | |
| *Agrostis capillaris* | 0.14 | 75.9 | 6 | 7 | 1.32 | 1 | 0.67 | 45.5 | 5.40 | 12.2 | 4 | 2.9 | 0 | 1 | 0 | 0 | 0 |
| *Cardamine flexuosa* | 0.13 | 41.3 | 4 | 10 | 1.32 | 1 | 0.67 | 47.6 | 5.41 | 11.9 | 5 | – | – | 0 | 1 | 1 | 0 |
| *Carex remota* | 0.12 | 25.8 | 6 | 7 | 1.37 | 1 | 0.75 | 45.7 | 5.38 | 12.3 | – | – | 1 | 1 | 1 | 0 | 0 |
| *Carex sylvatica* | 0.11 | 30.9 | 5 | 7 | 1.21 | 1 | 0.60 | 42.7 | 5.51 | 12.3 | 5 | -3.1 | 3 | 1 | 1 | 0 | 0 |
| *Chrysosplenium oppositifolium* | 0.13 | 23.4 | 4 | 6 | 1.38 | 0 | 0.00 | 58.5 | 5.59 | 16.6 | 5 | – | 1 | 0 | 1 | 1 | 0 |
| *Corylus avellana* | 0.11 | 21.5 | – | – | 1.09 | 1 | 0.00 | 43.7 | 5.45 | 12.5 | 5 | 1.0 | 2 | 0 | 0 | 0 | 0 |
| *Crataegus laevigata* s.l. | 0.11 | 30.3 | – | – | 1.11 | 1 | 0.00 | 41.3 | 5.41 | 11.7 | 5 | 3.2 | 3 | 0 | 1 | 0 | 0 |
| *Dryopteris carthusiana* | 0.11 | 22.4 | 7 | 8 | 1.02 | 1 | – | 46.1 | 5.15 | 12.4 | 3 | 17.3 | 2 | 0 | 0 | 0 | 0 |
| *Dryopteris dilatata* | 0.12 | 23.1 | 7 | 9 | 1.20 | 1 | – | 46.3 | 5.35 | 13.0 | 7 | 12.0 | – | 0 | 0 | 1 | 0 |
| *Frangula alnus* | 0.11 | 21.9 | – | – | 1.36 | 1 | 0.00 | 39.7 | 5.47 | 10.1 | – | -0.3 | 2 | 0 | 0 | 0 | 0 |
| *Galium aparine* | 0.12 | 32.6 | 6 | 10 | 1.22 | 1 | 0.31 | 38.6 | 5.22 | 10.6 | 8 | 1.9 | 1 | 0 | 1 | 0 | 0 |
| *Glechoma hederacea* | 0.12 | 33.7 | 4 | 6 | 1.27 | 1 | 0.30 | 41.5 | 5.48 | 11.9 | 7 | – | 1 | 0 | 0 | 0 | 0 |
| *Hedera helix* | 0.10 | 11.4 | – | – | 1.06 | 1 | 0.00 | 38.6 | 5.27 | 10.6 | – | -6.5 | 2 | 0 | 1 | 1 | 0 |
| *Holcus lanatus* | 0.14 | 47.0 | 6 | 8 | 1.59 | 1 | 0.60 | 43.8 | 5.06 | 9.4 | 4 | – | 2 | 1 | 1 | 1 | 0 |
| *Holcus mollis* | 0.11 | 60.2 | 6 | 8 | 0.80 | 1 | 0.00 | 42.7 | 5.09 | 11.6 | 3 | 5.2 | 1 | 1 | 1 | 1 | 0 |
| *Hypericum maculatum* s.l. | 0.18 | 21.2 | 7 | 8 | 3.00 | 1 | 0.56 | 45.9 | 5.64 | 12.8 | 2 | -1.2 | – | 0 | 0 | 0 | 0 |
| *Ilex aquifolium* | 0.10 | 6.8 | – | – | 1.15 | 1 | 0.00 | 37.6 | 5.01 | 9.1 | 5 | – | 1 | 0 | 1 | 1 | 0 |
| *Impatiens parviflora* | 0.13 | 101.9 | 6 | 9 | 1.41 | 0 | 0.00 | 37.4 | 4.84 | 8.2 | 6 | – | – | 0 | 0 | 0 | 1 |
| *Juncus effusus* | 0.15 | 6.5 | 6 | 8 | 1.95 | 1 | 0.87 | 45.4 | 5.24 | 10.5 | 4 | 11.6 | 1 | 1 | 0 | 0 | 0 |
| *Lonicera periclymenum* | 0.12 | 14.2 | – | – | 1.17 | 1 | 0.00 | 41.2 | 4.99 | 9.7 | 4 | -15.2 | – | 0 | 1 | 1 | 0 |
| *Luzula pilosa* | 0.10 | 25.1 | 4 | 5 | 0.96 | 0 | 0.73 | 42.1 | 4.94 | 9.1 | 4 | -6.9 | 1 | 1 | 0 | 0 | 0 |
| *Lythrum salicaria* | 0.20 | 27.1 | 7 | 9 | 1.20 | 1 | 0.38 | 53.6 | 5.57 | 16.7 | – | – | 4 | 0 | 0 | 0 | 0 |
| *Prunus serotina* | 0.12 | 22.5 | – | – | 1.23 | 1 | 0.50 | 41.4 | 4.29 | 4.3 | – | – | – | 0 | 1 | 1 | 1 |
| *Ribes rubrum* | 0.10 | 40.6 | – | – | 0.91 | 1 | – | 41.0 | 5.30 | 13.4 | 6 | – | 2 | 0 | 1 | 1 | 0 |
| *Rubus fruticosus* agg. | 0.13 | 19.5 | – | – | 1.42 | 1 | 0.44 | 42.2 | 5.18 | 11.2 | – | -1.7 | 4 | 0 | – | – | 0 |
| *Rumex sanguineus* | 0.14 | 25.0 | 6 | 8 | 1.59 | 1 | 0.75 | 45.9 | 5.43 | 11.2 | 7 | – | 1 | 0 | 1 | 1 | 0 |
| *Sambucus nigra* | 0.11 | 19.4 | – | – | 1.00 | 1 | 0.50 | 37.9 | 5.12 | 9.9 | 9 | – | 4 | 0 | 1 | 0 | 0 |
| *Scutellaria galericulata* | 0.13 | 39.6 | 6 | 9 | 1.20 | 1 | 0.00 | 47.7 | 5.31 | 12.9 | 6 | – | 0 | 0 | 0 | 0 | 0 |
| *Sorbus aucuparia* | 0.11 | 13.8 | – | – | 1.18 | 1 | 0.14 | 41.5 | 5.13 | 10.7 | – | 3.6 | 3 | 0 | 0 | 0 | 0 |
| *Taraxacum* sect. *Ruderalia* | 0.12 | 41.6 | 3 | 8 | 1.31 | 1 | 0.47 | 39.6 | 5.39 | 11.6 | 7 | -6.0 | 1 | 0 | 0 | 0 | 0 |
| *Veronica montana* | 0.11 | 38.4 | 5 | 6 | 1.31 | 1 | 0.60 | 43.0 | 5.31 | 10.9 | 6 | – | 1 | 0 | 1 | 1 | 0 |

**Table S2b.** Functional traits of loser species. For trait definitions see Table 1.

| | Light optimum (%) | SLA (mm$^2$ mg$^{-1}$) | Flowering | | Disturbance optimum | Long-distance dispersal | Seed longevity | Moisture optimum (vol %) | pH optimum | S-value optimum (mmol$_c$ (100g)$^{-1}$) | Ellenberg N | N$_{dev}$ | Browsing attractiveness | Graminoid | Latitudinal distribution | Oceanity | Exotic |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | onset | end | | | | | | | | | | | | | |
| *Adoxa moschatellina* | 0.10 | 38.5 | 3 | 5 | 1.00 | 1 | 0.00 | 40.1 | 5.30 | 10.7 | 8 | – | – | 0 | 0 | 0 | 0 |
| *Anemone nemorosa* | 0.11 | 27.7 | 3 | 5 | 1.07 | 1 | 0.07 | 40.9 | 5.26 | 11.0 | – | -5.1 | 1 | 0 | 0 | 0 | 0 |
| *Angelica sylvestris* | 0.14 | 19.1 | 7 | 9 | 1.00 | 1 | 0.21 | 54.1 | 5.83 | 21.6 | – | 2.2 | 3 | 0 | 0 | 0 | 0 |
| *Brachypodium sylvaticum* | 0.11 | 44.4 | 7 | 8 | 1.03 | 1 | 0.22 | 42.9 | 5.57 | 13.3 | 6 | -4.3 | 1 | 1 | 1 | 0 | 0 |
| *Circaea lutetiana* | 0.11 | 36.7 | 6 | 8 | 1.24 | 1 | 0.00 | 43.4 | 5.41 | 11.8 | 7 | – | 2 | 0 | 1 | 0 | 0 |
| *Crepis paludosa* | 0.11 | 37.0 | 6 | 8 | 1.01 | 1 | 0.00 | 45.0 | 5.66 | 14.3 | 6 | – | 4 | 0 | 0 | 0 | 0 |
| *Equisetum arvense* | 0.13 | 33.4 | 3 | 4 | 1.25 | 1 | – | 47.7 | 5.70 | 13.7 | 3 | – | 0 | 0 | 0 | 0 | 0 |
| *Equisetum hyemale* | 0.12 | 0.0 | 6 | 8 | 1.06 | 1 | – | 38.1 | 5.42 | 11.7 | 6 | – | 0 | 0 | 0 | 0 | 0 |
| *Equisetum sylvaticum* | 0.13 | 31.4 | 4 | 5 | 1.59 | 1 | – | 49.1 | 5.52 | 15.1 | 4 | 7.2 | 0 | 0 | 0 | 0 | 0 |
| *Festuca gigantea* | 0.12 | 28.7 | 7 | 8 | 1.40 | 1 | 0.20 | 43.4 | 5.47 | 12.5 | 6 | 6.2 | 2 | 1 | 1 | 0 | 0 |
| *Filipendula ulmaria* | 0.12 | 19.4 | 6 | 8 | 1.09 | 1 | 0.23 | 46.5 | 5.67 | 14.9 | 4 | 0.7 | 4 | 0 | 0 | 0 | 0 |
| *Galium odoratum* | 0.10 | 51.0 | 5 | 6 | 1.08 | 1 | 0.00 | 42.8 | 5.50 | 12.2 | 5 | 13.3 | 1 | 0 | 0 | 0 | 0 |
| *Geum rivale* | 0.12 | 27.8 | 4 | 7 | 1.03 | 1 | 0.00 | 50.5 | 5.81 | 15.5 | 4 | 0.1 | 2 | 0 | 0 | 0 | 0 |
| *Hepatica nobilis* | 0.10 | 24.2 | 3 | 4 | 1.15 | 0 | 0.00 | 41.5 | 5.53 | 12.5 | 5 | -3.4 | – | 0 | 1 | 0 | 0 |
| *Impatiens noli-tangere* | 0.12 | 45.4 | 7 | 8 | 1.39 | 0 | 0.00 | 44.0 | 5.47 | 12.0 | 6 | – | 1 | 0 | 0 | 0 | 0 |
| *Lamium galeobdolon* s.str. | 0.10 | 25.4 | 5 | 7 | 1.15 | 0 | 0.08 | 41.9 | 5.22 | 10.7 | 5 | 2.9 | 1 | 0 | 1 | 0 | 0 |
| *Lysimachia vulgaris* | 0.17 | 23.7 | 6 | 8 | 1.17 | 0 | 0.27 | 50.5 | 5.35 | 14.1 | – | – | 4 | 0 | 0 | 0 | 0 |
| *Mercurialis perennis* | 0.11 | 25.7 | 4 | 5 | 0.95 | 0 | 0.00 | 42.3 | 5.48 | 10.8 | 7 | 1.7 | 1 | 0 | 1 | 0 | 0 |
| *Milium effusum* | 0.11 | 33.4 | 5 | 7 | 1.15 | 1 | 0.25 | 40.6 | 5.13 | 10.1 | 5 | 8.6 | 2 | 1 | 0 | 0 | 0 |
| *Mycelis muralis* | 0.11 | 74.6 | 7 | 8 | 1.83 | 1 | 0.50 | 33.6 | 4.66 | 7.3 | 6 | 4.6 | 3 | 0 | 0 | 1 | 0 |
| *Myosotis scorpioides* agg. | 0.16 | 81.6 | 5 | 9 | 1.00 | 0 | 0.17 | 56.6 | 5.79 | 18.0 | 5 | – | 1 | 0 | 0 | 0 | 0 |
| *Oxalis acetosella* | 0.11 | 64.6 | 4 | 5 | 1.12 | 1 | 0.15 | 41.5 | 5.14 | 10.2 | 6 | -3.6 | 1 | 0 | 0 | 0 | 0 |
| *Paris quadrifolia* | 0.13 | 35.0 | 5 | 6 | 1.17 | 1 | 0.00 | 44.8 | 5.56 | 13.6 | 7 | 0.2 | 1 | 0 | 0 | 0 | 0 |
| *Phyteuma nigrum* | 0.09 | 42.7 | 5 | 7 | 0.97 | 1 | 0.00 | 32.3 | 5.13 | 10.3 | 4 | – | 4 | 0 | 1 | 0 | 0 |
| *Pulmonaria obscura* | 0.11 | 38.2 | 3 | 5 | 0.89 | 0 | 0.00 | 48.7 | 5.78 | 15.1 | 7 | 2.6 | 0 | 0 | 0 | 0 | 0 |
| *Ranunculus auricomus* agg. | 0.11 | 37.8 | 4 | 5 | 1.04 | 0 | 0.17 | 43.7 | 5.54 | 12.9 | – | 0.1 | 2 | 0 | 0 | 0 | 0 |
| *Ranunculus ficaria* | 0.11 | 31.8 | 3 | 5 | 1.12 | 0 | 0.00 | 41.6 | 5.33 | 11.3 | 7 | -1.2 | 3 | 0 | 1 | 0 | 0 |
| *Sanicula europaea* | 0.11 | 31.0 | 5 | 6 | 0.98 | 1 | 0.20 | 38.9 | 5.53 | 12.1 | 6 | -8.4 | 1 | 0 | 1 | 0 | 0 |
| *Stachys sylvatica* | 0.12 | 42.1 | 6 | 9 | 1.27 | 1 | 0.40 | 42.8 | 5.39 | 11.7 | 7 | 3.0 | 3 | 0 | 0 | 0 | 0 |
| *Valeriana officinalis* agg. | 0.13 | 32.5 | 5 | 8 | 0.87 | 1 | 0.00 | 49.6 | 5.42 | 13.3 | 5 | – | – | 0 | 0 | 0 | 0 |

