Urbanization causes shifts in species' trait state frequencies

Urbanizace způsobuje změny v zastoupení druhů určitých vlastností

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Urbanization is one of the most extreme forms of land transformation. It is supposed to change the frequencies of species trait states in species assemblages. We hypothesize that the flora of urban and rural areas differs in the frequency of trait states and ask which traits enable a plant to cope with the urban environment. We tested our hypothesis in Germany, which was divided into grid-cells of ca 130 km^2. We distinguished urbanized (with more than 33% urban land use; n = 59), agricultural (with more than 50% agricultural land use; n = 1365) and semi-natural (with more than 50% forest and semi-natural land use; n = 312) grid-cells and calculated the proportions of plant species per trait state in each grid-cell. Multiple linear regressions explained the log-transformed ratio of one proportion to another with land use (urban, agricultural, semi-natural) and the environmental parameters (climate, topography, soils and geology). Additionally, linear mixed effect models accounted for the effects of land use and biogeography and differences in sample size of the three grid-cell types. Urbanized and rural areas showed clear differences in the proportion of trait states. Urbanized grid-cells had e.g., higher proportions of wind-pollinated plants, plants with scleromorphic leaves or plants dispersed by animals, and lower proportions of insect-pollinated plants, plants with hygromorphic leaves or plants dispersed by wind than other grid-cells. Our study shows that shifts in land use can change the trait state composition of plant assemblages. Far-reaching urbanization might consequently homogenize our flora with respect to trait state frequency.

K e y w o r d s: compositional data, plant traits, species distribution patterns, urban ecology, urban flora, vascular plants

Introduction

Cities differ from rural landscapes in many ways: human densities peak in urbanized areas; concentrations of pollutants, energy and nutrients are higher there (Sukopp 1998); exotic species are more frequent and land use is more heterogeneous (Niemelä 1999, McKinney 2002, Kühn et al. 2004a); annual average air temperature is 0.5 to 1.5°C higher than in the non-urban surroundings and air moisture is reduced, at least in temperate and boreal zones (Sukopp 1998). In contrast to cities, many agricultural landscapes are homo-

geneous over large areas. They are often subjected to a highly industrialized agriculture, characterized by high pesticide and fertilizer input and water management aimed at maintaining favourable soil moisture conditions. Forested and semi-natural landscapes are often nutrient poor, like forests on siliceous rock or heathland, because many nutrient-rich habitats were transformed to agricultural or urban habitats (Pressey 1994).

Differences in land use lead to differences in species composition since functional traits (such as pollination) have different states (i.e., different classes of categorical traits, e.g. wind pollination, insect pollination, self-pollination) that respond differentially to environmental gradients and therefore show distinct biogeographic patterns (e.g., Kühn et al. 2006). In other words: different environments filter for species with different trait states (Zobel 1997). An example is the study of Wittig & Durwen (1982), which compared the spectra of environmental indicator values (Ellenberg et al. 2001) of spontaneous floras in four cities in the W Germany with those in the cities' rural surroundings, and revealed a greater proportion of high indicator values for e.g., light, temperature and nitrogen in the cities. Similar results were obtained for the central German city of Halle (Klotz 1989) and the Czech city of Plzeň (Chocholoušková & Pyšek 2003). Therefore, shifts in land use,
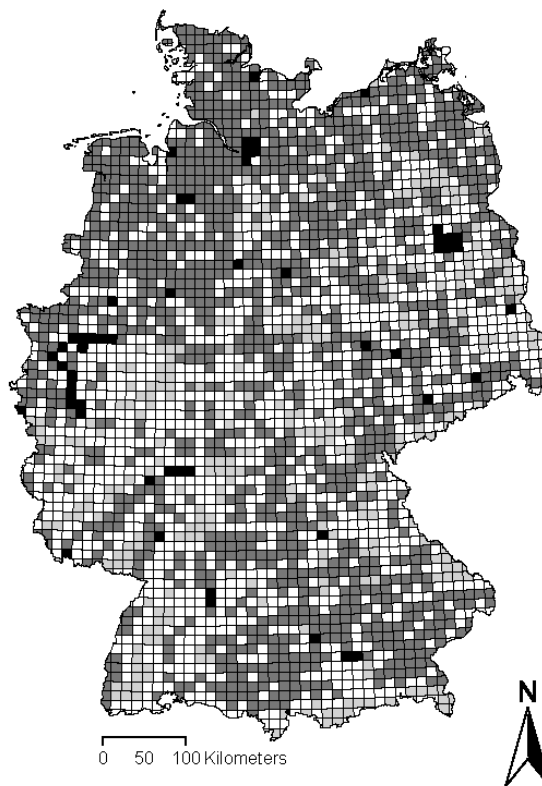

Fig. 1. – Study area (Germany, divided into grid-cells sized ca 12 × 11 km^2 ~ 130 km^2) Black – urbanized grid-cells, dark grey – agricultural grid-cells, light grey – semi-natural grid-cells, white – grid-cells not used due to insufficient number of control species or not meeting the selection criteria.

