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LETTER

Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany

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Abstract

Cities are hotspots of plant species richness, harboring more species than their rural surroundings, at least over large enough scales. However, species richness does not necessarily cover all aspects of biodiversity such as phylogenetic relationships. Ignoring these relationships, our understanding of how species assemblages develop and change in a changing environment remains incomplete. Given the high vascular plant species richness of urbanized areas in Germany, we asked whether these also have a higher phylogenetic diversity than rural areas, and whether phylogenetic diversity patterns differ systematically between species groups characterized by specific functional traits. Calculating the average phylogenetic distinctness of the total German flora and accounting for spatial autocorrelation, we show that phylogenetic diversity of urban areas does not reflect their high species richness. Hence, high urban species richness is mainly due to more closely related species that are functionally similar and able to deal with urbanization. This diminished phylogenetic information might decrease the flora's capacity to respond to environmental changes.

Keywords

Environmental filtering, evolutionary niche conservatism, macroecology, phylogeny, plant traits, urban ecology, urban flora.

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INTRODUCTION

The world is urbanizing rapidly. Today, *c.* 50% of the world's population lives in cities; in Europe, this proportion is higher than 70% (United Nations 2008). Often, cities are actually richer in species than their rural surroundings, as has been shown for Europe, North America, South America and sub-Saharan Africa (e.g. Balmford *et al.* 2001; Araújo 2003; Hope *et al.* 2003; Leveau & Leveau 2005). This higher species richness even in native species can be explained because (i) many cities developed in geologically and structurally heterogeneous landscapes (Kühn *et al.* 2004a); (ii) cities are highly structured themselves (Niemelä 1999); (iii) the high urban temperatures promote species whose distribution is limited by cold temperatures (Sukopp *et al.* 1979; Fig. 1a); and (iv) alien as well as native species tend to be introduced in urbanized areas (Kühn *et al.* 2004a). While Barthlott *et al.* (1999) argued that species richness in cities is an effect of sampling bias, this is not the case for Germany (Kühn *et al.* 2004a). Given the increasing concentration of human activities in such diverse landscapes (see e.g. Cincotta *et al.* 2000), we should provide habitats to conserve species diversity not only in natural landscapes but also within urban areas (Rosenzweig 2003).

However, biodiversity and species richness, i.e. the number of species in an area, are not equivalent. In terms of species richness, an assemblage of three *Poaceae* species seems as diverse as an assemblage of one *Poaceae*, one *Asteraceae* and one *Fagaceae* species; but the former assemblage appears much less diverse when considering their phylogenetic background: The three *Poaceae* species belong to one family and are thus closer related to each other than the species from the three families of *Poaceae, Asteraceae* and *Fagaceae*. Phylogenetic diversity, which measures the diversity of evolutionary relationships between species, reveals these underlying patterns, and so provides valuable information for species conservation and about mechanisms of species assembly (Vane-Wright *et al.* 1991).

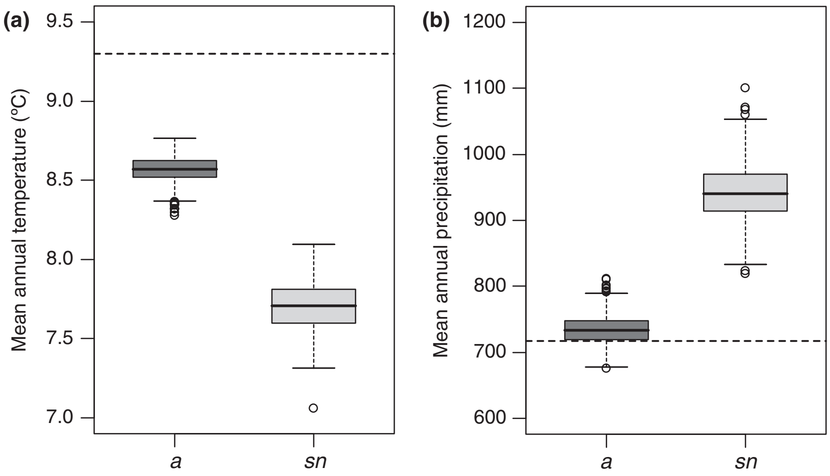

Figure 1 (a) Mean annual temperature and (b) mean annual precipitation in urbanized (– –), agricultural (*a*) and semi-natural (*sn*) grid-cells in Germany. Shown are the mean temperature/precipitation values for each of the three land-use types. Mean values for agricultural and semi-natural grid-cells are based on resampling (999*59 grid-cells) and shown as dark grey (agricultural) and light grey (semi-natural) boxplots representing median (line), 25–75% quartiles (boxes), ranges (whiskers) and extreme values (circles).

Phylogenetically closely related species often share specific traits through their common origin and evolutionary history (evolutionary niche conservatism; Harvey & Pagel 1991; Prinzing *et al.* 2001). Hence, phylogenetic diversity is usually interrelated with the frequency of species per functional trait, which is another aspect of biodiversity. However, phylogenetically closely related species can also develop different trait states because of adaptive radiation (e.g. Schluter 2000; Ackerly & Nyffeler 2004; Prinzing *et al.* 2008). In both cases, the environment influences the functional and phylogenetic structure of a species assemblage. We therefore expect differences in the functional and phylogenetic structure of floras from urbanized and non-urbanized areas. While influences of urbanization on functional traits have been confirmed for a range of plant traits (e.g. Kleyer 2002; Chocholoušková & Pyšek 2003; Williams *et al.* 2005; Lososová *et al.* 2006), little is known about the effects of urbanization on phylogenetic diversity (but see Ricotta *et al.* 2008).

