The flora of German cities is naturally species rich

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ABSTRACT

Previous studies on various scales and for various European regions and North America have shown that cities harbour more plant species than the surrounding landscape. It has been argued that the greater number of plant species is usually caused by a high number of alien plants promoted by human influence. We analysed native and naturalized vascular plant species distribution data from a comprehensive German database comparing city and non-city grid cells of 10 minutes latitude $\times$ 6 minutes longitude (*c.* 130 km^2). The number of city grid cells ($n = 68$) and non-city grid cells ($n = 1856$) differed by two orders of magnitude and species richness was highly autocorrelated. We therefore used resampling techniques. We resampled the species richness of 68 randomly selected grid cells 9999 times. This showed that not only naturalized alien but also native plant species richness was significantly higher in city grid cells. To relate environmental variables to species richness, we used 10,000 analyses of covariance of 68 city grid cells and 68 randomly selected non-city grid cells. We demonstrated that a large proportion of the higher native plant species richness could be explained by the number of geological types per grid cell (i.e. a measure of natural geological diversity). Additionally, we showed by resampling the number of geological types per grid cell that cities are not randomly distributed but are in fact in areas of high geological diversity. Hence, we conclude that city areas are preferentially located in pre-existing biodiversity hotspots and argue that they are species rich not because of but in spite of urbanization.

Keywords: alien plants, environmental correlates, environmental heterogeneity, native plants, resampling methods, species richness, urbanization.

INTRODUCTION

Across the globe and on various scales, strikingly similar patterns of correlation between human population density and species richness have been recorded. On the regional scale, Walters (1970) was the first to point out that cities harbour more spontaneous (not cultivated) plant species than the surrounding landscape. This pattern was confirmed on several scales and for various European regions (Haeupler, 1975; Klotz, 1990; Pyšek, 1993; Kowarik, 1995; Araújo, 2003; but see Roy *et al.*, 1999) and North America (Dobson *et al.*, 2001; McKinney, 2002a; Hope *et al.*, 2003).

This pattern is even more striking considering how changes and developments in human land use alter ecosystems. Such land-use changes induce changes in a variety of factors (e.g. Sukopp and Werner, 1983; Gilbert, 1989; Wittig, 1991; Collins *et al.*, 2000; Pickett *et al.*, 2001), including increases in temperature ('heat effect' in the city) and rainfall (Landsberg, 1981; Oke, 1982), pollution (Douglas, 1983), impervious surfaces, habitat fragmentation and disturbance (Kowarik, 1995; Trepl, 1995). However, fragments of semi-natural vegetation and agricultural land within or surrounding the cities contribute to higher biodiversity.

It is often argued that the majority of alien species establish in cities by means of cultivation (Barthlott *et al.*, 1999; Kent *et al.*, 1999). Thus, the higher species richness in cities could mainly be ascribed to alien species (e.g. McKinney and Lockwood, 2001). Plants that are adapted to stress or human land use and occur preferably within cities were termed 'urban specialists' by Hill *et al.* (2002). Such species could increase urban plant species richness (Pyšek, 1998) further. Similarly, disturbance or perturbation may lead to increased plant species richness at intermediate levels (Sukopp and Trepl, 1987; Kowarik, 1990, 1991, 1995; Pyšek, 1993; see Huston, 1994, for a general framework). Additionally, because botanical research institutes tend to be more often in big cities, some have argued that the species richness of cities is a sampling artefact (Barthlott *et al.*, 1999). Further general issues are the effect of area size on species richness (e.g. Rosenzweig, 1995) and the influence of spatial autocorrelation on statistical analyses (e.g. Fortin *et al.*, 1989; Lichstein *et al.*, 2002). These can cause severe problems but have largely been neglected by previous analyses.

Previous studies focused primarily on the increased richness of alien plant species due to human influence. However, richness patterns of plant species correlate, for example, with productivity (e.g. Waide *et al.*, 1999; Mittelbach *et al.*, 2001), landscape heterogeneity (e.g. Wohlgemuth, 1998; Deutschewitz *et al.*, 2003; Kühn *et al.*, 2003), climate (e.g. Wohlgemuth, 1998) and other 'natural' factors, which, in turn, may covary with human population density or settlements. As natural factors are important determinants for plant species richness and as naturalized aliens account usually for just a small fraction of urban plant species richness in Germany (e.g. Kowarik, 1995; Pyšek, 1998), we focus on the proportions of natural and man-made factors as correlates for native and naturalized alien plant species richness. From previous studies we know that natural factors such as geological diversity, soil diversity and landscape diversity are positively correlated with native and alien plant species richness (Deutschewitz *et al.*, 2003; Kühn *et al.*, 2003). Thus, we hypothesize that these natural factors are not only the most important correlates of plant species richness but are also relevant factors for the location of cities.

