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Plant richness patterns in agricultural and urban landscapes in Central Germany—spatial gradients of species richness

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Abstract

Urban areas are generally inhabited by greater numbers of plant species than rural areas of the same size. Though this phenomenon is well documented, scientists seem to be drawn to opposing views when it comes to explaining the high ratio of alien to native plants. Several ecological concepts claim that in cities, alien species displace native species. However, several studies show that both species groups increase proportionally. Another view tries to correlate the high species number in urban areas to the heterogeneity of the urban landscape. This correlation seems to be evident but still needs to be tested.

Most of these findings stem from studies performed on large or intermediate scales using data from official databases. We wanted to confront existing findings and opinions with our study comparing a typical urban with an agricultural landscape section on a local scale.

Our results support the view that plant species richness is higher in cities than in surrounding rural areas, partly because of a high rate of alien species brought into cities by humans. However, this species richness stems from an increase in alien as well as native species. Higher species richness is supported by a highly varying landscape structure mainly caused by anthropogenic land use.

Keywords: Plant species richness pattern; Native plants; Alien plants; Urbanisation; Landscape structure; Central Europe

1. Introduction

Since about two decades, a number of American and European botanists are dealing with the distribution patterns of alien plant species (e.g. Elton, 1958; Drake et al., 1989; di Castri et al., 1990; Williamson, 1996; Weber, 2003). One special interest is set on the ratio between alien plants and native species in the context of invasion ecology (e.g. Lonsdale, 1999; Stohlgren et al., 1999; Levine and D'Antonio, 1999; Sax, 2002; Sax and Gaines, 2003; Sax et al., 2002; Kühn et al., 2003). Introduced intentionally or unintentionally by humans from other regions and continents, some of

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the alien plants shortly disappear as others establish successfully, and in some cases even become a menace for native plant communities. Undoubtedly, alien plant species actually represent a considerable part of almost all regional floras (e.g. for Germany: Haeupler, 1999; Kühn and Klotz, 2002).

If we look on the distribution of plant species with regard to different land uses, cities undoubtedly play an important role. Even if the percentage of urban land cover is relatively low compared to other land uses on the earth's surface, it is growing irresistibly (Antrop, 2004). Besides the homogenisation of the landscape outside the city, urbanisation and linked processes altered the distribution pattern of plant species. At the beginning of the seventies, Walters (1973) was the first to recognise that the flora of cities is more species rich than the surrounding flora. Haeupler (1974) showed that within the area of Germany (Lower Saxony), cities showed higher species numbers than the open landscape. A number of studies followed and most of them confirmed the higher species numbers in cities (e.g. Pyšek and Pyšek, 1990; Klotz, 1990; Stadler et al., 2000; Deutschewitz et al., 2003; Kühn et al., 2004).

When looking for the reasons of the higher species numbers in urban regions, several recurring arguments are produced in scientific literature. Firstly, it is argued that the species richness of urban regions is due to higher alien species numbers (e.g. Bartlott et al., 1999). Secondly, the great variety of habitats within a town offering a wide range of living conditions is obviously one of the most important factors (Sukopp and Werner, 1983; Kowarik, 1995; Stadler et al., 2000; Kühn et al., 2004). Also, the homogenisation of the open landscape, particularly in regions dominated by agriculture, causes a loss in species richness outside the urban regions (Haeupler, 1974; Deutschewitz et al., 2003). Thus, cities may even represent habitat islands within the open landscape (Pyšek, 1993). Nevertheless, it is assumed that the role of urban regions as centres where foreign species are introduced to the native flora is very important or even fundamental for this phenomenon (Sukopp and Werner, 1983; Kowarik, 1990).

We would follow these findings and arguments by analysing the influence of landscape structure on species distribution. We addressed the following main questions:

- Is the higher plant species richness of urban regions induced by higher numbers of alien species?
- Are native and alien species numbers inversely correlated?
- How do landscape structure characteristics influence the distribution pattern of plant species in urban and agriculturally dominated landscapes in Central Europe?

Many of the studies on species distribution focussed on areas at least the size of administrative districts, using species data taken from official databases and compilations (Miller et al., 1997; Roy et al., 1999; Deutschewitz et al., 2003; Kühn et al., 2003). The intention of our study design was (1) to investigate the relationship between alien and native plant species at a much smaller scale–the local scale and (2) to investigate this relationship based on real field data compiled during one vegetation period and based on a unique and individual plant species knowledge of one research scientist (to prevent the unavoidable differences in species knowledge when several botanists are involved). In a first step, we wanted to find out whether the differences in species occurrence between cities and their wider surroundings can be determined on the finer local scale as well. And if so, we wanted to look for reasons for these differences in distribution patterns by focusing on the influence of land use and its varying surface characteristics as well as on the spatial arrangement of the different surfaces.

2. Material and methods

2.1. Location and plot selection

We selected two landscape sections in Central Germany, differing distinctly in land use pattern: the urban section of the city of Halle and an agriculturally cultivated section west of Halle (see Fig. 1). To avoid climatically caused differences in species occurrence, we selected both sections in one landscape region, called 'Mitteldeutsches Trockengebiet'. The region is situated in the rain shadow of the Harz Mountains, causing continental climate with annual rainfall less than 500 mm.

