



Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany

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ABSTRACT

Aim The aim of our study was to reveal relationships between richness patterns of native vs. alien plant species and spatial heterogeneity across varying landscape patterns at a regional scale.

Location The study was carried out in the administrative district of Dessau (Germany), covering around 4000 km².

Methods Data on plant distribution of the German vascular flora available in grid cells covering 5' longitude and 3' latitude (c. 32 km²) were divided into three status groups: native plants, archaeophytes (pre 1500 AD aliens) and neophytes (post 1500 AD aliens). Land use and abiotic data layers were intersected with 125 grid cells comprising the selected area. Using novel landscape ecological methods, we calculated 38 indices of landscape composition and configuration for each grid cell. Principal components analysis (PCA) with a set of 29 selected, low correlated landscape indices was followed by multiple linear regression analysis.

Results PCA reduced 29 indices to eight principal components (PCs) that explained 80% cumulative variance. Multiple linear regression analysis was highly significant and explained 41% to 60% variance in plant species distribution (adjusted

R²) with three significant PCs (tested for spatial autocorrelation) expressing moderate to high disturbance levels and high spatial heterogeneity. Comparing the significance of the PCs for the species groups, native plant species richness is most strongly associated with riverine ecosystems, followed by urban ecosystems, and then small-scale rural ecosystems. Archaeophyte and neophyte richness are most strongly associated with urban ecosystems, followed by small-scale rural ecosystems and riverine ecosystems for archaeophytes, and riverine ecosystems and small-scale rural ecosystems for neophytes.

Main conclusions Our overall results suggest that species richness of native and alien plants increases with moderate levels of natural and/or anthropogenic disturbances, coupled with high levels of habitat and structural heterogeneity in urban, riverine, and small-scale rural ecosystems. Despite differences in the order of relevance of PCs for the three plant groups, we conclude that at the regional scale species richness patterns of native plants as well as alien plants are promoted by similar factors.

Key words Alien plants, Central Europe, disturbance, landscape indices, native plants, plant species richness patterns, regional scale, spatial autocorrelation, spatial heterogeneity, species-environment relationships.

INTRODUCTION

A growing number of ecological studies have focused on invasive processes in order to predict further invasions and associated potentially negative effects. The introduction of alien plants or plant species new to an area due to human activity (definition following Richardson *et al.*, 2000) and their spread and

establishment is thought to cause a decline in the diversity of native species (Williamson, 1999). Furthermore, it is expected that invasive processes increase due to global climate changes (di Castri, 1990; Sukopp, 1998; Dukes & Mooney, 1999; Pyšek *et al.*, 2002a), fragmentation of natural ecosystems (Rejmánek, 1996; Faliński, 1998; Alpert *et al.*, 2000), and growing urbanization (Klotz, 1990; Sukopp, 1998; McKinney, 2002). Most studies investigate two main questions: what are the important ecosystem properties and/or what are the main plant characteristics that facilitate the establishment of alien species? (e.g. Ashton & Mitchell, 1989; Rejmánek, 1989; Faliński,

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1998; Sukopp, 1998; Alpert *et al.*, 2000). Studies focusing on ecosystem properties have examined different spatial scales and different geographical regions as for instance: global scales (Lonsdale, 1999), continental scales in tropical regions (Rejmánek, 1996), nationwide scales in Europe and North America (Kornaš, 1990; Pyšek *et al.*, 1998; Ernst *et al.*, 2000; McKinney, 2002), regional scales in Europe and Africa (Faliński, 1998; Stadler *et al.*, 2000), local scales in Australia, Europe and North America (McIntyre *et al.*, 1988; McIntyre & Lavorel, 1994; Hoffmann, 1998; Stohlgren *et al.*, 1999), or across a range of scales in Europe, North and South America (Planty-Tabacchi *et al.*, 1996; Sax, 2002). Despite a growing number of studies, few general answers have been found. Scale dependence of ecological systems and the variety of ecosystems studied might be two reasons for divergent results.

Most studies revealed that ecosystems with anthropogenic disturbances, such as cities or densely populated areas, contain high numbers of alien species (di Castri, 1989; Kornaš, 1990; McIntyre & Lavorel, 1994; Faliński, 1998; Pyšek *et al.*, 1998; Sukopp, 1998; McKinney, 2002), whereas natural or near-natural ecosystems (like natural forests or bogs) display a certain ecological resistance against the introduction of alien species (Elton, 1958; McIntyre *et al.*, 1988; Rejmánek, 1989; Faliński, 1998). Some studies on local scales show that high species richness of alien plants is coupled with low species richness of native plants in man-dominated habitats and with high richness in natural habitats (McIntyre *et al.*, 1988; McIntyre & Lavorel, 1994; Hoffmann, 1998). Levine (2000) concluded that at neighbourhood scales (species interaction scale level) native plant diversity increases community resistance against invading non-native species, at least as long as disturbance levels are low (Cornell & Karlson, 1997). But this pattern is not repeated at coarser scales, where several authors found high species richness of native and alien plants in ecosystems with moderate anthropogenic or natural disturbances (Planty-Tabacchi *et al.*, 1996; Lonsdale, 1999; Ernst *et al.*, 2000; Levine, 2000; Stadler *et al.*, 2000; McKinney, 2002; Sax, 2002). Positive relationships between richness of native and alien plant species were also reported for ecosystems obtaining highest anthropogenic disturbance levels, such as intensively managed agro-ecosystems, which were poor in both native and alien plants (Ernst *et al.*, 2000; Stadler *et al.*, 2000). One possible conclusion is that neighbourhood scales display species interactions, whilst at coarser scales (ranging from local to global) ecosystem determinants like habitat diversity, disturbance levels, or resource heterogeneity, control native as well as alien species richness in a similar way (Sukopp, 1998; Stohlgren *et al.*, 1999; Levine, 2000; Kennedy *et al.*, 2002). But whether these positive relationships between native and alien species richness can be generalized across various environments, still needs to be determined (Sax, 2002).

We conducted a study at a regional scale (a region being an area with similar natural and land use history) and observed

species richness patterns of three plant groups (native plants and two alien plant groups: archaeophytes and neophytes) and their relation to landscape characteristics using landscape indices in the administrative district of Dessau, Germany. We focused on the following questions:

- What is the relationship between richness of native and alien plant species in the Dessau region?
- What are the main landscape characteristics controlling species richness of alien plants (archaeophytes, neophytes) compared to native plants at the regional scale in such a Central European, man-dominated landscape?

MATERIALS AND METHODS

Study area

The study area covers *c.* 4000 km² and is located in the east of Germany (state of Sachsen-Anhalt, administrative district of Dessau). This region was formed during the last Ice Age and therefore contains typical geomorphologic features, such as glacial valleys with sandy soil and alluvial clay, end moraines with morainic till, dunes with nutrient poor sand, and periglacial areas with nutrient rich loess deposits (Schröder, 2000). Relief and climatic gradients are low, with elevation ranging from 49 m in the lowlands around Dessau to 187 m in southern (Dübener Heide) and northern (Fläming) parts of the Dessau district, and mean annual precipitation values between 450 mm in loess areas to the south-west of Dessau and 670 mm in Fläming and Dübener Heide. Three main rivers flow through the study area: Elbe, Saale and Mulde.

Geodiversity in the studied area is coupled with a high habitat and land use diversity, even if intensive agriculture and forestry are the main land uses (Fig. 1, 46% fields, 19% coniferous forests, 9% grassland, 5% mixed forests represent the main land uses in the Dessau district). Structuring elements in the study area are relicts of seminatural riparian forests, extensive grasslands, scrub, groves, bogs, lakes, lowland rivers, rural areas, parks and gardens in urban areas, open-cast mines and linear elements, such as hedgerows and tree rows. The main cities are Dessau and Lutherstadt Wittenberg (*c.* 85 000 and 50 000 inhabitants). These varying landscape and land use characteristics seemed to be ideal prerequisites for plant richness studies.