**Table S3.** Correlations among species traits. Upper triangle: Pearson *r*. Lower triangle: *P*-values. Significant ($P \leq 0.05$) correlation coefficients are printed in bold face.

| | Light optimum | SLA | Onset of flowering | End of flowering | Disturbance optimum | Long-distance dispersal | Seed longevity | Moisture optimum | pH optimum | S-value optimum | Ellenberg N | $N_{dev}$ | Browsing attractiveness | Graminoid | Latitudinal distribution | Oceanity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Light optimum | | 0.08 | **0.40** | **0.46** | **0.49** | 0.00 | **0.34** | **0.63** | **0.26** | **0.41** | -0.27 | 0.18 | 0.04 | -0.01 | **-0.31** | -0.05 |
| SLA | 0.562 | | 0.03 | 0.12 | -0.02 | -0.19 | -0.04 | -0.04 | -0.10 | -0.05 | 0.04 | 0.10 | -0.16 | 0.10 | -0.16 | -0.03 |
| Onset of flowering | **0.004** | 0.825 | | **0.74** | **0.31** | **0.30** | 0.25 | 0.05 | -0.14 | 0.06 | -0.13 | **0.46** | **0.32** | 0.23 | -0.02 | 0.14 |
| End of flowering | **0.001** | 0.397 | **< 0.001** | | 0.19 | **0.29** | 0.25 | 0.14 | -0.10 | 0.11 | 0.04 | 0.34 | **0.33** | 0.05 | -0.01 | 0.21 |
| Disturbance optimum | **0.001** | 0.877 | **0.027** | 0.192 | | 0.14 | **0.49** | 0.03 | -0.06 | -0.15 | **-0.28** | 0.10 | -0.08 | 0.08 | -0.11 | 0.09 |
| Long-distance dispersal | 0.985 | 0.147 | **0.043** | **0.047** | 0.295 | | 0.24 | -0.21 | -0.10 | -0.11 | -0.08 | 0.14 | 0.11 | 0.11 | 0.00 | 0.16 |
| Seed longevity | **0.012** | 0.774 | 0.090 | 0.097 | **< 0.001** | 0.077 | | 0.04 | -0.20 | -0.19 | -0.11 | 0.09 | 0.00 | **0.46** | 0.06 | 0.19 |
| Moisture optimum | **< 0.001** | 0.748 | 0.716 | 0.343 | 0.824 | 0.109 | 0.800 | | **0.58** | **0.78** | -0.27 | 0.30 | -0.10 | -0.02 | **-0.26** | -0.06 |
| pH optimum | **0.045** | 0.419 | 0.345 | 0.489 | 0.651 | 0.462 | 0.143 | **< 0.001** | | **0.85** | -0.02 | 0.00 | -0.11 | -0.12 | -0.22 | **-0.42** |
| S-value optimum | **0.002** | 0.700 | 0.679 | 0.455 | 0.214 | 0.410 | 0.167 | **< 0.001** | **< 0.001** | | -0.15 | 0.13 | 0.04 | -0.13 | **-0.28** | **-0.28** |
| Ellenberg N | 0.056 | 0.791 | 0.417 | 0.791 | **0.047** | 0.626 | 0.497 | 0.060 | 0.883 | 0.313 | | -0.10 | 0.10 | **-0.30** | 0.12 | -0.08 |
| $N_{dev}$ | 0.289 | 0.565 | **0.010** | 0.064 | 0.541 | 0.410 | 0.606 | 0.069 | 0.982 | 0.424 | 0.588 | | -0.02 | 0.11 | **-0.34** | -0.08 |
| Browsing attractiveness | 0.766 | 0.253 | **0.037** | **0.028** | 0.590 | 0.487 | 0.984 | 0.470 | 0.427 | 0.770 | 0.573 | 0.892 | | -0.15 | 0.06 | -0.07 |
| Graminoid | 0.958 | 0.426 | 0.143 | 0.740 | 0.511 | 0.670 | **< 0.001** | 0.895 | 0.359 | 0.311 | **0.040** | 0.520 | 0.323 | | 0.17 | -0.02 |
| Latitudinal distribution | **0.014** | 0.226 | 0.913 | 0.928 | 0.466 | 0.907 | 0.669 | **0.046** | 0.087 | **0.030** | 0.435 | **0.039** | 0.724 | 0.296 | | **0.46** |
| Oceanity | 0.682 | 0.849 | 0.379 | 0.177 | 0.486 | 0.272 | 0.173 | 0.663 | **0.001** | **0.027** | 0.640 | 0.632 | 0.663 | 1.000 | **< 0.001** | |

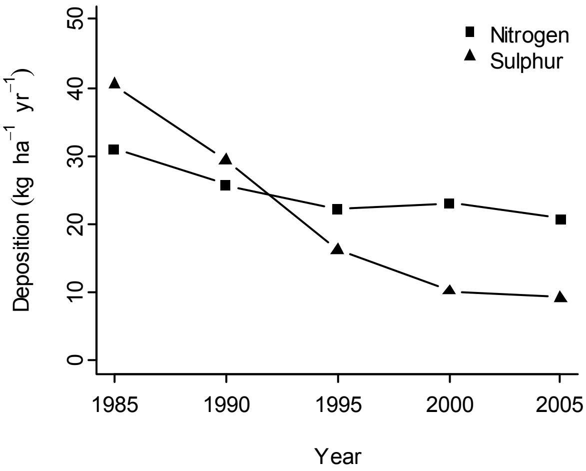

**Fig. S1.** Estimated deposition of sulphur and nitrogen in the Weser-Elbe-Region over the last two decades. Data from the EMEP database at http://www.emep.int.

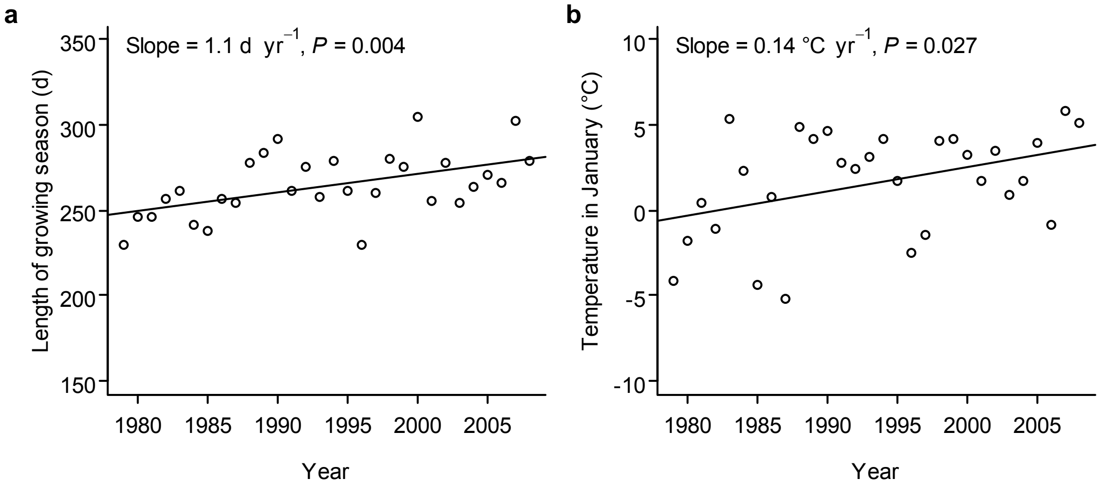

**Fig. S2.** Climate warming in Bremen over 30 years from 1979 to 2008. Length of growing season refers to the number of days with an average temperature of ≥5 °C. Data available at http://www.dwd.de.

# General Discussion

## Reliability of the results

Before I discuss how the four chapters contribute to achieving the objectives outlined in the General Introduction, it seems necessary to briefly address the data quality and possible sources of error. Like in most resurvey studies, the reliability of this study could be criticized for several shortcomings. These are a change of the person, who did the field work, not permanently marked plots and the lack of data for the years between the first and the recent survey. Although the person in charge changed, the likely bias in plant cover estimates could be reduced to a minimum, because the original researcher (M. Wulf) introduced me into the way, how she had proceeded during plant species recording. We calibrated my cover estimates by recording the plant species composition of several plots independently of each other until no further deviations occurred. We assume, therefore, that any deviations in cover-abundance between sampling periods are due to real plant population changes. M. Wulf also relocated all plots together with me. Although the original plots were not permanently marked, the exact position could be found by freehand sketches, made by M. Wulf at her work in 1990. These showed the constellation of the main tree and shrub stems and of other important structures such as stones and stumps along the plot margins. Relocation was therefore possible with an error of c. 2 m, which is little in relation to plot sizes of mostly 300 or 400 m². Furthermore, the original plots had been placed in an area of homogeneous vegetation (i.e., constant species composition), so that minor mismatches should not lead to biased results. The lack of data for any year between the first and the recent survey might be a more severe problem. It has been shown that the interannual variability in cover percentages can be substantial in forest plants, e.g., due to fluctuations in weather conditions (Dierschke & Brünn 1993; Brunet & Tyler 2000). However, we used cover-abundance classes for plant species recording (Chapter 1: Table 2), which appear more robust against interannual variation than percent cover estimates. Seedlings and saplings of tree species show the most pronounced interannual variation in abundance in dependence on the seed output of the surrounding mother trees. They were thus excluded in all analyses. Overall, I reckon that the reliability of our resurvey data can be considered relatively high compared to other resurvey studies.

Another problem that might affect the reliability of the results is spatial autocorrelation. Although we excluded pseudoreplicates (i.e., plots in close vicinity to each other within the same forest stand) when selecting plots for the resurvey, one might expect communities in nearby plots (within the same forest patch or in nearby fragments of a once contiguous patch) to respond in a more similar way to environmental changes than communities in plots located further apart. This autocorrelation may be induced by the patchiness of the environmental conditions or inherent in the forest vegetation, e.g., due to dispersal limitations and a restricted distribution pattern of some species in the study area (Legendre & Legendre 1998). If positive spatial autocorrelation occurred, the residuals in our statistical models would not be independent from each other and the risk of committing a type I error would be enhanced (Legendre 1993). Also, the parameter estimates in regression models would be unreliable (Kühn 2007).

During the last decade, the awareness of this problem has increased among ecologists and a large number of sophisticated methods has been introduced to account for spatial autocorrelation (Dale & Fortin 2002; Dormann et al. 2007). However, most methods are designed for lattice data, in which the autocorrelation structure can be approximated by a simple spherical, exponential or Gaussian model (Fortin & Dale 2005). In our study, the data points are irregularly distributed across the study area (Chapter 1: Fig. 1) and variables show mostly a complicated autocorrelation structure in which autocorrelation does not asymptotically decrease towards zero with increasing distance, but rises and falls below and above zero continuously (Fig. II). Under these circumstances, accounting for spatial autocorrelation appears more complicated (Fortin & Dale 2005). Therefore, this issue was neglected in the four manuscripts that were independently submitted for publication. On the one hand, it would have overloaded the methods sections that were already rather comprehensive. On the other hand, finding adequate methods and performing additional analyses to account for spatial autocorrelation would have been beyond the time frame set for manuscript preparation. The same is true for the correction for phylogenetic autocorrelation in the trait analyses in Chapter 4, which would require the knowledge of the phylogeny of all species (e.g., Diniz-Filho et al. 1998).

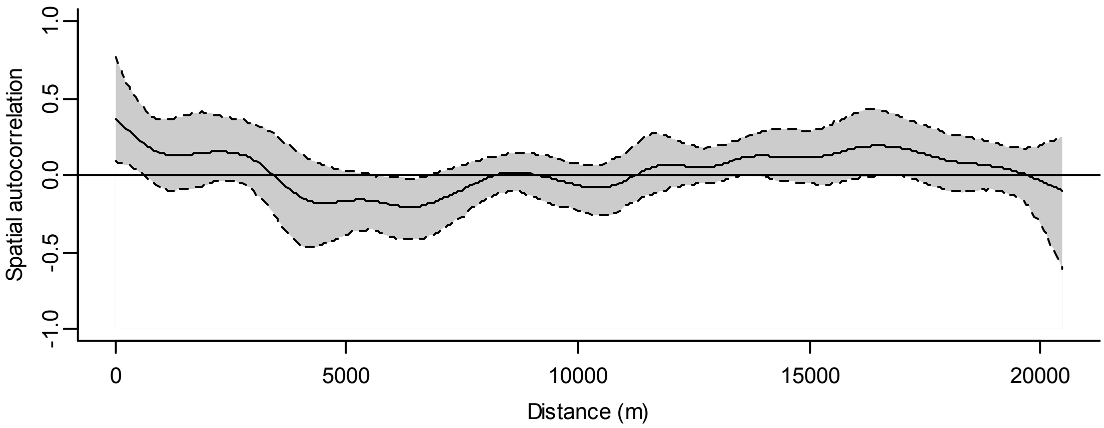

**Fig. II.** Spline correlogram (Bjørnstad & Falck 2001) showing the complex autocorrelation structure exhibited by some response variables in our data. As an example, the correlogram was calculated for the residuals of a multiple linear regression model of the first axis of a non-metric multidimensional scaling (as a measure of species composition; see Fig. III) against environmental variables (soil pH, S-value, soil moisture, light availability and degree of disturbance, see Chapter 4). The shaded region represents the 95% bootstrap confidence envelope for the autocorrelation function. The spline correlogram was calculated with the function *spline.correlog* of the R package *ncf* (Bjørnstad 2009). Note that significant positive autocorrelation occurs at short as well as far distances, while significant negative autocorrelation occurs at some intermediate distance.

