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Plant distribution patterns in Germany – Will aliens match natives?

With 2 Figures and 4 Tables

Summary

Using data on the distribution of the German vascular flora and a wide selection of environmental data we address questions regarding native and alien plant distribution patterns. We found highly significant positive relationships between plant species richness of natives and aliens on three spatial scales (c. 100 km², c. 1,000 km², c. 10,000 km²). Given the results of major axis regressions on log-transformed data, we conclude that alien species richness increases overproportionately compared to native species richness. To determine common factors for plant richness patterns, we used a principal component analysis (PCA) to reduce the number of environmental variables. The principal components were used in a multiple regression as independent variables to model plant species richness of aliens and natives, corrected for spatial autocorrelation. The diversity of geological substrates is considered most important for native and alien plant species richness. Furthermore, area of loess subsoils is important for archaeophyte richness, urbanisation is important for neophyte richness.

Comparisons of similarity matrices between natives and aliens using standardised similarities as well as Simpsons similarities of randomly selected grid cells showed a positive correlation. Similarity patterns provided by native plant species are traced by archaeophytes but not followed by neophytes. Similarities of archaeophytes were significantly higher than those of natives whereas similarities of neophytes were significantly lower than those of natives. Therefore, we concluded that archaeophytes lead to homogenisation of the German flora but are mainly plants of arable fields that are homogeneous due to human land use. Neophytes, however, did not lead to homogenisation but increase local biodiversity.

Zusammenfassung

Pflanzenverbreitungsmuster in Deutschland – zeigen Gebietsfremde ähnliche Verbreitungsmuster wie Einheimische?

Mit Hilfe von Umwelt- und Verbreitungsdaten zur Flora von Deutschland wurde untersucht, in wieweit sich einheimische und gebietsfremde Gefäßpflanzenarten voneinander unterscheiden. Wir haben hoch signifikante positive Zusammenhänge zwischen dem Artenreichtum der Einheimischen und der Gebietsfremden auf drei unterschiedlichen Skalenebenen (ca. 100 km², ca. 1000 km², ca. 10000 km²) festgestellt. Die Ergebnisse einer „Major Axis Regression“ der log-transformierten Daten zeigen, dass die Artenzahl der Gebietsfremden überproportional mit der der Einheimischen zunimmt.

Aus einer Vielzahl von relevanten Umweltvariablen wurden mit Hilfe einer Hauptkomponentenanalyse die wichtigsten Umweltgradienten bestimmt. Diese Hauptkomponenten wurden als Unabhängige Variable in einer multiplen Regression genutzt um die Artenzahlen der Einheimischen und Gebietsfremden zu erklären, wobei eine Korrektur hinsichtlich auftretender räumlicher Autokorrelation durchgeführt wurde. Das Ergebnis zeigt, dass geologische Heterogenität der wichtigste Faktor für die Artenzahlen sowohl der Einheimischen als auch der Gebietsfremden ist. Ferner sind bei den Gebietsfremden der Anteil an Lössgebieten für Archäophyten und die Urbanisierung für Neophyten die zweitwichtigsten Parameter.

Unterschiedliche Ähnlichkeitsindizes zwischen den Verbreitungsmustern der Einheimischen und Gebietsfremden in den untersuchten Rasterflächen sind jeweils positiv korreliert. Die Ähnlichkeitsmuster der Einheimischen, die durch biogeographische Muster vorgegeben sind, werden von Archäophyten nachvollzogen, nicht aber von Neophyten. Allerdings ist die Ähnlichkeit der Verbreitung der

Archäophyten untereinander signifikant höher als die der Einheimischen, wohingegen die Muster der Neophyten signifikant geringere Ähnlichkeiten zeigten. Daher schließen wir, dass Archäophyten zu einer Homogenisierung der Flora beitragen. Allerdings handelt es sich ohnehin meist um Arten der Äcker, also eines vergleichsweise homogenen Lebensraumes. Dagegen führen Neophyten nicht generell zu einer Homogenisierung der Flora sondern erhöhen die Artenvielfalt auf lokaler Ebene.

Introduction

Human land utilisation and transportation caused the immigration of species into biogeographic regions where they did not occur naturally (ELTON 1958). The introductions of these species alien to their new regions (cf. RICHARDSON et al. 2000) could be equalled to a breakdown of isolating barriers between biogeographical zones. The resulting patterns of diversity between native plant species and alien plant species were analysed by different authors and recent investigation on various spatial scales showed ambiguous results (e.g. ROBINSON et al. 1995; PLANTY-TABACCHI et al. 1996; STOHLGREN et al. 1999; LONSDALE 1999; STADLER et al. 2000; see also review by LEVINE & D'ANTONIO 1999). Central European analyses on large spatial scales on this topic are still missing (but see PYŠEK et al. 2002 for smaller scale).

One hypothesised effect is that biological invasions should homogenise flora and fauna (MCKINNEY & LOCKWOOD 1999). The authors argue that successful invaders displace native species which will lead to a few winners and many losers. The concept of homogenisation means that different biotas will become more similar. If this should be attributed to biological invasion of plant species, alien floras should be more similar (or have less species turnover) than native floras (MCKINNEY & LOCKWOOD 2001). However, to our knowledge evidence for a homogenisation on regional scale is still missing. The spatial distribution patterns of native and alien plant species and environmental factors influencing these patterns are still poorly studied on a regional scale.

Success of invasive plant species depends on three different components (LONSDALE

1999; WILLIAMSON 1999; ALPERT et al. 2000). First, species traits that enable a species to invade a new habitat, grow, and reproduce. Some effort is taken to answer this question (e.g. THOMPSON et al. 1995; CRAWLEY et al. 1996; ALPERT et al. 2000, PRINZING et al. 2002) but the search for traits has largely been unsuccessful (ALPERT et al. 2000). Second, propagule pressure, as the success highly depends on repeated introductions, competitive strength, or mere chance, all of which is increased with increasing propagule pressure. Third, the invaded object, namely its invasibility, as some communities, habitats, or biomes are more susceptible to invasions than others. However, native and alien plant species depend on environmental conditions and resources that influence their distribution patterns. Especially ecological factors covarying with species diversity are considered to be the common cause for alien and native plant species richness (LEVINE & D'ANTONIO 1999; LEVINE 2000), but this issue is not resolved.

In this study, we focus on the third point (invaded landscape) in combination with the environmental and geographical factors that directly or indirectly influence diversity and distribution patterns of native and alien plant species. Therefore, we will address following questions: 1) Is there a positive relationship between species richness of native and alien plants analysed at three different spatial scales (c. 100 km², c. 1,000 km², c. 10,000 km²)? 2) Which environmental factors determine species richness patterns of native and alien plants? 3) Is the biogeographic pattern of species similarities different for native compared with alien plant species? 4) Do invasive species lead to homogenisation of a regional flora?