Plant data

Plant presence/absence data were made available from a floristic survey throughout Germany performed over the past 20 years (Benkert *et al.*, 1996). It was presented in database format by the State Agency for the Environment Sachsen-Anhalt (Landesamt für Umweltschutz Sachsen-Anhalt, 1998). For the studied area, plants were recorded in grid cells covering 5' longitude and 3' latitude, which equals about 5.7 ×

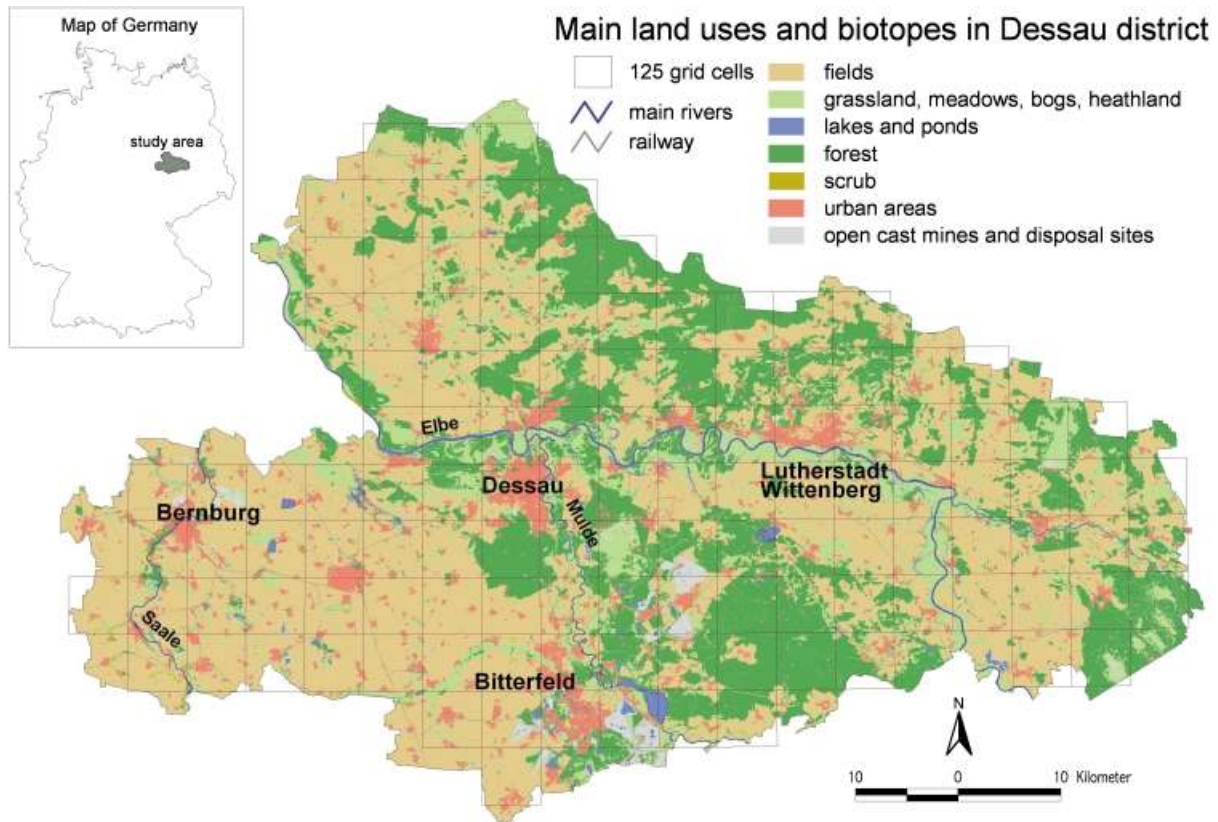


Fig. 1 Study area (approx. 4000 km²), 125 grid cells used in the analysis and main land use types in the administrative district of Dessau, state of Sachsen-Anhalt, Germany.

5.5 km or 32 km². Altogether, the study area contains 125 grid cells. Cells adjacent to the district border, with less than 75% area belonging to the Dessau district, were excluded from the study. Plants were aggregated in three status groups based on their time of arrival in Germany (Schroeder, 1969): native plants, archaeophytes (plants that reached the area before 1500 AD) and neophytes (plants that arrived since 1500 AD). The floristic survey included naturalized alien species (establishing sustainable populations, Richardson *et al.*, 2000) as well as casuals (no self-replacing populations, relying on repeated human induced introduction, Richardson *et al.*, 2000) being frequently introduced (repeated introductions every year). We did not distinguish between invasive and noninvasive plants, as a precise and unequivocal classification is not available for Germany at present, compared to other Central European studies (as in the Czech Republic; Pyšek *et al.*, 2002b).

Landscape indices

In recent years, landscape ecologists have focused on developing landscape indices to quantify spatial heterogeneity

and ecosystem patterns (O'Neill *et al.*, 1988; McGarigal & Marks, 1994). Following Gustafson (1998), spatial heterogeneity is characterized by composition, configuration, and temporal aspects of various system properties, such as abiotic conditions and landscape structure. As ecological processes are strongly related to spatial pattern, the number of ecological studies using landscape indices is growing (McGarigal & McComb, 1995; Miller *et al.*, 1997; Wagner *et al.*, 2000).

To quantify spatial heterogeneity, we combined a set of abiotic indices with a set of landscape composition and configuration indices derived from land use data. Climatic, relief, soil, ground water, and land use data layers in digital raster or vector format were intersected with the 125 grid cells of the study area, using techniques available in geographical information systems (GIS). From climatic data we used annual rainfall (1 km² grid scale, from 'Deutscher Wetterdienst') to calculate mean annual rainfall per grid cell. Mean elevation and elevation range (characterizing relief energy) per grid cell were calculated from a digital elevation model of the Dessau district (250 m² grid scale, Volk & Bannholzer, 1999). A digital soil map (captured from soil maps at a

scale of 1 : 200 000, Volk & Bannholzer, 1999) provided data on soil substrates (54 classes), main soil units (5 classes) and ground water levels (3 classes). We used soil substrates to calculate substrate diversity per grid cell, main soil units to calculate percentage area of sandy soils per grid cell and ground water levels to calculate percentage area of ground water level > 2 meters.

Land cover data were available from an aerial photo survey, carried out in Sachsen-Anhalt at a scale of 1 : 10 000 (Peterson & Langner, 1992). With a selection of 47 land use and habitat classes, we calculated indices of landscape composition (e.g. area per class type) and configuration (e.g. number, size and edge density of patches, where patches are defined as the basic units in a landscape according to McGarigal & Marks, 1994) for each grid cell. The calculation was carried out at the class level (considering patches per land use class) as well as the landscape level (indices combining patches of all classes per grid cell) using 'FRAGSTATS — Spatial pattern analysis program for quantifying landscape structure' (Version 2.0, McGarigal & Marks, 1994). We omitted calculations at the patch level (indices for each habitat patch), which has been shown to be more appropriate for studies on animal population dynamics (Wiens *et al.*, 1993). The landscape indices finally selected are shown in Table 1.

Pearson correlation

After normalizing skewed data, we used Pearson correlation to analyse the relationship between native and alien plant species richness. Testing the resulting correlation coefficients for significant differences was done with a *t*-test following Röhr *et al.* (1983). We used sequential Bonferroni testing to minimize the probability of type-I error (Rice, 1989). We used Pearson correlation to find out highly correlated and thus redundant landscape indices. This method is recommended for landscape analysis mainly because landscape configuration indices tend to correlate with landscape composition indices (O'Neill *et al.*, 1988; Riitters *et al.*, 1995; Gustafson, 1998). The threshold value for deciding on redundancy was set to a correlation coefficient of 0.8. Out of every highly correlated pair, one variable was retained for further analysis, following Riitters *et al.* (1995). The selection was somewhat arbitrary, but indices at the class level were preferred due to more straightforward interpretation compared to indices combining all classes at the landscape level.