Here we compare the phylogenetic diversity of German vascular plant assemblages between urbanized and two types of non-urbanized areas, i.e. agricultural and semi-natural including forests (both referred to as rural). Our approach is a macroecological one, suitable to reveal large-scale patterns and well suited to reflect the influence of urbanization on biodiversity that does not stop at city borders but acts on large areas. Moreover, the positive relation between urban land-use and species richness is especially strong at coarse scales (Pautasso 2007). We use a gridded data set for which previous analyses have shown that the species richness of vascular plants is higher in urbanized than in rural areas (Kühn *et al.* 2004a). Phylogenetic diversity in areas with dense human population might be even higher than expected from species numbers, as Sechrest *et al.* (2002) have shown for carnivores and primates in areas that are naturally species rich. Correspondingly, urbanized areas could be expected to have a higher phylogenetic diversity than rural areas, because heterogeneous landscapes provide a variety of niches for a variety of lineages (cf. Ricotta *et al.* 2008), while agricultural landscapes are homogeneous over large areas. On the other hand, if a trait is highly conserved, then the urban environment should filter for closely related species: Species groups characterized by a conservative trait that is suitable for urban environments should be phylogenetically clustered within urban landscapes (e.g. Cavender-Bares *et al.* 2006; Swenson *et al.* 2007).

There are environmental filters (Zobel 1997) in both urbanized and rural areas that might restrict species richness to species capable of passing the filters, i.e. plants with suitable trait states. These filters, such as the fragmentation of urban landscapes or the regular disturbance in agricultural landscapes, might increase the phylogenetic diversity of plants with well-suited traits but decrease the phylogenetic diversity of plants with less suited traits. Plants well-suited for urban environments should be able to colonize a range of urban habitats (cf. Kowarik 2008) and thus to establish a high phylogenetic diversity. Plants less suited for urban environments should be restricted to only a few urban habitats and consequently have a restricted phylogenetic diversity.

We therefore test the hypothesis that species-rich urbanized areas, given their high geological and structural heterogeneity, also have a higher phylogenetic diversity than rural areas. This should apply because the higher urban habitat heterogeneity is expected to hold a higher number of different lineages. We further test whether species richness and phylogenetic diversity patterns differ systematically between species groups characterized by different trait states, i.e. whether species richness or phylogenetic diversity are higher in groups with traits suitable for urban environments and lower in groups with more unsuitable traits. Our results show that the high urban species richness is mainly based on more closely related species, and that these are better adapted to the urban environment than a random selection of the overall species pool.

MATERIALS AND METHODS

Data sources

Plant species occurrences were calculated at a *c.* 12 × 11 km grid (*c.* 130 km^2; corresponding to 10′ longitude × 6′ latitude), taken from the database on the German flora (FLORKART, http://www.floraweb.de). FLORKART is maintained by the Federal Agency for Nature Conservation (Bundesamt für Naturschutz BfN) on behalf of the German Network for Phytodiversity (NetPhyD). The database contains > 14 million records of plant occurrences, acquired by thousands of volunteers. Occurrences are assigned to three periods: before 1950, 1950–1980 and after 1980. We did not use cultivated occurrences and only referred to the spontaneous flora. This means that occurrences of cultivated alien species that escaped from cultivation and form self-sustaining populations were mapped when occurring spontaneously. This applies, e.g. to *Robinia pseudoacacia* L. or *Ailanthus altissima* (Mill.) Swingle when growing spontaneously on, e.g. railway sites. Occurrences that were apparently planted, e.g. in any kind of garden, urban parks or on cemeteries, were not included in our analysis. All plant occurrences mapped by the volunteers were controlled for plausibility by specialists in floristic recording centres (see e.g. http://www.biologie.uni-regensburg.de/Botanik/Florkart/dbblber.htm). However, mapping intensity varies among grid-cells. Therefore, we only used occurrences from 1950 onwards and only grid-cells with at least 45 of 50 control species. These are the 45 most frequent species of the German flora according to Krause (1998) plus five generalists considered by the volunteers to be difficult to determine (Kühn *et al.* 2004a, 2006). Of 2995, 136 grid-cells were excluded because of an insufficient number of control species. Data on species traits and phylogeny were taken from BiolFlor, a database on the biological and ecological traits of the German flora (Klotz *et al.* 2002; Kühn *et al.* 2004b; http://www.ufz.de/biolflor). We used traits with distinct urban-rural patterns (see Table 1 and references therein).

On the basis of Corine land-cover data (http://www.corine.dfd.dlr.de/intro_en.html; Statistisches Bundesamt 1997), we selected those grid-cells with > 33% of urban land-use as urbanized grid-cells (*n* = 59) and all others as non-urbanized grid-cells (Fig. 2; Kühn & Klotz 2006). We split the latter into agricultural grid-cells having > 50% of agricultural land-use (*n* = 1365) and semi-natural grid-cells having > 50% of forests or semi-natural habitats (*n* = 312). Other environmental parameters known to act on biodiversity were used per grid-cell (Kühn *et al.* 2003). Originally, data on climate [mean annual temperature, mean July and mean January temperature, mean difference between July and January temperature (all 1960–1990), mean annual precipitation (1950–1980), mean wind speed] were provided by 'Deutscher Wetterdienst, Department Klima und Umwelt'. Data on topography (mean altitude above sea level) were taken from ESRI (ARCDeutschland 500 data set, 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), both provided by the German Federal Agency for Nature Conservation.