Material and methods

Plant distribution data

As data source for plant distribution we used the data base FLORKART of the German Centre for Phyto-diversity at the German Federal Agency for Nature Conservation. This database is compiled of data from current and former regional floristic mapping projects, based mainly on the field work of thousands of volunteers, co-ordinated by three Floristic Centres in Germany (HAEUPLER et al., unpublished). The species were assigned as natives, archaeophytes and neophytes after KÜHN & KLOTZ (2002). Archaeophytes are ancient immigrant that reached Germany before 1500, neophytes are recent immigrants that reached Germany after 1500 (SCHROEDER 1969). Both groups are summarised as aliens.

The localities of plant occurrences are referenced in FLORKART to 1:25,000 ordnance survey maps. The number of species was recorded on the different spatial scales where the grid cells are defined as follows:

1. one ordnance survey map (6' longitude \times 10' latitude, c. 130 km²).
2. 3 \times 3 ordnance survey maps (18' longitude \times 30' latitude, c. 1,135 km²).
3. 9 \times 9 ordnance survey maps (54' longitude \times 90' latitude, c. 10,300 km²).

As mapping was organised decentrally, mapping intensity proved to be heterogeneous throughout Germany. This might bias the data set towards lower species richness. To reduce this bias, we considered mapping intensity by designating 50 control species, all of which had to be present in order to include a grid into the analysis. These control species are ubiquitous and assumed to occur in every grid cell. Grid cells that lack any of the control species were regarded as not sufficiently sampled and excluded from the data set. 45 of the control species were the most ubiquitous species in Germany according to KRAUSE (1998) and five additional ubiquitous species which are either inconspicuous or difficult to determine (we do not want to publish their names as this may bias future mapping schemes; the names are available upon request from the corresponding author). This left 3,353 species for analysis (species in FLORKART and in BIOLFLOR excluding control species). For the analysis of species richness among grid cells, we could use 1,928 of the 2,995 grid cells. Despite the exclusions, species richness might still represent a lower bound; however, we expect that this bias is the same for native and alien species and therefore should not affect the results.

Species numbers were calculated for all doubtless occurrences after 1950; cultivated species or those brought intentionally to the wild for ornamental or dubious conservational reasons were excluded.

The grid cell area changes as Germany spans from c. 118 km² at 55° N to c. 140 km² at 47.2°. Therefore we corrected the numbers of species per grid cell according to the analysis of MALYSHEV et al. (1994) on the species area relationship in Central Europe as this is independent determined. The species area relationship of ARRHENIUS (1921) was used for correcting species number:

$$S_{\text{cor}} = S_0 \left(\frac{A_0}{A} \right)^{0.15} \quad (1)$$

where S_0 is the originally recorded species number at a grid cell with area A_0 and S_{cor} is the corrected species number at an area $A = 129.8$ km² (50° N). The exponent was empirically determined by MALYSHEV et al. (1994) for central western Germany (49.5°–51.5° N).

Environmental data

We used 45 environmental variables to explain differences in species richness among grid cells (c. 130 km²). Those parameters were transformed from digital maps with polygon-topology to the grid cells of the 1:25,000 ordnance survey topographical map by intersection, and exported into the database format that we used.

Spatial coordinates

We used the South and East enumeration of the 1:25,000 ordnance survey maps as southing and easting of the grid cells as explanatory variables and for the correction of spatial autocorrelation.

Land Cover

Corine Land Cover (CLC) data, provided by the "Statistisches Bundesamt" (1997) was used to calculate the following variables per grid cell: number of patches, average patch size, variation coefficient of patch size, number of different types, number of aggregated types (aggregated types are urban area, agricultural area, forests and near-nature area, wetland area, water surface area).

Soil data

Soil data was provided by the soil survey map (Bodenübersichtskarte) 1:1,000,000 of the "Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)" (<http://www.bgr.de>). We calculated number of patches, average patch size, variation coefficient of patch size, number of types, and number of aggregated types per grid cell. The soil types were aggregated to following classes: soils of coasts and bogs, soils of floodplains and valleys, soils of

lowlands, soils of loess landscapes, soils of low mountain, soils of high mountain, anthropogenic soils.

Geological data

For geological data, we used the geological survey map 1:1,000,000 (Geologische Übersichtskarte) of the “Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)”. For each grid cell, we calculated number of patches, average patch size, variation coefficient of patch size, number of geological types, number of aggregated types (aggregated types are lime, sand, loess, clay, others).

Climate data

Climate data on a 1 km² grid scale was provided by the “Deutscher Wetterdienst, Department Klima und Umwelt”. Recording period for temperature data was 1951–1980, for precipitation data 1961–1990. We calculated per grid cells averages and coefficients of variation of mean January temperature, mean July temperature, mean annual temperature, mean annual precipitation, difference mean July temperature – mean January temperature.

Altitude

Averages and coefficients of variation of altitude per grid cell were calculated after the ARCDaDeutschland500 dataset, scale 1:500,000, provided by ESRI.

Spatial autocorrelation

One of the most fundamental assumptions in statistical hypothesis testing is the independence of the observations. Spatial patterns which cause autocorrelation violate this assumption in many ecological analyses and thus overestimate the degrees of freedom which leads to wrong error probabilities (LEGENDRE & FORTIN 1989). Therefore, we corrected the significance of slopes in ordinary least square regressions by using corrected degrees of freedom (v_c) as proposed by DUTILLEUL (1993) which is a generalisation of the method of CLIFFORD et al. (1989). This test corrects the variance of the test statistics as well as the approximate degrees of freedom (LEGENDRE et al. 2002). The calculation was performed with MOD_T_TEST by LEGENDRE (2000). Thus we computed the modified t -statistic (t_c) from the correlation coefficient r :

$$t_c = \frac{r\sqrt{v_c}}{\sqrt{1-r^2}}, \quad (2)$$

where $v_c = v_{\text{Dut}} - k$; v_{Dut} is the corrected degrees of freedom calculated with the modified t -test algo-

rithm and k is the numbers of parameters fitted in the model (LEGENDRE et al. 2002). The corrected error probability p_c was computed from t_c . If no spatial autocorrelation is present in the data (and $v_c = v = n - 2 - k$), the value t_c is identical to the t -statistic used for testing the significance of a partial regression coefficient in multiple regression (LEGENDRE et al. 2002).

Species richness of native and alien species

The structural relationship between alien and native species richness was examined by Major Axis (MA) Regression, as all variables are in the same dimension and the errors on both axes are assumed to be in the same order of magnitude (LEGENDRE & LEGENDRE 1998). In contrast to Ordinary Least Square (OLS) Regression, where the sum of vertical squared deviations is minimised (regressing y on x), MA Regression minimises the sum of Euclidean distances to the regression line (i.e. minimising the orthogonal deviations). Therefore, the estimated MA regression line is the first principal component of a scatter of points and the absolute slope is always higher than in OLS Regression (LEGENDRE & LEGREND 1998). Permutation tests with 4,999 permutations were used to test if the slopes differ significantly from 0 and the 95% confidence intervals (C.I.) were calculated to test whether the slopes differ significantly from 1. The calculations were performed with the software Model II Regression by LEGENDRE (2001). The permutation procedure does not account for spatial autocorrelation, but it does not overestimate the degrees of freedom (or effective sample size) as in ordinary least square regression (cf. LENNON 2000). An R^2 -like ratio could be obtained by the ratio of the dominant eigenvalue to the total of eigenvalues $\lambda_1/\lambda_{\text{tot}}$, which could account for a proportion of the total variance (LEGENDRE & LEGENDRE 1998). Additionally, we used the R^2 of an OLS regression to compare the explained variances with the corresponding multiple linear regression of the environmental parameters. The error probability is corrected by a modified t -test (DUTILLEUL 1993), as described above.