Principal components analysis

Principal components analysis (PCA) with standardized Varimax-Rotation was used to reduce the number of landscape

Table 1 Overview on finally used landscape indices calculated at different scale levels (landscape or class) with FRAGSTATS (McGarigal & Marks, 1994) and patch types used at the class level

Abbreviation	Indices	Description	Unit	Scale level and patch types
Indices of landscape composition				
SIDI	Simpson's diversity index	Land use diversity considering amount and distribution of patches	None	Landscape level
PR	Patch richness	Number of patch types present per grid cell	No.	Landscape level
%LAND	Percent landcover	Percent landcover area of each patch type per grid cell	%	Class level: urban area, green area, fields, traffic patches, open-cast mines and disposal sites, grassland, scrub, groves, coniferous forest, riparian forest, rivers > 5 m, sandy soils, ground water > 2 m
Indices of landscape configuration				
MPS	Mean patch size	Mean patch size per class	ha	Class level: urban area, green area, fields
PD	Patch density	Number of patches per 100 ha	No./100 ha	Class level: vegetation of perennial herbs, urban areas, fields, short-grass meadow, heathland, bogs
ED	Edge density	Edge density of patches per 100 ha	m/ha	Landscape level; Class level: roads, railroad, vegetation of perennial herbs, ponds (< 1 ha); lakes (> 1 ha)
MPI	Mean proximity index	Neighbourhood index measuring the degree of connectivity between patches	None	Class level: deciduous forest, total forest area

indices and to minimize correlation effects between indices during multiple regression analysis. Principal components with eigenvalues greater than 0.8 were retained for further analysis. Interpretation of principal component axes was done by observing the common characteristics of landscape indices with high loadings per principal component.

Multiple linear regression

Multiple linear regression analysis was performed using plant species numbers of native plants, archaeophytes and neophytes, respectively, as dependent variables and PCA scores as independent variables. Variance in plant distribution was obtained from adjusted R^2 values, correcting for number of regressors and degrees of freedom. The significance of each principal component regarding plant species richness was determined from the standardized partial regression coefficient BETA.

As plant distribution patterns are likely to be influenced by spatial autocorrelation, neighbouring grid cells usually have a higher probability of being similar to each other than grid cells further apart (Fortin *et al.*, 1989; Stohlgren *et al.*, 1999). Therefore, data points are not independent and this contradicts basic presumptions of statistical tests. Testing significance without taking spatial autocorrelation into account usually results in overestimating the degrees of freedom (Legendre & Fortin, 1989). We used the modified t -test of Dutilleul (1993; Legendre, 2000) that takes spatial autocorrelation into account when calculating the degrees of freedom, and corrected the tests for the number of significant regressors (Legendre *et al.*, 2002). As principal components are orthogonal to each other, the resulting partial correlation coefficient ' r ' equals the partial regression coefficient BETA retained from multiple regression analysis. The significance of each regressor was corrected by employing the newly obtained degrees of freedom (Legendre *et al.*, 2002).

RESULTS

Species richness in the administrative district of Dessau

Altogether we counted 1685 different plant species for the 125 grid cells in the Dessau district: 1253 native species, 141 archaeophytes and 291 neophytes (198 naturalized, 98 casuals). The mean numbers of species per grid cell for the 125 grid cells were: 439 native species, 68 archaeophytes and 48 neophytes (42 naturalized, 6 casuals). High numbers of species, in all three species groups, are found near bigger cities and along main rivers (Fig. 2a–c). Low numbers are found in areas with intensive agriculture on large fields, i.e. on nutrient rich loess soils around Köthen and to the west of Bitterfeld, and in areas with a high percentage of forests, i.e. on nutrient poor sandy soils in southern and northern parts of the study area.

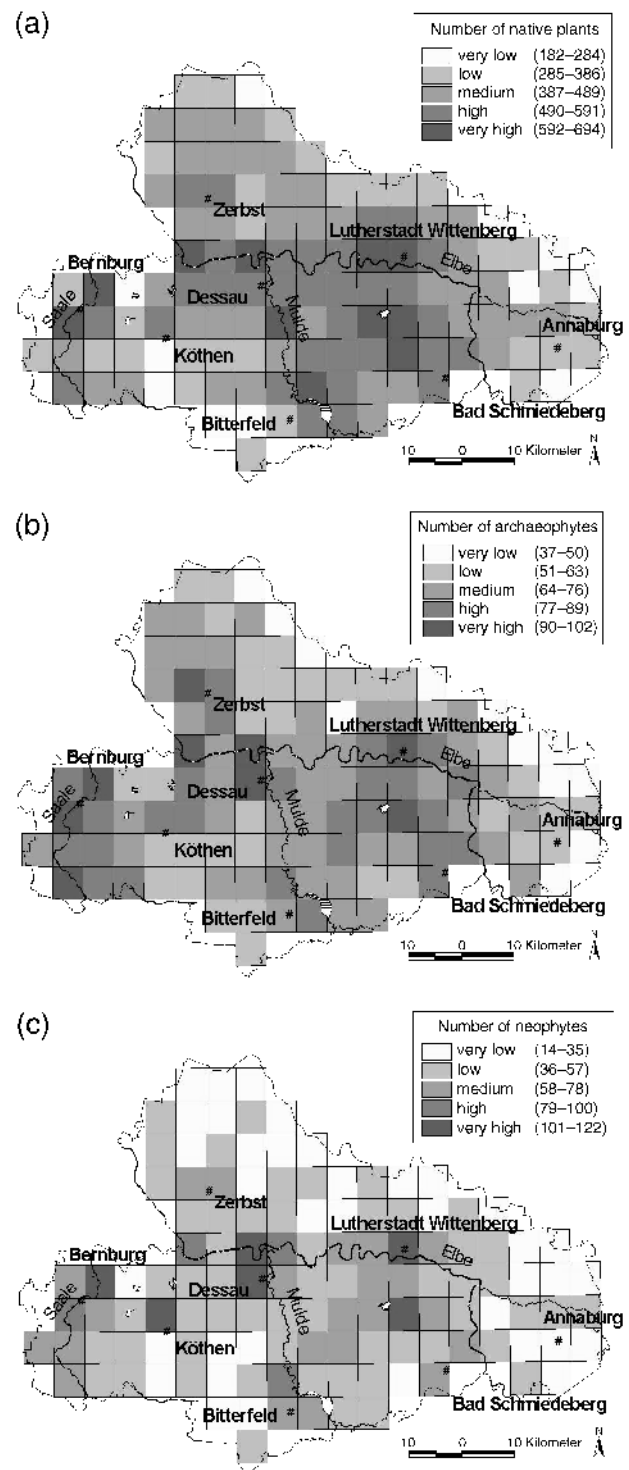


Fig. 2 Spatial distribution of plant species richness in the administrative district of Dessau (Germany) for 125 grid cells studied. (a) native plants; (b) archaeophytes (pre 1500 aliens); (c) neophytes (post 1500 aliens).

Pearson correlation between plant species groups revealed highly significant correlation coefficients, even after testing for spatial autocorrelation using Dutilleul's modified *t*-test. The highest correlation coefficient was found for the correlation between (a) archaeophytes and neophytes (0.833, $P < 0.001$) (Fig. 3a). But also native plant species are highly correlated with (b) neophytes and (c) archaeophytes with correlation coefficients of 0.767 and 0.742 (both $P < 0.001$) (Fig. 3b,c). All three correlation coefficients remained significant after sequential Bonferroni testing at the 0.05 alpha level.