Each section is defined by a grid of 11×10 cells, each cell of 1 km^2 size. The landscape in the agricultural section is not only dominated by arable fields and

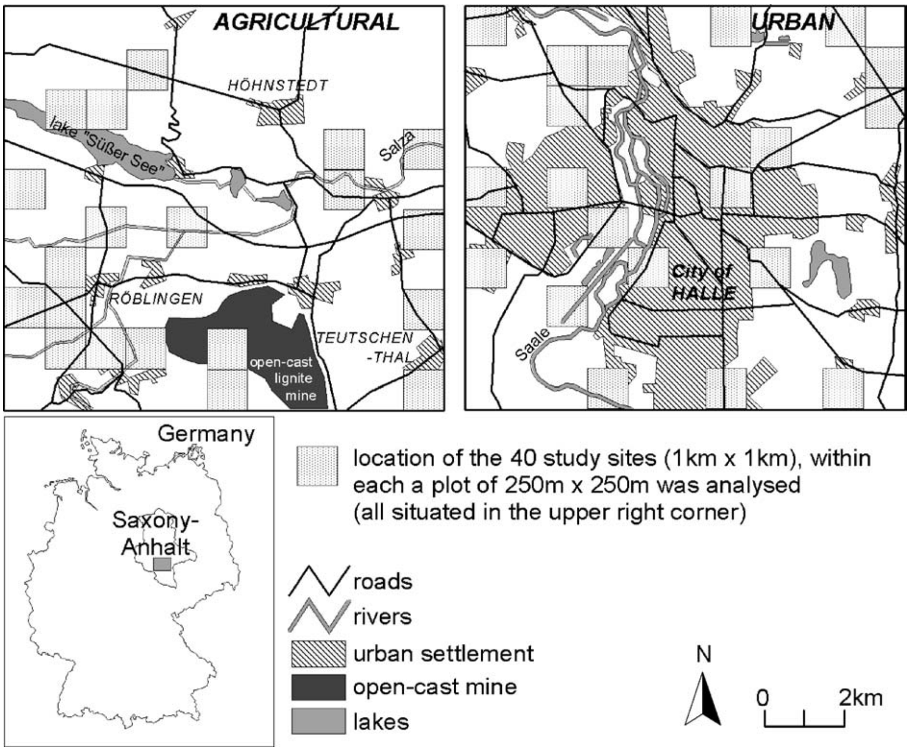

Fig. 1. Geographical situation of agricultural and urban landscape sections in the State Saxony-Anhalt, Central Germany. Within each of the landscape sections, 20 plots were randomly selected and analysed.

fruit-growing orchards, but also by aboveground and underground mining of mineral resources (coal, potassium salt and copper schist). Semi-natural structures are strongly reduced in space and number. The urban section is part of the Halle-Leipzig-conurbation, and apart from typical built-up and industrial/commercial areas, it also includes a complex of pasture and natural forest accompanying the river Saale as parts of recreational areas.

In each of these sections, 20 plots with a size of 250 m × 250 m were selected randomly (Fig. 1).

2.2. Data source

2.2.1. Floristic data

Within each plot, all species of spontaneous vascular plants were sampled, i.e. those populations that reproduce outside cultivation. Hence we excluded cultivated plants of flower beds, crop fields, planted trees or casual escapes. We assigned the ecological characteristics of the species according to the database of biological and ecological traits of the Eastern German Flora (Frank and Klotz, 1990) and BiolFlor (Klotz et al., 2002). Following this, we differentiated between natives and two groups of aliens according to the time of immigration, namely archaeophytes and neophytes. Archaeophytes are ancient immigrants that reached Germany before 1500, usually due to agriculture. Neophytes arrived after 1500 with the discovery of the Americas and the expansion of trade.

2.2.2. Land use data

Land use patterns were derived from field samplings and official habitat maps. We characterised each of the 37 land use types found by indicator value of land use intensity and degree of pavement[1]. The latter were taken from official habitat maps that differentiate

[1] The degree of pavement expresses the degree of anthropogenic soil alteration reaching from the lowest degree of soil compaction up to surface sealing, leading to impervious surfaces with no plant growth.

between 5 degrees: unpaved, low, medium, high, and very high. Land use intensity was assigned to each land use type using degrees of hemeroby by Kowarik (1988) which refer to the degree of habitat change. Since the investigated landscape region was strongly altered by human activities, we applied only 8 of the 11 degrees of the Kowarikian scale: natural habitats of the first 3 degrees of hemeroby did not occur in our landscape sections, and habitats are thus classed from the mesohemerobic up to the metahemerobic degree.

We applied landscape metrics after McGarigal and Marks (1994) to characterise landscape structure, i.e. configuration and composition.

Landscape configuration was described by number of patches (NUMP) and mean patch size (MPS). Because of the very large agricultural fields typical for the region, we calculated the coefficient of patch size variation (PSCOV) as well. Edges were quantified by the number of edges (NUMEDGE) and edge density (EDGED).

Landscape composition was quantified by the number of different land use types (NUMLand) as far as the number of different degrees of hemeroby (NUMHEM) and degrees of pavement (NUMPAV). Furthermore, we calculated the average degree of pavement (AWPAV, area weighted pavement) and the proportion of the 8 degrees of hemeroby (HEM 3 [mesohemerobic] up to HEM10 [metahemerobic]) and the 5 degrees of pavement (unpaved up to very highly paved). To evaluate the influence of linear structures, we analysed the density of roads and tracks (TRACKD) and calculated contrast values between neighbouring patches (CWED) according to the method of McGarigal and Marks (1994).

We did not use the percentage of each land use type for the following analysis because of the high number of zero-values causing an extremely skewed data distribution. They were only used to characterise the two areas by their land use in general.

The calculation for each of the 40 landscape sections was realised using PatchAnalyst (Rempel and Carr, 2003, http://flash.lakeheadu.ca/~rrempel/patch/) as an extension of the GIS program ArcView as well as own calculations.

2.2.3. Statistics

We calculated total species numbers per landscape section as well as their percentages and averages across plots. Furthermore, we compared the abundance of the species groups. We used a χ^2-test to test species association with one or the other landscape section.

To characterise the relationship between native species and the two alien species groups, we compared the logarithm of total species numbers in scatter-plots and performed a major axis regression using the FORTRAN program MODEL II by Legendre (2000). This method is more appropriate than ordinary least square regression, as all variables are in the same dimension and have the same error distribution. The significance of the slope was estimated by a test with 4999 permutations. The explained variance was obtained from the ratio of the dominant eigenvalue (λ Lambda) to the total of eigenvalues ($\lambda_1/[\lambda_1 + \lambda_2]$) (Legendre and Legendre, 1998).

Land use pattern and structure of the two landscapes in general were characterised by the percentage of main land use types (grouped single land use types), the 5 degrees of pavement and the average of three selected landscape metrics.