The relationship between natives and aliens is tested on all three spatial scales. Additionally, we tested the relationship between threatened or endangered species vs. neophytes. Threatened or endangered species (natives and archaeophytes) were taken from the “Red List of vascular plants of Germany” (KORNECK et al. 1996).

Environmental and ecological variables

To reduce the number of variables, we performed a Principal Components Analysis of the correlation matrix of these parameters using SPSS 9.0 (SPSS

Inc. 1999). Principal components that explained more than 4% of the variance (eigenvalues ≥ 2) were used for further analysis. Less important principal components proved to be difficult for interpretation.

Species richness and environment

The scores of the principal components were analysed as independent variables in multiple linear regression using ordinary least squares. The dependent variables were species numbers (corrected for area, see above) of natives, archaeophytes, and neophytes, respectively. As the axes of a PCA are orthogonal to each other, the final model gives the significant regressors without the necessity to use a (dubious) selection procedure. This calculation provides the structural relationship but does not account for spatial autocorrelation or spatial dependence. However, as latitudinal and longitudinal gradients (that are by definition spatially dependent) have a considerable importance for macroecology, we present these results, as well. We then corrected for spatial autocorrelation using the modified *t*-test (DUTILLEUL 1993) and tested each correlation of the resulting principal components with the species richness of native plants, archaeophytes and neophytes, respectively. As the principal components are orthogonal to each other (thus lacking any redundancy), the resulting correlation coefficient *r* corresponds to the standardised correlation coefficient BETA of the multiple regression.

Measures of similarity

To assess the effects of alien invasions onto native plant assemblages, especially regarding homogenisation, we calculated species similarities for natives, archaeophytes and neophytes, respectively. To minimise problems related to spatial autocorrelation and to avoid the calculation of all 1,857,628 similarities among 1,928 grid cells with further unresolved problems in test statistics, we calculated the indices among 30 randomly selected grid cells (1:25,000 ordnance survey maps)

Standardised similarity

Classical coefficients of similarity (such as JACCARD or SORENSEN) have the disadvantage, that they are heavily influenced by differences in species numbers. This problem is circumvented by the procedure of GILPIN & DIAMOND (1982) to calculate standardised similarities (S_s) between pairs of grid cells:

$$S_s = \frac{O_{ij} - E_{ij}}{\sqrt{SD_{ij}}}, \quad (3)$$

where O_{ij} is the observed number of shared species between grid cell *i* and *j*, E_{ij} is the expected number of shared species between grid cell *i* and *j* and SD_{ij} is the associated standard deviation. E_{ij} and SD_{ij} were derived from the marginal totals of the matrix, thus keeping the probability of occurrence proportional to the incidences of specific species and grid cell. When the probability of occurrence of a species in a particular case exceeds unity (which may rarely happen), this value is cut off to one, as this alters just marginally the results (GILPIN & DIAMOND 1982). This standardised similarity should be independent of species richness patterns and is used in our first analysis.

However, the range of values provided by the method of GILPIN & DIAMOND (1982) is positively correlated with species number. It is possible to calculate matrix correlations and it is very useful as a biogeographic tool for grouping sites on the basis of their similarity (GOTELLI & GRAVES 1996) as long as no between-group comparison is needed. But it is not possible to compare these similarity values between groups differing in species number as if similarity limits would be fixed.

Simpson similarity

To overcome this drawback, we then used a modification of SIMPSON'S (1943) index, which has a lower limit of zero (no species between two grid cells in common) and an upper limit of one (the complete flora of one grid cell is included in the other or both are identical). The Simpson index is calculated as:

$$S_i = \frac{a}{a + \min(b, c)} \quad (4)$$

where S_i is the similarity index, *a* the number of species present in both grid cells, *b* and *c* are those species just present in one or the other unit, respectively. As any difference in species richness will inflate either *b* or *c*, choosing the smaller of these decreases the influence of differences in species richness on similarity (LENNON et al. 2001). Accordingly, LENNON et al. (2001) could empirically verify (at least for birds in Britain) that a turnover gradient based on S_i is not influenced by local differences in species richness.

Similarities and homogenisation

Plotting the similarities of aliens against those of natives, enabled us to look for an effect towards homogenisation (MCKINNEY & LOCKWOOD 1999), i.e. a higher amount of similarity. When alien floras are more similar than natives, the resulting marks will scatter above the bisector and lead to an overall increase in similarity which indicates homogenisa-

tion compared to the pristine flora. The opposite is true, when the resulting scatter is below the bisector. A resulting scatter along the bisector would mean that those biogeographical patterns (as estimated by similarity) provided by natives are being followed by aliens. The former relationship was tested by Fischer's paired comparison randomisation test (MANLY 1991) with 4,999 randomisations. In this context, this procedure might be seen as a randomised form of a sign test. But as the 435 calculated similarities result from just 30 samples, a randomisation test was preferred over the sign test. To see if there is a correlation between the similarity matrices we performed a Mantel test (MANTEL 1967, 4,999 permutations). To compare the relationship between the two similarity matrices with the bisector (i.e. slope = 1, intercept = 0), we calculated the regression between alien and native similarities as Major Axis regressions (because both variables have similar errors) and used the 95% confidence intervals. The significance of the slope (against 0) was tested by a randomisation test with 4,999 permutations using Model II software (LEGENDRE 2001).

Results

Relationships of species richness between native and alien plants

There is a strong structural relationship between the number of natives and the number of aliens on the c. 130 km² scale (Fig. 1). Though there is considerable scatter around the regression, the ratio λ_1/λ_{1+2} is quite high (Table 1).

The slope of the MA regression line for archaeophytes vs. natives is >1 with 1 outside the 95% confidence interval; the slope of the regression for neophytes is even three times higher. This means, on a log-log scale, that the proportion of alien plant species increases with the richness of the native flora and much stronger for neophytes than for archaeophytes.