Using the *t*-test following Röhr *et al.* (1983) and applying the sequential Bonferroni testing at the 0.05 alpha level, we found a significant difference between correlation coefficient (a) (archaeophytes and neophytes) and correlation coefficient (c) (native plants and archaeophytes; $t = 2.781$, $P = 0.006$, $\alpha = 0.017$). Differences between correlation coefficients (a) (archaeophytes and neophytes) and (b) (native plants and neophytes; $t = 2.003$, $P = 0.05$, $\alpha = 0.025$) as well as between (b) (native plants and neophytes) and (c) (native plants and archaeophytes; $t = 0.778$, $P = 0.438$) were not significant. That is, only the correlation between archaeophytes and neophytes is significantly different to the correlation between native species and archaeophytes.

Landscape indices condensed to principal components

Testing for highly correlated indices retained 29 low correlated indices for further analysis (Table 1). Principal components analysis reduced 29 landscape indices to eight principal components (PCs) that explained 80% cumulative variance in total. PC and eigenvalue scores are shown in Appendix I. The spatial distributions of the first four principal components are shown in Fig. 4. They explained 62% cumulative variance with eigenvalues of two to eight. Searching for common characteristics per principal component regarding high loadings of landscape indices, resulted in the following interpretation:

PC 1 combines the two dominating land use types in the study area: agriculture and forestry. It is strongly negative correlated (high negative values) with percentage of fields and mean patch size of fields, but strongly positive correlated (high positive values) with percentage of coniferous forest, mean proximity index of mixed forest, percentage of sandy soil, and mean annual rainfall. In conclusion, PC 1 was interpreted as high values of forest (on nutrient poor soils and with high annual rainfall) vs. negative values of large-scale agriculture (large-scale in the sense of large extent).

PC 2 combines high positive loadings of percentage riparian forest, percentage rivers, percentage grassland, edge density of ponds and lakes and land use richness. It is strongly negatively correlated with percentage of ground water levels > 2 m. This assemblage of riverine indices was interpreted as high values of habitats and land use in riverine ecosystems.

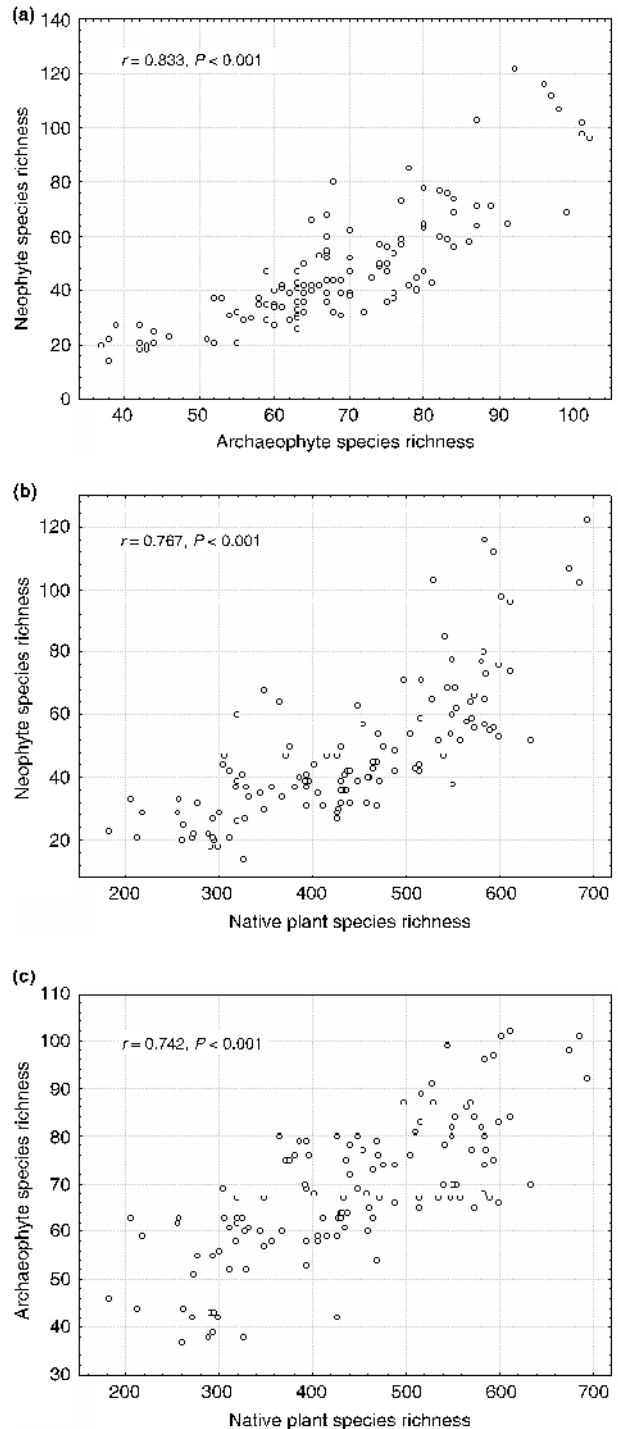


Fig. 3 Relationship between richness of (a) neophytic and archaeophytic plant species; (b) neophytic and native plant species; (c) archaeophytic and native plant species in the administrative district of Dessau (Germany) for 125 grid cells.