Table 1. – List of traits, units, trait states and their description (from BiolFlor: Klotz et al. 2002, Kühn et al. 2004b; http://www.ufz.de/biolflor, and LEDA: Kleyer et al. 2008; http://www.leda-traitbase.org/LEDAportal). cat = categorical, asterisks mark the trait state used in the denominator.

Trait	Unit	Trait state	Description
Mode of pollination	cat	Cleistogamy	Selfing in unopened, rudimentary flower
		Geitonogamy	Selfing by a neighbouring flower from the same plant
		Entomogamy	Pollination by insects
		Pseudocleistogamy	Selfing in unopened flower
		Selfing	Spontaneous pollination within a flower
		Anemogamy*	Pollination by wind
UV-reflection of flowers	cat	Yes*	UV reflectance pattern present
		No	No UV reflectance patterns
Leaf anatomy	cat	Helomorphic	With aeration tissue in the root (adapted to oxygen deficiency)
		Hydromorphic	Adapted to gas exchange in the water
		Hygromorphic*	Delicate plants of shade and semishade
		Mesomorphic	Without any characteristics, between scleromorphic and hydromorphic
		Scleromorphic	Firm and stiff leaves with thickened epidermis and cuticula but with mechanisms to promote water transport under beneficial conditions
		Succulent	With water storage tissue and thickened epidermis and cuticula
Specific leaf area (SLA)	$mm^2 \cdot mg^{-1}$	–	The ratio of fresh leaf area to leaf dry mass
Leaf dry matter content (LDMC)	$mg \cdot g^{-1}$	–	The ratio of dry leaf mass to fresh leaf mass; a measure of tissue density
Type of reproduction	cat	Only or mostly by seed	Plant reproduces by seed or spore, rarely vegetatively.
		By seed and vegetatively	Plant is able to reproduce by seed and vegetatively.
		Only or mostly vegetatively*	Plant reproduces vegetatively, rarely by seed or spore.
Life span	cat	Annual	The individual cycle lasts for a maximum of one year.
		Biennial	The plant grows for approx. one year vegetatively before reaching the generative phase after which it completes its life cycle.
		Pluriennial-monocarpic	The plant grows longer than one year (up to 5 years) vegetatively before completing its life cycle after the first and only generative reproduction.
		Pluriennial-polycarpic*	The plant has more than one generative phase in its life.
Life form	cat	Chamaephyte	Resting buds are situated on herbaceous or slightly lignified shoots some centimeters above the soil surface protected by foliage or snow.
		Geophyte	Resting buds are subterranean, often on storing organs within the soil.
		Hemicryptophyte	Resting buds are situated on herbaceous shoots close to the soil surface, protected by foliage or dead leaves.
		Hydrophyte	Resting buds are situated under water on the bed or in the mud.
		Phanerophyte	Resting buds are situated on (woody) shoots above the soil surface.
		Therophyte*	Summer annuals, which can only reproduce by generative diaspores
Dispersal type	cat	Anemochory*	Dispersal by wind
		Dysochory	Dispersal by scatter-hoarding animals
		Endozoochory	Dispersal by animals, after digestion
		Epizoochory	Adhesive dispersal by animals
		Hemerochory	Dispersal by man
		Nautochory	Dispersal by surface currents of water

e.g. increasing urbanization accompanied by an increase in temperature (Landsberg 1981, Oke 1982, Sukopp 1998), might lead to shifts in trait state frequency and, in extreme cases, to the loss of plants with certain trait states (Díaz & Cabido 1997). Tamis et al. (2005) showed that recent changes in the frequency of occurrence of vascular plant species across the Netherlands are at least partly related to both urbanization and climate change. However, they did not consider shifts in trait state frequency. If these shifts in trait spectra occur, they might affect ecosystem functioning: increased leaf dry matter content for example might decrease the rate of decomposition of litter (Kazakou et al. 2006).