When calculating the regression of the number of neophytes vs. the number of threatened or endangered species on the 130 km² scale, there is a high amount of variation explained with a slope not significantly differing from 1 (Table 1, a regression of archaeophytes on Red List species was not permissible as the "Red List" incorporates archaeophytes). Similar results as for the c. 130 km² scale are also found on the c. 1,135 km² scale and 10,300 km² scale (Table 1). However, the slope of the relationship between archaeophytes and

Table 1
Results of the major axis regressions and the ordinary least square regressions of native and alien plant species richness (\log_{10} -transformed) across several spatial scales

Scale	Dependent/Independent	major axis regression			ordinary least square regression						
		slope	95% C.I. of slope	λ_1/λ_{1+2}	p	slope	R^2	F	V_c	p_c	N
c. 130 km ²	Archaeophytes/Natives	1.56	[1.49, 1.64]	0.86	0.0002	0.92	0.46	91.27	108.49	<0.001	1928
c. 130 km ²	Neophytes/Natives	4.26	[3.96, 4.61]	0.9	0.0002	1.25	0.26	24.81	71.23	<0.001	1928
c. 130 km ²	Neophytes/"Red List"	1.14	[0.99, 1.31]	0.66	0.0002	0.32	0.1	19.74	185.03	<0.001	1928
c. 1,135 km ²	Archaeophytes/Natives	1.68	[1.42, 2.01]	0.82	0.0002	0.81	0.36	24.35	43.74	<0.001	243
c. 1,135 km ²	Neophytes/Natives	6.32	[5.18, 8.07]	0.94	0.0002	1.7	0.25	32.59	10.97	0.002	243
c. 10,300 km ²	Archaeophytes/Natives	1.03	[0.57, 1.90]	0.79	0.0014	0.6	0.35	7.98	17.97	0.01	27
c. 10,300 km ²	Neophytes/Natives	5.18	[2.91, 19.98]	0.91	0.0112	1.32	0.23	6.29	21.04	0.02	27
c. 1,135 km ²	Archaeophytes/Natives	1.68	[1.42, 2.01]	0.82	0.0002	0.81	0.36	24.35	43.74	<0.001	243
c. 1,135 km ²	Neophytes/Natives	6.32	[5.18, 8.07]	0.94	0.0002	1.7	0.25	32.59	10.97	0.002	243
c. 10,300 km ²	Archaeophytes/Natives	1.03	[0.57, 1.90]	0.79	0.0014	0.6	0.35	7.98	17.97	0.01	27
c. 10,300 km ²	Neophytes/Natives	5.18	[2.91, 19.98]	0.91	0.0112	1.32	0.23	6.29	21.04	0.02	27

neophytes does not differ significantly from 1 any more on the 10,300 km² scale whereas for neophytes vs. natives the slope is five times higher. As most of the results on the different scales considered are in the same order of magnitude we present just the results for archaeophytes and neophytes vs. natives on the c. 130 km² scale graphically (Fig. 1) and use this scale for further analyses. The results of an ordinary least square regression are provided in Table 1 for comparison. The slopes of the regression of neophyte species numbers vs. native species numbers are always >1, archaeophyte numbers vs. native numbers are always <1 on all analysed scales.

Environmental data

We hypothesised that a common mechanism determines native and alien plant species richness, in particular structural or landscape diversity. We reduced the numbers of environmental variables by principal components analysis prior to multiple regression. The resulting six principle components are presented in Table 2 and explain a cumulative total variance of c. 52%. PC 1 is strongly negatively influenced by the average altitude and variables that are strongly influenced by altitude such as area of

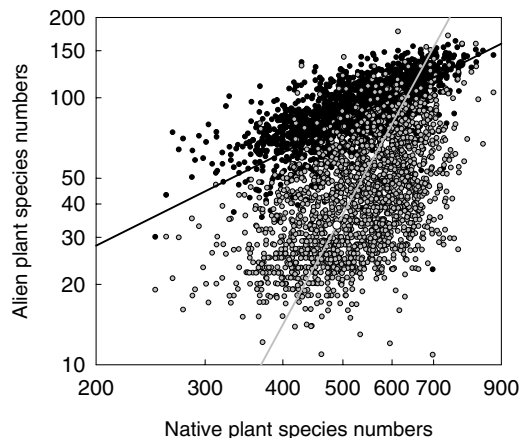


Fig. 1 Regression number of archaeophytes (black circles) and neophytes (grey circles), respectively, vs. number of native plant species in Germany on a logarithmic (log 10) scale. Species numbers are corrected for area using the species area relationship of ARRHENIUS (1921), see methods section for further details

soils of low mountains, coefficient of variation of annual temperature, coefficient of variation of July temperature. Low altitudes are also connected with a higher average of annual temperature and a lower average of annual precipitation, and less important an increase in average July temperature, decreasing coefficient of variation of annual precipitation, and increasing average January temperature. This gradient is almost parallel to a North-South gradient as the lowlands are in the North of Germany, highlands of medium altitude in the centre and the high Alps in the South. Additionally, this topography does also account for the area of woodlands or near-natural habitats, and number of aggregated soil types. Shortly, this PC 1 could be characterised as a gradient in altitude or a South-North gradient. PC 2 is positively related to the number of aggregated geological types, number of geological types, negatively influenced by area of soils of lowlands, and positively by urbanised area. It could be summarised as geological diversity. Relevant for PC 3 are a longitudinal gradient comprising a West-East gradient with decreasing average January temperature, increasing difference July–January temperature (as proxy of continentality), increasing geological patch number which results in decreasing average geological patch size, and increasing geological type number; it could be summed up as a West-East gradient. PC 4 just has temperature difference between July and January as the only important parameter which describes the continentality of the climate. This is not to be confounded with the West-East gradient, as there is some mitigating influence of the Baltic Sea in the Northeast. PC 5 is negatively correlated to the loess areas regardless whether it is subsoil geology or soil. Finally, PC 6 has negative loadings of the area of sandy subsoil, and positive ones of the area of other geological substrates, and urbanised areas.

Relationship between species richness and environment

The multiple regressions of the principal components as predictors of native and alien species richness without correcting for spatial autocorrelation provide highly significant models, but explain only 35% variation for

Table 2

Result of the Principal Component Analysis of the environmental variables (loadings >0.5| are presented in **bold**)

avg: average, cv: coefficient of variation, CLC: Corine Land Cover; numbers of specific types are counted as provided by the source; numbers of specific aggregated types are grouped as explained in the methods section