MATERIALS AND METHODS

Data sources

Species numbers were calculated from the database on German flora (FLORKART, see http://www.floraweb.de), maintained by the German Centre for Phytodiversity at the Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN). FLORKART is the central database that includes all provincial or regional mapping schemes throughout Germany. The data were mainly assembled by thousands of volunteers who recorded the flora of their respective grid cells. This work was initiated by a mapping scheme for Central Europe (Ehrendorfer and Hamann, 1965; Ellenberg *et al.*, 1968), which unfortunately could

not be realized in the desired manner. Nevertheless, a multitude of more regional mapping schemes led to distribution atlases for West Germany (Haeupler and Schönfelder, 1989) and East Germany (Benkert *et al.*, 1996). Both atlases, many publications on local or regional floras from the nineteenth century and the first half of the twentieth century, several very recent mapping schemes and corrections were incorporated into the recent version of FLORKART. We choose to use FLORKART for our analysis because it contains more than 14 million records, of which 2.6 million are unique for each species in a $6' \times 10'$ grid cell in the most recent time period, making it one of the most comprehensive European databases on plant species distribution. Therefore, we analysed this database. In our version of FLORKART, the time of recording is referenced as three time periods: before 1950, 1950 until 1979 and from 1980 (until 2001). We used the records from 1950 onwards. Localities of plant species are referenced within this database according to the German 1:25,000 Ordnance Survey Maps (10 minutes latitude $\times$ 6 minutes longitude, *c.* 130 km^2, hereafter called 'grid cells'). Species numbers were the sums of all occurrences of both natives and naturalized aliens (thus omitting casual and cultivated occurrences, i.e. in gardens, arboretums, managed road verges, etc.).

Mapping intensity in Germany is very heterogeneous. Hence, only sufficiently well mapped grid cells were used for analysis. Mapping intensity was evaluated by designating 50 'control' species. These control species were the 45 most frequent species mentioned by Krause (1998) and five additional species. The latter five species were generalists and preferably inconspicuous or regarded by many volunteers as difficult to identify. By this, we wanted to minimize potential observer bias towards obvious, easily identifiable species. All 50 control species had to be present to include a grid cell in the analysis. This control reduced the number of grid cells from 2995 to 1928. These control species were omitted from further analyses to avoid circular reasoning. However, as the number of control species is a constant in all grid cells under analysis, this does not change the general outcome. We also carried out preliminary tests to establish if we could work with less than 50 or up to 100 species. Using less than 50 species (e.g. 30 or 40) included too many grid cells not sufficiently well mapped (since we knew at least some regions that were poorly mapped). Having more than 50 species (e.g. 80 or 100) led partially to the exclusion of well mapped regions as the additional set of species included less common ones.

Despite this control mechanism, it was impossible to use data from smaller grid cells. Though there are some regions that have been extremely well mapped in the past on the scale of a quarter ordnance survey map ($5' \times 3'$) or smaller, such as Saxony (Hardtke and Ihl, 2000), Thuringia (Korsch *et al.*, 2002), Westphalia (Haeupler *et al.*, 2003) and the Dessau region (see Deutschewitz *et al.*, 2003), the chosen grid cell size for this study was the only one with a reasonably good coverage and quality for the whole of Germany.

We distinguished between native species (native to Germany) and alien species (species not native to Germany). Alien species were divided into pre-1500 aliens (so-called archaeophytes, promoted by agriculture from the Neolithic prior to the discovery of the Americas) and post-1500 aliens (so-called neophytes, introduced due to long-distance transport subsequent to the discovery of the Americas). We designated the immigration status according to BiolFlor (Kühn and Klotz, 2002). This distinction is established in Central European botanical research (e.g. Schroeder, 1969; Sykora, 1990; Pyšek, 1998; Hill *et al.*, 2002; Pyšek *et al.*, 2003), as both groups of aliens differ markedly (e.g. Pyšek *et al.*, 2002a,b), for example in ecology (the first are mainly species of arable fields, the latter occupy a wide variety of habitats), mode of introduction (the former immigrated across

short and medium distances without the assistance of man but into habitats provided by man, the latter arrived often by human mediated long-distance transport) and thus in evolutionary history. The combination of the two databases FLORKART and BiolFlor left 3150 species for analyses, of which 2411 are native, 239 are (presumed) pre-1500 aliens and 500 are post-1500 aliens. Furthermore, we used red list species ($n = 797$ within FLORKART) as another species group according to the German 'Red List' of threatened and endangered plants (Korneck *et al.*, 1996).