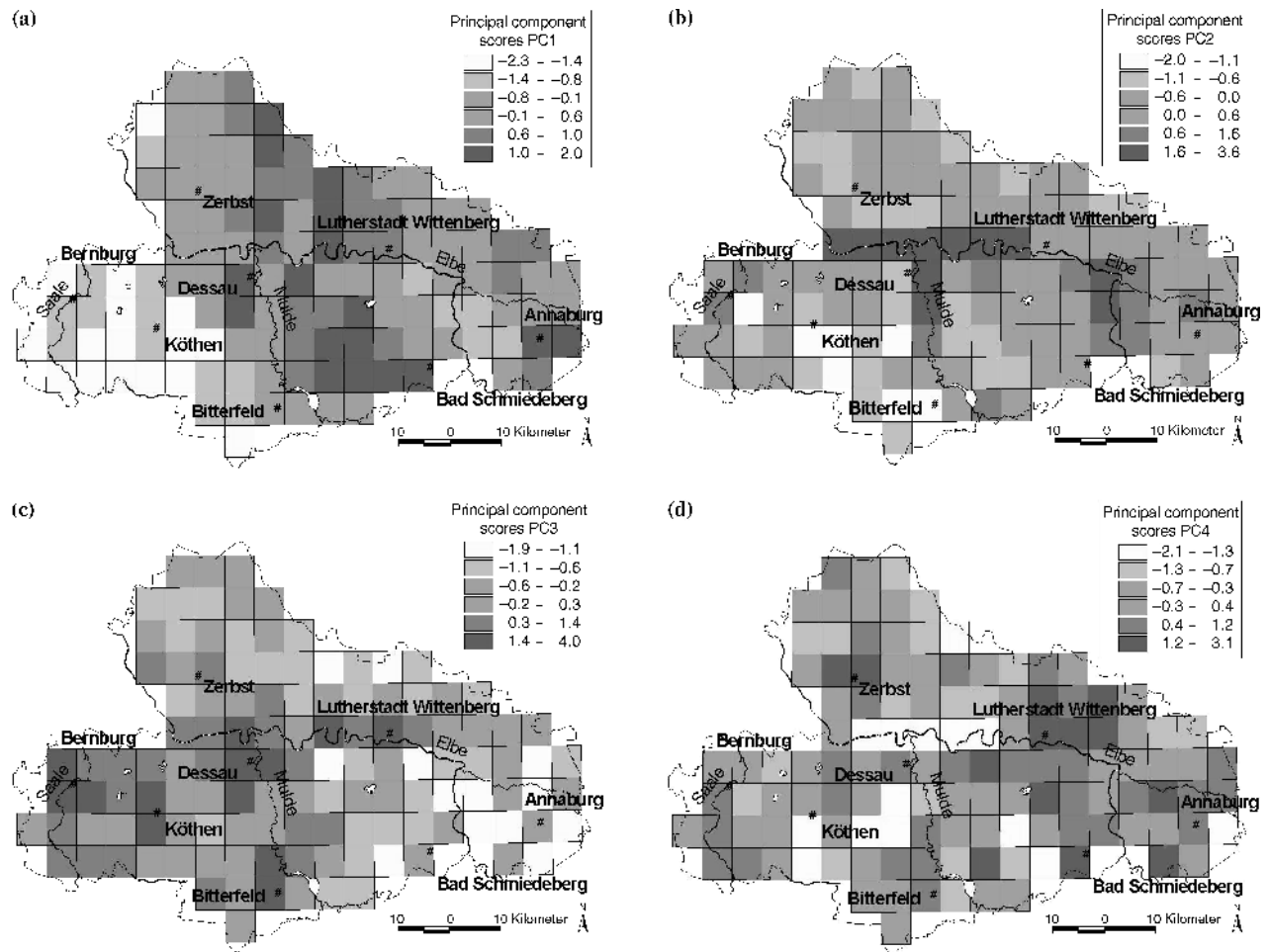


Fig. 4 Spatial distribution of the first four principal component scores in the administrative district of Dessau (Germany) for 125 grid cells. (a) PC 1 (forest vs. large-scale agriculture; positive values indicating dominance of forests, negative values indicating dominance of large-scale agriculture) (b) PC 2 (habitats and land use in riverine ecosystems, positive values indicating high amounts of riverine ecosystems); (c) PC 3 (large urban areas and traffic centres, positive values indicating urban centres in the study area); (d) PC 4 (small-scale land use and rural settlements, positive values indicating high patch densities of fields and settlements).

PC 3 is highly positive correlated with percentage urban area, mean patch size of urban area, mean patch size of greeneries, percentage scrub and tree groups, substrate diversity and edge density of railway lines and was therefore summarized as high values of large urban areas and traffic centres.

PC 4 combines two landscape configuration indices: patch density of fields and patch density of urban areas. Increasing values of PC 4 represent grid cells with a high number of small agricultural or urban patches and thus a high edge to area ratio. Therefore, PC 4 was interpreted as high values of small-scale land use and rural settlements (small-scale in the sense of small extent).

Four more PCs with eigenvalues < 2 were interpreted as: low patch densities of short-grass meadows and heathlands

(PC 5), high values of relief energy and mean elevation (PC 6), low values of percentage open-cast mines and disposal sites (PC 7), and high patch densities of bogs and perennial herb communities (PC 8).

Plant species richness in relation to spatial heterogeneity

Multiple linear regression analysis was highly significant and explained 55% of the variance (adjusted R^2) for native plants ($P < 0.001$), 56% for archaeophytes ($P < 0.001$), and 66% for neophytes ($P < 0.001$). Almost all principal components are highly correlated (BETA values) with the three studied plant groups, except PC 8 with archaeophytes and PC 1 and

Table 2 Results of multiple linear regression analysis for the three plant groups studied (**significant values bold**, confidence interval 0.95; $n = 125$; BETA: standardized partial regression coefficient, t : t -statistic, p : significance) and results after testing for spatial autocorrelation using Dutilleul's modified t -test (degrees of freedom of modified t -test reduced by number of parameters used to fit the model; v_m : degrees of freedom, t_m : t -statistic, P_m : significance)

PC	BETA	t	P -value	v_m	t_m	P_m
(a) native plants						
PC 1	0.211	3.499	< 0.001	16.75	0.882	n.s.
PC 2	0.467	7.747	< 0.001	47.03	3.618	< 0.001
PC 3	0.350	5.818	< 0.001	39.28	2.345	0.024
PC 4	0.294	4.873	< 0.001	61.11	2.400	0.019
PC 5	0.154	2.557	0.012	89.09	1.472	n.s.
PC 6	-0.224	-3.714	< 0.001	17.38	-0.957	n.s.
PC 7	-0.139	-2.303	0.023	68.98	-1.163	n.s.
PC 8	0.044	2.034	0.044	79.95	1.104	n.s.
(b) archaeophytes						
PC 1	-0.268	-4.488	< 0.001	19.06	-1.215	n.s.
PC 2	0.270	4.503	< 0.001	55.41	2.079	0.042
PC 3	0.491	8.221	< 0.001	30.11	3.092	0.004
PC 4	0.367	6.146	< 0.001	83.33	3.602	< 0.001
PC 5	0.147	2.469	0.015	-397.61	n.s.	n.s.
PC 6	-0.162	-2.718	0.008	14.19	-0.620	n.s.
PC 7	-0.135	-2.253	0.026	74.32	-1.171	n.s.
PC 8	0.016	0.273	n.s.	133.92	0.189	n.s.
(c) neophytes						
PC 1	-0.071	-1.357	n.s.	23.87	-0.346	n.s.
PC 2	0.356	6.839	< 0.001	62.17	3.008	0.004
PC 3	0.623	11.953	< 0.001	41.96	5.159	< 0.001
PC 4	0.301	5.781	< 0.001	78.16	2.794	0.007
PC 5	0.104	2.002	0.048	346.59	1.952	n.s.
PC 6	-0.195	-3.736	< 0.001	17.90	-0.840	n.s.
PC 7	-0.154	-2.948	0.004	82.40	-1.411	n.s.
PC 8	0.035	0.680	n.s.	105.53	0.364	n.s.

8 with neophytes (Table 2). However, after correcting for spatial autocorrelation and thus obtaining appropriate degrees of freedom, just three principal components remained significant for the three investigated plant groups: habitats and land use in riverine ecosystems (PC 2), large urban areas and traffic centres (PC 3), and small-scale land use and rural settlements (PC 4) (Table 2). They explained 41% of the variance (adjusted R^2) for native plants ($P < 0.001$), 43% for archaeophytes ($P < 0.001$), and 60% for neophytes ($P < 0.001$).

Examining the partial regression coefficients (Table 2), species richness of native plants mainly increases with the amount of habitats and land use in riverine ecosystems (PC 2), followed by the amount of large urban areas and traffic centres (PC 3), and small-scale land use and rural settlements (PC 4). The most important principal component for alien plants is PC 3: large urban areas and traffic centres. Further, species richness of archaeophytes increases with the amount of small-scale land use patches and rural settlements (PC 4) followed by habitats and land use in riverine ecosystems

(PC 2), whereas species richness of neophytes increases with the amount of habitats and land use in riverine ecosystems (PC 2) followed by small-scale land use patches and rural settlements (PC 4). Considering all three species groups, the highest partial regression coefficients were obtained for PC 3 (large urban areas and traffic centres), medium values for PC 2 (habitats and land use in riverine ecosystems) and the lowest for PC 4 (small-scale land use and rural settlements).

Overall, native as well as alien plant species richness is influenced by the same principal components, differing only in order of relevance. Further principal components, representing indices including percent forests, mean size of agricultural patches, percent sandy soils, mean annual rainfall, patch density of short-grass meadows, heathland and bogs, as well as relief energy, remained insignificant. In addition, we performed similar analyses but subdivided the two groups of aliens further into casuals and naturalized species. The results were basically the same, hence we conclude that our results are robust.