To be at least to some degree able to assess the level of spatial autocorrelation and the reliability of the presented results, I performed some additional analyses (Appendix II). These were confined to three types of analyses in Chapters 1 and 3: (a) the tests of significant changes over time in α and β diversity (Chapter 1: Tables 3 and 4), (b) the multiple regression analyses used to explain changes in β diversity by changes in species numbers (Chapter 1: Table 6) and (c) the correlations between trait distribution statistics and environmental gradients (Chapter 3: Tables 2-4). The changes in diversity and the residuals of the linear models were tested for spatial autocorrelation using the global Moran's *I* coefficient. If necessary, spatial autocorrelation was taken into account by (a) adjusting the effective sample size (Fortin & Dale 2005) or (b) and (c) removing spatial autocorrelation with a technique called 'spatial eigenvector filtering' (Dray et al. 2006; Griffith & Peres-Neto 2006). In Appendix II, it is shown that accounting for spatial autocorrelation does not substantially alter the results. Changes in α and β diversity (when calculated with Jaccard's index) exhibited significant spatial autocorrelation, but were still significant after adjusting the effective sample size. The residuals of the final regression models presented in Chapter 1 (Table 6) did not exhibit significant spatial autocorrelation. Also the residuals of the corresponding full models (i.e., with all potential predictors) were not spatially autocorrelated. Thus, spatial autocorrelation did not bias model selection. Any corrections were therefore not necessary. In contrast, most of the residuals of the simple linear regressions of the trait distribution statistics and their changes against the fertility and disturbance gradient (Chapter 3: Tables 3-4) exhibited significant spatial autocorrelation. This spatial autocorrelation could be reduced to an insignificant level in most cases by means of spatial eigenvector filtering. The resulting correlation coefficients were sometimes lower and less significant than the original coefficients. In most cases, however, the resulting correlation coefficients were even higher than the original ones. Changes in sign occurred only when the original correlation coefficient was small and not significant.

These additional analyses indicate that, although present in some response variables, spatial autocorrelation is probably not a serious problem for the reliability of our results. Another argument that may relieve concerns about the effects of spatial autocorrelation on the outcome of our statistical tests is the presence of negative autocorrelation at certain distances (Fig. II) which might mitigate the effects of positive autocorrelation at other distances to some degree (Fortin & Dale 2005, p. 248). To conclude, I think that accounting for spatial autocorrelation where necessary would be the more correct way, but neglecting spatial autocorrelation in our data kept the complexity of the applied methods at a comprehensible level and did probably not bias our results in such a way that our interpretations would be invalid.

## Distinguishing signal from noise

The four chapters demonstrate that the herb layer changes that occurred over the last two decades in the Weser-Elbe region were rather complex and not unidirectional.

This became obvious, for instance, by the relatively large scatter in the changes in α and β diversity (Chapter 1: Table 4, Fig. 2). Although, on average, these changes were positive and negative, respectively, there were also several sites, where diversity had changed in the opposite direction. Also, the group of winner species in Chapter 4 (Table S2a) appeared rather heterogeneous in terms of their life history, indicating that several different drivers were responsible for species shifts. Probably, even more drivers than those considered in Chapter 4 were responsible for the individual changes in each plot. This becomes obvious by the multidirectional shifts by the communities in ordination space (Fig. III). However, despite this considerable noise, we were able to find patterns of herb layer changes that were consistent across the study region.

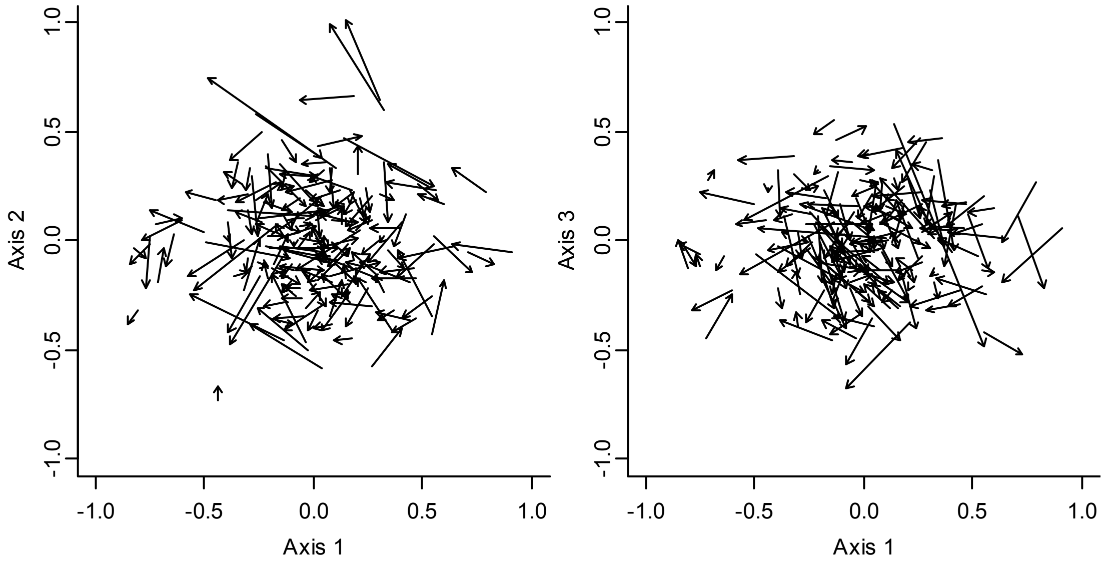

**Fig. III.** Non-metric multidimensional scaling of the joined dataset of both sampling periods. Vectors represent the shifts of the plots over time in ordination space. Total proportion of explained variation in species composition is 75.2%, with Axis 1, Axis 2 and Axis 3 explaining 41.4%, 22.5% and 11.4%, respectively (based on the $R^2$ between Euclidean distances in ordination space and Bray-Curtis distances in the original space).

## Changes in plant species diversity

Chapter 1 (Table 3 and 4) and Chapter 2 (Table 1) provide evidence that α diversity (species richness) increased over the last two decades, whereas β diversity decreased. The decrease in β diversity was most pronounced when considered as real turnover, i.e., when calculated with Lennon's index (Chapter 1: Fig. 2, Table 3). This study is one of the first studies in temperate Europe that demonstrate taxonomic homogenization of forest plant communities at a larger than local scale. In a 25 km$^2$ forest area in the more continental lowlands of SE Czech Republic, Hédl et al. (2010) observed a substantial decline of species typical for thermophilous oak forest vegetation over a time period of c. five decades, leading to a decrease in species richness both at the plot and landscape level. They also found an expansion of nutrient-demanding species of more mesic sites. However, no trend towards a homogenization of communities could be detected. Another recent study found an increased floristic similarity among woodland patches distributed throughout the southern English county of Dorset over a time period of seven decades (Keith et al. 2009). In contrast to our study, the authors observed no consistent change in species richness across sites. Instead, they found a remarkable turnover in the regional pool with a net loss of 70 species (i.e., a decrease in γ diversity). In the Weser-Elbe region, all significant loser species were still present in the pool, while five of the winner species were new in the dataset (Chapter 4), enhancing γ diversity (Chapter 2: Table 4 [here only a net increase by three species because woody species were excluded]). These differences between the studies demonstrate that the processes involved in the biotic homogenization of communities may be manifold (cf. Olden & Poff 2003). As shown in Chapter 1, the floristic homogenization in our study resulted mainly from species colonizations, although local species losses occurred as well (Chapter 4: Table S1).

The observed changes in α and β diversity were, however, only significant when species abundances were neglected (Chapter 1: Table 3; Chapter 2: Table 1). As discussed in Chapter 1, this demonstrates that the diversity changes based on presence-absence data resulted mainly from gains and losses of low-abundance species. The abundance of more dominant species shifted less consistently across sites, resulting in marked changes in individual plots (Chapter 1: Fig. 2), but not on average. Thus, the changes evident from data analysis may not be evident in the field yet.

The diversity changes found at the taxonomic level did not result in similar changes at the functional level, at least not consistently across traits and diversity components. For canopy height, all three diversity components (α, β and γ) slightly decreased, whereas for diaspore weight, they slightly increased (Chapter 2: Table 1). Changes in functional α diversity were most pronounced at sites that experienced disturbance by forest management activities between sampling periods. Here, the functional diversity of reproductive traits (including pollination mode, diaspore weight and seed longevity) increased, whereas that of canopy height decreased (Chapter 3: Table 4). However, when averaged across sites, the magnitude of change appeared low. No significant changes occurred, when functional diversity was calculated from multiple traits (Chapter 2: Table 1). Thus, on average, the herb layer communities neither gained functional richness nor experienced functional homogenization. A likely reason for this low response of the communities at the functional level is, as indicated in Chapter 2, that these communities are functionally "buffered". Single communities involve most of the functional diversity of the regional species pool, i.e., they are already functionally rich, while they are functionally redundant among each other, i.e., they are already homogeneous.

Changes in functional diversity and particularly functional β diversity have received little attention in resurvey studies on forest vegetation so far. For several plant traits, Smart et al. (2006) found a significant decline in functional α diversity averaged across different habitat types (including forest) within landscape windows throughout Britain. They did not test for changes in functional β diversity. Wiegmann & Waller (2006) claim to have observed functional homogenization in forest communities of northern Wisconsin due to the increasing dominance of graminoids. However, they did not explicitly test for it. Van Calster et al. (2007) found functional homogenization towards more ruderal species, based on C-S-R functional types (Grime 1979). This homogenization occurred within one single forest and could be clearly attributed to a change in forest management regime from coppice-with-standards to high forest. The present study suggests that, on a regional scale and taking multiple traits into account, functional homogenization will proceed slower than taxonomic homogenization. But for particular traits, which respond differently to environmental changes, this pattern may look different.

## Changes in species composition

### *Degree of biotic impoverishment*

In Chapter 1, we concluded that despite a broad trend toward homogenization of communities, no severe biotic impoverishment has taken place yet. The reason was that the observed taxonomic homogenization could be attributed mainly to the invasion of native habitat generalists and to a much lesser extent to the loss of habitat specialists. In Chapter 4, however, we showed that the number of loser species almost equaled the number of winner species. Among these loser species were also 12 ancient forest species (significantly more than among winner species as indicated by a $\chi^2$ randomization test as in Chapter 4: $\chi^2 = 7.56$, $P = 0.008$) and seven species listed on the Red List of endangered plant species in NW Germany. Based on these numbers, the level of biotic impoverishment must be considered more severe. This discrepancy in the assessment of biotic impoverishment is due to the fact that winner species were not generally habitat generalists and loser species were not generally habitat specialists. Both the number of habitat generalists among winner species and the number of habitat specialists among loser species were always higher than expected at random, but significantly only with respect to the specialization to soil pH (Table I). The results presented in Chapter 1 and 4 are consistent in view of the fact that the average number of pH specialists (species with an performance optimum at high soil pH) significantly decreased (Chapter 1: Table 4), while loser species had a higher pH optimum on average than winner species (Chapter 4: Fig. 2). Also, the average number of moisture specialists (species with an performance optimum at high soil moisture) did not change significantly (Chapter 1: Table 1), while winner and loser species did not differ significantly in their moisture optimum either (Chapter 4: Table 2). Inconsistently, however, the average number of forest specialists increased significantly (Chapter 1: Table 1), although there was a larger number of ancient forest species (which can be considered very specialized to forests) among loser species than among winner species. The forest specialists, as defined in Chapter 1, comprise both slow-colonizing forest specialists (i.e., ancient forest species sensu Wulf (1997)), such as *Adoxa moschatellina*, *Galium odoratum* or *Mercurialis perennis*, and fast-colonizing forest specialists (not closely tied to ancient forests), such as *Cardamine flexuosa*, *Dryopteris carthusiana* or *Impatiens parviflora*. Among the fast-colonizing forest specialists were several winner species, as those just mentioned (Chapter 4: Table S2a). But even if we had only considered slow-colonizing forest herbs as forest specialists in Chapter 1, the discrepancy between the chapters would remain: The average number of ancient forest species significantly increased by 0.56 species (paired-samples randomization test as in Chapter 1: $P = 0.001$). Thus, the number of ancient forest species in a plot may have increased due to the invasion of low-abundant species, and at the same time, the abundance of established ancient forest species may have decreased. Indeed, the average cumulative cover-abundance of ancient forest species significantly decreased by 7.6% (paired-samples randomization test as in Chapter 1: $P < 0.001$). This distinct development of species number and cumulative cover-abundance is partly due to some ancient forest species (*Brachypodium sylvaticum*, *Circaea lutetiana*, *Stachys sylvatica*) which decreased in abundance on average but increased in frequency (Appendix III).