City grid cells are those containing the centres of cities with more than 100,000 inhabitants (Statistisches Bundesamt, 2001). The centres of the German cities could easily be recognized on the map as the old town (often of medieval origin) with usually a cathedral and a marketplace in its centre and its often somewhat circular patterns (surrounded by ancient city walls, ring walls, circular roads, etc). The city of Kassel could not unambiguously be assigned to a grid cell (the city centre is located in the corners of four grid cells), and thus the corresponding grid cells were omitted from further analyses.

Rural grid cells were defined as those with less than 5% cover of urban land use according to the Corine Land Cover maps provided by the Federal Statistical Office of Germany (Statistisches Bundesamt, 1997). This resulted in 1924 grid cells for Germany, 68 of which contained city centres and 1099 of which were defined as rural. We calculated the number of geological patches and geological types according to the Geological Survey Map (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993) per grid cell. The 241 geological types were aggregated into five substrate classes: lime, sand, loess, clay and others. The number of natural soil types ($n = 69$) and six natural landscape types (coasts, valleys, plains, loess landscape, low mountains, high mountains) were calculated per grid cell according to the 1:1,000,000 German soil survey map (Bundesanstalt für Geowissenschaften und Rohstoffe, 1995).

For information on land cover, we used Corine Land Cover maps (Statistisches Bundesamt, 1997). These land cover types are hierarchically aggregated. The lowest (third) level contains 34 land cover type classes for Germany (represented by a three-digit code in the CLC legend, URL: http://reports.eea.eu.int/COR0-part2/en/) and will be called 'level 3 CLC classes' hereafter. The highest (first) level aggregates the lower level CLC type classes into five 'level 1 CLC classes' (artificial surfaces, agricultural areas, forests and semi-natural areas, wetlands and water bodies). From this information, we calculated the number of level 3 CLC patches, the number of level 3 CLC classes and the number of level 1 CLC classes per grid cell.

The Federal Agency for Nature Conservation provided the respective data in grid cell format, which were transformed from the digital maps mentioned above on geology, soil and land cover with polygon-topology.

Data analysis

To relate the native and alien species number of rural and city grid cells to natural and man-made factors, we used an analysis of covariance (ANCOVA; Crawley, 2002; Quinn and Keough, 2002). The number of city grid cells and non-city grid cells differed by two orders of magnitude, there was strong autocorrelation (see Fortin *et al.*, 1989) between a focus grid cell and the adjacent ones (native plant species of our analysis show a highly significant Moran's $I > 0.04$ [$P < 0.001$] up to a Euclidean distance of < 22 grid cells) and not all grid cells with a specific combination of abiotic features (potentially 'suitable' for cities) were

actually cities. Hence we used a combination of parametric and resampling methods. We used the 68 city grid cells and randomly sampled 68 non-city grid cells to perform an ANCOVA. This was repeated 10,000 times with random resampling of non-city grid cells each time. We used the species number of natives, pre-1500 aliens and post-1500 aliens as dependent variables in three analyses. The categorical predictor was 'city' versus 'non-city' grid cells, while the metric predictors were the number of geological patches, geological types, natural substrates, natural soil types and natural landscape types, level 3 Corine Land Cover patches, level 3 Corine Land Cover classes and level 1 Corine Land Cover classes per grid cell. We modelled the main effects as well as interactions between each of the metric variables and the categorical variable. We estimated the two-tailed error probability from the 95% confidence interval of the 10,000 sums of squares per variable of the ANCOVA. To get a minimum adequate model, we stepwise deleted the least non-significant variable(s) after one cycle of 10,000 resamples.

We partitioned the variation among natural factors (variables derived from geology natural soil types and natural landscape types), land use factors (variables derived from Corine Land Cover) and a city effect (city grid cell, 'yes/no') following the method proposed by Legendre and Legendre (1998). Variation could be partitioned among those fractions that (i) corresponded exclusively to one (group) of predictor(s), (ii) were joint contributions of each (group) of predictor(s) in conjunction with the other(s) and (iii) remained unexplained (see also Quinn and Keough, 2002). Given that there are only two predictor variables, it is possible to compute three linear models using both predictor variables: (model i) variable 1 as predictor and variable 2 as co-variable, (model ii) variable 2 as predictor and variable 1 as co-variable, (model iii) variables 1 and 2 as predictors. The R^2 coefficient of model iii yields the complete explained variation. Similarly, the R^2 coefficient of model i (or model ii) is the variation exclusively explained by variable 1 (or 2). Thus the fraction of joint contributions $R^2_{JC} = R^2_{model\ iii} - (R^2_{model\ i} + R^2_{model\ ii})$.