Data analyses

We first calculated the species richness of the total flora and of each species group with a specific functional trait. We tested whether the groups reflect the richness pattern of the total flora or vary according to their trait state. To control for spatial autocorrelation among grid-cells and for effects of environmental parameters other than land-use (see Data sources), we developed two spatial autoregressive error models (Dormann *et al.* 2007; Kissling & Carl 2008). One was an intercept-only model with species richness as the response (SARerr-null; correcting only for spatial autocorrelation), the other had species richness as response and climate, topography, soil, and geology as explanatory variables (SARerr-env; correcting for both spatial autocorrelation and environmental parameters). The lag-distance for which we considered the influence of autocorrelation was 2.5 grid-cells. We did not include land-use types in the models because of a highly imbalanced sampling design (1365 agricultural, 312 semi-natural, 59 urbanized grid-cells). We instead calculated the residuals from SARerr-null and SARerr-env models and assessed the effect of land-use type on the species richness of the total German flora and the 25 species groups by a resampling approach. We calculated the mean of the models' residuals per grid-cell type (agricultural, semi-natural, urbanized) and separately resampled, according to the number of urbanized grid-cells, 59 randomly chosen agricultural or semi-natural grid-cells 999 times. We then tested for significant differences in the residuals' mean values between urbanized and agricultural grid-cells and between urbanized and semi-natural grid-cells using the z-statistic (comparison of one value to a distribution of values; P-values calculated for absolute z standard normal deviates). The Mann–Whitney Wilcox U-test was used to test for differences between agricultural and semi-natural grid-cells (comparison of two distributions of values; Crawley 2002).

Table 1 List of traits, trait states and their description (from BiolFlor; http://www.ufz.de/biolflor)

Trait	Trait state	Description	Frequency in urbanized areas
Pollen vector	Insects	Pollination by insects	↓ (Lososová *et al.* 2006)
	Selfing	Spontaneous self-pollination within a flower	↓ (Lososová *et al.* 2006)
	Wind	Pollination by wind	↑ (Lososová *et al.* 2006)
Leaf anatomy	Hygromorphic	Delicate plants of shade and semi shade	↓ (Wittig 2002)
	Mesomorphic	Without any characteristics, between scleromorphic and hydromorphic	↓ (Wittig 2002)
	Scleromorphic	Firm and stiff leaves with thickened epidermis and cuticula but with mechanisms to promote water transport under beneficial conditions	↑ (Wittig 2002)
	Succulent	With water storage tissue and thickened epidermis and cuticula	↓ (Wittig 2002), ↑ (Knapp, S., Kühn, I., Wittig, R. & Klotz, S., unpublished data)
Life span	Annual	The individual cycle lasts for a maximum of 1 year	↓ (Lososová *et al.* 2006), ↑ (Chocholoušková & Pyšek 2003)
	Biennial	The plant grows for *c.* 1 year vegetatively before reaching the generative phase after which it completes its life cycle	↑ (Chocholoušková & Pyšek 2003; Lososová *et al.* 2006)
	Pluriennial	The plant has more than one generative phase in its life	↓ (Chocholoušková & Pyšek 2003)
Life form	Chamaephyte	Resting buds are situated on herbaceous or only slightly lignified shoots some centimeters above the soil surface protected by parts of the plant itself and/or by a snow cover	↑ (Williams *et al.* 2005), ↓ (Knapp, S., Kühn, I., Wittig, R. & Klotz, S., unpublished data)
	Geophyte	Resting buds are subterranean, often on storing organs protected within the soil	↓ (Wittig 2002; Williams *et al.* 2005)
	Hemicryptophyte	Resting buds are situated on herbaceous shoots close to the soil surface, protected by foliage or dead leaves	↓ (Wittig 2002; Williams *et al.* 2005)
	Phanerophyte	Resting buds are situated on (woody) shoots above the soil surface	→ (Lososová *et al.* 2006), ↓ (Knapp, S., Kühn, I., Wittig, R. & Klotz, S., unpublished)
	Therophyte	Summer annuals, which can only reproduce by means of generative diaspores	↑ (Wittig 2002)
Strategy type	c	Competitors: trees and shrubs with high competitive power due to their morphological and/or physiological life history traits	↑ (Wittig 2002; Chocholoušková & Pyšek 2003)
	cr	Intermediate type between competitors and ruderals	↑ (Wittig 2002; Chocholoušková & Pyšek 2003)
	cs	Intermediate type between competitors and stress-tolerators	↑ (Wittig 2002)
	csr	Intermediate type, usually rosette plants or small, perennial species which can utilize spatio-temporal niches very well and have an intermediate life span	↓ (Chocholoušková & Pyšek 2003)
	r	Ruderals: usually annual, weedy plant species which produce many seeds and can easily colonize pioneer habitats	↓ (Lososová *et al.* 2006), ↑ (Wittig 2002)
	s	Stress tolerators: species with only little growth and morphological and/or physiological adaptations to conditions that may be either very rare or overabundant (e.g. water or drought)	→ (Wittig 2002; Chocholoušková & Pyšek 2003)
	sr	Intermediate type between stress-tolerators and ruderals	↓ (Chocholoušková & Pyšek 2003)