Today's differences in the trait state composition of urban and rural floras might point to potential future shifts with further urbanization. We compared the proportions of several trait states of vascular plants in urbanized, agricultural and semi-natural areas in Germany. We ask which trait states enable a plant to cope with urban environments, e.g. the urban climate (Sukopp 1998), irregular disturbance, and spatial and temporal heterogeneity (Niemelä 1999). We chose traits that we expect to respond to these urban conditions: leaf traits [leaf anatomy, specific leaf area (SLA), leaf dry matter content (LDMC)] should respond to climate, because gas exchange and water storage make leaves key organs in the adaptation to changes in air temperature and moisture content (Wright et al. 2005). Further, we chose type of reproduction, life span and life form, as traits related to persistence and regeneration after disturbance (which is true for SLA and LDMC as well; Lavorel & Garnier 2002, Wittig 2002, Sudnik-Wójcikowska & Galera 2005). Both spatial and temporal heterogeneity call for the ability of plants to disperse in space, therefore we included dispersal type as another trait. Poschlod & Bonn (1998) record shifts in dispersal processes in man-made landscapes, especially after land-use intensification, which may cause a decrease or increase in species frequency (Römermann et al. 2008). Last, we chose pollination type and UV-reflection of flowers; both are related to a plant's fecundity and reflect the suitability of the environment for pollinating insects. We discuss possible urban and rural filters and consequences of shifts in trait expression.

Materials and methods

Data sources

Data on species' traits come from BiolFlor, a database on biological and ecological traits of the German flora (Klotz et al. 2002, Kühn et al. 2004b; http://www.ufz.de/biolflor) and from LEDA, a database on life-history traits of the Northwest European flora (Kleyer et al. 2008; http://www.leda-traitbase.org; see Table 1 for a complete overview and description of traits and trait states).

Plant species occurrences come from the database on the German flora (FLORKART, http://www.floraweb.de), maintained by the German Centre for Phytodiversity at the Federal Agency for Nature Conservation (Bundesamt für Naturschutz BfN). In FLORKART, Germany is divided into grid-cells of 10 minutes longitude × 6 minutes latitude (corresponding to ca 12 × 11 km or 130 km^2). To ensure a sufficient mapping quality we used only grid-cells with at least 45 of 50 so called control species (see Kühn et al. 2006 for details) that are either very frequent in Germany (Krause 1998) or generalists (Kühn et al. 2004a). The latter are inconspicuous or difficult to identify.

Land-use data for each grid-cell are based on Corine Land Cover data (Statistisches Bundesamt 1997; http://www.corine.dfd.dlr.de/intro_en.html) and differentiate between artificial (i.e., urban), agricultural, and forested/semi-natural land use, wetlands and water bodies. We classified grid-cells with more than 33% urban land as urbanized (n = 59) (Kühn & Klotz 2006; Fig. 1) and split the remaining grid-cells into agricultural, those with more than 50% agriculture (n = 1365) and semi-natural, those with more than 50% forest or semi-natural land use (n = 312). Grid-cells not meeting the criteria were omitted (n = 1259).

To account for the effects of environmental parameters other than land use on the trait state proportions, we used co-variables calculated per grid-cell and known to act on species diversity (Kühn et al. 2003). Data on climate [mean annual, mean July and mean January temperature, mean difference between July and January temperature (all 1961–1990), mean annual precipitation (1951–1980), mean wind speed] were provided by "Deutscher Wetterdienst Department Klima und Umwelt"; on topography (mean altitude above sea level) by ESRI (ARCDeutschland 500 dataset, 1: 500,000); data on soils (number of soil types, number of soil patches) and geology (number of geological types, number of geological patches) are based on the German soil survey map (Bundesanstalt für Geowissenschaften und Rohstoffe 1995) and the Geological survey map (Bundesanstalt für Geowissenschaften und Rohstoffe 1993) provided by the German Federal Agency for Nature Conservation.

Data analysis

Log-ratios of proportions

We combined the matrices on species per grid-cell and trait state per species (by matrix multiplication), creating a matrix on trait state frequency per grid-cell, from which we calculated the trait state proportions (for numbers of species analyzed per trait state see Table 2). Because the proportions add up to 100%, they depend on each other. To break this unit sum constraint, we used log-ratios of proportions (e.g., Aitchison 1982, Billheimer et al. 2001, Kühn et al. 2006). The log-ratio of two trait states a and b is log (a/b). For traits with more than two states the denominator should always be the same and independent of which trait it is.