To detect relationships between landscape structure and species numbers, we combined principal component analysis (PCA) and multiple linear regression (both performed in SPSS version 10.0). The application of this combination follows a lot of several publications dealing with landscape analysis (Riitters et al., 1995; Cain et al., 1997; Deutschewitz et al., 2003). As a multivariate procedure, PCA is designed to reduce a large number of variables to a small number of principal components and is based on the correlation matrix of these variables.

Before starting PCA, we checked for sampling adequacy to detect whether or not the data will factor well. With regard to skewness of data distribution, this was especially necessary to avoid strong distortion of the results. In SPSS, sampling adequacy is measured by the Kaiser–Meyer–Olkin criterion (KMO). The diagonal elements in the anti-image correlation matrix are the KMO individual statistics for each variable. KMO varies from 0 to 1 and the overall KMO should be 0.5 or higher to proceed principal component analysis. In case of KMO < 0.5, the variable with the lowest KMO is dropped until the overall KMO value rises above 0.5. Another criteria in this sampling adequacy procedure is the Bartlett Test of Sphericity, which should be significant as well.

Despite the skewness of data distribution, neither floristic data nor land use data were transformed for the multivariate analysis.

The loadings or variances of extracted principal components were optimised by Varimax Rotation. For further analysis, principal components with eigenvalues >1 were retained. Furthermore, we looked at the number of variables with high loadings (>0.5) and the possible interpretation of PCs.

The following multiple linear regression was performed using the scores of the principal components as independent variables and plant species numbers in general, numbers of natives, archaeophytes, and neophytes, respectively, as dependent variables. As all principal components are orthogonal to each other, we could simply delete the insignificant variables to derive the simplified (minimum adequate) model.

This procedure reduced highly covarying landscape metrics to their relevant dimensions. We thus ensured that we did not use redundant metrics and that the results might be blurred by highly correlated landscape metrics. The use of several indices within the principal component makes interpretation easier.

3. Results

3.1. Species richness and abundance

The total number of species of the urban landscape section is higher than that of the agricultural landscape section (Table 1). The same applies for the three individual species groups. Regarding the proportion of each species group, only the group of neophytes shows a higher proportion in the urban landscape section than in the agricultural one. The proportion of natives and archaeophytes is higher in the agricultural landscape section. Fig. 2 shows the average values for the species groups per plot. The average species numbers are significantly higher in the urban landscape section, meaning that both the number of alien and native species is higher in the urban landscape section. With regard to the aliens, it is remarkable that the number of archaeophytes exceeds the number of neophytes in the agricultural landscape section, whereas in the urban area, the neophytes dominate the alien species group.

Table 1
Total species number, number of natives and the two alien groups and proportion of each in agricultural and urban landscape sections (Halle, Central Germany)

	Agricultural landscape		Urban landscape	
	Total number	(%)	Total number	(%)
Total	415	100	539	100
Natives	268	65	332	62
Archaeophytes	62	15	64	12
Neophytes	85	20	143	26

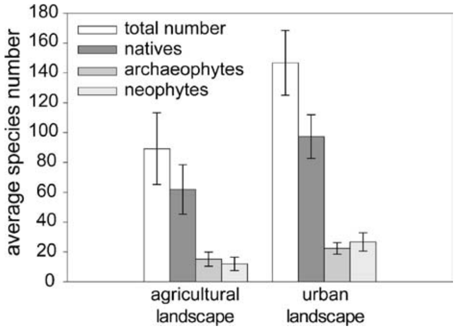

Fig. 2. Average species numbers and confidence intervals across all plots for native and alien plant species in the agricultural and urban landscape section (Halle, Central Germany). Both alien as well as native species numbers are significantly higher in the urban landscape (levels of significance between species numbers of the landscape sections: total species number $p < 0.001$, natives $p < 0.001$, archaeophytes $p = 0.02$, neophytes $p < 0.001$, Mann–Whitney U-Test). In the agricultural landscape, the average number of archaeophytes exceeds those of the neophytes, whereas in the urban landscape, the opposite is true.

χ^2-test yielded 90 species with an affinity to one of the two landscape sections, 83 associated with the urban landscape (56 natives, 16 neophytes, 11 archaeophytes) and 7 associated with the agricultural landscape (6 natives, one archaeophyte) (Table 2).

3.2. Relationship between native and alien species numbers

The results of the major axis regression show that there is a strong relationship between native and alien species numbers (Table 3). The number of all aliens increases with the number of natives; in detail: compared to the species number of archaeophytes, the number of neophytes increases much faster and higher with increasing numbers of natives.

Table 2
Species with significant affiliation in either agricultural or urban landscape sections (Halle, Central Germany), results of the χ^2-test (F: application of the exact Fisher-Test in the case of an expected frequency <5, result of this test is only a level of significance) $N = 20$ in each landscape section