Principal Components	1	2	3	4	5	6
southing	-0.614	0.466	-0.079	0.191	-0.219	-0.112
easting	0.146	-0.437	0.672	0.386	-0.197	0.168
avg July temperature	0.604	0.332	-0.075	0.422	-0.337	0.020
cv of July temperature	-0.736	0.317	0.137	-0.047	0.047	0.014
avg January temperature	0.557	0.359	-0.623	-0.232	0.066	-0.053
cv of January temperature	0.039	-0.024	-0.062	-0.014	-0.046	0.016
temperature difference July-January	-0.060	-0.087	0.571	0.590	-0.350	0.071
avg mean annual temperature	0.715	0.360	-0.396	0.098	-0.174	0.016
cv of mean annual temperature	-0.765	0.221	0.134	-0.019	0.061	0.107
avg annual precipitation	-0.702	0.176	-0.276	-0.153	0.195	-0.016
cv of annual precipitation	-0.581	0.329	0.169	-0.099	0.042	0.043
avg altitude	-0.889	0.131	0.125	0.015	-0.034	-0.030
cv of altitude	-0.007	0.087	0.116	-0.096	0.083	0.291
number of CLC patches	-0.383	0.405	-0.283	0.190	0.386	-0.035
number of CLC types	0.299	0.429	-0.188	0.340	0.366	0.266
avg size of CLC patches	0.220	-0.408	0.243	-0.270	-0.297	-0.016
cv of size of CLC patches	0.221	-0.237	0.130	-0.394	-0.202	-0.047
number of aggregated CLC types	0.365	-0.228	0.104	0.237	0.406	0.256
agricultural area	0.286	-0.174	0.054	-0.466	-0.104	-0.208
wetlands area	0.183	-0.173	-0.097	-0.245	0.323	0.123
urbanised area	0.208	0.520	-0.229	0.250	0.032	0.503
forest or near-nature area	-0.612	0.003	0.070	0.347	0.168	-0.200
watersurface area	0.165	-0.178	0.099	0.202	0.236	0.329
number of geological patches	0.120	0.332	0.528	0.023	0.266	-0.147
number of geological types	0.120	0.547	0.504	-0.140	0.146	-0.005
avg size of geological patches	-0.240	-0.237	-0.520	0.001	-0.253	0.162
cv of size of geological patches	-0.156	-0.106	0.091	0.119	0.165	-0.225
number of aggregated geological types	0.212	0.602	0.148	-0.313	-0.112	-0.112
area of lime subsoil	-0.205	0.304	0.123	-0.173	-0.088	-0.231
area of loess subsoil	0.137	0.386	0.076	-0.175	-0.538	0.253
area of sandy subsoil	0.315	0.067	-0.194	0.471	-0.013	-0.615
area of clay subsoil	0.160	0.030	-0.177	-0.355	0.204	0.122
area of other subsoil	-0.411	-0.279	0.184	-0.160	0.123	0.540
number of soil patches	0.407	0.361	0.434	-0.140	0.240	-0.089
number of soil types	0.403	0.429	0.422	-0.137	0.218	-0.112
avg size of soil patches	-0.468	-0.255	-0.388	0.099	-0.213	0.090
cv of size of soil patches	0.095	0.032	0.173	0.009	0.147	-0.073
number of aggregated soil types	0.510	0.396	0.266	-0.057	0.129	0.022
area of anthropogenic soils	0.216	0.304	-0.091	0.272	0.003	0.491
area of soils of high mountains	-0.081	0.027	0.059	-0.015	0.023	-0.036
area of coastal soils	0.370	-0.351	-0.064	-0.360	0.379	0.081
area of soils of loess landscape	0.052	0.446	0.152	-0.287	-0.569	0.223
area of soils of low mountains	-0.840	0.175	-0.023	-0.051	0.117	-0.083
area of soils of planes	0.363	-0.534	0.145	0.196	0.140	-0.071
area of soils of valleys and floodplains	0.464	0.174	-0.235	0.274	-0.008	-0.287
eigenvalues	7.933	4.547	3.481	2.777	2.430	2.087
percentage variance	17.630	10.104	7.736	6.172	5.401	4.638
cumulative percentage variance	17.630	27.734	35.471	41.643	47.043	51.682

native species richness (5 significant principal components, $F_{5, 1922} = 212.4$), 43% for archaeophyte richness (6 significant principal components, $F_{6, 1921} = 243.7$), and just 37% for neophyte richness (6 significant principal components, $F_{6, 1921} = 189.4$). The most important principal component in the multiple regression models for species richness of natives and aliens as well is PC 2 “geological diversity” (Table 3) with a positive influence. The first five PC’s are the most important ones for native plant species richness, PC 1 “south north gradient” (negatively related to native species richness) being second and PC 3 “west east gradient” (positively related to species richness) third most important. On the other hand, the second most important components for alien plant species richness are PC 5 “low proportion of loess area”, negatively related to archaeophyte species richness, and PC 6 “no sandy soils but urbanisation” positively related to neophyte species richness. However, the third most important component for the two later groups is PC 1 “south north gradient” again, but with an inverse relation.

When taking spatial autocorrelation into account, the main gradients (latitudinal and longitudinal) are removed (Table 3). The only significant principal component for native plant species richness is PC 2 “geological diversity”. High archaeophyte diversity is also associated with geological diversity (and urbanisation, PC 2), and also with a high proportion of loess landscapes (PC 5). Beside PC 2, high numbers of neophytes are associated with a low proportion of sandy soils but a high proportion of urban areas (PC 6).

To estimate archaeophyte species richness, native plant species richness is a much better predictor (R^2 OLS regression: 0.49; $p_c < 0.001$) than all the significant environmental variables combined (see Table 3). Neophytes however, are relatively poorly predicted by the chosen environmental variables (see Table 3), but the estimate from native plant species richness is even poorer (R^2 OLS regression: 0.24; $p_c < 0.001$).

Species similarities and homogenisation

The floristic similarities using the model of GILPIN & DIAMOND (1982) show a clear relationship between the similarities of native and

archaeophytes as well as neophytes (Fig. 2a, b, Table 4). The results when using Simpson similarities are comparable, though the correlation is much weaker, albeit still highly significant. Furthermore, we compared the resulting Simpson similarities with the bisector (Fig. 2c, d, Table 4), as Simpson’s index has fixed limits. Fishers paired comparison test of archaeophytes vs. natives shows highly significant more occurrences above the bisector (archaeophytes’ similarities are higher than corresponding natives’ similarities), but the bisector is within the 95% confidence intervals of the major axis regression’s slope and intercept. Neophytes vs. natives show a different picture: There are significantly more neophytes below the bisector (neophytes similarities are lower than corresponding native similarities), but the slope is much steeper and the intercept much lower than of the bisector, excluding the bisector from the respective confidence intervals.

Discussion

Relationships of species richness between native and alien plants

One may argue that plant species richness patterns are mere artefacts of biased mapping intensity (cf. BARTHLOTT et al. 1999a, b). Yet, HAEUPLER (2000) claims that this is unlikely because areas with high plant species richness do not coincide with centres of floristic research. Furthermore we corrected for possible bias in mapping intensity by some “control species” (see methods section) and proved that those areas exceptionally species rich (natives, natives and aliens) are not related to centres floristic research (unpublished). But even if there would be some bias, this would probably be the same for native and alien species and therefore should not affect the results. Thus we hypothesised that common factors underlie natives’ as well as aliens’ plant species richness.