To assess the significance of differences between species richness and the number of geological types in city grid cells and randomly selected (rural) grid cells, we used the means of 68 cells resampled 9999 times ('simple resampling') and compared this distribution to the mean of the city grid cells.

We present the results from analyses where we performed both the resampling ANCOVA and the simple resampling (to compare mean species richness) without replacement. For the simple resampling, we included the city grid cells into the universe for random sampling. This analysis was also performed with different resampling techniques (i.e. with and without replacement, including and excluding city grid cells into the universe for random selection) and definitions of city grid cells (e.g. > 30% urban land use as the definition for 'city grid cells'). The results were not influenced by these differences.

To regress species richness of red list species versus the number of natives plus pre-1500 aliens (both of which are pooled together in the red list of Korneck *et al.*, 1996), we used a major axis regression (Legendre and Legendre, 1998). This method was more appropriate for our data than an ordinary least square regression for two reasons. First, the numbers of red list species and of native + naturalized pre-1500 alien plant species were in the same dimension and sampled with the same error structure. Secondly, the error probability of the major axis regression was assessed after 1000 permutations. Therefore, we did not infer an error probability from an inflated number of degrees of freedom due to spatial autocorrelation (see Dutilleul, 1993).

All analyses were performed using R (http://www.r-project.org/).

RESULTS

First, we checked if the use of control species resulted in a higher proportion of up-to-date records compared with those grid cells that were omitted due to a lack of control species. On average, 82% (standard deviation 17.5%) of the data of city grid cells used in this analysis were from after 1980. Similarly, an average of 80% (standard deviation 23.5%) of the non-city data were from after 1980. There were no significant differences among the groups of natives and aliens, or between city and non-city cells. In contrast, the average proportion of the data from 1980 onwards of those cells that were omitted was 40% (standard deviation 36%). This differed significantly from the former groups (ANOVA, $P < 0.001$).

A brief overview of mean, quartiles and ranges of plant species richness in city or non-city grid cells is given by Fig. 1. The average numbers of native species were roughly five to six times higher than those of pre-1500 aliens and eight to twelve times higher than those of post-1500 aliens. While the average species number outside city grid cells was always lower than within city grid cells, their ranges were higher, as was their sample size (68 city grid cells, 1856 non-city grid cells).

The simple resampling analysis showed that the number of pre-1500 aliens, post-1500 aliens and native plant species were significantly higher in city grid cells than expected by random or than in rural grid cells (Fig. 2). The mean species number differed significantly between city grid cells and both randomly sampled grid cells and randomly sampled rural
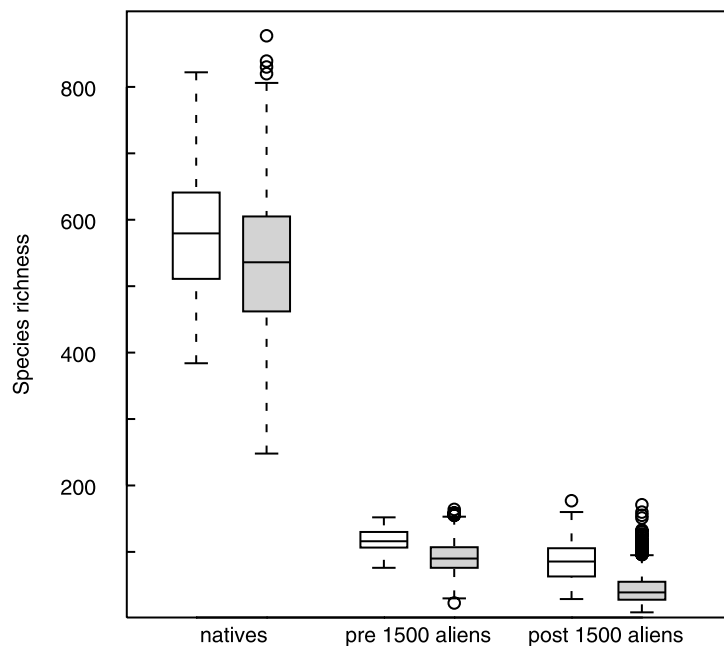