**Table I.** Association between species performance (winner vs. loser) and niche breadth (specialists vs. generalists) as tested by $\chi^2$ randomization tests with 10000 permutations (cf. Chapter 4). Expected frequencies are given in parentheses.

| | | Winner | Loser | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Forest | specialist | 12 (15.8) | 19 (15.2) | 3.70 | 0.072 |
| | generalist | 19 (15.2) | 11 (14.8) | | |
| Moisture | specialist | 2 (3.2) | 5 (3.8) | 0.97 | 0.392 |
| | generalist | 19 (17.8) | 20 (21.2) | | |
| pH | specialist | 3 (6.6) | 12 (8.4) | 5.00 | 0.026 |
| | generalist | 18 (14.4) | 15 (18.6) | | |

These results demonstrate that looking at species numbers alone without taking into account species abundances might be misleading. In conclusion, the degree of biotic impoverishment associated with taxonomic homogenization can be considered low. As discussed in Chapter 1, taxonomic homogenization is mainly a result of the invasion of high-frequent habitat generalists and forest specialists (including some ancient forest species). However, independent of taxonomic homogenization, the abundance of 30 species decreased significantly. If these decreases continue over the next decades, local extinctions of ancient forest species populations may result. This biotic impoverishment would seriously conflict with regional conservation goals (Wulf & Kelm 1994).

Changes in the number or the abundance of ancient forest species have rarely been explicitly addressed in resurvey studies on forest vegetation. In a resurvey of “woods” distributed throughout Britain, Kirby et al. (2005) found that “woodland specialists” (defined as ancient woodland indicator species) were more likely to decrease in abundance compared to the whole species pool. In a forest patch in south Sweden (Dalby Söderskog) von Oheimb & Brunet (2007) observed a decline in the plot occupancy of many forest specialists (defined as in Chapter 1; e.g., *Adoxa moschatellina*, *Platanthera chlorantha*, *Sanicula europaea*), resulting in an overall decline in the number of forest specialists both at the plot and forest level. Further studies report significant decreases of the abundance or frequency of species generally considered to exhibit an affinity to ancient forests (cf. Hermy et al. 1999), e.g., *Anemone nemorosa*, *Paris quadrifolia* and *Primula elatior* in Meerdal forest in central Belgium (Baeten et al. 2009), and *Galium odoratum*, *Mercurialis perennis* and *Polygonatum multiflorum* in forests of Skåne (south Sweden; Falkengren-Grerup & Tyler 1991). Together with these studies, our results suggest that there may be a general trend for ancient forest species to decrease in abundance, although the local and regional drivers may differ for the individual studies. The actual drivers for the Weser-Elbe region will be discussed in the subsection after the next.

### *Changes in community assembly mechanisms*

The comparison of the functional herb layer compositions over time indicated only little changes in community assembly mechanisms over the last two decades, at least at the regional level (Chapter 2). The null model tests and the comparison of functional and taxonomical diversity components revealed that, in general, species composition is determined by limiting similarity mechanisms, which cause a high functional differentiation within communities and functional redundancy among communities. At the same time, environmental filters are operating, resulting in a functional turnover across sites that is, although low, higher than expected at random (Chapter 2: Fig. 1). Although these general mechanisms remained stable over time, trait distribution patterns and associated assembly mechanisms changed significantly at certain sites, mainly at those that experienced disturbance by forest management activities between the sampling periods. At these sites, the functional diversity of several reproductive traits increased, that of pollination mode and seed longevity to a level significantly higher than expected at random (Chapter 3: Table 3 and 4). Also the diversity of diaspore weight values increased at disturbed sites, resulting in an overall increase in average functional α diversity (Chapter 2: Table 1) and an increase in functional β diversity to a level higher than expected at random (Chapter 2: Fig. 1). These changes in reproductive trait diversity indicate that disturbance events relaxed the environmental filters that limited reproduction strategies in 1988. After sites had experienced disturbance, several reproductive strategies coexisted in 2008. Species with a persistent seed bank, the ability of long-distances dispersal and a flowering period late in the season were among the winner species (Chapter 4: Table 3, Fig. 2). At the same time, the enhanced light availability associated with tree removal or windthrow enhanced the competitive adversity and tightened competitive filters. These limited the functional diversity with respect to canopy height and selected for taller species (Chapter 3: Table 3 and 4). Thus, despite the continuity of basic assembly mechanisms at the regional level, assembly mechanisms changed considerably at the local level, i.e. at sites that experienced disturbance.

Other studies on long-term vegetation changes in temperate forests have, to my knowledge, not yet addressed the question of changes in community assembly mechanisms. Effects of disturbance by forest management activities on species composition have mostly been investigated along spatial gradients of disturbance (e.g., Brunet et al. 1996; Decocq et al. 2004; Aubin et al. 2007). As demonstrated in Chapter 3 (Table 3 and 4), this approach may lead to very similar conclusions to those obtained by comparisons over time. However, resurvey studies provide additional information on the amount of time that is needed to observe a significant response in terms of trait composition. As the present study comprises only two surveys with a time lag of 20 years, and disturbance events may have occurred at any time during this period, we can conclude that the altered assembly mechanisms, which start operating immediately after an disturbance event has occurred, resulted in an altered functional composition and diversity already after a few years. It is known that disturbance in forests may lead to a higher functional diversity of reproductive traits (Degen et al. 2005; Biswas & Mallik 2010). But this has not yet been interpreted with respect to community assembly mechanisms and has not been contrasted with simultaneous effects on the functional diversity of competitive traits. Schamp & Aarssen (2009) analyzed the distribution of canopy height in forest plant communities along a gradient of disturbance to find evidence for assembly mechanisms, but, as discussed in Chapter 3, did not succeed. They did not include reproductive traits in their analyses.

The present study demonstrates that disturbance in temperate forests alters community assembly mechanisms in two ways: (i) it relaxes environmental filters and allows the coexistence of different reproduction strategies, and (ii) it tightens competitive filters, which lead to an exclusion of small-growing species. These findings represent evidence for the validity of hypotheses in community ecology (Grime 2006; Navas & Violle 2009) that have not been sufficiently tested yet (Chapter 3). In this respect, the present study fills an important gap.

## Likely environmental drivers

The many directions of change in species composition (Fig. III) indicate a multitude of environmental drivers with different relative importance for each plot. However, some drivers caused consistent signals across the study region (Chapter 4). The observed changes in functional composition, as shown in Chapters 2-4, provide evidence that disturbance is the most important driver for species shifts. Disturbance refers mainly to forest management interventions, i.e., the selective cutting of one or few trees, and to a lesser extent to natural tree mortality due to windthrow or old age. Generally, disturbance involves both the opening of the canopy and damage of the soil surface (Chapter 3: Study system). As discussed in the previous section, disturbance altered the operating assembly mechanisms, leading to marked changes in species composition. Besides the mentioned effects on the distribution of reproductive traits and canopy height within communities, disturbance affected species' performance via their SLA (Chapter 4: Table 3). As discussed in Chapter 4, the more open canopies at disturbed sites may have favored species with a lower SLA, which are better able to tolerate higher solar radiation and lower humidity than species with high SLA as adaptation to the low-light environments in closed forests. In consequence, the average SLA tended to decrease over time on more disturbed sites (Chapter 3: Table 4).

Although the observed changes in functional composition demonstrate that the average degree of disturbance due to forest management activities increased in the sample of sites, they do not indicate an increase in forest management intensity within the study area. As mentioned in all four chapters, the sample was biased because the sites for the first survey were chosen to reflect undisturbed forest vegetation. While some of these sites experienced some disturbance during the last two decades, other sites not included in the sample may have developed from disturbed sites to undisturbed sites. Several resurvey studies demonstrated that a gradual canopy closure in formerly disturbed and more open forests leads to a gradual decline in species that are less shade-tolerant and adapted to disturbed sites, while at the same time, shade-tolerant forest species increase in abundance (e.g., Wilmanns & Bogenrieder 1986; Dahlgren et al. 2006; Baeten et al. 2009). Thus, the observed changes in the present study can be assumed to be to some degree reversible in the long term. However, the impacts of forest management interventions may represent a problem in small, isolated forest patches with small populations of slow-colonizing forest herbs. If these are negatively affected or even extinguished by disturbance events, a recovery or re-colonization may be difficult. The relatively large number of slow-colonizing forest herbs among the loser species in the present study indicates that, in the long term, regular disturbance by forest management activities may have a negative impact on forest species diversity (cf. Bossuyt et al. 2002).

In contrast to other resurvey studies in Europe, this study failed to provide evidence that eutrophication and acidification due to atmospheric deposition are important drivers of herb layer changes. The likely reason was discussed in Chapter 4. Instead, this study is one of the first that provide some indication that climate warming and enhanced deer browsing affect the herb layer composition in temperate European forests. While this issue was discussed for climate warming in Chapter 4, it shall be stressed for deer browsing here. It is known that deer densities have increased in many regions of temperate Europe over the recent decades (Ward 2005; Milner et al. 2006; Ellenberg & Leuschner 2010, p. 75) as a result of several causes, including land-use changes and mild winters (Fuller & Gill 2001). It is also known from numerous studies that deer exert a profound impact on the ground vegetation in forests (e.g., Klötzli 1965; Kirby 2001; Rooney & Waller 2003; Takatsuki 2009). However, in contrast to North America (e.g., Taverna et al. 2005; Barret et al. 2006; Wiegmann & Waller 2006; Thiemann et al. 2009), only few resurvey studies in Europe consider an enhanced browsing pressure as a driver for changes in herb layer composition (Appendix I). Kirby & Thomas (2000) observed a decline in the cover of *Rubus fruticosus* agg. and the expansion of some grasses as likely responses to increased deer densities in a south British wood. Hédl et al. (2010) attribute the overall decline in species richness and the expansion of ruderal species at least partly to a deer overabundance in thermophilous oakwoods in Czech Republic. Together with these studies, our results indicate that deer browsing should receive more attention as potential driver in future resurvey studies of European forests.

Although the analyses in Chapter 4 took into account many drivers and related plant species traits, I see that our findings explain quite well the high performance of winner species, but less exhaustive the low performance of loser species. While winner species were favored by disturbance and climate warming due to a low SLA, a high seed longevity, the ability of long-distance dispersal or an oceanic distribution, loser species were partly inhibited by disturbance and deer browsing due to a high SLA or high browsing attractiveness (Chapter 4: Table 3). However, several loser species have neither a markedly high SLA nor a high browsing attractiveness, e.g. *Equisetum sylvaticum, Mercurialis perennis* or *Sanicula europaea* (Chapter 4: Table S2b). Another suggestion was that acidification may be responsible for the low performance of loser species due to a low tolerance to more acidic soil conditions (Chapter 4: Fig. 2), but, as discussed in Chapter 4, there was no evidence for this suggestion when all traits were considered simultaneously (Chapter 4: Table 3). Thus, the decline in abundance of several loser species has not been well explained so far. Therefore, I want to suggest an additional driver here that was neglected in Chapter 4. This is forest fragmentation. The level of forest fragmentation in the study area did certainly not change over the last two decades. However, as mentioned in the General Introduction, the forest fragments may still have to pay off their “extinction debt” (Vellend et al. 2006). All sites sampled in this study were located in ancient forest stands of which many represent remnants of a once continuous forest area (Kelm 1994). In these patches, populations of long-lived forest species, which are able to persist via prolonged clonal growth (Inghe & Tamm 1985; Ehrlén & Lehtilä 2002), may have survived and show today a delayed response to the effects of forest fragmentation as outlined in the General Introduction. In fact, as already mentioned, the proportion of ancient forest species was significantly higher among loser than among winner species. Regarding the affinity to ancient forests as low colonization capacity (cf. Vellend et al. 2006) and using this plant trait as an additional predictor in the multiple logistic regression model in Chapter 4 (Table 3), we get a proportion of explained deviance of 57.0% with a unique contribution of colonization capacity of 9.6% (Table II). The sign of this predictor is negative, thus colonization capacity significantly helps to explain the low performance of loser species. Assuming that colonization capacity reflects species’ susceptibility to fragmentation effects (Kolb & Diekmann 2005; Vellend et al. 2006), we must consider fragmentation as another important driver that exerts a delayed effect on species composition.

**Table II.** Multiple logistic regression model for the discrimination between winner ($n = 22$) and loser ($n = 24$) species from Chapter 4 (Table 3), extended by the plant trait "colonization capacity" as an additional predictor. The proportion of deviance explained by the model is 57.0% ($P < 0.001$). The area under the receiver operating characteristic curve (*AUC*) is 0.94.

| Significant predictors | Sign | Unique proportion of deviance explained (%) | $P$ [a] |
|---|---|---|---|
| Seed longevity | + | 19.4 | 0.002 |
| SLA | − | 17.0 | 0.004 |
| Browsing attractiveness | − | 11.4 | 0.020 |
| Oceanity | + | 9.9 | 0.031 |
| Colonization capacity | − | 9.6 | 0.034 |
| Long-distance dispersal | + | 8.7 | 0.047 |

[a] Partial $\chi^2$ randomization test

## Conclusions

The results of this study add significantly to our understanding of the current long-term changes, occurring in the herb layer of European temperate forests. Using a reliable and comprehensive dataset, the study provides evidence for both quantitative and qualitative changes in species composition, which are consistent across the Weser-Elbe region. After 20 years, the degree of biotic homogenization is still low and mostly coupled with the expansion of low-abundant habitat generalists. The observed changes in taxonomic diversity do not imply similar changes in functional diversity. Marked changes in community assembly mechanisms were not found, except at sites that experienced disturbance by forest management activities. Overall, the changes in species diversity at different spatial and abstraction levels do not indicate major biotic impoverishment of the herb layer communities. However, looking at abundance changes of individual species, the study reveals a consistent decline in 30 species, including several slow-colonizing forest specialists. These declines cause concern from a conservational point of view. The study indicates that the observed changes in species composition are the result of several, partly competing forces, which are acting on different spatial scales. Disturbance by forest management activities is certainly the most important driver, which means that some of the observed changes may be reversible within the next decades. However, other important drivers, including climate warming, deer browsing and (as a legacy from the past) forest fragmentation, are unlikely to change their impact on forest vegetation within the near future. Therefore, I expect the corresponding species shifts to become more pronounced over the next decades. Because climate warming, increased deer densities and a high level of fragmentation are drivers that are operative in many regions of the European lowlands, the results of this study may be partly representative beyond NW Germany.