We could clearly demonstrate that there is a positive relationship between natives and aliens on all investigated scales. This is similar to results of LONSDALE 1999; STOHLGREN et al. 1999; STADLER et al. 2000; PYŠEK et al. 2002. Contrasting, there are theoretical considerations at community scale that increasing diver-

Table 3

Results of multiple linear regression of native and alien plant species richness and principal component scores;

Beta: standardised partial regression coefficient; t : t -statistic; R^2 : coefficient of determination adjusted for number of predictors; SE: standard error; ν : degrees of freedom; F : F -statistic; p : two-tailed error probability. R_c , ν_c , t_c , p_c : results after corrected degrees of freedom due to autocorrelation by using a modified t -test (DUTILLEUL 1993); ns.: not significant

Models summaries and ANOVA

Dependent variables

	adj. R^2	SE	ν	F	p	adj. R_c^2
natives	0.35	78.367	5, 1922	212.45	<0.001	0.222
archaeophytes	0.43	17.105	6, 1921	243.73	<0.001	0.359
neophytes	0.37	18.635	6, 1921	189.38	<0.001	0.322

Coefficients

Dependent variables and predictors

	Beta	t	p	ν_c	t_c	p_c
natives						
constant		300.60	<0.001			
PC 2	0.47	25.78	<0.001	37.84	3.25	0.003
PC 1	-0.26	-13.99	<0.001	35.3		n.s.
PC 3	0.23	12.5	<0.001	33.71		n.s.
PC 4	0.11	6.07	<0.001	49.89		n.s.
PC 5	0.05	2.96	0.006	93.39		n.s.
PC 6	0.01		n.s.	192.88		n.s.
archaeophytes						
constant		237.43	<0.001			
PC 2	0.56	32.59	<0.001	77.19	5.87	<0.001
PC 5	-0.21	-12.47	<0.001	116.95	-2.35	0.02
PC 1	0.17	9.84	<0.001	74.49		n.s.
PC 3	0.12	7.19	<0.001	39.55		n.s.
PC 4	0.12	7.01	<0.001	64.24		n.s.
PC 6	0.12	6.87	<0.001	216.96		n.s.
neophytes						
constant		108.58	<0.001			
PC 2	0.51	28.42	<0.001	96.95	5.40	<0.001
PC 6	0.24	13.35	<0.001	202.46	3.52	<0.001
PC 1	0.17	9.63	<0.001	64.38		n.s.
PC 3	-0.09	-5.06	<0.001	54.52		n.s.
PC 4	0.08	4.62	<0.001	80.93		n.s.
PC 5	-0.06	-3.25	0.002	122.35		n.s.

sity decreases invasibility (e.g. PIMM 1984; CASE 1990; DRAKE 1990; LAW & MORTON 1996). On the neighbourhood scale, the pattern is already not that clear. In a short review, LEVINE & D'ANTONIO (1999) present investigations with a positive as well as a negative correlation between diversity and invasibility. Similarly, STOHLGREN et al. (1999) had positive as well as negative correlations between

native and alien plants species on a 1 m² scale. An analysis by LEVINE (2000) shows that species loss at small scales may reduce invasion resistance. He argues that at community scales, an overwhelming effect of ecological factors spatially covarying with diversity makes the most diverse communities most likely to be invaded. However, even the smallest scale of our analysis is much larger than the neighbour-

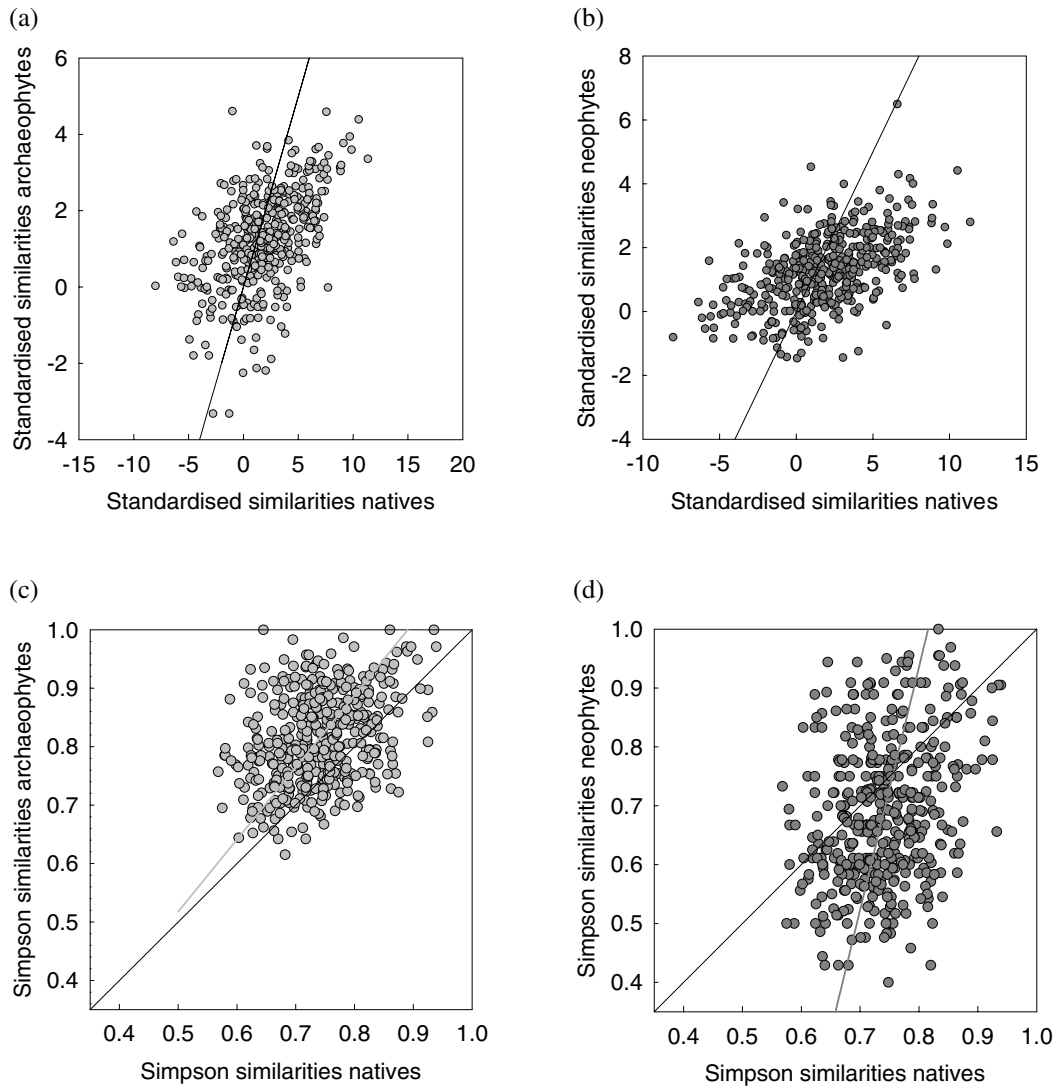


Fig. 2

Pairwise comparisons of similarities between aliens and natives: standardised similarities (GILPIN & DIAMOND 1982) of archaeophytes vs. natives (a) and neophytes vs. natives (b); Simpson similarities of archaeophytes vs. natives (c) and neophytes vs. natives (d). Black lines are bisectors, grey lines are regression lines

hood or the community scale. When ELTON (1958) presented his ideas about diversity and resistance to invasions, he did not care about scale: in this context he changes among landscape, ecological system, community, and habitat scale (pp. 116–117, 145–150).