Fig. 1. Box-and-whisker plots of the species richness of native, pre-1500 alien and post-1500 alien plant species. White bars represent city grid cells ($n = 68$), grey bars represent non-city grid cells ($n = 1856$). The figure shows median species richness (lines), 25% to 75% quartiles (boxes) and ranges (whiskers). Open circles are shown if extreme values are more than 1.5 times the interquartile range of the box.
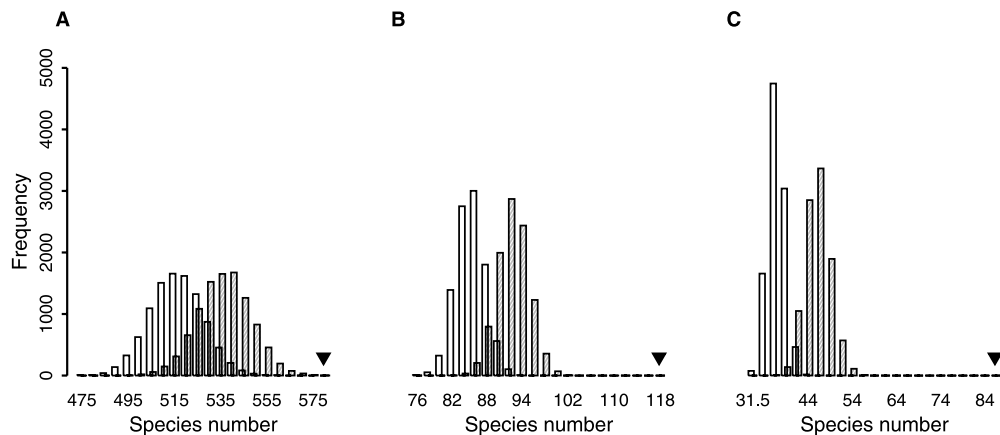
Fig. 2. Histograms of mean species richness per grid cell in Germany for (a) native plant species, (b) pre-1500 alien plant species and (c) post-1500 alien plant species of 68 grid cells randomly sampled 9999 times. Hatched bars represent the frequency of randomly sampled grid cells ($n = 1924$), white bars represent the frequency of randomly sampled rural grid cells ($n = 1099$). The labels of the x-axis provide the number of the midpoint of species richness classes. The interval range for native plant species is 5, for pre-1500 alien species it is 2 and for post-1500 alien species it is 2.5. The mean species number of city grid cells ($n = 68$) is indicated by the black triangle. City grid cells contain centres from cities with more than 100,000 inhabitants; rural grid cells contain less than 5% urban land cover.

Table 1. Average richness of different groups of plant species per grid cell in Germany

	City grid cells	Random grid cells	Random rural grid cells
Species richness of native plant species	580.7	536.1***	516.3***
Species richness of pre-1500 alien plant species	116.7	92.4***	85.3***
Species richness of post-1500 alien plant species	85.7	46.0***	37.1***
Species richness of threatened or endangered plant species	42.6	38.7*	36.7**

Note: Species richness in city grid cells was the average of 68 city grid cells with more than 100,000 inhabitants. The number of random grid cells equalled the number of city grid cells and were 9999 times randomly selected for (i) all German grid cells or (ii) only for rural grid cells (<5% cover of urban land use). *One-tailed error probability (compared with species number in city grid cells) <0.05. **One-tailed error probability <0.01. ***One-tailed error probability <0.001.

grid cells for all groups (all $P < 0.001$) (Table 1). Additionally, those species threatened or endangered on the national scale were more abundant in city grid cells than in randomly selected grid cells ($P = 0.03$) or in randomly selected rural grid cells ($P = 0.001$; see Table 1).

The resampling analysis of covariance showed for native plant species richness no significant effect of grid cell type (city or non-city). There was a significant effect of the number of different geological types and a marginally significant effect of land use on the number of native species (Table 2). The species number of aliens was significantly influenced by all three variables. For all three species groups, the analysis showed no interaction between city and geological, soil or land use variables, respectively. The number of red list

Table 2. Error probabilities of the minimum adequate model of a resampling analysis of covariance on the species number of natives and aliens between city and non-city grids in Germany

	Native species		Pre-1500 aliens		Post-1500 aliens	
	Sums of squares	*P*	Sums of squares	*P*	Sums of squares	*P*
Number of geological types	238521.0	<0.001	12290.1	<0.001	12523.5	0.001
Number of level 3 land cover classes	78489.6	0.040	18082.4	<0.001	44013.4	<0.001
City/non-city	4866.2	0.981	4401.1	0.035	16787.1	<0.001
Residuals	905685.3		48178.9		88065.0	

Note: Categorical factors were all 68 'city' and 68 randomly selected 'non-city' grid cells, resampled 10,000 times. Metric predictors of the full model were the number of geological patches, number of geological types, number of natural geological substrates, number of natural soil types, number of natural landscape types, number of level 3 Corine Land Cover (CLC) patches, number of level 3 CLC classes and number of level 1 CLC classes per grid cell.

species was influenced by almost the same variables as that of native species, namely the number of geological patches and the number of land use types but not by a city effect (I. Kühn *et al.*, unpublished).