DISCUSSION

Native compared to alien plant species richness

As seen in the results, Pearson correlation coefficients for between species group relations were highly significant. That is, alien plant richness patterns follow the richness patterns of native plant species (Levine, 2000; Stadler *et al.*, 2000; Sax, 2002). Our analysis revealed that plant species richness depends on the same principal components. These three PCs have in common that they are characterized by anthropogenic or natural disturbances in association with a high habitat and structural heterogeneity. Increasing landscape heterogeneity usually leads to increasing species richness (Planty-Tabacchi *et al.*, 1996; Duhme & Pauleit, 1998; Lonsdale, 1999). In this sense, native and alien plant richness patterns are favoured by similar landscape conditions (Davis *et al.*, 2000; Levine, 2000; Sax, 2002).

Whether these patterns apply to common as well as to rare or threatened native species (Duhme & Pauleit, 1998) and whether the number of individuals per species is of any relevance (Alpert *et al.*, 2000) has to be analysed in further studies. In addition, no causal relationship between native and alien species richness, as proposed by Williamson (1999), could be detected at the investigated regional scale. Declining native plant species richness due to increased alien species richness might be restricted to small local scales or to neighbourhood scales (Rejmánek, 1996; Lonsdale, 1999; Levine, 2000).

Although we found significant correlations between all three species groups, the *t*-test following Röhr *et al.* (1983) revealed a significant difference only between the highest correlation coefficient (neophyte to archaeophyte richness) and the lowest correlation coefficient (native plant to archaeophyte richness). This underlines that the two alien species groups are more similar to each other than native plant richness patterns to archaeophyte richness. Underlying factors responsible for similarities between archaeophyte and neophyte richness patterns could be time of introduction, origin of plants, or their potential to spread, but these were not considered in our study. Factors responsible for dissimilarities between native plants and archaeophytes could be the different habitat preferences, as seen in the results: native plant richness mainly increases with natural habitats such as habitats and land use in riverine ecosystems, whilst archaeophyte richness mainly increases with frequently disturbed anthropogenic habitats such as large urban areas and traffic centres and small-scale land use patches and rural settlements. Pyšek *et al.* (2002a) also found the positive relationship between native species and neophytes to be stronger than between native species and archaeophytes and showed that alien compared to native species richness was influenced by different environmental determinants.

The role of urban areas for alien and native plant species richness

In our study, neophyte species numbers increase with an increasing amount of urbanization and associated features such as percentage of urban area, mean patch size of urban area, percentage of greenery, mean patch size of greenery, edge density of railway lines, diversity of substrates, and percentage of scrub and groves (PC 3). This is consistent with a number of studies that claim factors such as high nutrient inputs, warmer climate, high light availability, disturbances in soil structure, and direct or indirect introduction of exotic species in parks, gardens, ruderal places, or along transportation routes, to be responsible for high alien species richness with increased city area (Kowarik, 1995; Pyšek *et al.*, 1998, 2002a; Sukopp, 1998; Ernst *et al.*, 2000; Stadler *et al.*, 2000; McKinney, 2002).

At first glance, it seems surprising that increasing amounts of urbanization also support native species richness, as shown in our study. But besides being permanently influenced by moderate to high anthropogenic disturbances, cities contain a variety of different habitats like parks, gardens, cemeteries, recreational sites, remnants of natural vegetation like old forests or riparian habitats (e.g. in Dessau and Lutherstadt-Wittenberg along the rivers Elbe and Mulde), fallow lands, ruderal places, or construction sites with bare soil. This habitat diversity is responsible for high species richness of alien as well as native plant species (Duhme & Pauleit, 1998; Ernst *et al.*, 2000; Stadler *et al.*, 2000). In our analysis, such habitat heterogeneity in urban areas is indicated by high loadings of greenery, scrub, and groves in PC 3 (large urban areas and traffic centres). In this sense, urban ecosystems provide much better living conditions for native and alien plant species, compared to surrounding large, monotonous, and intensively used agricultural areas (e.g. large fields to the west of Dessau are species poor despite nutrient rich loess soils) or forested areas with low light availability (Haeupler, 1975; Ernst *et al.*, 2000). In our study area, species poorness in forests is increased by the dominance of monotonous stands of coniferous forest on nutrient poor sandy soils (e.g. Dübener Heide in the south and Fläming in the north) and might therefore be lower compared to Central European forests elsewhere.

Plant species richness and riverine ecosystems

Our study reveals a significant correlation of riverine ecosystems (PC 2) with native species richness as well as with archaeophyte and neophyte species richness. High native species richness in this case might be due to a considerably higher assemblage of near-natural habitats, such as river banks, riverine forests, oxbow lakes, meadows, and groves (Wohlge-muth, 1998). Secondly, land use intensity along parts of the main rivers Elbe and Mulde is low, as they are part of conservation areas, such as the biosphere reserve 'Mittlere Elbe'.

Therefore, near-natural riverine ecosystems, surrounded by man-dominated landscapes, may act as retreat areas for a large number of native plant species.

Furthermore, riverine ecosystems experience moderate to strong disturbances resulting from repeated flooding. This leads to nutrient inputs, erosion, sedimentation, exposure of bare soil on gravel bars as well as habitat heterogeneity, which altogether support species richness of native as well as alien plant species (Planty-Tabacchi *et al.*, 1996; Pyšek *et al.*, 1998). Di Castri (1989) summarizes that openness (availability of light and bare soil, as in riverine ecosystems) and disturbance (natural and/or anthropogenic) are possibly the driving forces for alien introductions in Central European ecosystems. Repeated flooding as well as human transportation activities on and along rivers also allow for species distribution and migration, as riverine ecosystems represent a connected network (Rejmánek, 1989; Planty-Tabacchi *et al.*, 1996). This might further explain high species richness patterns of native as well as alien species in riverine landscapes.

Large-scale vs. small-scale land use

As shown in the results, PC 4 (small-scale land use and rural settlements) combines two configuration indices: high patch densities of agricultural fields and of urban areas. High patch densities are equivalent to large patch numbers per grid cell. This stands for an increasing proportion of edges and transition zones between patches of these two land use types and surrounding types. Therefore, grid cells with high values in PC 4 comprise increased landscape heterogeneity and structural diversity, compared to grid cells dominated by large agricultural patches (low values in PC 4). PC 4 was strongly correlated with all three plant groups considered. In conclusion, species richness of native as well as alien plants is positively influenced by increased structural diversity and landscape heterogeneity in rural areas. These results are consistent with results in a case study of Haeupler (1975), where plant species richness in grid cells with small-scale land use was higher than in grid cells dominated by large fields. Even archaeophytes, known to be typical 'weeds' adapted to agricultural land use, were not able to keep pace with the rapid agricultural intensification in the past century. They are nowadays more or less restricted to edges, gardens and extensively used patches (Kornaš, 1990).

Summing the last three headings up, anthropogenic and/or natural disturbances in association with a high habitat and structural heterogeneity, as for instance in urban, riverine, or small-scale rural ecosystems, promote species richness of native as well as alien plant species at the regional scale in a Central European, man-dominated landscape. This supports the findings of Planty-Tabacchi *et al.* (1996), Sukopp (1998) and Stohlgren *et al.* (1999), who conclude that spatial heterogeneity is responsible for overall high plant species richness. Also,

even in strongly competitive species assemblages, spatial heterogeneity favours local enrichment from the regional species pool (Cornell & Karlson, 1997). In general, the number of species at the investigated scale depends on the number of available species at the next coarser scale (Zobel, 1997). This might be an additional factor influencing native and alien plant species richness, but was not considered in our analysis.