Table 1 (*Continued*)

Trait	Trait state	Description	Frequency in urbanized areas
Floristic status	Archaeophyte	Taxon immigrated before the discovery of the Americas	↓ (Lososová *et al.* 2006)
	Native	Taxon native to Germany	↓ (Kowarik 2008)
	Neophyte	Taxon immigrated after the discovery of the Americas	↑ (Lososová *et al.* 2006; Kowarik 2008)

It is indicated whether the respective trait is generally more (↑) or less (↓) frequent in urbanized areas or shows no trend (→).

Figure 2 The study area (Germany) divided into grid-cells of 10′× 6′ of arc degrees (i.e. *c.* 12 × 11 km). Black: urbanized grid-cells; dark grey: agricultural grid-cells; light grey: semi-natural grid-cells; white: grid-cells not used because not meeting the selection criteria; cross-hatched: grid-cells not used due to insufficient number of control species.

To compare phylogenetic diversity among the land-use types, we combined the matrices on species per grid-cell and on phylogenetic code per species to calculate phylogenetic diversity per grid-cell. The phylogenetic code of a species (as assigned to each species in BiolFlor; Durka 2002; Kühn *et al.* 2004b) marks its position in the phylogenetic tree and therefore its position relative to other species in the tree. In BiolFlor, only the topology of a species tree is given, not the branch lengths. Consequently, all branches are treated as having the same length and the phylogenetic distance between species can be derived from the number of nodes separating one species from another. This is a good alternative for the calculation of phylogenetic diversity indices if exact branch lengths are unknown (Faith 1992). Since our aim was to disentangle the effects of species richness and phylogenetic diversity, we used average taxonomic distinctness (Δ^+) following Warwick & Clarke (1998). Δ^+ is unbiased by species richness, i.e. it does not automatically increase with increasing species richness. There are several mathematically related indices such as Rao's quadratic entropy (Rao 1982) or Webb's Net Relatedness Index (NRI; Webb *et al.* 2002). However, NRI was defined for slightly different questions, as it quantifies the distribution of taxa in a sample relative to a pool. Additionally, a comparative study shows that only Warwick and Clarke's Δ^+ is exactly independent of species richness and reflects the phylogenetic structure of a subset from a phylogenetic tree best (Schweiger *et al.* 2008). Δ^+ originally was developed on taxonomic relationships but it can be easily adapted to phylogenetic information by substituting the taxonomically weighted distance by phylogenetic distance (see also Schweiger *et al.* 2008). The index was calculated as

$$\Delta^+ = \frac{\sum\sum_{i<j} d_{i,j}}{[s\,(s-1)/2]}$$

where $d_{i,j}$ is the distance matrix of nodes and s is the number of species. Thus, the index is based on a pairwise distance matrix defined by the number of nodes that separate one species from another and can be interpreted as the mean distance between two randomly chosen species independent from their distance from the root of the tree.

We calculated Δ^+ per grid-cell; first for the total German flora, then for 25 groups of species characterized by a specific trait state, e.g. for all insect, self or wind pollinated species, or for all species with scleromorphic or hygromorphic leaves (Table 1). For all species groups, both native and exotic species were considered; except, of course, when grouping was based on natives, archaeophytes and neophytes. As for species richness, SARerr-null models corrected for effects of spatial autocorrelation on Δ^+ and

SARerr-env models corrected for effects of spatial autocorrelation, climate, topography, soil and geology. We also resampled the models' residuals for agricultural and semi-natural grid-cells and compared the residuals' mean values for urbanized, agricultural and semi-natural grid-cells with the z-statistic and Mann–Whitney Wilcox U-test.

If SARerr-null and SARerr-env models yield the same result, e.g. higher urban than rural phylogenetic diversity, then the parameters causing this pattern should be 'urban-intrinsic' (or 'rural-intrinsic'). Examples for urban-intrinsic parameters are the density of built-up area or disturbance intensity. If the SARerr-null model shows a difference between urbanized and rural areas but the SARerr-env model does not, then the differences shown by the former could be explained by the parameters accounted for in the latter, such as higher temperatures in urbanized areas (Fig. 1). If the SARerr-null model shows no differences between urbanized and rural areas but the SARerr-env model does, then 'urban-intrinsic' and environmental parameters are operating in opposite directions. All analyses were performed with the software R, version 2.6.0 (http://www.R-project.org; R Development Core Team 2007).