To test the assumption that the high number of red list species in cities was not caused by urbanization, we tested whether the species richness of red list plant species was a constant property of the species richness of natives + naturalized pre-1500 aliens. A major axis regression of the log-transformed species number yielded a slope of 3.8 ($P = 0.001$) and unity was outside of the confidence interval [3.52, 4.04]. (The slope of the ordinary least square regression was 1.5 [$P < 0.001$] and differed significantly from 1 [t-test, $P < 0.001$].) The results were similar whether city grid cells were included or not.

Partitioning the variation among the variables revealed that geology was especially important for natives, whereas land use and in particular the city effects were increasingly important for aliens (Fig. 3). Joint contributions or effects were those where, for example, geology might influence land use or where land use is inseparable from city effects. Calculating how much each of these factors contributed to the total (native and alien) additional species in cities showed that geology was the most important single factor (30%), while land use and city/non-city each accounted for 12% of the additional species; 46% was attributed to combined effects.

We hypothesized that natural factors influencing plant species richness covary with urbanization – that is, they were more abundant in city grid cells and not randomly distributed. To test this hypothesis, we resampled (i) randomly selected and (ii) randomly selected rural grid cells in Germany and compared these to city grid cells. This showed that the single most important factor influencing plant species richness was significantly higher in city areas (number of geological types = 7.4) than on average (number of geological types = 6.6, $P = 0.007$) or than in rural grid cells (number of geological types = 6.2, $P < 0.001$) (Fig. 4). Of course, there are less level 3 CLC classes outside city grid cells (10.0) than in city grid cells (15.1), but as this is trivial and not the focus of our analysis it was not analysed further.
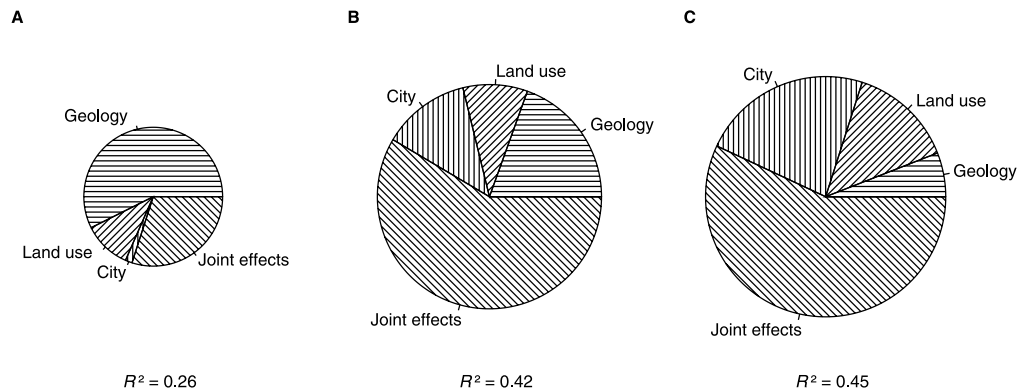
Fig. 3. Partitioning the variance of variables correlating with plant species richness in Germany. Slices represent the average proportions of explained variance. These are calculated as the averages of R^2 values of 10,000 analyses of covariance, each with 68 city grid cells and 68 randomly sampled grid cells from Germany. The pie charts show the independent contribution to the explained variance of geology (i.e. number of geological types), land use (number of level 3 Corine Land Cover classes) and city (city or non-city grid cell); joint contributions are those that could only be explained by two or three of the previous components together. Note that circle sizes are proportional to the explained variances (R^2).
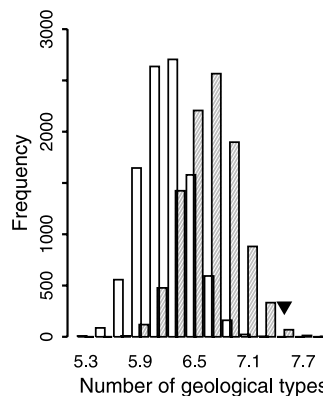

Fig. 4. Histogram of the mean number of geological types of 68 grid cells randomly sampled 9999 times. Hatched bars represent the frequency of randomly sampled grid cells ($n = 1924$), white bars represent the frequency of randomly sampled rural grid cells ($n = 1099$). The labels of the x-axis provide the number of the midpoint of species richness classes with ranges of 0.2. The mean number of geological types in city grid cells ($n = 68$) is indicated by the black triangle. City grid cells contain centres from cities with more than 100,000 inhabitants; rural grid cells contain less than 5% urban land cover.