Bias of the results due to sampling intensity

It may be argued that our results are strongly biased by different sampling intensities, i.e. cities are better sampled than rural areas (cf. Barthlott *et al.*, 1999a,b). Then, the resulting correlation of species numbers between native and alien plant species would be artificial. Unfortunately, we do not have any information about mapping intensity in the Dessau district. However, we could infer sampling intensity by using a set of 50 control species that are ubiquitous and which are assumed to occur in every grid cell. Forty-five of the control species are the most ubiquitous species in Germany, according to Krause (1998). Five additional ubiquitous species are either inconspicuous or difficult to determine. We argue that the more control species are present, the better an area is sampled. Of the 125 grid cells in the Dessau district, just seven contained 49 species and the rest all 50 control species. Thus we think that sampling bias may be of minor importance for results.

Abiotic characteristics in relation to plant species richness

In our study, abiotic conditions like soil substrate character, precipitation, or ground water levels, show high loadings together with a range of land use indices in PC 1, 2 or 3. Apart from relief indices, they do not appear in separate principal components. On the one hand, this is due to historical land use and settlement that followed distribution patterns of natural resources and constraints. But as technical solutions developed, land use became increasingly independent of natural restrictions, resulting in strong changes of natural qualities such as soil characteristics or ground water levels. In this way, abiotic landscape characteristics became more and more overruled by land use characteristics. Studies by Roche *et al.* (1998) and Roy *et al.* (1999) showed that plant distribution was mainly explained by land use characteristics, especially in areas lacking extreme abiotic conditions or gradients. Other studies have shown that natural site conditions are strongly determined by anthropogenic influences in cultural landscapes (Miller *et al.*, 1997; Saunders *et al.*, 1998; Walz, 1999; Wagner *et al.*, 2000).

Principal components analysis revealed high loadings of relief energy and mean elevation in PC 6. However, the partial linear regression coefficient (after correcting for spatial autocorrelation) of PC 6 showed no significant relationships with

the three species groups. It can be assumed that the investigated regional scale and the moderate topographic differences in our study area are not appropriate to detect correlations with relief, or even with climatic gradients. In studies at coarser scales, abiotic gradients such as substrate diversity patterns or altitude, increase in relevance for plant distribution patterns (Pyšek *et al.*, 2002a; Kühn *et al.*, unpublished observation).

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REFERENCES

- Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 52–66.
- Ashton, P.J. & Mitchell, D.S. (1989) Aquatic plants: patterns and modes of invasion, attributes of invading species and assessment of control programmes. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 111–154. Wiley, Chichester.
- Barthlott, W., Biedinger, N., Braun, G., Feig, F., Kier, G. & Mutke, J. (1999a) Terminological and methodological aspects of the mapping and analysis of the global biodiversity. *Acta Botanica Fennica*, **162**, 103–110.
- Barthlott, W., Kier, G. & Mutke, J. (1999b) Globale Artenvielfalt und ihre ungleiche Verteilung. *Courier Forschungsinstitut Senckenberg*, **215**, 7–22.
- Benkert, D., Fukarek, F. & Korsch, H. (1996) *Verbreitungsatlas der Farn- und Blütenpflanzen Ostdeutschlands*. Gustav Fischer Verlag, Jena.
- di Castri, F. (1989) History of biological invasions with special emphasis on the Old World. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 1–30. Wiley, Chichester.
- di Castri, F. (1990) On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. di Castri, A. J. Hansen and M. Debussche), pp. 3–16. Kluwer Academic Publishers, Dordrecht.
- Cornell, H.V. & Karlson, R.H. (1997) Local and regional processes as controls of species richness. *Spatial ecology the role of space in population dynamics and interspecific interactions* (ed. by D. Tilman and P. Kareiva), pp. 250–268. Princeton University Press, Princeton.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- Duhme, F. & Pauleit, S. (1998) Some examples of different landscape systems and their biodiversity potential. *Landscape and Urban Planning*, **41**, 249–261.
- Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135–139.
- Dutilleul, P. (1993) Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Ernst, D., Felinks, B., Henle, K., Klotz, S., Sandermann, H. & Wiencke, C. (2000) Von der numerischen zur funktionellen Biodiversität: Neue Forschungsansätze. *GAIA — Mitt Hermann Von Helmholtz-Gemeinschaft Deutscher Forschungszentren*, **9**, 140–145.
- Faliński, J.B. (1998) Invasive alien plants and vegetation dynamics. *Plant invasions: ecological mechanisms and human responses* (ed. by U. Starfinger, K.R. Edwards, I. Kowarik and M. Williamson), pp. 3–21. Backhuys Publishers, Leiden.
- Fortin, M.-J., Drapeau, P. & Legendre, P. (1989) Spatial autocorrelation and sampling design in plant ecology. *Vegetatio*, **83**, 209–222.
- Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems*, **1**, 143–156.
- Haeupler, H. (1975) Statistische Auswertung von Punktrasterkarten der Gefäßpflanzen flora Süd-Niedersachsens. *Scripta Geobotanica*, **8**, 1–141.
- Hoffmann, J. (1998) Assessing the effects of environmental changes in a landscape by means of ecological characteristics of plant species. *Landscape and Urban Planning*, **41**, 239–248.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.
- Klotz, S. (1990) Species/area and species/inhabitants relations in European cities. *Urban ecology plants and plant communities in urban environments* (ed. by H. Sukopp, S. Hejny and I. Kowarik), pp. 99–104. SPB. Academic Publishing, The Hague.
- Kornaś, J. (1990) Plant invasions in Central Europe: historical and ecological aspects. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. di Castri, A.J. Hansen and M. Debussche), pp. 19–36. Kluwer Academic Publishers, Dordrecht.
- Kowarik, I. (1995) On the role of alien species in urban flora and vegetation. *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek, and M. Wade), pp. 85–103. SPB. Academic Publishing, Amsterdam.
- Krause, A. (1998) Floras Alltagskleid oder Deutschlands 100 häufigste Pflanzenarten. *Natur Landschaft*, **73**, 486–491.
- Landesamt für Umweltschutz. Sachsen-Anhalt (1998) *Datenbank Blütenpflanzen Sachsen-Anhalt*. Landesamt für Umweltschutz, Halle (Saale), unpublished.
- Legendre, P. (2000) *Program Mod_t_Test*. Département de sciences biologiques. Université de Montreal. <http://www.fas.umontreal.ca/biol/legendre>.
- Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M. & Myers, D. (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, **25**, 601–615.