Relationship between species richness and environment

Interestingly, though PC 1 could be considered a “natural” gradient as it consists mainly of variables related to topography and climate, it is in opposite direction to a global north-south gradient. A probable reason for this is the dis-

Table 4
 Relationships between native and alien similarities
r: correlation coefficient; *p*: two tailed error probability; C.I.: confidence interval; λ : eigenvalue; see methods section for details

Test	Mantel test		Fishers paired comparison design test				major axis regression ($y = a+bx$)				
	<i>r</i>	<i>p</i>	≤observed	≥observed	as far as or further from 0 than observed	<i>a</i>	C.I. of <i>a</i>	<i>b</i>	C.I. of <i>b</i>	λ_1/λ_{tot}	<i>p</i>
standardised similarities											
archaeophytes vs. natives	0.50	<0.001									
neophytes vs. natives	0.52	<0.001									
Simpson similarities											
Archaeophytes vs. natives	0.34	<0.001	0.02%	100.00%	0.02%	-0.10	[-0.38, 0.11]	1.23	[0.96, 1.62]	0.67	<0.001
Neophytes vs. natives	0.28	<0.001	100.00%	0.02%	0.02%	-2.37	[-3.78, -1.61]	4.13	[3.11, 6.04]	0.77	<0.001

tribution of mountains in Germany, resulting in a reversal of global climatic gradients on a regional scale. PC 2 could be interpreted mainly as a component of geological substrate diversity. This supports the principal idea of “geodiversity” (in a wider sense) as a determinant of biological diversity (e.g. BARTHOLOTT et al. 1996). The principal component “geological diversity” has an additional positive loading for area of urbanisation. This could indicate that human settlement was preferably in areas of high (natural) geological diversity. Therefore we consider PC 2 as a “natural gradient”, as well. PC’s 3 and 4 could also be interpreted as “natural”, as all of them have high loadings of natural variables (climate, geology), whereas PC 6 regards to land utilisation, in particular urbanisation. Nevertheless, PC 6 has a negative loading of the area of sandy geological subsoil. As sandy subsoils are very poor in nutrient content and thus not very good arable land, they could historically not provide enough food from the land to supply big cities, which may explain the negative relationship between areas of sandy subsoil and urbanisation. PC 5 “low proportion of loess areas” is a natural component but it is the main reason for long lasting very intense agricultural use, as the best soils for agriculture derived from loess subsoil (cf. CATT 2001). Thus, we could interpret this principal component in terms of “natural” as well as “anthropogenic” component. However, as agriculture has much more area (though of lower quality) on non-loess subsoil, it does not load very high on PC 5.

Considering spatial autocorrelation, geological substrate diversity remains as one common cause that determines species richness of alien and native plants. This means that the natural diversity of different substrates promotes species richness (probably through resource availability or habitat diversity, e.g. LEVINE & D’ANTONIO 1999; LONSDALE 1999; STOHLGREN et al. 1999; DAVIS et al. 2000; STADLER et al. 2000; DEUTSCHEWITZ et al. 2003). Additionally, archaeophytes are promoted by subsoil that provided the best arable land in Germany and thus had the longest history in land utilisation. Neophytes are promoted by urbanisation, as already noticed by many authors (e.g. KOWARIK 1990; ROY et al.

1999). However, the results suggest that the diversity of geological substrates (or more generally: habitat or landscape diversity) promotes native as well as alien species richness and our data do not indicate that threatened natives are replaced by aliens due to a direct causal link (e.g. human impact). Thus, we disagree with conclusions of MCKINNEY & LOCKWOOD (2001) who show a positive correlation between the numbers of established non-native plant species and threatened plant species for various regions of the world. MCKINNEY & LOCKWOOD (2001) argue that this correlation between extinction and introduction is related to habitat loss of native species followed by habitat gain for introduced species.

At least for archaeophyte richness, native plant species richness is a better predictor than all the significant environmental variables of our analysis. One reason may be that we did not choose the correct (or enough) variables. But one should be aware that human perception of the environment is completely different from plants' perception and that native plants' perception of the environment is closer to that of archaeophytes than to that of neophytes (e.g. due to a longer common post-glacial evolutionary history).

Species similarities and homogenisation

Our analyses of the similarities showed that there is a highly significant correlation between the similarity matrices. Furthermore, we found that archaeophytes tend towards homogenisation *and* follow the biogeographic pattern provided by natives. Most archaeophytes are plants of arable fields, which themselves are very homogenous habitats due to human land utilisation. Thus it is evident that they seem to promote homogenisation. On the other hand, they mapped the pattern of natives for which we suggest two complementary hypotheses: (1) they are quite dependent on characteristic soils and climatic factors; (2) being here for many hundreds (or even thousands) of years, they had enough time to match existing patterns. Contrary, we could not support the idea that neophytes lead to homogenisation of the German flora on a regional scale *and* the similarity pattern provided by natives is not followed

completely. While natives display a comparably small range of Simpson similarities neophytes span almost the complete range. Our findings support the idea of environmental conditions that act as filters generating patterns of distribution in the flora of aliens that correspond to the pattern of native flora (STADLER et al. 2000): Archaeophytes, though mainly restricted to a homogenous habitat, react usually sensitive to climatic or soil factors (e.g. MÜLLER 1963). Contrary, neophytes (e.g. generally grow on a variety of different substrates under different conditions. Thus, archaeophytes are "Kulturfolger" (ROSENZWEIG 2001a, or cultural followers) in anthropogenic homogenised habitats whereas neophytes might be a true enrichment of regional biodiversity. Our results are corroborated by STADLER et al. (2000), who also found a high correlation between similarities of natives and aliens in Kenya. However, as the global area and the global species pool is limited, a global homogenisation due to species exchange between biota could be demonstrated by WEBER & PYŠEK (2001), but is not inevitable in the long run (ROSENZWEIG 2001b).

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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.
- ARRHENIUS, O. 1921: Species and area. – *J. Ecol.* **9**: 95–99.