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# Summary

Human-induced alterations of the environment are causing biotic changes worldwide, including the extinction of species and a mixing of once disparate floras and faunas. One type of biological communities that is expected to be particularly affected by environmental alterations are herb layer plant communities of fragmented forests such as those in the west European lowlands. However, our knowledge about current changes in species diversity and composition in these communities is limited due to a lack of adequate long-term studies.

In this thesis, I resurveyed the herb layer communities of ancient forest patches in the Weser-Elbe region (NW Germany) after two decades using 175 semi-permanent plots. The general objectives were (i) to quantify changes in plant species diversity considering also between-community (β) and functional diversity, (ii) to determine shifts in species composition in terms of species' niche breadth and functional traits and (iii) to find indications on the most likely environmental drivers for the observed changes. These objectives were pursued with four independent research papers (Chapters 1-4) whose results were brought together in a General Discussion.

The observed herb layer changes were rather complex and not unidirectional. However, several patterns and processes were consistent across the study region. Alpha diversity (species richness) increased by almost four species on average, whereas β diversity tended to decrease (Chapter 1). The latter is interpreted as a beginning floristic homogenization. The magnitude of change in β diversity depended on the β diversity measure applied. The observed changes were primarily the result of a spread of native habitat generalists that are able to tolerate broad pH and moisture ranges. A distinction between forest specialists (closely tied to forest habitats) and generalists (also found in open habitats) did not help explain changes in β diversity. The observed changes in α and β diversity were only significant when species abundances were neglected (Chapters 1 and 2), demonstrating that the diversity changes resulted mainly from gains and losses of low-abundance species. This study is one of the first studies in temperate Europe that demonstrates floristic homogenization of forest plant communities at a larger than local scale.

The diversity changes found at the taxonomic level did not result in similar changes at the functional level (Chapter 2). On average, the herb layer communities neither gained functional richness nor experienced functional homogenization (Chapter 2). The likely reason is that these communities are functionally "buffered". Single communities involve most of the functional diversity of the regional pool, i.e., they are already functionally rich, while they are functionally redundant among each other, i.e., they are already homogeneous.

The degree of biotic impoverishment associated with the beginning taxonomic homogenization can be considered low, because the homogenization resulted mainly from the invasion of high-frequent habitat generalists (Chapter 1). However,

independent of taxonomic homogenization, the abundance of 30 species decreased significantly (Chapter 4). These species included 12 ancient forest species (i.e., species closely tied to forest patches with a habitat continuity > 200 years) and seven species listed on the Red List of endangered plant species in NW Germany. If these decreases continue over the next decades, local extinctions may result. This biotic impoverishment would seriously conflict with regional conservation goals.

The functional herb layer composition changed little over time, indicating that the essential community assembly mechanisms remained stable, at least at the regional level (Chapter 2). Null model tests and the comparison of functional and taxonomical diversity components as a result of a multiplicative diversity partitioning approach revealed that, in general, species composition is determined by limiting similarity mechanisms that cause a high functional differentiation within communities and functional redundancy among communities. At the same time, environmental filters are operating, as reflected by a functional turnover across sites that was higher than expected at random. Despite the continuity of basic assembly mechanisms at the regional level, assembly mechanisms changed considerably at the local level, particularly at sites that experienced disturbance by forest management activities between the sampling periods (Chapter 3). Disturbance altered community assembly mechanisms in two ways: (i) it relaxed environmental filters and allowed the coexistence of different reproduction strategies, as reflected by a higher diversity of reproductive traits at the time of the resurvey, and (ii) it enhanced light availability and tightened competitive filters. These limited the functional diversity with respect to canopy height and selected for taller species.

Thirty-one winner and 30 loser species, which had significantly increased or decreased in abundance, respectively, were characterized by various functional traits and ecological performances to find indications on the most likely environmental drivers for the observed floristic changes (Chapter 4). Winner species had higher seed longevity, flowered later in the season and had more often an oceanic distribution compared to loser species. Loser species tended to have a higher specific leaf area, to be more susceptible to deer browsing and to have a performance optimum at higher soil pH values compared to winner species. Multiple logistic regression analyses in combination with a deviance partitioning approach indicated that disturbances due to forest management interventions were the primary cause of the species shifts. Here, disturbance involved both the opening of the tree canopy and damage of the soil surface. As one of the first European resurvey studies, this study provides indications that an enhanced browsing pressure due to increased deer densities and increasingly warmer winters are important drivers. The study failed to demonstrate that eutrophication and acidification due to atmospheric deposition substantially drive herb layer changes. The restriction of the sample to the most base-rich sites in the region is discussed as a likely reason. Furthermore, the decline of several ancient forest species is discussed as an indication that the forest patches are still paying off their “extinction debt”, i.e., exhibit a delayed response to forest fragmentation.

# Zusammenfassung

Durch den Menschen hervorgerufene Umweltveränderungen führen weltweit zu Veränderungen der Tier- und Pflanzenwelt. Diese umfassen auch das Aussterben von Arten und die Vermischung von ursprünglich räumlich getrennten Floren und Faunen. Zu den besonders beeinträchtigten Lebensgemeinschaften gehören die Krautschichtgemeinschaften fragmentierter Wälder, wie sie im westeuropäischen Tiefland vorkommen. Unser Wissen über die Veränderung von Artenvielfalt und -zusammensetzung in diesen Gemeinschaften ist begrenzt, da es bislang nicht genug Langzeitstudien gibt.

In dieser Arbeit wurden Untersuchungen an Krautschichtgemeinschaften historisch alter Waldfragmente im Elbe-Weser-Dreieck (NW-Deutschland) nach zwei Jahrzehnten wiederholt. Dazu wurden 175 semi-permanente Aufnahmeflächen verwendet. Die Ziele der Arbeit waren (i) die Quantifizierung von Veränderungen der Pflanzenartenvielfalt unter Berücksichtigung der β-Diversität und der funktionalen Diversität, (ii) die Feststellung von Artenverschiebungen in Bezug auf Nischenbreite und funktionale Merkmale der Arten und (iii) die Identifizierung der wahrscheinlich verantwortlichen Umweltveränderungen. Diese Ziele wurden im Rahmen von vier unabhängigen Forschungsartikeln (Kapitel 1-4) verfolgt, deren Ergebnisse in einer allgemeinen Diskussion zusammengeführt wurden.

Die beobachteten Veränderungen in der Krautschicht waren ausgesprochen komplex und verliefen in verschiedene Richtungen. Dennoch erwiesen sich einige Muster und Prozesse auf regionaler Ebene als konsistent. Die α-Diversität (Artenzahl) stieg durchschnittlich um fast vier Arten an. Die β-Diversität nahm hingegen tendenziell ab (Kapitel 1). Letzteres wird als Beginn einer floristischen Homogenisierung interpretiert. Das tatsächliche Ausmaß der β-Diversitätsveränderung hing von dem verwendeten Index ab. Die beobachteten Veränderungen waren in erster Linie auf die Ausbreitung von heimischen Standortgeneralisten zurückzuführen, die eine weite Spanne der Bodenfeuchtigkeit und des pH-Wertes tolerieren. Die Unterscheidung von Waldspezialisten (an geschlossene Wälder gebunden) und Waldgeneralisten (kommen auch im Offenland vor) trug nicht zur Erklärung der β-Diversitätsveränderungen bei. Die beobachteten Veränderungen von α- und β-Diversität waren nur signifikant, wenn die Artabundanzen vernachlässigt wurden (Kapitel 1 und 2). Die Diversitätsveränderungen resultierten also hauptsächlich aus dem Hinzukommen oder Ausfallen von Arten mit geringer Abundanz. Diese Studie ist eine der ersten im gemäßigten Europa, die eine floristische Homogenisierung von Waldpflanzengemeinschaften auf einer größeren als der lokalen Ebene aufzeigt.

Die Diversitätsveränderungen auf taxonomischer Ebene führten nicht zu vergleichbaren Veränderungen auf funktionaler Ebene. Im Durchschnitt gewannen die Krautschichtgemeinschaften weder an funktionaler Vielfalt, noch erfuhren sie eine funktionale Homogenisierung (Kapitel 2). Der Grund liegt in der funktionalen „Pufferung“ der Pflanzengemeinschaften. Einerseits wiesen einzelne

Pflanzengemeinschaften bereits den Großteil der funktionalen Vielfalt des regionalen Artenpools und damit ein Maximum an funktionaler Diversität auf. Andererseits waren sie untereinander funktional redundant, also bereits homogen.

Die mit der beginnenden taxonomischen Homogenisierung verbundene floristische Verarmung wird als gering eingestuft, da die Homogenisierung im Wesentlichen das Ergebnis der Zuwanderung häufig vorkommender Standortgeneralisten war (Kapitel 1). Unabhängig von der taxonomischen Homogenisierung gingen jedoch 30 Arten signifikant in ihrer Abundanz zurück (Kapitel 4). Diese Arten umfassen 12 an historisch alte Wälder gebundene Arten sowie sieben Arten, die auf der Roten Liste von NW-Deutschland stehen. Sollte die Abundanz dieser Arten im Verlauf der nächsten Jahrzehnte weiter zurückgehen, kann dies zu einem lokalen Aussterben der Populationen führen. Diese Form der floristischen Verarmung stünde in deutlichem Widerspruch zu regionalen Naturschutzzielen.

Die geringfügigen Veränderungen der funktionalen Krautschichtzusammensetzung zeigen, dass die wesentlichen Mechanismen für die Vergesellschaftung der Arten stabil blieben, zumindest auf der regionalen Ebene (Kapitel 2). Nullmodelltests sowie der Vergleich von funktionalen und taxonomischen Diversitätskomponenten (als Ergebnis einer multiplikativen Diversitätspartitionierung) ergaben, dass die Artenzusammensetzung in den untersuchten Wäldern im Wesentlichen von limiting similarity-Mechanismen bestimmt wird. Diese bewirken eine hohe funktionale Differenzierung innerhalb der Gemeinschaften und funktionale Redundanz zwischen den Gemeinschaften. Gleichzeitig sind Umweltfilter wirksam, was durch den funktionalen turnover zwischen den Standorten angezeigt wird, der höher war als bei einer zufälligen Verteilung der Arten erwartet. Trotz der zeitlichen Konstanz dieser grundlegenden Vergesellschaftungsmechanismen auf der regionalen Ebene, veränderten sich die Vergesellschaftungsmechanismen auf der lokalen Ebene erheblich, insbesondere auf Standorten, die Störung durch forstwirtschaftliche Maßnahmen erfuhren (Kapitel 3). Störung veränderte die Vergesellschaftungsmechanismen in zweierlei Hinsicht. Einerseits führte sie zu einer Abschwächung der Umweltfilter, was die Koexistenz von Arten mit unterschiedlichen Reproduktionsstrategien ermöglichte. Andererseits erhöhte sie die Lichtverfügbarkeit und verstärkte damit die Konkurrenzfilter. Diese führten zu einer Einschränkung der funktionalen Diversität in Bezug auf die Wuchshöhe und zu einer Selektion hochwüchsiger Arten.

Einunddreißig Gewinner- und 30 Verliererarten, die in ihrer Abundanz signifikant zu- bzw. abnahmen, wurden anhand funktionaler Merkmale und ihres ökologischen Verhaltens charakterisiert mit dem Ziel, Hinweise auf die verantwortlichen Umweltveränderungen zu finden (Kapitel 4). Gewinnerarten wiesen eine höhere Langlebigkeit der Samen auf, blühten später in der Vegetationsperiode und hatten öfter eine ozeanische Verbreitung im Vergleich zu Verliererarten. Verliererarten hatten eine höhere spezifische Blattfläche, einen höheren Attraktivitätswert als Wildäsung und ein ökologisches Optimum bei höheren pH-Werten im Vergleich zu Gewinnerarten. Multiple Logistische Regressionsanalysen in Kombination mit einer Devianzpartitionierung ließen erkennen, dass Störung durch forstwirtschaftliche

Eingriffe hauptverantwortlich für die Artenverschiebungen war. Diese Störung umfasst sowohl die Öffnung des Kronendaches als auch die Verletzung der Bodenoberfläche. Zusätzlich liefert diese Wiederholungsstudie als eine der ersten in Europa Hinweise darauf, dass ein erhöhter Äsungsdruck durch erhöhte Wilddichten sowie zunehmend mildere Winter entscheidende Einflussfaktoren darstellen. Es gelang hingegen nicht zu zeigen, dass Eutrophierung und Versauerung als Folge atmosphärischer Deposition die Krautschichtveränderungen maßgeblich beeinflussten. Die Beschränkung der Stichprobe auf die basenreichsten Standorte der Region wird als Grund diskutiert. Darüber hinaus wird der Rückgang mehrerer an historisch alte Wälder gebundener Arten als Anzeichen dafür diskutiert,  dass die untersuchten Waldfragmente noch dabei sind, ihre „Aussterbeschuld“ zu begleichen, also eine verspätete Reaktion auf die Waldfragmentierung zeigen.