Species name	Observed frequencies in the landscape sections		χ^2-value	*p*-level	Occurrence in landscape section	Immigration status
	Agricultural	Urban				
Acer negundo	3	12	8.64	<0.01	Urban	N
Acer platanoides	3	12	8.64	<0.01	Urban	I
Acer pseudoplatanus	5	15	0.00	<0.01	Urban	I
Aesculus hippocastanum	1	8	F	0.02	Urban	N
Ailanthus altissima	0	6	F	0.02	Urban	N
Alcea rosea	0	5	F	0.05	Urban	N
Alliaria petiolata	2	12	10.99	<0.01	Urban	I
Arctium lappa	8	17	8.64	0.03	Urban	A
Arrhenatherum elatius	12	18	4.80	0.03	Urban	I
Artemisia absinthium	1	7	F	0.04	Urban	A
Aster novi-belgii	0	5	F	0.05	Urban	N
Bellis perennis	0	7	F	0.01	Urban	I
Betula pendula	3	10	5.58	0.02	Urban	I
Bidens frondosa	0	5	F	0.05	Urban	N
Bromus inermis	2	8	4.80	0.03	Urban	I
Calamagrostis epigejos	9	16	5.23	0.02	Urban	I
Calystegia sepium	6	14	6.40	0.01	Urban	I
Carlina vulgaris	5	0	F	0.05	Agricultural	I
Cerastium holosteoides	7	17	10.42	<0.01	Urban	I
Chaerophyllum temulum	5	13	6.47	0.01	Urban	I
Chelidonium majus	5	13	6.47	0.01	Urban	I
Chenopodium hybridum	8	2	4.80	0.03	Agricultural	I
Cichorium intybus	6	15	8.12	<0.01	Urban	A
Clematis vitalba	5	12	5.01	0.03	Urban	I
Cornus sanguinea	6	13	4.91	0.03	Urban	I
Corylus avellana	1	9	8.53	<0.01	Urban	I
Crepis biennis	7	15	6.47	0.01	Urban	I
Cynoglossum officinale	8	1	F	0.02	Agricultural	I
Deschampsia cespitosa	3	11	7.03	0.01	Urban	I
Diplotaxis tenuifolia	6	13	4.36	0.04	Urban	N
Echinochloa crus-galli	2	10	7.62	0.01	Urban	A
Epilobium ciliatum	2	11	9.23	<0.01	Urban	N
Epilobium tetragonum	9	16	5.23	0.02	Urban	I
Erigeron annuus	0	7	F	0.01	Urban	N
Euphorbia cyparissias	11	4	5.23	0.02	Agricultural	I
Euphorbia exigua	5	0	F	0.05	Agricultural	A
Euphorbia peplus	3	10	5.58	0.02	Urban	A
Festuca rubra	10	16	3.96	0.05	Urban	I
Fraxinus excelsior	4	11	5.23	0.02	Urban	I
Geranium robertianum	3	9	4.29	0.04	Urban	I
Glechoma hederacea	5	13	6.47	0.01	Urban	I
Hedera helix	1	9	8.53	<0.01	Urban	I
Humulus lupulus	2	11	9.23	<0.01	Urban	I
Hypochoeris radicata	0	8	F	<0.01	Urban	I
Inula conyzae	8	2	4.80	0.03	Agricultural	I
Juncus effusus	0	5	F	0.05	Urban	I
Lamium purpureum	6	18	15.00	<0.001	Urban	I
Lapsana communis	3	14	12.38	<0.001	Urban	I
Lathyrus pratensis	0	5	F	0.05	Urban	I

Table 2 (*Continued*)

Species name	Observed frequencies in the landscape sections		χ^2-value	*p*-level	Occurrence in landscape section	Immigration status
	Agricultural	Urban				
Lepidium latifolium	1	7	F	0.04	Urban	I
Ligustrum vulgare	4	10	3.96	0.05	Urban	I
Linum catharticum	5	0	F	0.05	Agricultural	I
Lolium perenne	10	19	10.16	<0.01	Urban	I
Malus domestica	4	11	5.23	0.02	Urban	N
Medicago lupulina	9	16	5.23	0.02	Urban	I
Medicago × varia	6	15	8.12	<0.01	Urban	N
Melilotus alba	3	11	7.03	0.01	Urban	A
Plantago lanceolata	10	16	3.96	0.05	Urban	A
Plantago major	11	17	4.29	0.04	Urban	A
Poa annua	6	17	12.38	<0.001	Urban	I
Poa nemoralis	1	12	13.79	<0.001	Urban	I
Polygonum amphibium	2	9	6.14	0.01	Urban	I
Polygonum persicaria	0	10	13.33	<0.001	Urban	I
Populus × canadensis	3	11	7.03	0.01	Urban	N
Quercus robur	1	8	F	0.02	Urban	I
Rubus armeniacus	0	6	F	0.02	Urban	N
Rumex acetosa	0	5	F	0.05	Urban	I
Rumex obtusifolius	4	15	12.13	<0.001	Urban	I
Rumex thyrsiflorus	1	12	13.79	<0.001	Urban	I
Sagina procumbens	1	7	F	0.04	Urban	I
Salix caprea	0	7	F	0.01	Urban	I
Saponaria officinalis	0	5	F	0.05	Urban	I
Sedum acre	0	6	F	0.02	Urban	I
Senecio vulgaris	3	11	7.03	0.01	Urban	I
Silene latifolia	13	19	F	0.04	Urban	I
Sisymbrium officinale	0	11	15.17	<0.001	Urban	A
Solanum dulcamara	2	8	4.80	0.03	Urban	I
Solanum nigrum	0	8	F	<0.01	Urban	A
Solanum tuberosum	0	5	F	0.05	Urban	N
Solidago canadensis	12	18	4.80	0.03	Urban	N
Sonchus asper	5	12	5.01	0.03	Urban	I
Sonchus oleraceus	7	18	12.91	<0.001	Urban	A
Stellaria media	9	19	11.91	<0.01	Urban	I
Symphoricarpos albus	2	9	6.14	0.01	Urban	N
Taraxacum officinale agg.	13	19	F	0.04	Urban	I
Trifolium campestre	3	12	8.64	<0.01	Urban	I
Trifolium pratense	8	18	10.99	0.01	Urban	I
Trifolium repens	3	15	14.55	<0.001	Urban	I
Ulmus laevis	0	7	F	0.01	Urban	I
Urtica dioica	11	17	4.29	0.04	Urban	I

Immigration status: I: Indigenous, N: Neophyte, A: Archaeophyte.