DISCUSSION

The results of this study clearly showed that not only naturalized alien plant species but also native plant species contributed to higher plant species richness in urban areas. Thus, the high species richness of cities was not only due to cultivated or introduced alien plants, as suggested by several authors (e.g. Barthlott *et al.*, 1999; Kent *et al.*, 1999; McKinney,

2002a). The number of geological types was the most important environmental correlate for native and for total plant species richness. However, geological diversity itself was probably not directly responsible for plant species richness, but within a climatic zone, geology defines resource availability through other factors, for example soil chemistry, (micro) relief or habitats. All this adds to environmental heterogeneity caused by geological richness, which contributes to species richness (e.g. Wohlgemuth, 1998; Levine and D'Antonio, 1999; Lonsdale, 1999; Stohlgren *et al.*, 1999; Davis *et al.*, 2000; Stadler *et al.*, 2000; Deutschewitz *et al.*, 2003).

A possible source of error might have been the use of our 50 control species. Two of the authors (I.K. and S.K.) have in-depth experience in floristic mapping and were involved in several schemes incorporated in FLORKART. Therefore, some experience in plant distribution, plant habitat preferences, mapping procedures and mapping accuracy exists that, unfortunately, could not be quantified in any way that we are aware without either employing circular reasoning or calibrating to a benchmark, which does not yet exist. As far as the distribution maps in Haeupler and Schönfelder (1989) and Benkert *et al.* (1996), the experience of the authors as well as the species' ecological behaviour (very broad generalists) are concerned, it is reasonable to assume that all of the 50 control species occur in every $6' \times 10'$ grid cell. However, without using the 50 control species, our randomly resampled grid cells would have included many more insufficiently mapped grid cells, largely from more rural areas (for mainly stochastic and not methodological reasons). This would have resulted in an even lower plant species richness in randomly selected or rural grid cells while having only a minor effect on the species number per city grid cell.

An inconsistency might be the different scales for plant species distribution (1:25,000), geology and soil (1:1,000,000) and land cover (1:100,000). Unfortunately, there is no information available for the complete area of Germany on geology, soil and land cover at a scale of 1:25,000. Scaling up the grid cells of plant species distribution would have resulted in levelling off differences between city and non-city grid cells. Recognizing the appropriate scale of an analysis is important (e.g. Allen and Hoekstra, 1991, 1992; Scheiner *et al.*, 2000). Scheiner *et al.* (2000) distinguished three different components of scale: (1) the *grain*, which is the level of resolution at which the sampling took place; (2) the *focus*, being the level at which the analysis takes place, which can be the same size or larger than the grain; and (3) the *extent*, which is the span of the geographic area of the samples. Although we employed different scales for plant species distribution and environmental variables, we used the same focus and the same extent; differences were only in the grain. Using a relatively coarse grain for environmental variables may result in underestimating the number of different patches, and less in underestimating the number of different classes which were defined very broadly. Therefore, we believe that the use of a smaller grain would probably lead to reduced noise in the analysis but would not influence the general outcome of our study.

We showed that anthropogenic activities, namely land use heterogeneity, is least important for native plant species richness and most important for the post-1500 aliens. This is to be expected, since native plant species were once independent of humans (during evolution and colonization of pre-human habitats) while post-1500 aliens have been largely dependent on humans in their new range. Indeed, they would not have crossed biogeographic barriers into foreign areas without human facilitation.

We showed that cities are not randomly distributed among areas of different geological heterogeneity. There are good reasons why big cities are more often in areas of high geological heterogeneity, namely to provide enough means for founding a settlement and

facilitating development into big cities. Analyses from prehistoric settlements in ancient Greece (Davidson, 1972) and Roman settlements in Britain (Branigan, 1972) demonstrated the importance of geomorphology for the placement of settlements and traffic routes. Theoretical considerations (Blouet, 1972) and empirical evidence (Southall, 2000) showed that the availability of numerous things, such as drinking water (i.e. rivers), arable soils, defence (e.g. outlooks) and mineral resources, promoted the growth of cities. All these factors add to geological richness compared to average areas. Actually, most German cities are situated on large, usually navigable, rivers. As the number of geological patches was the most important correlate for native plant species richness in our analysis, we reason that areas where cities were developed were already species rich before the arrival of man. This means that, at least for native species, today's city areas were species rich independent of the presence of a city.