# Appendix I

## Resurvey studies on temperate, deciduous forest vegetation

The list is probably not exhaustive. Country codes refer to ISO 3166-1. The spatial extent indicates the extent of the study area: sf single forest (one single, continuous forest area), l landscape (1-1000 km²), r region (1000-100 000 km²), c country (>100 000 km²). The resurvey method indicates if permanent plots (pp), semi-permanent plots (sp) or no relocation of plots, but instead a comparison within phytosociological types (pt) were used to determine changes in species composition. The codes for the considered drivers mean: 1a succession towards a closed canopy due to grazing abandonment, a conversion from coppice to high forest or other changes in management, 1b succession towards an altered tree layer composition involving a change in litter quality and light availability, 2 disturbance by forest management activities or natural windthrow, 3 change in water regime, 4a atmospheric deposition causing acidification, 4b atmospheric deposition causing eutrophication, 5 (enhanced) browsing pressure, 6 climate change, 7 invasion of exotic species, 8 habitat fragmentation, S special drivers (see footnotes).

| Reference | Country code | Time lag (years) | Spatial extent | Resurvey method | Considered drivers |
|---|---|---|---|---|---|
| Baeten et al. 2009 | BE | 46 | sf/l | sp | 1a, 4a |
| Bernhardt et al. 2005 | DE | 42; 18 | sf | pt; pp | 1a, 4b |
| Bjørnstad 1991 | NO | 20 | l | pp | 4a, 4b |
| Brewer 1980 | US | 39-54 | sf | sp | 1b |
| Brunet et al. 1996 | SE | 10 | r | pp | 1a, 2, 4a |
| Brunet et al. 1997a | SE | 10 | r | pp | 2, 4a |
| Brunet et al. 1997b | SE | 10 | r | pp | 1a, 2 |
| Brunet & Tyler 2000 | SE | 10 | sf | pp | 4a |
| Buck-Feucht 1986 | DE | 30 | l | sp | 1a, 4a |
| Bürger 1991 | DE | 8-45 | r | pt | 4a, 4b |
| Dahlgren et al. 2006 | SE | 42 | sf | pp | 1a |
| Davison & Forman 1982 | US | 30 | sf | pp | 2, S[a] |
| Diekmann & Dupré 1997 | DE | *variable* | r | pt | 4a, 4b |
| Diekmann et al. 1999 | SE | 11 | r | pp | 2, 4a, 4b |
| Drayton & Primack 1996 | US | 100 | l | pp | 2, 4b, 8, S[b] |
| Durak 2010 | PL | 50 | r | sp | 1a, 2, 4a |
| Elliot et al. 1999 | US | 20 | l | pp | 2 |
| Falkengren-Grerup 1986 | SE | 14-36 | r | pp? | 4a, 4b |
| Falkengren-Grerup & Eriksson 1990 | SE | 35-40 | r | sp | 2, 4a, 4b |
| Falkengren-Grerup & Tyler 1991 | SE | 10 | r | sp | 2, 4a |
| Fischer 1993 | DE | 10 | l | pp | 1a, 3, 5, 4b |
| Haveman & Schaminee 2005 | NL | *variable* | r | pt | 1a, 4b |
| Hédl 2004 | CZ | 60 | l | sp | 2, 4a |
| Hédl et al. 2010 | CZ | 39+14 | sf/l | sp | 1a, 1b, 5 |
| Holeska & Woźniak 2005 | PL | c. 30 | l | pt | 2, 5 |
| Holland et al. 2000 | US | 23 | sf | pp | 3 |
| Hülber et al. 2008 | AT | 12 | l | pp | 4a |
| Keith et al. 2009 | GB | c. 70 | r | sp | 1a, 4b |
| Kirby & Thomas 2000 | GB | 17 | sf/l | pp | 5, 4b |
| Kirby et al. 2005 | GB | 30 | c | sp | 1a, 5, 4a, 4b, 6 |

| Reference | Country code | Time lag (years) | Spatial extent | Resurvey method | Considered drivers |
|---|---|---|---|---|---|
| Kirkpatrick 2004 | AU | 27 | l | sp | 1a, 1b |
| Kuhn et al. 1987 | CH | 37-50 | r | pp | 1a, 4b |
| Kwiatkowska 1994 | PL | 24 | sf | pp | 1a, 1b |
| Lameire et al. 2000 | BE | 20 | sf | sp | 3, 4b |
| Liu & Bråkenhielm 1996 | SE | 12 | c | pp | 4a, 4b |
| Lysik 2008 | PL | 10 | sf | pp | 1b, 6, 7 |
| Lysik 2009 | PL | 13 | sf | pp | 1b |
| Madĕra 2001 | CZ | 21+4 | l | pp | 3 |
| Medwecka-Kornas & Gawronski 1991 | PL | 30 | l | sp | 4a, 4b, S[c] |
| Persson et al. 1980 | SE | 41 | sf | sp | 1b |
| Persson et al. 1987 | SE | 41 | sf | sp | 1b, 4a |
| Röder et al. 1996 | DE | 40 | l | sp | 1a, 4a, 4b, S[d] |
| Rogers et al. 2008 | US | c. 53 | r | sp | 1a, 1b, 7, 8 |
| Rooney & Dress 1997 | US | 66 | sf | pt | 5, 4a, 8 |
| Rooney 2009 | US | 16 | sf | pp | 5 |
| Rooney et al. 2004 | US | 50 | r | sp | 1a, 2, 5, 7 |
| Rost-Siebert & Jahn 1988 | DE | 25-50 | l | pp | 1a, 2, 4a |
| Schmidt 1993 | DE | 30-35 | l | pp | 4a |
| Taverna et al. 2005 | US | 23 | sf/l | pp | 1a, 2, 5 |
| Thimonier et al. 1992 | FR | 20 | sf/l | pp | 4a, 4b |
| Thimonier et al. 1994 | FR | 19 | sf/l | pp | 4a, 4b |
| Tyler et al. 2002 | SE | 12 | sf | pp | 1a, 4a, 6 |
| van Calster et al. 2007 | BE | 38 | sf/l | sp | 1a, 2, 4a |
| van Calster et al. 2008 | BE | 38-48 | l | sp | 1a, 1b |
| von Oheimb & Brunet 2007 | SE | 34+7+26 | sf | sp | 1a, S[e] |
| Wiegmann & Waller 2006 | US | 50 | r | sp | 1a, 2, 5, S[f] |
| Wilmanns 1989 | DE | 35 | l | sp | 1a, 4b |
| Wilmanns & Bogenrieder 1986 | DE | 37 | l | pt | 1a |
| Wilmanns et al. 1986 | DE | 24-38 | l | pt | 1a, 4b |
| Wittig et al. 1985 | DE | 8 | r | sp | 2, 4a, 4b |
| Zukrigl et al. 1993 | AT | 7-32 | r | sp | 4b |

[a] fertilization

[b] intensive recreational use

[c] deposition of dust with gypsum, dolomit and calcit

[d] amelioration liming

[e] slug invasion and Dutch elm disease

[f] loss of pollinators and exotic earthworm invasion

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# Appendix II

## Accounting for spatial autocorrelation (SAC) in the analyses of Chapters 1 and 3

Spatial autocorrelation was quantified with the global Moran's $I$ statistic, which was calculated and tested for significance using the R function *moran.mc* in the package *spdep* (Bivand et al. 2010). The spatial weights ($w$) needed to calculate Moran's $I$ were calculated as Gaussian function of the distances between the plot locations: $w_{ij} = \begin{cases} 0 & \text{for } d_{ij} > d_{\max} \\ e^{-(4d_{ij}/d_{\max})^2} & \text{for } d_{ij} \leq d_{\max} \end{cases}$, where $d_{ij}$ is the geographical distance between plots $i$ and $j$, and $d_{\max}$ is the maximum distance in the minimum spanning tree that connects all plots (cf. Dray et al. 2006; Griffith & Peres-Neto 2006).

In Chapter 1, the change in α diversity and the change in β diversity when calculated with Jaccard's index exhibited weak but significant SAC (Table A-I). To account for this SAC in testing the changes in diversity against zero, I performed a one-sample $T$-test instead of the paired-samples randomization test used originally and adjusted the effective sample size (Fortin & Dale 2005). The effective sample size $n'$ in the presence of SAC was calculated from the autocorrelation matrix: $n' = \frac{n^2}{\sum_{i=1}^{n}\sum_{j=1}^{n}\mathrm{Cor}(x_i, x_j)}$, where n is the original sample size and $\mathrm{Cor}(x_i, x_j)$ is the spatial autocorrelation between observations $i$ and $j$ (Fortin & Dale 2005, p. 223). The autocorrelation matrix contains a correlation value for each pair of observations and was estimated from a spline correlogram that provides a correlation estimate as a continuous function of distance (Bjørnstad & Falck 2001). The spline correlogram was calculated with the function *spline.correlog* of the R package *ncf* (Bjørnstad 2009). Estimating the autocorrelation matrix from the sample data itself rather than using an autocorrelation matrix that corresponds to a known or assumed correlation structure in the statistical population might be misleading (Dale & Fortin 2002), because the data points represent only one realization of theoretically many others that might give different estimates. However, if the correlation structure cannot be described by a simple autoregressive model that would allow the simulation of many realizations in order to derive the distribution of the test statistic (Dale & Fortin 2002), estimating the autocorrelation matrix from the data appears to be the only way possible. I calculated the effective sample size using three different autocorrelation matrices to account to some degree for the effects of arbitrary choices in calculating the autocorrelation matrix: (a) correlations at all distances ≤ $d_{\max}$ were considered; (b) only significant correlations according to the 95% confidence envelope around the spline correlogram were used, while non-significant correlations were set to zero; (c) only correlations up to the smallest distance, where the correlation is zero (correlation length; (Bjørnstad & Falck 2001) were used. The $T$-statistic was then calculated as $T = \frac{\bar{x}}{s / \sqrt{n'}}$, where $\bar{x}$ is the sample mean and $s$ is the sample standard deviation, and compared to the $T$ distribution with $n'$ degrees of freedom (Dale & Fortin 2002).

In general, the modified *T*-tests indicated a significant increase in α diversity and a significant decrease in β diversity as did the paired-samples randomization tests in the original chapter (Table A-II). Noticeable is the effective sample size of variant (a) for the change in α diversity, which was larger than the original sample size. This may occur if SAC is mostly negative at far distances (Fortin & Dale 2005, p. 228). Also noticeable is the effective sample size of variant (a) for the change in β diversity, which was negative. The corresponding *T*-test could, of course, not be performed in that case. A negative $n'$ can only occur if the autocorrelation structure is estimated from the data, which represents only one possible realization. The sum over the autocorrelation matrix that represents the statistical population cannot be less than zero (Fortin & Dale 2005, p. 229). Here, the autocorrelation structure estimated from the data was apparently not reliable.

**Table A-I.** Spatial autocorrelation (measured by global Moran's *I* and tested with the function *moran.mc* in the R package *spdep* (Bivand et al. 2010) with 999 permutations) of changes in α diversity (Δα; cf. Chapter 1: Table 4) and changes in β diversity (Δβ; cf. Chapter 1: Table 3).

| | Global Moran's *I* | *P* |
|---|---|---|
| Δα | 0.20 | 0.001 |
| Δβ(Jaccard) | 0.05 | 0.030 |
| Δβ(Lennon) | 0.00 | 0.310 |
| Δβ(Bray-Curtis) | 0.03 | 0.107 |

**Table A-II.** Test for significant deviations of the change in α diversity (Δα) and the change in β diversity (Δβ) measured with Jaccard's index from zero using modified *T*-tests with an adjusted effective sample size $n'$. See text for explanations of variants. Original sample size: $n = 175$.

| | Mean | Variant | $n'$ | *T* | *P* |
|---|---|---|---|---|---|
| Δα | 3.7 | a | 1871.3 | 21.2 | <0.001 |
| | | b | 99.7 | 4.90 | <0.001 |
| | | c | 51.9 | 3.53 | <0.001 |
| Δβ(Jaccard) | -2.3 | a | -7.5 | - | - |
| | | b | 175.0 | -8.34 | <0.001 |
| | | c | 103.0 | -6.40 | <0.001 |

The residuals of the final regression models presented in Chapter 1 (Table 6) did not exhibit significant SAC (Table A-III). Also the residuals of the corresponding full models (i.e., with all potential predictors) were not spatially autocorrelated. Thus, no SAC did bias model selection. Any corrections were therefore not necessary.

**Table A-III.** Spatial autocorrelation (measured by global Moran's *I* and tested with the function *moran.mc* in the R package *spdep* (Bivand et al. 2010) with 999 permutations) of the residuals of the linear regression models shown in Chapter 1 (Table 6) and of the corresponding full models with all potential predictors.

| Model | | Global Moran's *I* | *P* |
|---|---|---|---|
| Jaccard | reduced | 0.00 | 0.393 |
| | full | -0.01 | 0.457 |
| Lennon | reduced | 0.01 | 0.235 |
| | full | 0.02 | 0.159 |
| Bray-Curtis | reduced | -0.02 | 0.618 |
| | full | -0.02 | 0.610 |

In Chapter 3, most of the residuals of the simple linear regressions of the trait distribution statistics and their changes against the fertility and disturbance gradient (Chapter 3: Table 3-4) exhibited significant SAC (Tables A-IV – A-VII). This SAC could be reduced to an insignificant level in most cases by means of spatial eigenvector filtering (Dray et al. 2006; Griffith & Peres-Neto 2006). This method has the advantages that it can be used with non-lattice data and does not require the definition of an autocorrelation structure. It also does not strictly assume spatial isotropy and stationarity as most other methods (Dormann et al. 2007). It is, however, confined to models in which the effects of one or several explanatory variables on one or several response variables are to be elucidated. It can not account for spatial autocorrelation in one-sample tests such as those described above. During spatial eigenvector filtering, an eigenvector decomposition of the spatial weights matrix $[w_{ij}]$ is performed and then the resulting eigenvectors are used as additional predictors in the linear regression models (Dormann et al. 2007). Spatial eigenvector filtering was carried out using the R function *ME* in the *spdep* package (Bivand et al. 2010). In a first step, this function calculates the eigenvectors of the doubly centered spatial weights matrix. Each eigenvector represents a particular spatial pattern of the data points. In a second step, these eigenvectors are used one by one as additional predictor in the linear regression model and the eigenvector that produces the lowest Moran's *I* of the regression residuals is selected. This procedure is repeated until the remaining Moran's *I* value has a permutation-based probability value above a defined significance level $\alpha$ (here $\alpha = 0.05$). Afterwards, the effects of the fertility gradient and the disturbance gradient on the trait distribution statistics before and after accounting for SAC were compared using the Pearson correlation coefficient. Without accounting for SAC, the simple correlation coefficient was used. With accounting for SAC, the partial correlation coefficient was calculated using the selected spatial eigenvectors as covariables. The partial correlation coefficients were sometimes lower and less significant than the original coefficients (Tables A-IV – A-VII). In most cases, however, the partial correlation coefficients were even higher than the original ones. Changes in sign occurred only when the original correlation coefficient was small and not significant. Thus, accounting for SAC did not substantially alter the results or their interpretation.