Zero values can neither be log-transformed nor used in the denominator. Therefore, we replaced each zero with the proportion one trait state would have if expressed by only one out of all species of a grid-cell, and reduced the respective non-zero values by a corresponding amount (Fry et al. 2000, Martin-Fernandez et al. 2000). Each log-ratio was used separately in subsequent analyses.

SLA and LDMC are the only continuous traits in our analysis, i.e. they were used directly as responses in the linear models without preceding log-transformation.

Linear models

We explained each log-ratio, SLA and LDMC by using multiple linear regressions with the land-use types as categorical predictors and the parameters on climate, topography, soils and geology as continuous predictors. We reduced each model via backward selection to a minimal adequate version (model selection by AIC; Mac Nally 2000). In the output of a linear model, the first level of a categorical predictor (in this case the level 'urbanized grid-cells' of the predictor 'land-use types') is the intercept. For the other levels (in this case agricultural grid-cells and semi-natural grid-cells), the parameter estimate shows whether they differ

Table 2. – Number of species per trait state that were available for analysis (species data from FLORKART, http://www.floraweb.de; trait data from BiolFlor http://www.ufz.de/biolflor and LEDA http://www.leda-traitbase.org).

Trait	Trait state	Number of species
Mode of pollination	Cleistogamy	98
	Geitonogamy	74
	Entomogamy	2676
	Pseudocleistogamy	42
	Selfing	1905
	Anemogamy	741
UV-reflection of flowers	No	533
	Yes	349
Leaf anatomy	Helomorphic	448
	Hydromorphic	132
	Hygromorphic	325
	Mesomorphic	2210
	Scleromorphic	784
	Succulent	72
Specific leaf area	–	1168
Leaf dry matter content	–	981
Type of reproduction	Only or mostly by seed	1702
	By seed and vegetatively	1798
	Only or mostly vegetatively	168
Life span	Annual	748
	Biennial	266
	pluriennial-monocarpic	76
	pluriennial-polycarpic	2828
Life form	Chamaephyte	178
	Geophyte	438
	Hemicryptophyte	1955
	Hydrophyte	148
	Phanerophyte	746
	Therophyte	722
Dispersal type	Anemochory	468
	Dysochory	168
	Endozoochory	406
	Epizoochory	781
	Hemerochory	510
	Nautochory	253

from the first level. Because we are only interested in differences between urbanized and agricultural, and urbanized and semi-natural grid-cells, but not in differences between agricultural and semi-natural grid-cells, it was not necessary to perform post-hoc tests.

Choosing environmental variables to minimize non-land-use effects on log-ratios is difficult, because we might miss important variables. To corroborate the results of our first analysis, we additionally explained the log-ratios using linear mixed effect models that allow for random and fixed effects: We assigned the urbanized grid-cells to six regions that are reasonably homogeneous with respect to biogeography (Fig. 2). Within each region, we selected as many agricultural and semi-natural grid-cells as there were urbanized
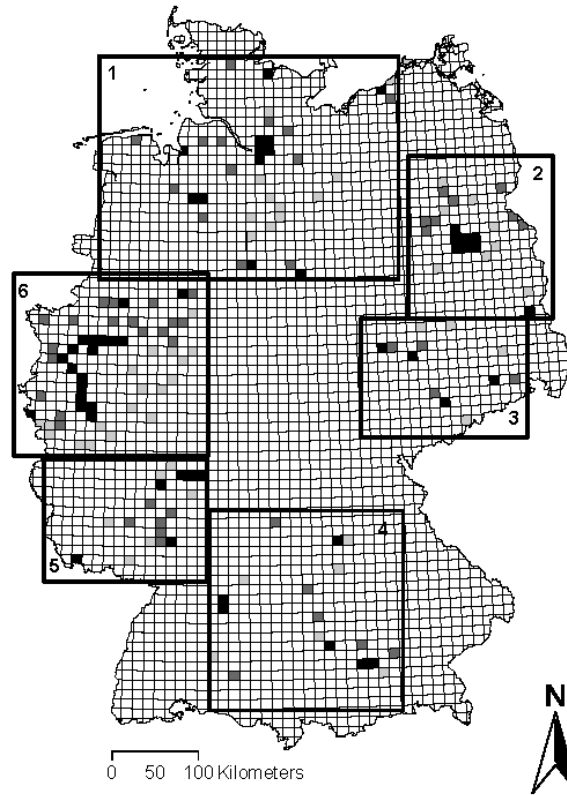
Fig. 2. – Six regions in Germany selected for comparison of effects of biogeography and land use. 1 – Northern Germany, 2 – Berlin and Brandenburg, 3 – Saxony and Saxony-Anhalt, 4 – Southern Germany, 5 – Rhine-Main region, 6 – Rhine-Ruhr region. Black – urbanized grid-cells, dark grey – agricultural grid-cells, light grey – semi-natural grid-cells.

grid-cells to account for the differences in sample size of grid-cell types. We explained the log-ratios (and SLA and LDMC) within the regions as random effects and land use as a fixed effect. On this, we performed a variance components analysis.