Comparing the two investigated landscape sections, the slopes for the regression of natives versus archaeophytes are the same, which contrasts the slope of the regression of natives versus neophytes, where the slope is higher in the urban landscape section. For both landscape sections combined, the slope of log archaeophyte versus log native species richness is less than one and for log neophyte versus log native species richness is larger than one (excluding unity from their respective confidence intervals). Latter statement still holds true when considering the urban landscape section only. Thus, neophyte plant species number increases

Table 3
Results of the major axis regressions of the species number of native species and the two alien plant species groups ($\log_{10}$-transformed)

	Slope	95% C.I. slope	$\lambda_1/(\lambda_1+\lambda_2)$	*p*
Both landscapes (40 plots)				
Natives vs. archaeophytes	0.75	[0.57, 0.97]	0.90	<0.001
Natives vs. neophytes	1.30	[1.11, 1.53]	0.95	<0.001
Agricultural landscape (20 plots)				
Natives vs. archaeophytes	0.73	[0.45, 1.12]	0.88	<0.001
Natives vs. neophytes	1.09	[0.86, 1.40]	0.95	<0.001
Urban landscape (20 plots)				
Natives vs. archaeophytes	0.73	[0.56, 1.14]	0.85	<0.01
Natives vs. neophytes	1.69	[1.32, 2.24]	0.95	<0.001

C.I.: confidence interval; λ: eigenvalue; *p*: one-tailed probability of H_0, see statistics section for details).

overproportionately with native species number in the urban landscape area in the pooled landscapes, whereas archaeophyte species number shows diminishing returns with increasing native plant species number. The slopes of the other relationships do not differ significantly from unity.

3.3. Landscape structure

We grouped the 37 land use types into eight main groups to characterise both landscape sections by their land use (Fig. 3). The agricultural landscape section is mainly dominated by agricultural and forestry land use representing more than half of the total area. Semi-natural land uses also make up a high proportion in this landscape section. Although semi-natural land uses have the highest single proportion in the urban landscape, joint urban land uses such as industry/commercial, residential, traffic and urban green spaces dominate this landscape.

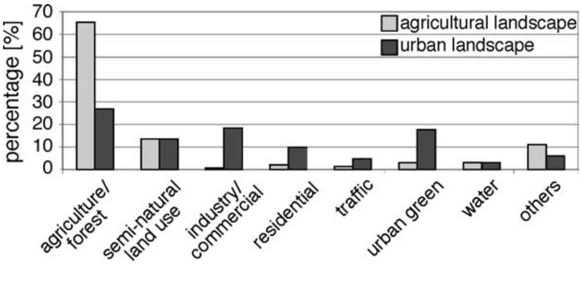

Fig. 3. Characterisation of agricultural and urban landscape sections (Halle, Central Germany) by the percentage of land use types (aggregated). Semi-natural land use includes tall herb communities, natural shrubbery, extensive orchards, natural forest.

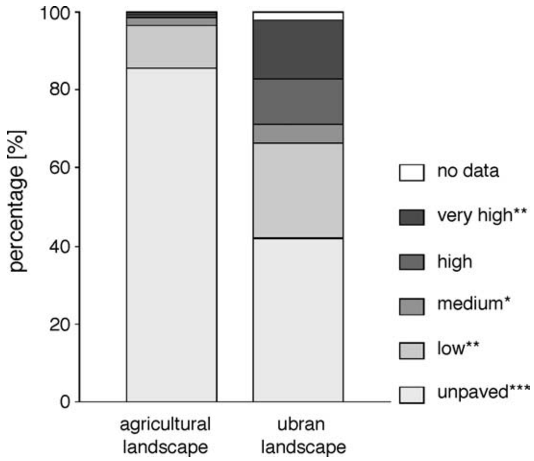

Fig. 4. Comparison between the percentages of the 5 degrees of pavement in agricultural and urban landscape sections (Halle, Central Germany). The difference between both landscape sections is emphasised by the high amount of paved surfaces in the urban landscape and opposite to this the amount of unpaved surfaces exceeding more than 80% in the agricultural landscape (levels of significance: unpaved < 0.001, low = 0.01, medium = 0.03, high = 0.17, very high = 0.01, Mann–Whitney *U*-Test).

Low to medium paved and very highly paved areas differ significantly between urban and agricultural landscape section (Fig. 4). The open character of the agricultural landscape contrasts the intensive pavement in the urban landscape. The calculated average amount of pavement (area weighted pavement AW-PAV) reaches 0.2 in the agricultural landscape and 1.2 in the urban landscape ($p < 0.001$; Mann–Whitney *U*-Test).

Both landscape sections differ significantly in their landscape structure. The urban landscape section has higher numbers of patches (mean patch number in the urban landscape section: 6.10, agricultural landscape section: 4.15, $p = 0.02$, *U*-Test), smaller mean patch sizes (urban: 1.43 ha, agricultural: 2.58 ha, $p = 0.03$) and a more heterogeneous land use pattern (mean number of different land use types, urban: 5.05, agricultural: 3.35, $p = 0.01$).

3.4. Influence of landscape structure on species richness

To quantify the influence of landscape structure on species richness and distribution, we performed three analyses. With regard to the different landscape characteristics, we calculated the influences within each of the two landscape sections (within each of it 20 plots). A third analysis used all 40 plots pooled.

The first principle component analysis was performed in the 20 plots of the *agricultural landscape* (Table 4). Regarding the loadings of each variable, the principal components are interpreted as follows: as PC 1 includes the percentage of semi-natural habitats and summarises almost all of the landscape metrics representing a small structured landscape that is high in contrasts of land use, we interpreted it as highly differentiated landscape structure and semi-natural habitats. PC 2 combines variables as variation in degree of pavement and especially high degrees of pavement. It is therefore, interpreted as extremely paved habitats. PC 3 combines two variables that express a high density of edge elements with special regard to contrasts due to different land use intensities (hemeroby). It is interpreted as high density of roads and tracks. PC 4 combines the percentages of two higher hemerobic degrees and was interpreted as intense land use. Except from the fourth, all principal components remained in the regression models (Table 5).

Overall, highly paved habitats or even just the presence of built-up area contribute essentially to higher species numbers in the agricultural landscape. Above all, the standardised slope values of the second principal component for the regression of archaeophytes and neophytes prove a strong relation to this factor. More important for native species in the agricultural landscape seems to be the presence of semi-natural habitats.

The second principal component analysis was performed in the 20 plots of the *urban landscape* (Table 6). Similar to the first analysis, the first principle component includes almost all parameters expressing a small structured landscape that is high in contrasts of land use but with no relation to the degree of hemeroby.