**Table A-IV.** Effects of the fertility gradient (PC1) on trait distribution statistics as measured by Pearson's correlation coefficient (*r*) before (cf. Chapter 3: Table 2) and after accounting for spatial autocorrelation (SAC).

| Trait | Statistic | | Before accounting for SAC | | | | After accounting for SAC | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *r* | *P* | Moran's *I* | *P* | *r* | *P* | Moran's *I* | *P* |
| Competitive trait set | FD | | -0.04 | 0.633 | 0.17 | 0.001 | -0.06 | 0.448 | 0.03 | 0.139 |
| | *z*-score | | -0.27 | < 0.001 | 0.10 | 0.002 | -0.28 | < 0.001 | 0.03 | 0.141 |
| Canopy height | Mean | | 0.39 | < 0.001 | 0.10 | 0.001 | 0.46 | < 0.001 | 0.02 | 0.194 |
| | FD | | -0.49 | < 0.001 | 0.08 | 0.006 | -0.50 | < 0.001 | 0.04 | 0.053 |
| | *z*-score | | -0.41 | < 0.001 | 0.08 | 0.007 | -0.44 | < 0.001 | 0.03 | 0.111 |
| Lateral spread | Mean | | -0.12 | 0.128 | 0.12 | 0.001 | -0.11 | 0.141 | 0.03 | 0.120 |
| | FD | | 0.11 | 0.164 | 0.15 | 0.001 | 0.11 | 0.154 | 0.04 | 0.072 |
| | *z*-score | | -0.13 | 0.085 | 0.09 | 0.003 | -0.14 | 0.066 | 0.04 | 0.077 |
| Specific leaf area | Mean | | -0.40 | < 0.001 | 0.07 | 0.011 | -0.39 | < 0.001 | 0.02 | 0.189 |
| | FD | | -0.24 | 0.002 | 0.11 | 0.002 | -0.22 | 0.004 | 0.03 | 0.109 |
| | *z*-score | | -0.30 | < 0.001 | 0.12 | 0.001 | -0.29 | < 0.001 | 0.03 | 0.100 |
| Reproductive trait set | FD | | 0.12 | 0.122 | 0.28 | 0.001 | 0.17 | 0.026 | 0.03 | 0.105 |
| | *z*-score | | -0.05 | 0.513 | 0.29 | 0.001 | 0.00 | 0.995 | 0.03 | 0.124 |
| Onset of flowering | Mean | | 0.36 | < 0.001 | 0.13 | 0.001 | 0.45 | < 0.001 | 0.03 | 0.083 |
| | FD | | -0.01 | 0.896 | 0.00 | 0.390 | NA | NA | NA | NA |
| | *z*-score | | -0.04 | 0.561 | 0.01 | 0.258 | NA | NA | NA | NA |
| End of flowering | Mean | | 0.38 | < 0.001 | 0.18 | 0.001 | 0.51 | < 0.001 | 0.02 | 0.135 |
| | FD | | 0.30 | < 0.001 | 0.14 | 0.001 | 0.40 | < 0.001 | 0.01 | 0.213 |
| | *z*-score | | 0.05 | 0.551 | 0.11 | 0.001 | 0.07 | 0.392 | 0.02 | 0.133 |
| Pollination | Mean | Insects | 0.13 | 0.082 | 0.20 | 0.001 | 0.14 | 0.058 | 0.05 | 0.047 |
| | | Wind | -0.05 | 0.498 | 0.33 | 0.001 | 0.00 | 0.963 | 0.02 | 0.154 |
| | | Self | -0.08 | 0.285 | 0.11 | 0.001 | -0.13 | 0.093 | 0.02 | 0.178 |
| | FD | | 0.00 | 0.995 | 0.35 | 0.001 | -0.01 | 0.924 | 0.03 | 0.095 |
| | *z*-score | | -0.11 | 0.155 | 0.36 | 0.001 | -0.13 | 0.090 | 0.03 | 0.096 |
| Diaspore weight | Mean | | -0.42 | < 0.001 | 0.08 | 0.007 | -0.41 | < 0.001 | 0.05 | 0.049 |
| | FD | | 0.22 | 0.003 | 0.09 | 0.009 | 0.24 | 0.001 | 0.03 | 0.091 |
| | *z*-score | | 0.09 | 0.248 | 0.05 | 0.036 | 0.11 | 0.162 | 0.03 | 0.100 |
| Seed longevity | Mean | | 0.40 | < 0.001 | 0.11 | 0.002 | 0.45 | < 0.001 | 0.03 | 0.089 |
| | FD | | 0.41 | < 0.001 | 0.08 | 0.014 | 0.47 | < 0.001 | 0.03 | 0.084 |
| | *z*-score | | 0.27 | < 0.001 | 0.08 | 0.012 | 0.28 | < 0.001 | 0.04 | 0.077 |

**Table A-V.** Effects of the disturbance gradient (PC2) on trait distribution statistics as measured by Pearson's correlation coefficient (*r*) before (cf. Chapter 3: Table 3) and after accounting for spatial autocorrelation (SAC).

| Trait | Statistic | | Before accounting for SAC | | | | After accounting for SAC | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *r* | *P* | Moran's *I* | *P* | *r* | *P* | Moran's *I* | *P* |
| Competitive trait set | FD | | 0.10 | 0.175 | 0.16 | 0.001 | 0.10 | 0.198 | 0.02 | 0.190 |
| | *z*-score | | 0.05 | 0.484 | 0.08 | 0.009 | 0.03 | 0.673 | 0.02 | 0.192 |
| Canopy height | Mean | | 0.47 | < 0.001 | 0.02 | 0.172 | NA | NA | NA | NA |
| | FD | | -0.33 | < 0.001 | 0.00 | 0.305 | NA | NA | NA | NA |
| | *z*-score | | -0.36 | < 0.001 | 0.03 | 0.125 | NA | NA | NA | NA |
| Lateral spread | Mean | | 0.03 | 0.693 | 0.12 | 0.002 | -0.01 | 0.941 | 0.04 | 0.055 |
| | FD | | 0.19 | 0.013 | 0.14 | 0.001 | 0.19 | 0.013 | 0.03 | 0.123 |
| | *z*-score | | 0.14 | 0.059 | 0.08 | 0.006 | 0.13 | 0.096 | 0.04 | 0.064 |
| Specific leaf area | Mean | | -0.14 | 0.064 | 0.07 | 0.008 | -0.15 | 0.055 | 0.01 | 0.276 |
| | FD | | 0.22 | 0.004 | 0.11 | 0.004 | 0.23 | 0.003 | 0.01 | 0.224 |
| | *z*-score | | 0.19 | 0.010 | 0.11 | 0.001 | 0.20 | 0.007 | 0.01 | 0.257 |
| Reproductive trait set | FD | | 0.43 | < 0.001 | 0.29 | 0.001 | 0.47 | < 0.001 | 0.03 | 0.117 |
| | *z*-score | | 0.39 | < 0.001 | 0.31 | 0.001 | 0.44 | < 0.001 | 0.03 | 0.112 |
| Onset of flowering | Mean | | 0.49 | < 0.001 | 0.05 | 0.027 | 0.50 | < 0.001 | 0.03 | 0.147 |
| | FD | | -0.24 | 0.001 | 0.00 | 0.352 | NA | NA | NA | NA |
| | *z*-score | | -0.23 | 0.002 | 0.02 | 0.206 | NA | NA | NA | NA |
| End of flowering | Mean | | 0.41 | < 0.001 | 0.12 | 0.001 | 0.43 | < 0.001 | 0.04 | 0.086 |
| | FD | | 0.15 | 0.043 | 0.09 | 0.005 | 0.10 | 0.175 | 0.02 | 0.157 |
| | *z*-score | | 0.05 | 0.538 | 0.10 | 0.001 | 0.01 | 0.892 | 0.02 | 0.164 |
| Pollination | Mean | Insects | -0.36 | < 0.001 | 0.21 | 0.001 | -0.38 | < 0.001 | 0.04 | 0.072 |
| | | Wind | 0.30 | < 0.001 | 0.34 | 0.001 | 0.30 | < 0.001 | 0.02 | 0.169 |
| | | Self | 0.14 | 0.068 | 0.10 | 0.004 | 0.10 | 0.209 | 0.02 | 0.132 |
| | FD | | 0.36 | < 0.001 | 0.38 | 0.001 | 0.39 | < 0.001 | 0.02 | 0.189 |
| | *z*-score | | 0.33 | < 0.001 | 0.37 | 0.001 | 0.36 | < 0.001 | 0.01 | 0.245 |
| Diaspore weight | Mean | | -0.31 | < 0.001 | 0.08 | 0.004 | -0.32 | < 0.001 | 0.03 | 0.128 |
| | FD | | 0.15 | 0.042 | 0.09 | 0.008 | 0.16 | 0.041 | 0.03 | 0.120 |
| | *z*-score | | 0.09 | 0.219 | 0.05 | 0.034 | 0.11 | 0.157 | 0.03 | 0.114 |
| Seed longevity | Mean | | 0.39 | < 0.001 | 0.05 | 0.028 | 0.40 | < 0.001 | 0.00 | 0.300 |
| | FD | | 0.34 | < 0.001 | 0.03 | 0.094 | NA | NA | NA | NA |
| | *z*-score | | 0.36 | < 0.001 | 0.04 | 0.068 | NA | NA | NA | NA |

**Table A-VI.** Effects of the fertility gradient (PC1) on the differences in trait distribution statistics between the sampling periods as measured by Pearson's correlation coefficient (*r*) before (cf. Chapter 3: Appendix 1) and after accounting for spatial autocorrelation (SAC).

| Trait | Statistic | | Before accounting for SAC | | | | After accounting for SAC | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *r* | *P* | Moran's *I* | *P* | *r* | *P* | Moran's *I* | *P* |
| Competitive trait set | FD | | 0.07 | 0.337 | 0.03 | 0.104 | NA | NA | NA | NA |
| | *z*-score | | -0.03 | 0.728 | -0.01 | 0.444 | NA | NA | NA | NA |
| Canopy height | Mean | | -0.15 | 0.051 | 0.10 | 0.005 | -0.11 | 0.157 | 0.03 | 0.094 |
| | FD | | 0.09 | 0.262 | 0.07 | 0.020 | 0.06 | 0.453 | 0.04 | 0.058 |
| | *z*-score | | 0.09 | 0.214 | 0.07 | 0.009 | 0.06 | 0.411 | 0.04 | 0.084 |
| Lateral spread | Mean | | -0.01 | 0.903 | 0.04 | 0.065 | NA | NA | NA | NA |
| | FD | | 0.06 | 0.456 | 0.05 | 0.040 | 0.05 | 0.492 | 0.01 | 0.282 |
| | *z*-score | | -0.05 | 0.527 | 0.01 | 0.210 | NA | NA | NA | NA |
| Specific leaf area | Mean | | 0.04 | 0.608 | -0.02 | 0.609 | NA | NA | NA | NA |
| | FD | | 0.00 | 0.983 | 0.06 | 0.014 | 0.01 | 0.859 | 0.00 | 0.382 |
| | *z*-score | | -0.03 | 0.705 | 0.06 | 0.030 | -0.02 | 0.808 | -0.01 | 0.481 |
| Reproductive trait set | FD | | -0.08 | 0.273 | 0.05 | 0.030 | -0.08 | 0.303 | 0.03 | 0.108 |
| | *z*-score | | -0.12 | 0.122 | 0.08 | 0.006 | -0.11 | 0.154 | 0.01 | 0.296 |
| Onset of flowering | Mean | | -0.08 | 0.268 | 0.13 | 0.002 | -0.09 | 0.259 | 0.02 | 0.170 |
| | FD | | 0.16 | 0.035 | 0.07 | 0.011 | 0.18 | 0.020 | 0.01 | 0.271 |
| | *z*-score | | 0.19 | 0.010 | 0.06 | 0.016 | 0.21 | 0.005 | 0.00 | 0.427 |
| End of flowering | Mean | | -0.04 | 0.621 | 0.17 | 0.001 | -0.04 | 0.617 | 0.03 | 0.103 |
| | FD | | 0.07 | 0.362 | 0.17 | 0.001 | 0.07 | 0.333 | 0.03 | 0.098 |
| | *z*-score | | 0.06 | 0.417 | 0.08 | 0.005 | 0.08 | 0.289 | 0.01 | 0.309 |
| Pollination | Mean | Insects | 0.17 | 0.026 | 0.03 | 0.092 | NA | NA | NA | NA |
| | | Wind | -0.22 | 0.004 | 0.15 | 0.002 | -0.22 | 0.004 | 0.02 | 0.159 |
| | | Self | 0.12 | 0.116 | 0.06 | 0.024 | 0.12 | 0.127 | 0.03 | 0.126 |
| | FD | | -0.14 | 0.067 | 0.06 | 0.028 | -0.14 | 0.073 | 0.03 | 0.096 |
| | *z*-score | | -0.16 | 0.038 | 0.09 | 0.007 | -0.15 | 0.042 | 0.05 | 0.042 |
| Diaspore weight | Mean | | -0.08 | 0.272 | 0.05 | 0.025 | -0.09 | 0.244 | 0.04 | 0.080 |
| | FD | | 0.08 | 0.305 | 0.03 | 0.113 | NA | NA | NA | NA |
| | *z*-score | | 0.05 | 0.517 | -0.01 | 0.501 | NA | NA | NA | NA |
| Seed longevity | Mean | | 0.02 | 0.794 | 0.06 | 0.023 | 0.03 | 0.694 | -0.01 | 0.490 |
| | FD | | 0.01 | 0.947 | 0.05 | 0.045 | 0.01 | 0.854 | -0.01 | 0.453 |
| | *z*-score | | -0.05 | 0.481 | 0.04 | 0.085 | NA | NA | NA | NA |