- 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 Bot. Fennica* **162**: 103–110.
- BARTHLOTT, W.; KIER, G. & MUTKE, J. 1999b: Globale Artenvielfalt und ihre ungleiche Verteilung. – *Courier Forsch.-Inst. Senckenberg* **215**: 7–22.
- BARTHLOTT, W.; LAUBER, W. & PLACKE, A. 1996: Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. – *Erdkunde* **50**: 317–327.
- CASE, T. J. 1990: Invasion resistance arises in strongly interacting species-rich model competition communities. – *Proc. Natl. Acad. Sci. United States of Amer.* **87**: 9610–9614.
- CATT, J. A. 2001: The agricultural importance of loess. – *Earth Sci. Rev.* **54**: 213–229.
- CLIFFORD, P.; RICHARDSON, S. & HÉMON, D. 1989: Assessing the significance of the correlation between two spatial processes. – *Biometrics* **45**: 123–134.
- CRAWLEY, M. J.; HARVEY, P. H. & PURVIS, A. 1996: Comparative ecology of the native and alien floras of the British Isles. – *Phil. Trans. Roy. Soc. London, Ser. B, Biol. Sci.* **351**: 1251–1259.
- DAVIS, M. A.; GRIME, J. P. & THOMPSON, K. 2000: Fluctuating resources in plant communities: a general theory of invasibility. – *J. Ecol.* **88**: 528–534.
- DEUTSCHEWITZ, K.; LAUSCH, A.; KÜHN, I. & KLOTZ, S. 2003: Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. – *Global Ecol. Biogeogr.* **12**: 299–311.
- DRAKE, J. A. 1990: The mechanics of community assembly and succession. – *J. Theor. Biol.* **147**: 213–233.
- DUTILLEUL, P. 1993: Modifying the *t*-test for assessing the correlation between two spatial processes. – *Biometrics* **49**: 305–314.
- ELTON, C. 1958: *The ecology of invasions by animals and plants.* – London.
- GILPIN, M. E. & DIAMOND, J. M. 1982: Factors contributing to non-randomness in species co-occurrences on islands. – *Oecologia* **52**: 75–84.
- GOTELLI, N. J. & GRAVES, G. R. 1996: Null models in ecology. – Herndon.
- HAEUPLER, H. 2000: Die ungleiche Verteilung der Artenvielfalt innerhalb Deutschlands – eine Antwort. – *Flor. Rundbr.* **34**: 17–24.
- KORNECK, D.; SCHNITTLER, M. & VOLLMER, I. 1996: Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Deutschlands. – *Schriftenr. Vegetationskde.* **28**: 21–187.
- KOWARIK, I. 1990: Some responses of flora and vegetation to urbanization in central Europe: 45–74. – In: H. SUKOPP & S. HEJNÝ (eds.), *Urban ecology: Plants and plant communities in urban environments.* – The Hague.
- KRAUSE, A. 1998: Floras Alltagskleid oder Deutschlands 100 häufigste Pflanzenarten. – *Natur und Landschaft* **73**: 486–491.
- KÜHN, I. & KLOTZ, S. 2002: Floristischer Status und gebietsfremde Arten. – In: S. KLOTZ; I. KÜHN & W. DURKA (eds.), *BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland.* – *Schriftenr. Vegetationskde.* **38**: 47–56.
- LAW, R. & MORTON, R. D. 1996: Permanence and the assembly of ecological communities. – *Ecology* **77**: 762–775.
- LEGENDRE, P. 2000: Program Mod_t_test. Montreal, Département de sciences biologiques, Université de Montreal. (<http://www.fas.umontreal.ca/BIOL/legendre>)
- LEGENDRE, P. 2001: Model II regression – User's guide. Montréal, Département de sciences biologiques, Université de Montréal. (<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.
- LEGENDRE, P. & LEGENDRE, L. 1998: *Numerical ecology.* – Amsterdam.
- LENNON, J. J. 2000: Red-shifts and red herrings in geographical ecology. – *Ecography* **23**: 101–113.
- LENNON, J. J.; KOLEFF, P.; GREENWOOD, J. J. D. & GASTON, K. J. 2001: The geographical structure of British bird distributions: diversity, spatial turnover and scale. – *J. Animal Ecol.* **70**: 966–979.
- LEVINE, J. M. 2000: Species diversity and biological invasions: Relating local process to community pattern. – *Science* **288**: 852–854.
- LEVINE, J. M. & D'ANTONIO, C. M. 1999: ELTON revisited: a review of evidence linking diversity and invasibility. – *Oikos* **87**: 15–26.
- LONSDALE, W. M. 1999: Global patterns of plant invasions and the concept of invasibility. – *Ecology* **80**: 1522–1536.
- MALYSHEV, L. I.; NIMIS, P. L. & BOLOGNINI, G. 1994: Essays on the modelling of spatial floristic diversity in Europe: British Isles, West Germany, and East Europe. – *Flora* **189**: 79–88.
- MANLY, B. F. J. 1991: *Randomization and Monte Carlo methods in biology.* – London.

- MANTEL, N. A. 1967: The detection of disease clustering and a generalized regression approach. – *Cancer Res.* **27**: 209–220.
- MCKINNEY, M. L. & LOCKWOOD, J. L. 1999: Biotic homogenization: a few winners replacing many losers in the next mass extinction. – *Trends Ecol. & Evol.* **14**: 450–453.
- MCKINNEY, M. L. & LOCKWOOD, J. L. 2001: Biotic homogenization: a sequential and selective process 1–17. – In: M. L. MCKINNEY & J. L. LOCKWOOD (eds.), *Biotic homogenization*. – New York.
- MÜLLER, G. 1963: Die Bedeutung der Ackerunkrautgesellschaften für die pflanzensoziologische Gliederung West- und Mittelsachsens. – *Hercynia*, N.F. **1**: 82–166; 213–313.
- PIMM, S. L. 1984: The complexity and stability of ecosystems. – *Nature* **307**: 321–326.
- PLANTY-TABACCHI, A. M.; TABACCHI, E.; NAIMAN, R. J.; DEFERRARI, C. & DECAMPS, H. 1996: Invasibility of species rich communities in riparian zones. – *Conservat. Biol.* **10**: 598–607.
- PRINZING, A.; DURKA, W.; KLOTZ, S. & BRANDL, R. 2002: Which species become aliens? – *Evol. Ecol. Res.* **4**: 385–405.
- PYŠEK, P.; JAROSIK, V. & KUČERA, T. 2002: Patterns of invasion in temperate nature reserves. – *Biol. Conservat.* **104**: 13–24.
- REJMÁNEK, M. 1996: Species richness and resistance to invasions: 153–172. – In: G. H. ORIANI; R. DIRZO & J. H. CUSHMAN (eds.), *Biodiversity and ecosystem processes in tropical forests*. – Berlin, Heidelberg, New York.
- RICHARDSON, D. M.; PYŠEK, P.; REJMANEK, 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.
- ROBINSON, G. R.; QUINN, J. F. & STANTON, M. L. 1995: Invasibility of experimental habitat islands in a California winter annual grassland. – *Ecology* **76**: 786–794.
- ROSENZWEIG, M. L. 2001a: Loss of speciation rate will impoverish future diversity. – *Proc. Natl. Acad. Sci. United States of Amer.* **98**: 5404–5410.
- ROSENZWEIG, M. L. 2001b: The four questions: What does the introduction of exotic species do to diversity? – *Evolutionary Ecol. Res.* **3**: 361–367.
- 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.
- SCHROEDER, F.-G. 1969: Zur Klassifizierung der Anthropochoren. – *Vegetatio* **16**: 225–238.
- SIMPSON, G. G. 1943: Mammals and the nature of continents. – *Amer. J. Sci.* **241**: 1–31.
- SPSS Inc. 1999: SPSS, 9. 0: Applications guide. – Chicago.
- 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.
- Statistisches Bundesamt 1997: Daten zur Bodenbedeckung für die Bundesrepublik Deutschland 1:100.000. – Wiesbaden.
- 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. – *Ecol. Monographs* **69**: 25–46.
- THOMPSON, K.; HODGSON, J. G. & RICH, T. C. G. 1995: Native and alien invasive plants: more of the same? – *Ecography* **18**: 390–402.
- WEBER, E. & PYŠEK, P. 2001: Exotic plant species lead to a biotic homogenization. – *Verh. Gesell. Ökol.* **31**: 319.
- WILLIAMSON, M. 1999: Invasions. – *Ecography* **22**: 5–12.

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