We performed all analyses with open source software R, Version 2.6.0 (R Development Core Team 2007), calculating the linear mixed-effect models with the R-function lme from the package nlme (Pinheiro et al. 2006) and variance components analysis with the R-function varcomp from the package ape (Paradis et al. 2004).

Results

Linear models

Most differences in trait state composition between urbanized and non-urbanized grid-cells were significant (Table 3). Urbanized grid-cells had relatively more wind-pollinated plants and correspondingly less insect and self-pollinated plants than agricultural grid-cells but did not differ from semi-natural grid-cells. There were more plants with UV-reflecting flowers

Table 3. – Differences in trait state ratios between urbanized (u) and agricultural (a) and urbanized and semi-natural (sn) grid-cells. Shown are the intercepts (Int; parameter estimate) of the linear models with their P-values: P > 0.1 n.s., 0.1 ≥ P > 0.05 +, P ≤ 0.05 *, P ≤ 0.01 **, P ≤ 0.001 ***. P-values indicate the differences between urbanized and agricultural (Int$_a$) or urbanized and semi-natural grid-cells (Int$_{sn}$). Where only n.s. is given without numbers, land use was not significant at all. (u, a) and (u, sn) indicate whether a trait state ratio is higher (>) or lower (<) in urbanized than in agricultural or semi-natural grid-cells or whether the grid-cell types have equal values (=). Model R^2 (adjusted for number of predictors) gives the total explained variance of the model including P-values.

Trait	Trait state ratio	Int$_u$	Int$_a$	Int$_{sn}$	u, a	u, sn	Model R^2
Mode of pollination	Cleistogamy/anemogamy	–1.44	–1.38***	–1.36***	u < a	u < sn	0.23***
	Geitonogamy/anemogamy	–2.23	–2.2 n.s.	–2.25 n.s.	u = a	u = sn	0.22***
	Entomogamy/anemogamy	1.77	1.8*	1.77 n.s.	u < a	u = sn	0.51***
	Pseudocleistogamy/anemogamy	–1.3	–1.29 n.s.	–1.32 n.s.	u = a	u = sn	0.20***
	Selfing/anemogamy	1.65	1.68*	1.65 n.s.	u < a	u = sn	0.40***
UV-reflection of flowers	No/yes	0.64	0.66*	0.67***	u < a	u < sn	0.08***
Leaf anatomy	Helomorphic/hygromorphic	–1.23	–1.29**	–1.26 n.s.	u > a	u = sn	0.49***
	Hydromorphic/hygromorphic	–4.04	–4.12 n.s.	–4.23**	u = a	u > sn	0.47***
	Mesomorphic/hygromorphic	0.21	0.08***	0.12***	u > a	u > sn	0.42***
	Scleromorphic/hygromorphic	–1.82	–2.0***	–1.9**	u > a	u > sn	0.37***
	Succulent/hygromorphic	–6.83	–7.2***	–7.02**	u > a	u > sn	0.25***
Specific leaf area	–	34.92	34.92 n.s.	34.55***	u = a	u > sn	0.25***
Leaf dry matter content	–	233.14	239.29***	241.55***	u < a	u < sn	0.20***
Type of reproduction	Only or mostly by seed/only or mostly vegetatively	1.92	1.84*	1.88 n.s.	u > a	u = sn	0.43***
	By seed and vegetatively/only or mostly vegetatively	n.s.	n.s.	n.s.			0.64***
Life span	Annual/pluriennial-polycarpic	–1.28	–1.42***	–1.4***	u > a	u > sn	0.70***
	Biennial/pluriennial-polycarpic	–2.59	–2.68***	–2.66***	u > a	u > sn	0.44***
	pluriennial-monocarpic/ pluriennial-polycarpic	n.s.	n.s.	n.s.			0.31***
Life form	Chamaephyte/therophyte	–1.0	–0.88***	–0.8***	u < a	u < sn	0.71***
	Geophyte/therophyte	–0.21	–0.06 n.s.	–0.08***	u < a	u < sn	0.60***
	Hemicryptophyte/therophyte	0.9	1.02***	1.03***	u < a	u < sn	0.71***
	Hydrophyte/therophyte	–2.44	–2.28**	–2.44 n.s.	u < a	u = sn	0.27***
	Phanerophyte/therophyte	0.55	0.7***	0.68***	u < a	u < sn	0.44***
Dispersal type	Dysochory/anemochory	–0.85	–0.83+	–0.84 n.s.	u < a	u = sn	0.42***
	Endozoochory/anemochory	0.25	0.22*	0.22*	u > a	u > sn	0.49***
	Epizoochory/anemochory	0.27	0.17***	0.17***	u > a	u > sn	0.59***
	Hemerochory/anemochory	0.3	0.23***	0.22***	u > a	u > sn	0.56***
	Nautochory/anemochory	–1.0	–1.07***	–1.08***	u > a	u > sn	0.62***