Table 4
Scores of principal component analysis of landscape structure indices for agricultural landscape (loadings >0.5 in bold)

Landscape structure metrics (acronym meaning)	Principal components			
	PC 1	PC 2	PC 3	PC 4
Proportion of total variance explained by PC (%)	**52.6**	16.2	10.1	7.1
Eigenvalues				
Patch number (NUMP)	**0.98**	0.06	0.11	0.10
Number of different land use types (NUMLand)	**0.95**	0.20	0.06	0.06
Mean patch size (MPS)	**−0.83**	−0.27	−0.18	0.23
Coefficient of patch size variation (PSCOV)	**0.80**	0.15	0.12	−0.34
Number of edges (NUMEDGE)	**0.89**	0.04	0.25	0.15
Edge density (EDGED)	**0.90**	0.13	0.20	0.15
Contrast weighted edge density (CWED)	**0.77**	0.20	**0.52**	0.01
Number of different degrees of pavement (NUMPAV)	0.42	**0.76**	−0.01	−0.13
Area weighted degree of pavement (AWPAV)	0.08	**0.96**	0.07	0.06
Density of roads and tracks (TRACKD)	0.20	0.28	**0.86**	−0.02
Number of different degrees of hemeroby (NUMHEM)	**0.93**	0.11	−0.17	−0.14
Proportion of meso- to β-euhemerob surfaces (Hem 4)	**0.76**	−0.28	0.28	0.29
Proportion of α-euhemerob to polyhemerob surfaces (Hem 8)	−0.21	−0.02	−0.18	**−0.83**
Proportion of polyhemerob surfaces (Hem 9)	−0.24	0.15	−0.40	**0.69**
Proportion of unpaved surfaces	0.01	**−0.90**	−0.28	−0.17

The four principal components (PC) explain 86.1% of the total variance.

Table 5
Multiple regression of species number for the agricultural landscape

Species group	Adjusted R^2	Principal components included in the model		Standardised slope	*p*-level
		Nb	Interpretation		
Total	0.70	PC 2	Extremely paved habitats	0.56	<0.001
		PC 1	Highly differentiated landscape structure and semi-natural habitats	0.55	<0.001
		PC 3	High density of roads and tracks	0.36	0.01
Natives	0.63	PC 1	Highly differentiated landscape structure and semi-natural habitats	0.65	<0.001
		PC 2	Extremely paved habitats	0.38	0.02
		PC 3	High density of roads and tracks	0.36	0.02
Archaeophytes	0.63	PC 2	Extremely paved habitats	0.81	<0.001
Neophytes	0.71	PC 2	Extremely paved habitats	0.71	<0.001
		PC 1	Highly differentiated landscape structure and semi-natural habitats	0.37	0.01
		PC 3	High density of roads and tracks	0.34	0.01

Results of the regression between PCs and species groups. PCs listed with decreasing standardised coefficients (slope).

Furthermore, the variation of patch size shows no high loadings and in contrast to the former analysis the density of roads and tracks is involved in this principle component. Finally, PC 1 was interpreted as highly differentiated landscape structure. The second principal component refers to the proportion of intensively used and paved land use types. Considering the negative loading of the contrast value, PC 2 is interpreted as dense urban areas. The third principal component combines the proportion of semi-natural habitats showing high variance in patch size and was named semi-natural habitats. All principal components mentioned here were included in the following multiple regressions for the species groups (Table 7).

Table 6
Scores of principal component analysis of landscape structure indices for urban landscape (loadings >0.5 in bold)

Landscape structure metrics (Acronym meaning)	Principal components		
	PC 1	PC 2	PC 3
Proportion of total variance explained by PC (%)	**45.1**	21.9	8.1
Eigenvalues			
Patch number (NUMP)	**0.91**	0.06	0.31
Number of different land use types (NUMLand)	**0.89**	0.22	0.06
Mean patch size (MPS)	**−0.75**	−0.18	−0.37
Coefficient of patch size variation (PSCOV)	0.15	0.22	**0.89**
Number of edges (NUMEDGE)	**0.78**	0.14	0.22
Edge density (EDGED)	**0.83**	−0.24	0.42
Contrast weighted edge density (CWED)	**0.69**	**−0.54**	0.38
Number of different degrees of pavement (NUMPAV)	**0.74**	0.44	0.14
Area weighted degree of pavement (AWVERS)	0.21	**0.90**	0.06
Density of roads and tracks (TRACKD)	**0.69**	−0.07	0.03
Number of different degrees of hemeroby (NUMHEM)	**0.93**	0.19	−0.01
Proportion of meso- to β-euhemerob surfaces (Hem 4)	0.25	−0.32	**0.71**
Proportion of α-euhemerob to polyhemerob surfaces (Hem 8)	−0.49	−0.28	−0.48
Proportion of polyhemerob surfaces (Hem 9)	0.06	**0.86**	0.20
Proportion of unpaved surfaces	−0.06	**−0.86**	0.09
Proportion of very highly paved surfaces	0.09	**0.67**	−0.04

The three principal components (PC) explain 75.2% of the total variance.

Table 7
Multiple regression of species number for the urban landscape

Species group	Adjusted R^2	Principal components included in the model		Standardised slope	*p*-level
		Nb	Interpretation		
Total	0.40	PC 1	Highly differentiated landscape structure	0.66	<0.01
Natives	0.54	PC 1	Highly differentiated landscape structure	0.69	<0.001
		PC 3	Semi-natural habitats	0.33	0.05
Archaeophytes	0.40	PC 2	Dense urban areas	0.66	<0.01
Neophytes	0.56	PC 2	Dense urban area	0.57	<0.01
		PC 1	Highly differentiated landscape structure	0.53	<0.01

Results of the regression between PCs and species groups. PCs listed with decreasing standardised coefficients (slopes).

Altogether, the influence of a highly structured landscape becomes much more distinct in the urban landscape. But after that, the presence of semi-natural habitats is also important for native species. Most important for the alien species are as in the agricultural landscape urban habitats with a high amount of paved surfaces. It is also the only principal component showing influence on the number of archaeophytes.