**Table A-VII.** Effects of the disturbance gradient (PC2) on the differences in trait distribution statistics between the sampling periods as measured by Pearson's correlation coefficient (*r*) before (cf. Chapter 3: Table 4) and after accounting for spatial autocorrelation (SAC).

| Trait | Statistic | | Before accounting for SAC | | | | After accounting for SAC | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *r* | *P* | Moran's *I* | *P* | *r* | *P* | Moran's *I* | *P* |
| Competitive trait set | FD | | 0.03 | 0.676 | 0.03 | 0.142 | NA | NA | NA | NA |
| | *z*-score | | -0.01 | 0.845 | -0.01 | 0.479 | NA | NA | NA | NA |
| Canopy height | Mean | | 0.48 | < 0.001 | 0.08 | 0.007 | 0.47 | < 0.001 | 0.05 | 0.045 |
| | FD | | -0.26 | 0.001 | 0.08 | 0.007 | -0.29 | < 0.001 | 0.02 | 0.133 |
| | *z*-score | | -0.28 | < 0.001 | 0.09 | 0.005 | -0.32 | < 0.001 | 0.03 | 0.096 |
| Lateral spread | Mean | | 0.03 | 0.732 | 0.04 | 0.063 | NA | NA | NA | NA |
| | FD | | 0.10 | 0.182 | 0.03 | 0.110 | NA | NA | NA | NA |
| | *z*-score | | 0.05 | 0.474 | 0.01 | 0.240 | NA | NA | NA | NA |
| Specific leaf area | Mean | | -0.18 | 0.019 | -0.02 | 0.657 | NA | NA | NA | NA |
| | FD | | 0.14 | 0.064 | 0.06 | 0.026 | 0.15 | 0.053 | -0.01 | 0.483 |
| | *z*-score | | 0.10 | 0.167 | 0.05 | 0.030 | 0.11 | 0.150 | -0.01 | 0.578 |
| Reproductive trait set | FD | | 0.38 | < 0.001 | 0.02 | 0.203 | NA | NA | NA | NA |
| | *z*-score | | 0.37 | < 0.001 | 0.05 | 0.036 | 0.39 | < 0.001 | 0.01 | 0.174 |
| Onset of flowering | Mean | | 0.45 | < 0.001 | 0.08 | 0.005 | 0.44 | < 0.001 | 0.04 | 0.083 |
| | FD | | -0.14 | 0.072 | 0.07 | 0.009 | -0.17 | 0.026 | 0.02 | 0.196 |
| | *z*-score | | -0.12 | 0.105 | 0.06 | 0.011 | -0.16 | 0.040 | 0.00 | 0.347 |
| End of flowering | Mean | | 0.33 | < 0.001 | 0.14 | 0.001 | 0.30 | < 0.001 | 0.02 | 0.167 |
| | FD | | 0.10 | 0.201 | 0.15 | 0.001 | 0.05 | 0.487 | 0.03 | 0.096 |
| | *z*-score | | 0.03 | 0.718 | 0.08 | 0.008 | -0.01 | 0.923 | 0.01 | 0.306 |
| Pollination | Mean | Insects | -0.28 | < 0.001 | 0.03 | 0.133 | NA | NA | NA | NA |
| | | Wind | 0.36 | < 0.001 | 0.13 | 0.001 | 0.40 | < 0.001 | 0.04 | 0.093 |
| | | Self | -0.08 | 0.316 | 0.07 | 0.011 | -0.09 | 0.218 | 0.03 | 0.089 |
| | FD | | 0.34 | < 0.001 | 0.03 | 0.109 | NA | NA | NA | NA |
| | *z*-score | | 0.32 | < 0.001 | 0.07 | 0.013 | 0.34 | < 0.001 | 0.02 | 0.183 |
| Diaspore weight | Mean | | -0.37 | < 0.001 | 0.03 | 0.123 | NA | NA | NA | NA |
| | FD | | 0.23 | 0.002 | 0.01 | 0.270 | NA | NA | NA | NA |
| | *z*-score | | 0.17 | 0.024 | -0.02 | 0.698 | NA | NA | NA | NA |
| Seed longevity | Mean | | 0.31 | < 0.001 | 0.05 | 0.052 | NA | NA | NA | NA |
| | FD | | 0.30 | < 0.001 | 0.03 | 0.112 | NA | NA | NA | NA |
| | *z*-score | | 0.27 | < 0.001 | 0.02 | 0.146 | NA | NA | NA | NA |

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# Appendix III

## Mean abundance change and frequencies of winner and loser species

The table equals Table S1 in Chapter 4, but species’ frequencies were added.

| | Abundance | | Change in abundance | $P$ [a] | Frequency | |
|---|---|---|---|---|---|---|
| | 1988 | 2008 | | | 1988 | 2008 |
| Winner species: | | | | | | |
| *Agrostis capillaris* | 0.7 | 3.5 | 2.8 | 0.001 | 3 | 19 |
| *Cardamine flexuosa* | 1.1 | 1.7 | 0.7 | 0.002 | 24 | 50 |
| *Carex remota* | 1.6 | 2.8 | 1.2 | < 0.001 | 60 | 93 |
| *Carex sylvatica* | 2.6 | 3.5 | 0.8 | < 0.001 | 91 | 115 |
| *Chrysosplenium oppositifolium* | 0.6 | 3.2 | 2.6 | < 0.001 | 1 | 5 |
| *Corylus avellana* | 1.3 | 1.8 | 0.5 | 0.001 | 66 | 99 |
| *Crataegus laevigata* s.l. | 1.2 | 1.5 | 0.3 | 0.008 | 80 | 117 |
| *Dryopteris carthusiana* | 0.5 | 1.6 | 1.2 | < 0.001 | 8 | 31 |
| *Dryopteris dilatata* | 0.8 | 1.5 | 0.7 | < 0.001 | 36 | 78 |
| *Frangula alnus* | 0.0 | 1.4 | 1.4 | < 0.001 | 0 | 8 |
| *Galium aparine* | 1.9 | 2.3 | 0.3 | 0.046 | 52 | 69 |
| *Glechoma hederacea* | 2.0 | 3.3 | 1.3 | < 0.001 | 42 | 60 |
| *Hedera helix* | 1.5 | 2.9 | 1.4 | < 0.001 | 104 | 151 |
| *Holcus lanatus* | 0.3 | 2.7 | 2.4 | 0.010 | 1 | 9 |
| *Holcus mollis* | 0.0 | 2.9 | 2.9 | < 0.001 | 0 | 7 |
| *Hypericum maculatum* s.l. | 0.0 | 1.6 | 1.6 | < 0.001 | 0 | 5 |
| *Ilex aquifolium* | 0.8 | 1.9 | 1.2 | < 0.001 | 21 | 52 |
| *Impatiens parviflora* | 0.3 | 3.0 | 2.7 | < 0.001 | 2 | 19 |
| *Juncus effusus* | 0.6 | 1.8 | 1.2 | < 0.001 | 14 | 42 |
| *Lonicera periclymenum* | 1.8 | 2.1 | 0.3 | 0.015 | 73 | 83 |
| *Luzula pilosa* | 1.3 | 1.9 | 0.6 | 0.039 | 19 | 23 |
| *Lythrum salicaria* | 0.0 | 1.4 | 1.4 | < 0.001 | 0 | 7 |
| *Prunus serotina* | 0.0 | 1.4 | 1.4 | < 0.001 | 0 | 9 |
| *Ribes rubrum* | 0.8 | 1.8 | 1.0 | < 0.001 | 10 | 25 |
| *Rubus fruticosus* agg. | 1.5 | 2.1 | 0.6 | 0.003 | 72 | 93 |
| *Rumex sanguineus* | 0.6 | 1.5 | 0.9 | 0.002 | 6 | 22 |
| *Sambucus nigra* | 0.5 | 1.4 | 0.9 | < 0.001 | 8 | 28 |
| *Scutellaria galericulata* | 0.8 | 1.9 | 1.1 | 0.008 | 7 | 21 |
| *Sorbus aucuparia* | 1.0 | 1.1 | 0.2 | 0.036 | 58 | 76 |
| *Taraxacum* sect. *Ruderalia* | 0.6 | 1.1 | 0.5 | 0.001 | 22 | 43 |
| *Veronica montana* | 2.1 | 3.4 | 1.3 | < 0.001 | 45 | 76 |
| Loser species: | | | | | | |
| *Adoxa moschatellina* | 3.5 | 2.8 | -0.7 | < 0.001 | 118 | 115 |
| *Anemone nemorosa* | 6.9 | 5.9 | -1.1 | < 0.001 | 168 | 173 |
| *Angelica sylvestris* | 1.8 | 0.2 | -1.6 | < 0.001 | 20 | 2 |
| *Brachypodium sylvaticum* | 2.9 | 2.0 | -0.9 | < 0.001 | 59 | 65 |
| *Circaea lutetiana* | 3.6 | 3.4 | -0.2 | 0.027 | 140 | 145 |
| *Crepis paludosa* | 3.2 | 2.2 | -0.9 | < 0.001 | 116 | 96 |
| *Equisetum arvense* | 1.6 | 1.4 | -0.3 | 0.049 | 35 | 29 |
| *Equisetum hyemale* | 3.0 | 2.3 | -0.7 | 0.015 | 20 | 15 |
| *Equisetum sylvaticum* | 2.3 | 1.6 | -0.7 | 0.018 | 19 | 13 |
| *Festuca gigantea* | 2.4 | 1.1 | -1.3 | < 0.001 | 85 | 66 |
| *Filipendula ulmaria* | 2.7 | 2.1 | -0.6 | < 0.001 | 85 | 70 |
| *Galium odoratum* | 5.1 | 3.7 | -1.5 | < 0.001 | 97 | 91 |
| *Geum rivale* | 3.2 | 2.4 | -0.7 | < 0.001 | 46 | 40 |
| *Hepatica nobilis* | 2.9 | 2.2 | -0.7 | 0.010 | 19 | 16 |
| *Impatiens noli-tangere* | 3.3 | 1.7 | -1.6 | < 0.001 | 53 | 40 |
| *Lamium galeobdolon* s.str. | 4.9 | 4.5 | -0.4 | 0.007 | 137 | 148 |
| *Lysimachia vulgaris* | 2.0 | 0.9 | -1.1 | 0.001 | 28 | 17 |
| *Mercurialis perennis* | 7.3 | 5.6 | -1.7 | < 0.001 | 56 | 55 |
| *Milium effusum* | 3.5 | 3.3 | -0.2 | < 0.001 | 132 | 141 |
| *Mycelis muralis* | 1.7 | 0.5 | -1.2 | 0.019 | 11 | 5 |
| *Myosotis scorpioides* agg. | 3.2 | 0.6 | -2.5 | < 0.001 | 11 | 3 |
| *Oxalis acetosella* | 4.7 | 3.4 | -1.3 | < 0.001 | 148 | 150 |
| *Paris quadrifolia* | 3.1 | 2.8 | -0.3 | 0.021 | 54 | 49 |
| *Phyteuma nigrum* | 2.6 | 1.9 | -0.7 | 0.032 | 16 | 13 |
| *Pulmonaria obscura* | 3.5 | 2.3 | -1.2 | < 0.001 | 28 | 23 |
| *Ranunculus auricomus* agg. | 2.8 | 2.6 | -0.3 | 0.004 | 120 | 121 |
| *Ranunculus ficaria* | 5.8 | 5.4 | -0.4 | < 0.001 | 154 | 168 |
| *Sanicula europaea* | 3.1 | 2.2 | -1.0 | < 0.001 | 79 | 69 |
| *Stachys sylvatica* | 2.9 | 2.5 | -0.4 | < 0.001 | 120 | 123 |
| *Valeriana officinalis* agg. | 2.5 | 1.2 | -1.3 | 0.004 | 17 | 11 |

[a] Fisher’s sign test

# Declaration

All chapters of this thesis were written by myself and are based on my own research. The four main chapters, that have been published or have been submitted for publication in international, peer-reviewed journals, were co-authored by Prof. Dr. Monika Wulf. Her contributions were stated in the General Introduction (p. 6). Any research not carried out by myself or M. Wulf is fully acknowledged in the text. The two chapters that are already published (Chapter 1) or accepted for publication (Chapter 4) were improved following the comments of the referees and editors.

# Erklärung

Die geltende Promotionsordnung der Mathematisch-Naturwissenschaftlichen
Fakultät der Universität Potsdam ist mir bekannt.

Die vorliegende Dissertation habe ich selbständig angefertigt und hierbei
alle verwendeten Hilfsmittel und Quellen angegeben.

Ich habe weder die vorliegende Arbeit noch eine in wesentlichen Teilen ähnliche Abhandlung bei einer anderen Hochschule als Dissertation eingereicht.

Potsdam, den 19. Januar 2011

Tobias Naaf

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