Table 4. – Percentage of variation explained in linear mixed effect models by land use (urbanized, agricultural, semi-natural) and differences in biogeography between six selected regions in Germany that are relatively homogenous biogeographically (see Materials and Methods). Model intercepts for urbanized (Int_u), agricultural (Int_a) and semi-natural (Int_{sn}) grid-cells show whether there are significant differences between urbanized and agricultural (see Int_a) or between urbanized and semi-natural grid-cells (see Int_{sn}). Levels of significance are indicated as follows: n.s. – not significant, * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

Trait	Trait state ratio	Land use	Biogeography	Int_u	Int_a	Int_{sn}
Mode of pollination	Cleistogamy/anemogamy	85	15	-1.88	-1.85 n.s.	-1.83*
	Geitonogamy/anemogamy	92	8	-2.25	-2.20 n.s.	-2.21 n.s.
	Entomogamy/anemogamy	55	45	1.02	1.03 n.s.	1.04 n.s.
	Pseudocleistogamy/anemogamy	85	15	-2.44	-2.44 n.s.	-2.47 n.s.
	Selfing/anemogamy	58	42	0.68	0.68 n.s.	0.69 n.s.
UV-reflection of flowers	No/yes	96	4	0.45	0.46 n.s.	0.48**
Leaf anatomy	Helomorphic/hygromorphic	62	38	0.29	0.25 n.s.	0.16***
	Hydromorphic/hygromorphic	83	17	-1.25	-1.30 n.s.	-1.65****
	Mesomorphic/hygromorphic	94	6	1.58	1.44***	1.41***
	Scleromorphic/hygromorphic	77	23	0.57	0.35***	0.34***
	Succulent/hygromorphic	96	4	-2.37	-2.63***	-2.72***
Specific leaf area	–	75	25	26.99	26.94 n.s.	26.74*
Leaf dry matter content	–	68	32	211.62	218.70***	223.33***
Type of reproduction	Only or mostly by seed/only or mostly vegetatively	61	39	2.27	2.16**	2.17**
	By seed and vegetatively/ only or mostly vegetatively	61	39	1.93	1.95 n.s.	2.02***
Life span	Annual/pluriennial-polycarpic	91	9	-0.83	-0.99***	-1.11***
	Biennial/pluriennial-polycarpic	93	7	-1.99	-2.09***	-2.14***
	pluriennial-monocarpic/ pluriennial-polycarpic	82	18	-3.26	-3.27 n.s.	-3.36**
Life form	Chamaephyte/therophyte	89	11	-1.99	-1.88***	-1.60***
	Geophyte/therophyte	89	11	-0.84	-0.68***	-0.58***
	Hemicryptophyte/therophyte	87	13	0.70	0.86***	0.97***
	Hydrophyte/therophyte	78	22	-1.74	-1.53**	-1.75 n.s.
	Phanerophyte/therophyte	84	16	-0.72	-0.54***	-0.42***
Dispersal type	Dysochory/anemochory	80	20	-0.67	-0.62**	-0.67 n.s.
	Endozoochory/anemochory	63	37	0.05	0.04 n.s.	0.01*
	Epizoochory/anemochory	78	22	0.60	0.51***	0.45***
	Hemerochory/anemochory	88	12	0.37	0.32**	0.24***
	Nautochory/anemochory	53	47	-0.45	-0.47 n.s.	-0.56***

