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Which traits influence the frequency of plant species occurrence in urban habitat types?

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Abstract Plants in cities must cope with various anthropogenic environments that differ from surrounding landscapes. Moreover, the differences in biotic and abiotic conditions among these habitats filter species with suitable traits and niche requirements. Here we aim to identify those attributes that promote species occurrence across and within urban habitat types of large cities. Species composition of spontaneously occurring vascular plant species was recorded in 1-ha plots in seven different urban habitat types in each of 32 European cities. Each species was characterized in terms of dispersal type, growth form, height, seed bank longevity, seed mass, selected leaf traits and ecological indicators including Ellenberg indicator values, Grime's life strategies, and immigration pathways using information from available species-trait databases. For each species, total frequency of occurrence across all plots and habitat frequency of occurrence across plots of given habitat types were calculated and regression trees were used to relate them to traits and ecological indicators. The most frequently occurring species in the cities tended to be human-dispersed, nutrient-demanding plants that prefer drier to mesic soil conditions. These species do not possess the S-strategy and usually produce seeds of low mass forming short-term persistent seed banks. Habitat-specific responses were also revealed, indicating the effects of between- and within-habitat heterogeneity on trends in species performance in cities. Such patterns can be overlooked when differences in species occurrences in particular urban habitat types are not considered; thus, habitat-specific responses can resolve inconsistencies found when whole urban floras are analysed as a whole.

Keywords City · Europe · Ellenberg indicator values · Plant traits · Regression tree · Seed bank · Urban ecology

Introduction

Urbanisation results in specific environments in cities, where abiotic conditions and biotic interactions affecting plant species performance are strongly altered by human activities (Sukopp and Starfinger 1999; Niemelä et al. 2009). Urban environments differ from the surrounding landscapes in many ways: temperatures are higher due to the urban heat island effect (Oke 1982; Sukopp 1998); traffic and industry pollute the air and soil (Horbert et al. 1983; Thorton 1991); aerial nutrient deposition and higher decomposition lead to eutrophication (McDonnell et al. 1997; Williams et al. 2015); and sealed surfaces decrease water infiltration and ground water regeneration (Sukopp and Starfinger 1999). Whereas abiotic conditions vary among locations within a city, human impacts increase from the suburbs to the city centre (Sukopp and Starfinger 1999; Pickett et al. 2001), with both resulting in distinct habitat heterogeneity (Kowarik 2011). Cities contain mosaics of remnants of pre-urban habitats and new urban habitats resulting from various types of human disturbance (Kleyer 2002; Godefroid and Koedam 2007; Williams et al. 2009).

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One can assume that not all species are able to survive in such conditions. Indeed, both differences in species compositions between cities and their surroundings and changes over time in floras due to urbanisation have been reported (e.g. Chocholoušková and Pyšek 2003; Pyšek et al. 2004; van der Veken et al. 2004; Knapp et al. 2010). Moreover, different land use is reflected not only in the differences in the compositions of floras of cities and surrounding rural landscapes, but also in shifts in functional trait distributions of species along the rural-urban gradient (Knapp et al. 2008a, 2009; Thompson and McCarthy 2008). Because functional trait analyses could make an important contribution to understanding processes that shape urban plant communities and the functioning of urban ecosystems (Suding et al. 2008; Lavorel et al. 2011), increasing effort has been devoted to identify which traits enable plant species to cope with urban environments.

The plant functional trait approach has mainly been applied to floras in particular European cities (e.g. Landolt 2000; Hill et al. 2002; Kühn et al. 2004; Kühn and Klotz 2006; Godefroid and Koedam 2007) to identify those traits that promote or inhibit species occurrence there. In these studies, several traits have been found to relate to the frequency of occurrence of plant species within urbanized areas, e.g. height (Kleyer 2002; Knapp et al. 2009), dispersal strategies (Knapp et al. 2010), life forms (Godefroid and Koedam 2007; Knapp et al. 2009), leaf traits such as specific leaf area and leaf dry matter content (Knapp et al. 2008a; Thompson and McCarthy 2008), and seed bank characteristics (Kleyer 2002).

Whereas plant functional traits directly influence species occurrence through impacts on growth, reproduction and survival (Violle et al. 2007), species occurrence can also be investigated in relationship to ecological niche indicators (see Williams et al. 2015). Of these, Ellenberg indicator values and categorization in terms of CSR (competitive, stress-tolerant, and ruderal) strategies have been employed most often. Ellenberg values estimate species ecological optima along environmental gradients and thus indicate realized niches (Ellenberg et al. 1992), while CSR strategies reflect variation in life-strategies among species (Grime 1979). Both of them have relationships to groups of traits that enable species to withstand particular environmental conditions (Lavorel and Garnier 2002). They show responses on the urbanization gradient resulting from the different demands of species in urban areas for temperature, light and nitrogen from those in rural surroundings (Wittig and Durwen 1982; Klotz 1989; Knapp et al. 2009) and from changes in proportions of particular ecological life-strategies with increasing urbanization (Preston 2000; Chocholoušková and Pyšek 2003).