Finally, we performed an analysis including the data of all 40 plots (neglecting whether they belong to the agricultural or urban landscape). As these results confirm the results above, we will not present them here in detail. Variation in landscape structure has a positive influence on species numbers as well. It is the main factor for high species numbers in general, and for native plant species numbers in particular. In the case of both alien species groups, this factor is superposed by the proportion of intensively human influenced land use types and their degree of pavement. The archaeophytes depend once more on the presence of urban habitats. In contrast, the influence of intensively human altered land use types with lower degree of pavement are most important for the neophytes.

4. Discussion

4.1. Species richness in urban and agricultural landscapes

We demonstrated that at a local scale, urban regions support more species than surrounding landscapes. Previously, this was usually known for larger scales (e.g. Haeupler, 1974; Klotz, 1990; Kowarik, 1995; Pyšek, 1993; Stadler et al., 2000; Deutschewitz et al., 2003; Kühn et al., 2004). We showed that this higher number of species is not only related to higher alien species numbers, but to higher numbers of native species as well. Stadler et al. (2000), Deutschewitz et al. (2003), Kühn et al. (2004) had similar results analysing much larger landscape units. Both, the average number of native as well as of alien species were higher in the urban landscape. Percentages of natives and archaeophytes were slightly higher in the agricultural landscape section compared to the urban landscape section. In contrast, the neophytes shared a remarkably high proportion in the urban landscape section. Thus it seems that the percentage of neophytes is most important for the difference between both landscapes concerning species composition. We do not conclude however that species richness in cities is mainly due to higher alien species numbers. While Lonsdale (1999) showed on the global diversity pattern that communities which were richer in native species were richer in aliens as well, Deutschewitz et al. (2003); Stohlgren et al. (1999); Stadler et al. (2000); Sax (2002); Kühn et al. (2003) demonstrated this for intermediate scales. The highly significant regression coefficients of the major axis regressions prove a strong structural relationship between the species groups. We conclude that the richness patterns of native and alien plants are rather similar. That is that the richness patterns of native species could be used to describe those of the alien species and vice versa. Nevertheless, Roy et al. (1999) could not show on intermediate scale that the species richness of cities is higher compared to their surroundings. But this may be due to the experimental design with a different definition of urban plots. In their study, Roy et al. consider plots in Great Britain as being “urban” if the area of urban land use exceeds 10%.

However, it seems that declining native species richness due to increased alien species richness is restricted to small spatial scales (community level) (Rejmánek, 1996; Levine, 2000; Lonsdale, 1999; Shea and Chesson, 2002; Byers and Noonburg, 2003).

4.2. The role of landscape structure and landscape characteristics

The richness pattern of native and alien plant species is influenced by the landscape structure caused by land use variability. Within our study, this is first of all the most important factor for both, alien and native plants (see also Haeupler, 1974; Wohlgemuth, 1998; Wagner et al., 2000; Deutschewitz et al., 2003; Kühn et al., 2003). Our results support the assumption that habitat variability might be decisive for the species richness of cities (Kowarik, 1995; Stadler et al., 2000; Kühn et al., 2004). The influence of a highly diverse landscape structure is more distinct in the urban landscape, but it is not clear whether it is connected to semi-natural or even more urban habitats.

In our study, variability is mainly correlated with human influence in general. This applies to our landscapes today, where variability is mainly induced by human activities (Kowarik, 1988; Wagner et al., 2000). Obviously only on large scales, environmental variability has an impact on species pattern (Mutke and Barthlott, 2000; Kühn et al., 2003). Regarding the investigated landscape types, dominating smaller patches of different land use promote habitat heterogeneity in urban areas, whereas in agricultural landscapes, large homogenous patches dominate, finally leading to a lack of variability.

Apart from the influence of the structural variability, our results show that the land use characteristics themselves were of distinctive influence as well. Even if structural diversity is of high importance for native species, there is a strong influence of the presence of more natural habitats. Kent et al. (1999) indicate that green “nature-like” structures act as refuges or even local hot spots and emphasise their special role in cities. Our results support these findings and also indicate that not only native, but alien species as well are drawn to such areas. Furthermore, aliens are much more influenced by the presence of human activities.

The described variation in the type and intensity of human activities and resulting structural diversity is typical for Central Germany, which is dominated by large agricultural fields and industrial and urban construction, interspersed with habitat islands, where alien and native species concentrate and find adequate living conditions.

5. Conclusion

The results show how plant species distribution patterns are linked to the different kinds of landscape use in general. Large scale agricultural land use reduces structural diversity and the availability of adequate habitats, leading finally to the homogenisation of the landscape. We assume that on the scale of our study, species are displaced more by this pressure than by alien species.

Concerning the role of cities in the distribution of species, our results support the idea that cities represent islands inside the homogenous agricultural landscape. They might serve as an important refuge for many species, offering a highly diverse selection of habitats (Pyšek, 1998).

We also showed that urban ecosystems may serve as an important environment for biodiversity as well (Savard et al., 2000). As cities serve as an important habitat for alien species, they might be an important habitat or refuge for native plant species as well (Pyšek, 1998). With landscapes modified to suit the needs of humans, many plants and animals move from their original habitats and adapt to new living conditions. Hence, green spaces within cities may promote biodiversity and therefore deserve our special interest. Apart from the obvious, however, we must not ignore the role of other urban habitats, such as walls, yards, gardens and even flower-pots!

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References

Antrop, M., 2004. Landscape change and the urbanisation process in Europe. Landscape Urban Plann. 67, 9–26.

Bartlott, W., Biedinger, N., Braun, G., Feig, F., Kier, G., Mutke, J., 1999. Terminological and methodological aspects of the mapping and analysis of the global biodiversity. Acta Bot. Fenn. 162, 103–110.

Byers, J.E., Noonburg, E.G., 2003. Scale dependent effects of biotic resistance to biological invasion. Ecology 84, 1428–1433.

Cain, D.H., Riitters, K., Orvis, K., 1997. A multi-scale analysis of landscape statistics. Landscape Ecol. 12, 199–212.

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.

di Castri, F., Hansen, A.J., Debussche, G., 1990. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M., 1989. Biological Invasions: A Global Perspective. Wiley, New York.