RESULTS

Species richness and phylogenetic diversity

Species richness was significantly higher in urbanized than in agricultural or semi-natural grid-cells, not only regarding the total flora but also throughout all tested trait state groups (Table 2). This was true when only accounting for spatial autocorrelation as well as when accounting for both spatial autocorrelation and environmental variables. Despite this high urban species richness, the phylogenetic distinctness of the total flora was not higher in urbanized than in rural areas (Fig. 3a; Table 2), but rather showed a tendency towards

Table 2 Differences in mean between the species richness and average phylogenetic distinctness of the flora of urbanized (u), agricultural (a) and semi-natural (sn) grid cells in Germany

	Species richness				Phylogenetic distinctness			
	SARerr-null		SARerr-env		SARerr-null		SARerr-env	
Total flora	sn < u***	a < u***	sn < u***	a < u***	sn > u+	a = u	sn = u	a = u
Insect pollination	sn < u***	a < u***	sn < u***	a < u***	sn < u*	a = u	sn = u	a = u
Self-pollination	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u*	sn < u***	a < u**
Wind pollination	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u***
Hygromorphic leaves	sn < u***	a < u***	sn < u***	a < u**	sn > u***	a > u*	sn > u**	a = u
Mesomorphic leaves	sn < u***	a < u***	sn < u***	a < u***	sn > u**	a > u*	sn > u**	a > u+
Scleromorphic leaves	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u**	sn < u**	a < u*
Succulent leaves	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u**	sn < u***	a < u***
Annual	sn < u***	a < u***	sn < u***	a < u***	sn = u	a = u	sn = u	a = u
Biennial	sn < u***	a < u***	sn < u***	a < u***	sn < u**	a < u***	sn < u***	a < u***
Pluriennial	sn < u***	a < u***	sn < u***	a < u***	sn > u**	a > u*	sn = u	a = u
Chamaephytes	sn < u***	a < u***	sn < u***	a < u***	sn < u**	a = u	sn = u	a = u
Geophytes	sn < u***	a < u***	sn < u***	a < u***	sn > u***	a > u*	sn > u*	a = u
Hemicryptophytes	sn < u***	a < u***	sn < u***	a < u***	sn = u	a < u*	sn = u	a < u**
Phanerophytes	sn < u***	a < u***	sn < u***	a < u***	sn > u***	a = u	sn > u**	a = u
Therophytes	sn < u***	a < u***	sn < u***	a < u***	sn = u	a = u	sn = u	a = u
Archaeophytes	sn < u***	a < u***	sn < u***	a < u***	sn = u	a = u	sn = u	a = u
Natives	sn < u***	a < u***	sn < u***	a < u***	sn = u	a = u	sn = u	a = u
Neophytes	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u**
c-strategists	sn < u***	a < u***	sn < u***	a < u***	sn > u***	a > u***	sn > u**	a > u+
cr-strategists	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u***	sn < u**	a < u**
cs-strategists	sn < u***	a < u***	sn < u***	a < u***	sn < u***	a < u*	sn < u**	a < u**
csr-strategists	sn < u***	a < u***	sn < u***	a < u***	sn = u	a = u	sn = u	a < u*
r-strategists	sn < u***	a < u***	sn < u***	a < u***	sn > u**	a > u+	sn = u	a = u
s-strategists	sn < u+	a < u***	sn < u***	a < u***	sn > u*	a = u	sn = u	a = u
sr-strategists	sn < u***	a < u***	sn < u***	a < u***	sn < u**	a < u*	sn = u	a = u

SARerr-null is corrected for spatial autocorrelation; SARerr-env is corrected for spatial autocorrelation and environmental variables (see *methods* section for details). P-values: $0.05 < P \leq 0.1$+, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, for nonsignificant differences equal values are assumed.