in urbanized than in agricultural and semi-natural grid-cells. Proportions of plants with hygromorphic leaves were lower and those with mesomorphic, scleromorphic or succulent leaves were higher in urbanized grid-cells. Plants in urbanized grid-cells had a higher SLA than those in semi-natural grid-cells but did not differ from those in agricultural grid-cells. LDMC was lower in urbanized than in both types of non-urbanized grid-cells. Plants in urbanized grid-cells reproduced more often by seeds than those in agricultural grid-cells and were more often annual or biennial than those in agricultural or semi-natural grid-cells. There were relatively more therophytes in urbanized than in non-urbanized grid-cells, and accordingly fewer chamaephytes, geophytes, hemicryptophytes and phanerophytes in proportion to therophytes in the urbanized grid-cells. There were proportionally more plants dispersed by animals, man or water in urbanized grid-cells than plants dispersed by wind, which were relatively more frequent in the two types of non-urbanized grid-cells.

The linear mixed effect models, which corrected for biogeographic effects, mainly corroborated these results. Land use explained more variance than the biogeographic differences between the six regions, for all the trait state ratios tested (Table 4).

Discussion

The urban environment clearly favours plants with trait states other than those found in agricultural or semi-natural environments. The trait state patterns we found are due to typical urban filters. First, the urban heat island (Landsberg 1981, Oke 1982) favours plants either able to cope with drought, e.g. plants with succulent or scleromorphic leaves, or that avoid drought, e.g. annuals that complete their life cycle in a temporal niche like springtime, when temperatures and drought stress are still low (Wittig 2002). Low air moisture promotes wind pollination by increasing the probability of pollen reaching receptive surfaces (Culley et al. 2002). Secondly, the intensive and irregular disturbances in urbanized areas favour annuals (Kleyer 1999) and plants with leaves with a high specific leaf area and low leaf dry matter content (Díaz et al. 1999). Thirdly, the spatial and temporal heterogeneity of cities should promote plants with high dispersal abilities. Although all the dispersal types studied can potentially result in long-distance seed dispersal (Knevel et al. 2005), our results suggest that wind is less adequate for long-distance dispersal within urbanized areas. Wind is channelled along streets and often follows the increasing temperatures towards the city centre, thus seeds end up more often on sealed surfaces. Moreover, calm periods occur more frequently in than outside cities (Kuttler 1993) and seeds do not reach potential habitats in the lee of houses or walls. In contrast to wind dispersal, animal dispersal (endo- and epizoochory) seems to work as well in urbanized areas as that by man. On the one hand, birds, cats, dogs and some wild mammals like foxes (Gloor et al. 2001) are potential dispersers. However, birds mainly disperse fleshy fruits and rarely other types of seed (Kollmann 1994). On the other hand, animal-dispersal and man-dispersal might overlap, with epizoochorous species using man or even cars as vehicles for dispersal instead of animals (Hodkinson & Thompson 1997, von der Lippe & Kowarik 2007, 2008). Finally, cities have a high proportion of unstable habitats (e.g., urban brownfields) that favour annuals and biennials, reproduction by seeds and therophytes (Brandes & Oppermann 1995, Wittig 2002, Sudnik-Wójcikowska & Galera 2005). Note that therophytes are annuals and reproduce by seeds (Table 1), thus, the results confirm both as the traits are correlated and partly depend on the same environmental factors. The same is true for

specific leaf area and low leaf dry matter content, which are negatively correlated (Roche et al. 2004). Higher SLA and higher proportions of plants with scleromorphic leaves in urbanized areas seem contradictory, but again point to the high heterogeneity of urban areas (Niemelä 1999) with dry, nutrient poor habitats like urban brownfields, which favour plants with scleromorphic leaves, and nutrient rich watered habitats like urban parks and cemeteries (Sukopp 1998), which favour those with a high SLA (Wright et al. 2005).

The rural filters differ from the urban filters: Temperatures are lower, disturbances are more regular, land use is more homogeneous (Lososová et al. 2006). Additionally, rural environments seem to be more suitable for insects than urban environments, due to less pollution and different land-use structure (e.g., fewer buildings) and consequently favour insect-pollinated over wind-pollinated plants (Lososová et al. 2006). It seems contradictory to have more wind-pollinated but fewer wind-dispersed species in urbanized grid-cells, but pollinating insects might be more sensitive to urban land use than seed-dispersing animals, and animal-dispersed species might also be dispersed by humans (see above). A sensitivity of insects to urban land use can also explain the higher frequency of plants with UV-reflecting flowers in urbanized grid-cells: UV-reflection in BiolFlor is mainly documented for insect-pollinated plants, which seem to attract fewer insects in urban than in rural areas. Nevertheless, we cannot tell from our data whether a low proportion of insect-pollinated species decreases pollinator richness or vice versa. It might be a parallel response to urbanization (Biesmeijer et al. 2006).

