



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

Tobias Naaf*, Monika Wulf

Leibniz-Centre for Agricultural Landscape Research (ZALF e. V.), Institute of Land Use Systems, Eberswalder Straße 84, D-15374 Müncheberg, Germany

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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.

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1. Introduction

A gradual increase in compositional similarity among formerly distinct biological communities is called biotic homogenization (Olden and Rooney, 2006). This process has received much attention during the last decade (McKinney and Lockwood, 1999; Olden and Rooney, 2006). Biotic homogenization has been observed across an array of different taxonomic groups and at various spatial scales (Lockwood and 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; McKinney, 2004; Schwartz et al., 2006; Castro et al., 2007; Qian et al., 2008). 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 (Rooney et al., 2004; Smart et al., 2006; Rogers et al., 2008). Such studies are most relevant for con-

servation goals because conservation planning is often implemented at that scale (Margules and Pressey, 2000; Ferrier, 2002). 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 and Rooney, 2006). In the present study, we were able to use a broad historical dataset from 1986 to 1988 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 and Lockwood, 1999; Olden and Poff, 2003). For instance, studies on the impact of atmospheric depositions and forest management on herb layer vegetation observed an increase in

* Corresponding author. Tel.: +49 33432 82114; fax: +49 33432 82387.

E-mail addresses: naaf@zalf.de (T. Naaf), mwulf@zalf.de (M. Wulf).

‘weedy’ species, including ruderal, nitrophilous or non-forest species (Thimonier et al., 1992; Falkengren-Grerup, 1995; van Calster et al., 2007). Others found a loss of specialized forest herbs that require high pH (Falkengren-Grerup and Tyler, 1991; Tyler et al., 2002; Hédli, 2004). 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., Smart et al., 2006; Jurasinski and Kreyling, 2007) 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 and Rooney, 2006). Beta diversity is most often quantified with similarity or dissimilarity metrics (Jurasinski et al., 2009) and among the many available metrics (Wolda, 1981; Koleff et al., 2003), Jaccard’s index (Table 1) has been the most frequently used in studies on biotic homogenization (Olden and 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 and 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 and 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.

The main objectives of this study were: (i) to quantify the degree of homogenization or differentiation of forest plant communi-

ties 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.

2. Methods

2.1. 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 7600 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).

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 and 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 1–2 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 sev-

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 and Curtis (1957)	$BC = \frac{\sum x_{ij} - x_{ik} }{\sum (x_{ij} + x_{ik})}$	x_{ij} and x_{ik} are the abundances of species i at sites j and k , respectively

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