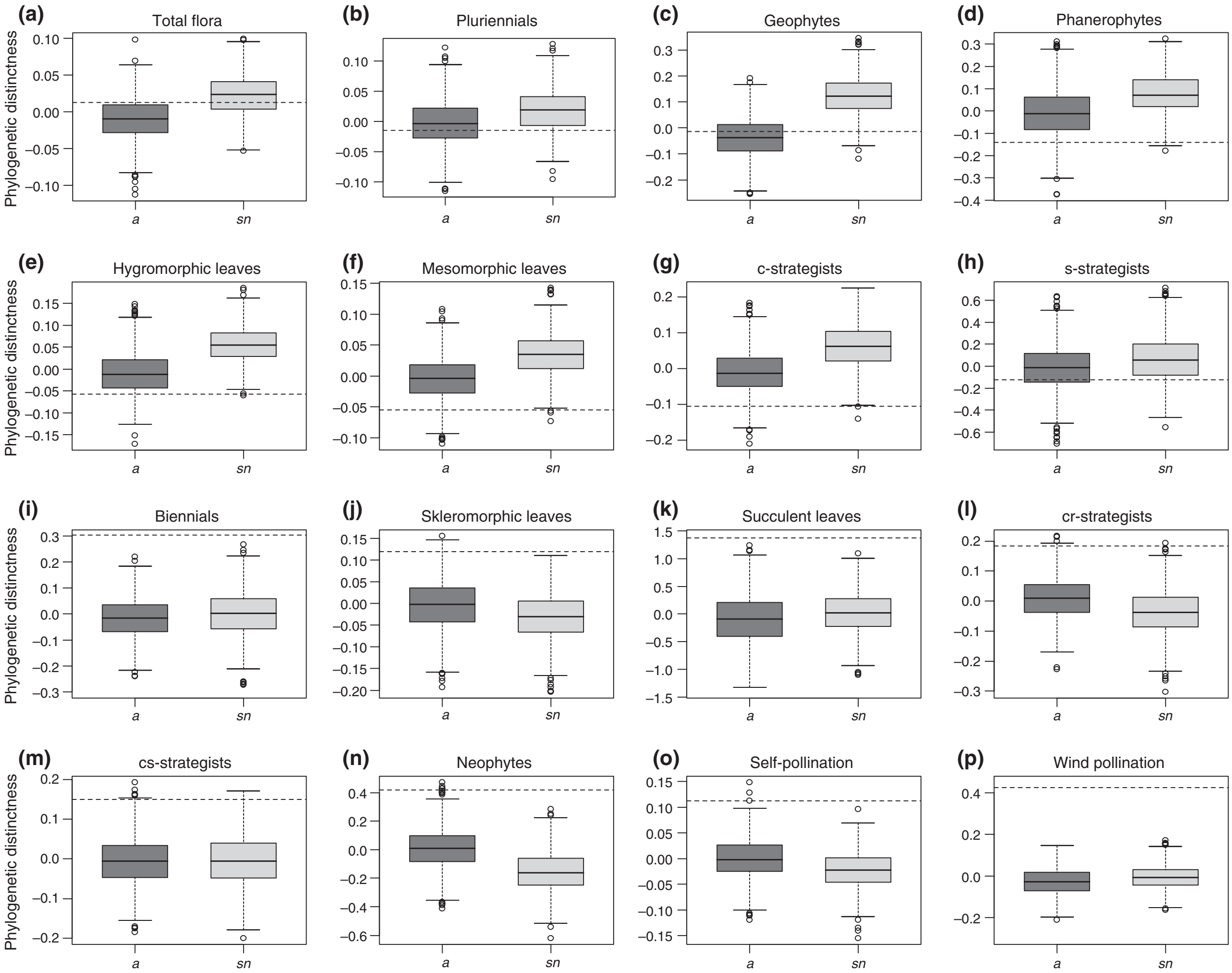

Figure 3 Phylogenetic distinctness of (a) all plants, and (b-p) all plant species sharing the same type of a functional trait in urbanized (- -), agricultural (*a*) and semi-natural (*sn*) grid-cells in Germany, corrected for spatial autocorrelation and climatic, topographic, edaphic and geologic parameters: (b–h) are species groups that share the pattern or tendency of the total flora: (b) pluriennial plants, (c) geophytes, (d) phanerophytes, (e) plants with hygromorphic leaves, (f) plants with mesomorphic leaves, (g) c-strategists, (h) s-strategists. (i–p) are species groups with a higher urban than agricultural or semi-natural phylogenetic diversity: (i) biennials, (j) plants with scleromorphic leaves, (k) plants with succulent leaves, (l) cr-strategists, (m) cs-strategists, (n) neophytes, (o) self-pollinated plants, (p) wind pollinated plants. Boxplots represent median (line), 25–75% quartiles (boxes), ranges (whiskers) and extreme values (circles). Dashed line: urban grid-cells; dark grey boxplots: agricultural grid-cells; light grey boxplots: semi-natural grid-cells. Values for agricultural and semi-natural grid-cells are based on resampling (999*59 grid-cells); shown are residuals (see *methods* section for details).

being decreased. The phylogenetic diversity of the total flora was higher in semi-natural than in urbanized grid-cells in the SARerr-null model, but showed no differences between the urbanized and the two types of rural grid-cells in the SARerr-env model.

Phylogenetic diversity across plant functional groups

For particular species groups, different patterns occurred according to their trait states. Phylogenetic distinctness of geophytes (i.e. plants with subterranean overwintering organs; see Table 1), phanerophytes (shrubs and trees), plants with hygromorphic or mesomorphic leaves, and Grime's c-strategists (Grime 1979) was highest in semi-natural grid-cells in both the SARerr-null and the SARerr-env models. The phylogenetic distinctness of pluriennial plants and s-strategists was highest in semi-natural grid-cells in the SARerr-null models (Fig. 3b–h; Table 2). Plants that have a biennial life cycle, scleromorphic or succulent leaves, or are cr- or cs-strategists, neophytes (i.e. alien species immigrated after the discovery of the Americas; Table 1) or self- or wind pollinated had a higher phylogenetic distinctness in urbanized than in agricultural and semi-natural grid-cells in both the SARerr-null and SARerr-env models (Fig. 3i–p; Table 2).

DISCUSSION

Our study highlights a pronounced discrepancy between species richness and phylogenetic diversity in urbanized areas. Generally, we expect phylogenetic diversity to be higher in heterogeneous than in homogeneous landscapes, because the former provide more niches for a variety of lineages (Ricotta *et al.* 2008). Due to the high heterogeneity of urban landscapes (Niemelä 1999) and because modern agricultural habitats as well as heavily managed forested habitats are very homogeneous, we expected phylogenetic diversity to be higher in urbanized than in rural areas. However, our results suggest the opposite: Phylogenetic diversity does not reflect the high species richness of urbanized areas.