It seems surprising that self-pollinated species are less frequent in urbanized than rural areas, although many urban habitats are quite young. Newly created habitats should be first invaded by plants that are independent of insects or other pollinating animals, since if pollinator availability is low, successful reproduction is only possible by wind or self-pollination (Culley et al. 2002, Düring 2004). However, selfers are only more frequent in agricultural than urbanized grid-cells and do not differ in frequency in semi-natural and urbanized grid-cells. Agricultural areas are tilled and harvested often several times a year. Therefore, many agricultural habitats are even younger than urban brownfields or industrial habitats.

Germany covers a range of biogeographic regions from the Alps in the South to the coasts in the North. There are more cities in the N and W Germany than in the South (Fig. 1); most cities are situated on rivers and below 300 m a.s.l. (Kühn & Klotz 2006). Thus they have a biogeographically biased distribution (Kühn et al. 2004a), and the trait state patterns might not reflect differences between urban and rural land use but also biogeographic gradients. Although we accounted for climate, topography, soils and geology, there are other environmental parameters that might influence trait state patterns, such as variation in altitude, sunshine duration or length of vegetation period. To account for all these biogeographic effects, we applied the linear mixed effect models. Nevertheless, in these models land use explains even more of the variation than differences in biogeography (Table 4).

Our results might be influenced by phylogenetic relatedness of species and spatial autocorrelation. Both can alter parameter estimates of linear models (Kühn 2007, Tremlová & Münzbergová 2007). Though we are aware of this, we neither corrected for phylogeny nor for spatial autocorrelation. We think that our results are reliable as including or excluding phylogenetic relatedness produced similar results for most traits in an urban-rural comparison of plant trait patterns in the Czech Republic (Lososová et al. 2006). In addition, analyses without phylogenetic correction pose fewer problems when dealing with large rather than small species groups (Tremlová & Münzbergová 2007). Besides, we are not aware of any method suitable to account for spatial as well as phylogenetic autocorrelation.

Our study clearly shows that on a coarse spatial scale shifts in land use can change the trait state composition of plant assemblages. This finding is remarkable, given the fact that grid-cells are rather heterogeneous; there is still 66% non-urban land in a grid-cell with 34% urban land. However, modern cities are not restricted to a few square kilometers bordered by city walls. They spread into the surroundings where they mingle with rural land use, creating urbanized landscapes. Given this spatial heterogeneity it is expected that, in addition to the effects of urban land use on coarse spatial scales, there are additional effects of urbanization on smaller spatial scales. There is, however, some evidence that the positive relation between urban land use and species richness (Araújo 2003, Hope et al. 2003, Kühn et al. 2004a) is especially strong at coarse scales (Pautasso 2007).

In conclusion, our study shows that shifts in land use can change the trait state composition of plant assemblages. Further urbanization might consequently homogenize the flora with respect to trait state frequency.

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Souhrn

Urbanizace je jedním z nejextrémnějších způsobů využívání krajiny. Článek je založen na předpokladu, že se flóra městských a venkovských stanovišť liší v zastoupení druhů určitých vlastností, a zjišťuje, které vlastnosti rostlinám umožňují vyrovnat se s urbanizovaným prostředím. V Německu byly rozlišeny čtverce (o velikosti ca 130 km^2) s urbanizovaným (více než 33 % zastavěné plochy, n = 59), zemědělským (více než 50 % zemědělské plochy, n = 1365) a polopřirozeným (více než 50 % lesní a polopřirozené vegetace, n = 312) krajinným pokryvem. V jednotlivých čtvercích bylo vypočteno zastoupení druhů s určitými vlastnostmi. Rozdíly v poměrném zastoupení druhových vlastností závisely na krajinném pokryvu a parametrech prostředí (klima, topografie, půda a geologie). Městské a venkovské oblasti se jasně lišily ve frekvenci výskytu druhů určitých vlastností. V urbanizovaných čtvercích byly více zastoupeny druhy opylované větrem, se skleromorfními listy a šířené zvířaty, méně pak druhy opylované hmyzem, s hygromorfními listy a šířené větrem. Studie ukazuje, že pokud jde o frekvenci zastoupení druhů s určitými vlastnostmi, urbanizace může vést k homogenizaci flóry.

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