Unlike natives, the groups of alien species showed a significant city effect (i.e. higher richness within versus outside urban areas). This might be due to variables not included in our model (for example, location of transportation corridors). Another argument is that centres of floristic research (such as universities or research centres) and hobby botanists were more often in larger cities than in rural areas and thus the observed pattern might simply be a sampling artifact (Barthlott *et al.*, 1999). On balance, we think that this result is unlikely to be a sampling artifact, for the following reasons. While we omitted all grid cells that were poorly mapped, there might still be a 'positive' bias for areas mapped extraordinarily well, but there is little reason to expect that alien plant species would be sampled differently from natives, which showed no city effect.

We believe that the clear pattern of enhanced plant species diversity seen for German flora at the national scale is likely to be similar across large parts of temperate Europe; for example, areas of high natural heterogeneity with high native plant species richness are also areas of high population density. However, in other climatic zones (e.g. Hope *et al.*, 2003), areas with another history of settlement and land use, at other spatial scales or with different definitions of 'urbanization' (e.g. Roy *et al.*, 1999), the pattern might be different. Therefore, we need to conduct similar analyses especially from other biogeographic regions.

Our data do not allow us to infer directly whether the high number of red list species in city grid cells is due to or in spite of urbanization. While Dobson *et al.* (2001) could only show a correlation between population density and proportions of imperilled plants in California, analyses from Britain clearly showed a decline of rare species with increasing population density (Thompson and Jones, 1999). However, our results may be caused by similar underlying processes, as almost the same factors correlate with native plant species richness and with those of the red list plant species.

We demonstrated that species richness of red list species is a constant property of native + naturalized pre-1500 alien plant species richness and that the proportion of red list plant species increases more than proportionately. Hence we reason that species-rich grid cells have a considerably larger proportion of rare (and endangered) species than species-poor grid cells. As city grid cells are relatively species rich, the number of red list species is quite high as well. Thus it can also be reasoned that endangered plant species survived in small (semi-) natural areas or those that were not intensely utilized and which are frequently found in and around city areas and are themselves promoted by geological diversity. However, as underlying mechanisms for plant species richness may be co-correlated (Loreau *et al.*, 2001), cause and effect are easily confounded (e.g. Araújo, 2003).

Another reason for this pattern might be too long a time frame of the plant species records. If the time frame was too long, species that never co-existed together might co-occur together in the analysis. However, we used only records after 1950, when city centres were already completely developed. Furthermore, there were on average less than 20% of the records from before 1980 with no significant differences between city or non-city grid cells. Thus, the proportions of species that could not be recorded later from city and non-city grid cells were the same. Therefore, it is unlikely that the results are derived from a higher number of pseudo co-occurrences in cities that were separated in time.

It is well documented that urbanization is one of the major threats to biodiversity (Wilson, 1988; Thompson and Jones, 1999; McKinney, 2002b; Liu *et al.*, 2003). When this takes place in areas of high biodiversity, the threat of species loss will increase. Recent analyses on a global scale (Cincotta *et al.*, 2000; Liu *et al.*, 2003) have shown that the human population and the number of households grow extraordinarily in biodiversity hotspots. It appears that human habitat selection (a preference of urban over rural habitats) is consistent with an evolutionarily stable strategy and that this pattern of habitat use is associated with increased threats to the biodiversity of several animal groups and higher plants (Morris and Kingston, 2002). For Germany, Korneck *et al.* (1998) state that urbanization is one threat among others to biodiversity. Combining these observations with our results, we reason that cities are still rich in native species despite urbanization.

Additionally, cities form new habitats for completely human-managed cultivated plant communities (e.g. Whitney and Adams, 1980; Wittig, 1991; Pickett *et al.*, 2001; Hope *et al.*, 2003). These artificial (e.g. horticultural) plant assemblages, which are discussed as functioning ecosystems and placed in conceptual frameworks (e.g. Savard *et al.*, 2000; Löfvenhaft *et al.*, 2002), may add considerably to the biodiversity of cities. So besides the effect on native as well as naturalized alien plant species richness demonstrated in this study, the diversity of cities consists of these assemblages in gardens, parks, cemeteries or other habitats completely maintained by humans.

In summary, our findings show that German cities, both currently and in the past, were preferentially located in pre-existing biodiversity hot spots. We suspect that this pattern is similar for other temperate cities in Europe and elsewhere under similar environmental conditions and histories of settlement, and that urban areas are even more important for the conservation of floristic biodiversity than previously realized. We conclude that to maintain species diversity it is vital to increase conservation activities in human-dominated ecosystems, particularly those in and around cities (cf. Balmford *et al.*, 2001; Rosenzweig, 2003; but see Dobson *et al.*, 2001) and that a full understanding of the importance of urban biodiversity be incorporated into urban development and planning (Niemelä, 1999).

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