Moreover, when changing perspective from the total flora to species groups, it is apparent that the patterns of phylogenetic diversity differ between species groups characterized by specific functional traits. Using different approaches, studies have shown that the phylogenetic structure of a community can depend on taxonomic or spatial scale (Cavender-Bares *et al.* 2006 for all seed plants and single lineages in Floridian plant communities; and Swenson *et al.* 2007 for size classes of tropical trees). Our results suggest the presence of selective environmental filters in urbanized areas which differ from those of rural areas. When species are assembled from the species pool, they have to pass a series of filters whose properties determine the structure of the assemblage according to species-specific trait compositions (e.g. Zobel 1997; Schweiger *et al.* 2005). The urban filters act on all species, but depending on their trait states, some plants are able to pass the filters, while others are not. The reduction of phylogenetic diversity in urbanized areas may then be caused by the presence of only particular species groups that can be regarded as adapted to non-urban conditions (species groups in Fig. 3b–h). Some of these groups have not only the highest phylogenetic diversity in semi-natural areas but also the highest frequency in the German flora, e.g. pluriennials, plants with mesomorphic leaves, or c-strategists (Fig. 4). This partly explains why they reflect the pattern of the total flora (or vice versa). Furthermore, some species groups are intercorrelated, e.g. phanerophytes are usually pluriennial. Therefore, the low phylogenetic diversity of pluriennials in urbanized grid-cells might mainly reflect the even more significant reduction in urbanized phylogenetic diversity for phanerophytes.

Species groups with a reduced phylogenetic diversity in rural grid-cells (Fig. 3i–p) might be more sensitive to non-urban filters, e.g. higher competition because of low disturbance frequency. However, they are adapted to urban conditions, such as biennial or wind-pollinated plants which are adapted to disturbance and fragmentation (Lososová *et al.* 2006). These species consequently are more frequent in urbanized than in rural areas. But why are they also phylogenetically more diverse in urbanized grid-cells?

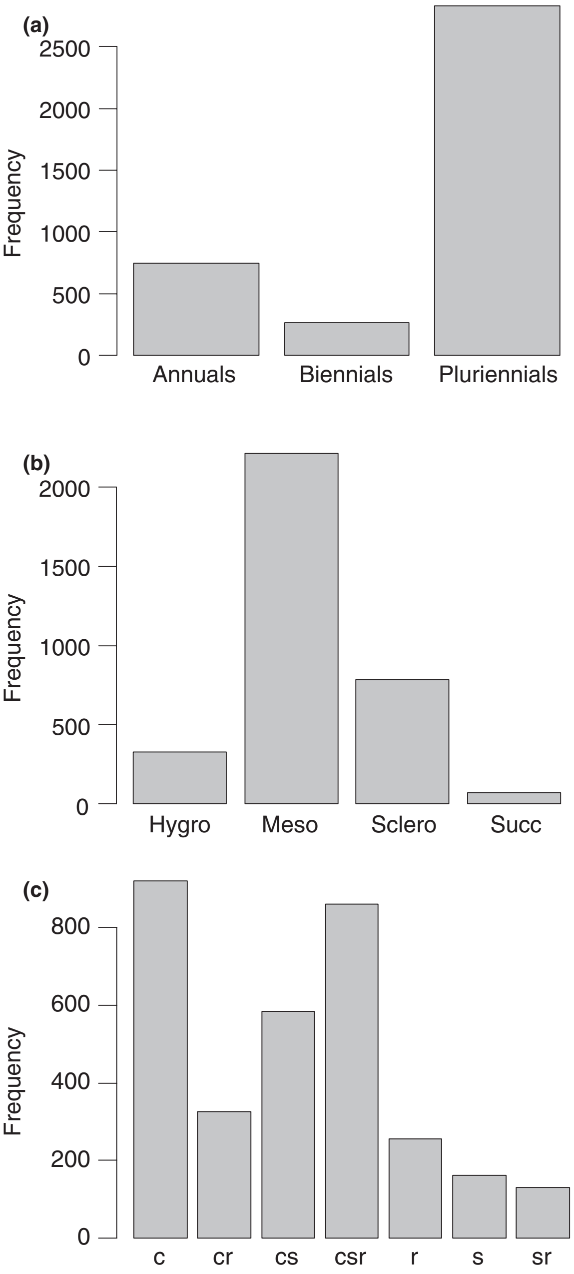

Figure 4 Frequency of trait states in the German flora for (a) life span, (b) leaf anatomy: hygro, hygromorphic; meso, mesomorphic; sclero, scleromorphic; succ, succulent; (c) strategy types.