Elton, C.S., 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, UK.

Frank, D., Klotz, S. (Eds.), 1990. Biologisch-ökologische Daten zur Flora in der DDR, vol. 32 (P41), 2nd ed. Wissenschaftliche Beiträge Martin-Luther-Univ., Halle-Wittenberg, Halle, Germany.

Haeupler, H., 1974. Statistische Auswertung von Punktrasterkarten der Gefäßpflanzenflora Süd-Niedersachsens. Scripta Geobot. 8, 1–141.

Haeupler, H., 1999. Zur Phytodiversität Deutschlands, eine aktualisierte Bilanz. Cour. Forsch. -Inst. Senckenberg 215, 103–109.

Kent, M., Stevens, A., Zhang, L., 1999. Urban plant ecology patterns and process: a case study of the flora of the City of Plymouth, Devon, UK. J. Biogeogr. 26, 1281–1298.

Klotz, S., 1990. Species/area and species/inhabitants relations in european cities. In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), Urban ecology–Plants and plant communities in urban environments. SPB Academic Publishing, The Hague, The Netherlands, pp. 99–103.

Klotz, S., Kühn, I., Durka, W. (Eds.), 2002. BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde, vol. 38. Bundesamt für Naturschutz, Bonn, 334 pp.

Kowarik, I., 1988. Zum menschlichen Einfluß auf Flora und Vegetation–Theoretische Konzepte und ein Quantifizierungsansatz am Beispiel von Berlin (West). Landschaftsentwicklung und Umweltforschung TU Berlin, Bd. 56.

Kowarik, I., 1990. Some responses of flora and vegetation to urbanization in Central Europe. In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), Urban ecology–Plants and plant communities in urban environments. SPB Academic Publishing, The Hague, The Netherlands, pp. 45–74.

Kowarik, I., 1995. On the role of alien species in urban flora and vegetation. In: Pyšek, P., Prach, K., Rejmánek, M., Wade, M. (Eds.), Plant invasions–General Aspects and Special Problems. SPB Academic Publishing, Amsterdam, pp. 85–103.

Kühn, I., Klotz, S., 2002. Floristischer Status und gebietsfremde Arten. In: Klotz, S., Kühn, I., Durka, W. (Eds.), BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde, vol. 38. Bundesamt für Naturschutz, Bonn, pp. 47–56.

Kühn, I., May, R., Brandl, R., Klotz, S., 2003. Plant distribution patterns in Germany—Will aliens match natives? Feddes Repertor. 114, 559–573.

Kühn, I., Brandl, R., Klotz, S., 2004. The flora of German cities is naturally species rich. Evol. Ecol. Res. 6, 749–764.

Legendre, P., 2000. Model II Regression—User's guide. Département de sciences biologiques, Univ. de Montreal, Quebec, Canada, http://www.fas.umontreal.ca/biol/legendre.

Legendre, P., Legendre, L., 1998. Numerical Ecology, Developments in Environmental Modelling, vol. 20. Elsevier Science B.V., Amsterdam.

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.

McGarigal, K., Marks, B.J., 1994. Fragstats–spatial pattern analysis programme for quantifying landscape structure, Version 2.0. Oregon State University, Corvallis.

Miller, J.N., Books, R.P., Croonquist, M.J., 1997. Effects of landscape patterns on biotic communities. Landscape Ecol. 12, 137–153.

Mutke, J., Barthlott, W., 2000. Some aspects of North American phytodiversity and its biogeographic relationships. In: Breckle, S.-W., Schweizer, B., Arndt, U. (Eds.), Proceedings of the First Symposium by the A.F.W. Schimper-Foundation. Results of worldwide ecological studies. Heimbach, Stuttgart, pp. 435–447.

Pyšek, P., 1993. Factors affecting the diversity of flora and vegetation in central European settlements. Vegetatio 106, 89–100.

Pyšek, P., 1998. Alien and native species in Central European urban floras. A quantitative comparison. J. Biogeogr. 25, 155–163.

Pyšek, P., Pyšek, A., 1990. Comparison of vegetation and flora of West Bohemian towns. In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), Urban Ecology—Plants and Plant Communities in Urban Environments. SPB Academic Publishing, The Hague, pp. 105–112.

Rejmánek, M., 1996. Species richness and resistance to invasions. In: Orians, G.H., Dirzo, R.J. (Eds.), Biodiversity and Ecosystem Processes in Tropical Forests. Ecological studies, vol. 122. Springer-Verlag, Berlin, pp. 153–172.

Rempel, R.S., Carr, A.P., 2003. Patch Analyst extension for ArcView: version 3. Centre for Northern Forest Ecosystem Research, Lakehead University Campus, Thunder Bay, Ontario, http://flash.lakeheadu.ca/∼rrempel/patch.

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 Ecol. 10, 23–39.

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.

Savard, J.-P., Clergeau, P., Mennechez, G., 2000. Biodiversity concepts and ecosystems. Landscape Urban Plann. 48, 131–142.

Sax, D.F., 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity Dist. 8, 193–210.

Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. Trends Ecol. Evol. 18, 561–566.

Sax, D.F., Gaines, S.D., Brown, J.H., 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. Am. Nat. 160, 766–783.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. 17, 170–176.

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. Ecol. Monogr. 69, 25–46.

Sukopp, W., Werner, P., 1983. Urban environments and vegetation. In: Holzner, W., Werger, M.J.A., Ikusima, I. (Eds.), Man's Impact on Vegetation. Dr. W. Junk Publishers, The Hague, pp. 247–260.

Wagner, H., Wildi, O., Ewald, K.C., 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. Landscape Ecol. 15, 219–227.

Walters, S.M., 1973. The next twenty years. In: Perring, F. (Ed.), The Flora of a Changing Britain. Classey, Hampton, UK, pp. 136–141.

Weber, E., 2003. Invasive Plant Species of the World. CABI Publishing, Wallingford, UK.

Williamson, M., 1996. Biological Invasions. Chapman & Hall, London.

Wohlgemuth, T., 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. Biodivers. Conserv. 7, 159–177.

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