- Legendre, P. & Fortin, M.-J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852–854.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- McGarigal, K. & Marks, B.J. (1994) *FRAGSTATS — Spatial Pattern Analysis Program for Quantifying Landscape Structure*. Oregon State University, Corvallis.
- McGarigal, K. & McComb, W.C. (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs*, **65**, 235–260.
- McIntyre, S., Ladiges, P.Y. & Adams, G. (1988) Plant species-richness and invasion by exotics in relation to disturbance of wetland communities on the Riverine Plain, NSW. *Australian Journal of Ecology*, **13**, 361–373.
- McIntyre, S. & Lavorel, S. (1994) Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conservation Biology*, **8**, 521–531.
- McKinney, M.L. (2002) Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Global Ecology and Biogeography*, **11**, 343–348.
- Miller, J.N., Brooks, R.P. & Croonquist, M.J. (1997) Effects of landscape patterns on biotic communities. *Landscape Ecology*, **12**, 137–153.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmont, B., Christensen, S.W., Dale, V.H. & Graham, R.L. (1988) Indices of landscape pattern. *Landscape Ecology*, **1**, 153–162.
- Peterson, J. & Langner, U. (1992) *Katalog der Biotoptypen und Nutzungstypen für die CIR-luftbildgestützte Biotoptypen- und Nutzungskartierung im Land Sachsen-Anhalt*. Berichte des Landesamtes für Umweltschutz Sachsen-Anhalt (4), Halle.
- Planty-Tabacchi, A.-M., Tabacchi, E., Naiman, R.J., Deferrari, C. & Decamps, H. (1996) Invasibility of species-rich communities in riparian zones. *Conservation Biology*, **10**, 598–607.
- Pyšek, P., Jarošík, V. & Kučera, T. (2002a) Patterns of invasion in temperate nature reserves. *Biological Conservation*, **104**, 13–24.
- Pyšek, P., Prach, K. & Mandák, B. (1998) Invasions of alien plants into habitats of Central European Landscape: an historical pattern. *Plant invasions: ecological mechanisms and human responses* (ed. by U. Starfinger, K.R. Edwards, I. Kowarik and M. Williamson), pp. 23–32. Backhuys Publishers, Leiden.
- Pyšek, P., Sádlo, J. & Mandák, B. (2002b) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
- Rejmánek, M. (1989) Invasibility of plant communities. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 369–388. Wiley, Chichester.
- Rejmánek, M. (1996) Species richness and resistance to invasions. *Ecological Studies 122: Biodiversity and ecosystem processes in tropical forests* (ed. by G.H. Orians and R.J. Dirzo), pp. 153–172. Springer Verlag, Berlin.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B. & Jackson, B.L. (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology*, **10**, 23–39.
- Roche, Ph, Taton, T. & Médail, F. (1998) Relative importance of abiotic and land use factors in explaining variation in woody vegetation in a French rural landscape. *Journal of Vegetation Science*, **9**, 221–228.
- Röhr, M., Lohse, H. & Ludwig, R. (1983) *Statistische Verfahren Statistik für Soziologen, Pädagogen und Mediziner, Bd. 2*. Verlag H. Deutsch, Frankfurt am Main.
- Roy, D.B., Hill, M.O. & Rothery, P. (1999) Effects of urban land cover on the local species pool in Britain. *Ecography*, **22**, 507–515.
- Saunders, S.C., Chen, J., Crow, T.R. & Brososke, K.D. (1998) Hierarchical relationships between landscape structure and temperature in a managed forest landscape. *Landscape Ecology*, **13**, 381–395.
- Sax, D.F. (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions*, **8**, 193–210.
- Schröder, F. (2000) *Abriß der Physischen Geographie und Aspekte Des Natur- und Umweltschutzes Sachsen-Anhalts. Forschungen zur deutschen Landeskunde, Band 247*. Deutsche Akademie für Landeskunde, Flensburg.
- Schroeder, F.-G. (1969) Zur Klassifizierung der Anthropochoren. *Vegetatio*, **16**, 225–238.
- Stadler, J., Trefflich, A., Klotz, S. & Brandl, R. (2000) Exotic plant species invade diversity hot spots: the alien flora of northwestern Kenya. *Ecography*, **23**, 169–176.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.
- Sukopp, H. (1998) On the study of anthropogenic plant migrations in central Europe. *Plant invasions: ecological mechanisms and human responses* (ed. by U. Starfinger, K.R. Edwards, I. Kowarik and M. Williamson), pp. 43–56. Backhuys Publishers, Leiden.
- Volk, M. & Bannholzer, M. (1999) Auswirkungen von Landnutzungsänderungen auf den Gebietswasserhaushalt: Anwendungsmöglichkeiten des Modells 'ABIMO' für regionale Szenarien. *Geökodynamik*, **20**, 193–210.
- Wagner, H.H., Wildi, O. & Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology*, **15**, 219–227.
- Walz, U. (1999) Erfassung und Bewertung der Landnutzungsstruktur. *Erfassung und Bewertung der Landschaftsstruktur Auswertung Mit GIS und Fernerkundung* (ed. by U. Walz), pp. 1–8. Institut für ökologische Raumentwicklung e. V., Dresden.
- Wiens, J.A., Stenseth, N.C., Van Horne, B. & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369–380.
- Williamson, M. (1999) Invasions. *Ecography*, **22**, 5–12.
- Wohlgemuth, T. (1998) Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodiversity Conservation*, **7**, 159–177.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, **12**, 266–269.

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APPENDIX I

Scores of principal components analysis (highest loading per index in bold; %LAND: percent landcover; MPS: mean patch size; PD: patch density; ED: edge density; MPI: mean proximity index; PR: patch richness)

Landscape indices	Principal components							
	1	2	3	4	5	6	7	8
%LAND urban area	-0.09	0.07	0.88	0.32	0.08	-0.07	-0.07	0.16
%LAND fields	-0.86	-0.20	-0.14	0.13	0.18	-0.16	0.13	-0.18
%LAND open-cast and disposal sites	0.06	-0.08	0.13	-0.03	0.03	0.03	-0.92	0.05
%LAND grassland	0.18	0.67	0.04	0.29	0.18	-0.26	0.22	0.08
%LAND scrub	-0.36	0.20	0.50	0.17	-0.28	0.14	-0.36	0.26
%LAND groves	-0.23	0.52	0.54	0.30	-0.10	0.08	-0.08	0.16
%LAND riparian forest	0.05	0.73	0.37	-0.21	0.03	-0.02	0.10	-0.08
%LAND rivers	-0.03	0.77	0.37	-0.16	0.03	0.05	0.08	0.06
%LAND coniferous forest	0.80	-0.10	-0.43	-0.10	-0.04	0.19	0.06	-0.12
MPS urban area	-0.05	0.22	0.88	-0.18	0.06	-0.14	-0.06	-0.04
MPS greenery	-0.14	0.23	0.82	-0.09	0.00	0.06	0.00	-0.07
MPS fields	-0.72	-0.25	-0.10	-0.39	0.14	-0.14	0.16	-0.17
PD vegetation of perennial herbs	0.18	0.28	0.31	0.19	-0.13	0.03	-0.29	0.61
PD urban areas	-0.06	-0.09	0.40	0.74	0.05	0.02	-0.01	0.29
PD fields	-0.30	0.04	-0.09	0.85	0.15	-0.08	0.04	-0.10
PD short-grass meadows	0.05	-0.07	-0.03	0.01	-0.93	0.12	0.01	-0.03
PD heathlands	0.26	-0.11	-0.15	-0.18	-0.86	-0.18	0.01	0.01
PD bogs	-0.10	0.32	0.05	0.01	0.08	-0.15	0.04	0.83
ED railroads	0.03	-0.12	0.65	0.23	0.11	-0.23	-0.29	0.33
ED ponds	0.01	0.79	0.04	-0.06	0.04	-0.07	0.02	0.17
ED lakes	-0.08	0.70	-0.02	0.07	0.07	-0.19	-0.16	0.19
MPI mixed forest	0.74	0.06	0.00	-0.25	-0.13	-0.16	0.04	-0.10
PR land use	0.37	0.56	0.13	0.43	-0.03	0.05	-0.21	0.28
Mean annual rainfall	0.77	0.02	-0.42	0.01	0.15	0.24	0.13	-0.01
Relief energy	0.14	-0.14	0.05	0.04	0.01	0.90	-0.09	-0.07
Mean elevation	0.24	-0.40	-0.36	-0.14	0.00	0.72	0.10	-0.04
PR substrates	-0.32	0.10	0.57	0.16	0.24	0.25	0.02	0.33
%LAND sandy soils	0.73	-0.30	-0.34	-0.08	-0.09	-0.01	-0.06	-0.13
%LAND ground water level > 2 m	-0.08	-0.65	0.07	-0.42	0.06	0.46	-0.02	-0.09
Eigenvalues	8.04	4.62	2.93	2.33	1.89	1.41	1.16	0.83
Percentage variance	4.36	4.46	4.74	2.48	1.96	2.05	1.38	1.77
Cumulative percentage variance	0.15	0.15	0.16	0.09	0.07	0.07	0.05	0.06