The phylogenetic urban–rural patterns may result from a combination of phenotypic clustering and phylogenetic overdispersion (Cavender-Bares *et al.* 2006). Plants that share trait states are able to pass the same environmental filters and thus tend to occur in similar habitats. For example, biennials occur more often in cities and pluriennials more often in semi-natural habitats; they are phenotypically clustered. However, if species are too similar because they share critical trait states, they cannot coexist (e.g. Chesson 2000; Prinzing *et al.* 2008). Accordingly, the phylogenetic overdispersion within species groups characterized by traits suitable to pass the urban (or rural) environmental filters can be due to several mechanisms: Firstly, the species within a species group do not share trait states because of trait conservatism within lineages (e.g. Prinzing *et al.* 2001) but due to convergent trait evolution (Cavender-Bares *et al.* 2006). Secondly, closely related species get replaced with less related species, i.e. competitive exclusion limits similarity (Diamond 1975, cit. in Helmus *et al.* 2007; Swenson *et al.* 2007). However, competition acts on a much smaller scale than the one of our study and is thus unlikely to cause the patterns we found. Thirdly, similar and closely related species differentiated through adaptive radiation (Schluter 2000) independent of urbanization. Radiation enables species to use different resources within the same environment, e.g. in an urban landscape. This means that plants with traits well-suited for urban areas find several niches and thus can contribute to a high phylogenetic diversity of the urban flora. Conversely, plants with traits less well adapted to the urban environment can only grow in a few urban habitats and thus only contribute with a reduced phylogenetic diversity to the urban flora. With this last point, we can explain best why species richness is high in urbanized grid-cells, while phylogenetic diversity is reduced within the total flora but increased within 'urban-adapted' species groups. The high urban species richness seems to rest upon single (or few) but speciose lineages characterized by conservative traits that enable them to pass the urban filters and to settle many different habitats within a city. Grasses for example are very speciose and wind pollinated (Gorelick 2001), a trait that is phylogenetically conserved (Chazdon *et al.* 2003). Similarly, the genus *Oenothera* is a speciose lineage especially occurring in urban habitats (cf. Sukopp *et al.* 1979). Most *Oenothera* species are biennials and hemicryptophytes, which are both traits with a higher phylogenetic diversity in urbanized grid-cells (Table 2). Biennials and hemicryptophytes, in turn, are usually non-woody, a trait that is also phylogenetically conserved (Ackerly & Donoghue 1995). Cavender-Bares *et al.* (2006) and Swenson *et al.* (2006) showed that phylogenetic overdispersion is more likely at finer taxonomic levels. In our study, phylogenetic overdispersion occurs at the level of species groups characterized by certain trait states, which is finer than the level of the total flora.

Differences between models correcting for spatial autocorrelation (SARerr-null) and models correcting for both spatial autocorrelation and environmental variables (SARerr-env) indicate whether the environmental variables that we accounted for or 'urban-intrinsic' filters influence phylogenetic diversity. SARerr-null and SARerr-env models yielded no fundamental differences across most species groups (Table 2). Therefore, the acting filters seem to be 'urban-intrinsic' (i.e. they were not accounted for in the models, e.g. strong fragmentation of habitats by high proportions of built-up area, high disturbance frequencies, and high temporal land-use turnover; Sukopp *et al.* 1979; Kleyer 2002). The phylogenetic diversity of the total flora, insect pollinated plants, chamaephytes and geophytes, plants with hygromorphic leaves, r-, s- and sr-strategists differs between urbanized and agricultural or urbanized and semi-natural grid-cells in the SARerr-null models. One or both of these differences disappear in the SARerr-env models (Table 2). Thus, the climatic, topographic, edaphic and geologic variables that we accounted for are relevant for differences in the phylogenetic diversity of these species groups between urbanized and non-urbanized grid-cells. For example, increased temperatures and reduced rainfall in urban grid-cells (Fig. 1) are probably major filters reducing the phylogenetic diversity of hygromorphic plants in urbanized areas: They restrict these plants to special habitats within a city, such as urban parks along rivers which are cooler and more humid than other urban habitats. Regarding self-pollinated plants, plants with succulent leaves, biennials, hemicryptophytes, cs- and csr-strategists, it seems that the environmental filters and the 'urban-intrinsic', or 'rural-intrinsic' filters partly mask each other (Table 2): Differences in phylogenetic diversity between urbanized and rural grid-cells are even stronger in the SARerr-env than in the SARerr-null models. All these species groups have the highest phylogenetic diversity in urbanized grid-cells. The SARerr-null and SARerr-env models differ with respect to differences between urbanized and agricultural grid-cells (except for biennials; Table 2). Succulent leaves, for example, might be especially suitable with respect to the relatively warm and dry city climate (Fig. 1) and therefore develop a high phylogenetic diversity in urbanized grid-cells. They might as well be suitable with respect to the high density of sealed surfaces in urban areas and the accordingly high proportion of surface runoff that increases the aridity of urban habitats. Surface runoff would then be an 'urban-intrinsic' filter not accounted for in the SARerr-env models. Its effects might be masked by the effects of high temperatures and reduced precipitation.

With grid-cells sized *c.* 12 × 11 km, the scale of our study is fairly large. As biodiversity patterns can vary between large and small spatial scales (e.g. Cavender-Bares *et al.* 2006; Pautasso 2007), the results of our analyses might change when tested on a smaller scale. Unfortunately, plant occurrence data for the whole area of Germany are not available for a higher resolution than the grid used. Further research is needed to clarify whether the patterns we found are robust over varying scales.

Our study shows that the generally high plant species richness of urbanized areas is not reflected in phylogenetic diversity but is mainly due to more closely related plants with (pre-) adaptations to urban environments. The loss of phylogenetic information decreases the capacity of species assemblages to respond to environmental changes and might negatively affect ecosystem functioning (e.g. Maherali & Klironomos 2007). Therefore, nature conservation should, besides the number and identity of species, also account for phylogenetic diversity to sustain the capacity of species assemblages to respond to changing environmental conditions. As urbanization is unlikely to stop, we need strategies for protecting biodiversity in spite of urbanization, i.e. also within urbanized areas. To give valuable recommendations for the protection of biodiversity in urbanized areas, we need further analyses that explore the phylogenetic diversity of semi-natural vs. typical urban habitats within urbanized areas. Such studies might assess the potential of semi-natural areas within urban landscapes in conserving a high phylogenetic diversity (across all functional groups). The consideration of both the phylogenetic relationships and traits of species in addition to species richness is crucial for a detailed understanding of how species assemblages develop and change with a changing environment.

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