Nevertheless, previous studies have usually not accounted for an important factor: the intrinsic habitat heterogeneity of cities (but see Kleyer 2002; Lososová et al. 2011). Species composition of urban communities varies according to habitat disturbance regimes (Celesti-Grapow et al. 2006; Godefroid and Koedam 2007; Lososová et al. 2011), and traits of species are likely to differ among urban habitats as well. Habitat-specific sets of conditions act as filters that determine which species can coexist in given habitat based on species traits and niche requirements (Zobel 1997; Williams et al. 2009). Therefore, particular species traits and ecological indicators could respond differently when comparing across whole-city floras, only a part of the habitat spectrum or particular urban habitats per se. At the habitat scale, local filters together with biotic interactions are important for predicting plant species composition, so that considering data at only larger scales (e.g., whole cities) habitat-specific relationships can be overlooked (Williams et al. 2015).

Urbanization is a rapidly increasing driver of land-use change, often at the expense of natural ecosystems (Vitousek et al. 1997); Therefore, knowledge of species' abilities to withstand land-use changes and processes forming communities in novel urban habitats is important not only from an ecological, but also from a conservation perspective (Zerbe et al. 2003; La Sorte et al. 2007; Hautekèete et al. 2015).

In our study, we investigated the influence of plant traits and ecological indicators on frequency of species occurrence across and within particular urban habitats. Our dataset covers habitats located along the disturbance gradient from the city centre to the city outskirts in a large number of cities across Central and North-Western Europe. This enables us to identify traits generally promoting plant vascular occurrence in urban environments and to also discern potential habitat-specific differences. Thus, we aim mainly to identify: (1) which traits characterize plant species occurring frequently in the cities; and (2) which traits influence plant species occurrence in particular urban habitats.

Materials and methods

Species data

Data sampling was conducted during summers from 2007 to 2009 in Central and North-Western Europe in 32 cities with population sizes greater than 100,000 inhabitants (Table 1). Seven urban habitat types were chosen to reflect different regimes of disturbance characteristic of the gradient from the city centre to the suburbs: (1) historical city square, > 90 % paved or sealed area surrounded by generally pre-nineteenth century houses; (2) boulevard, > 70 % paved or sealed area with nineteenth century houses, small lawns or lines of trees; (3) residential area with compact building pattern, consisting of family houses at least 50 years old and private gardens; (4) residential area with open building pattern, consisting of block of flats built in the 1960s to 1980s, with lawns, scattered trees and shrubs; (5) city park with old deciduous trees (tree cover

Table 1 A list of the sampled cities and their locations in Central and North-Western Europe (ISO 3166–1 country codes)

City	Country	Latitude	Longitude	City	Country	Latitude	Longitude
Amsterdam	NLD	52°21'N	04°52'E	Cologne	DEU	50°55'N	06°56'E
Antwerp	BEL	51°12'N	04°25'E	Košice	SVK	48°43'N	21°15'E
Augsburg	DEU	48°22'N	10°53'E	Kraków	POL	50°04'N	19°55'E
Bern	CHE	46°57'N	07°27'E	Linz	AUT	48°17'N	14°17'E
Bratislava	SVK	48°08'N	17°07'E	Ljubljana	SVN	46°02'N	14°30'E
Brno	CZE	49°12'N	16°35'E	Maribor	SVN	46°33'N	15°39'E
Budapest	HUN	47°30'N	19°03'E	Munich	DEU	48°08'N	11°33'E
Debrecen	HUN	47°31'N	21°37'E	Oldenburg	DEU	53°08'N	08°12'E
Freiburg	DEU	48°01'N	07°51'E	Ostrava	CZE	49°50'N	18°16'E
Geneva	CHE	46°12'N	06°07'E	Prague	CZE	50°05'N	14°23'E
Groningen	NLD	53°13'N	06°34'E	Regensburg	DEU	49°00'N	12°06'E
Halle	DEU	51°29'N	11°57'E	Salzburg	AUT	47°48'N	13°02'E
Hamburg	DEU	53°33'N	09°57'E	Stuttgart	DEU	48°46'N	09°10'E
Chemnitz	DEU	50°50'N	12°55'E	Szczecin	POL	53°25'N	14°33'E
Innsbruck	AUT	47°16'N	11°23'E	Utrecht	NLD	52°05'N	05°07'E
Kassel	DEU	51°18'N	09°29'E	Würzburg	DEU	49°46'N	09°55'E

10–50 %) and frequently mown lawns; (6) early successional sites, strongly disturbed 1–3 years ago, mostly bare ground and only sparse vegetation, usually in or around construction sites; and (7) mid-successional sites, abandoned for 5–15 years, dominated by perennial grasses, with scattered shrubs and young trees.

The presence of all spontaneously occurring vascular plant species was recorded in one 1-ha plot of rectangular size in each urban habitat in each city. Thus, only intentionally planted species were not recorded, whereas garden escapes and seedlings of spontaneously regenerating trees and shrubs were included. The data set consisted of information from 224 plots (32 plots per habitat type) on a total of 1065 vascular plant taxa (529.14 ± 107.03 taxa per habitat type; mean ± SD). The taxonomy and species nomenclature we used follows Jäger et al. (2005) and Jäger et al. (2008). For more details on field data sampling and taxonomic delimitation of taxa see Lososová et al. (2011, 2012); all taxa are hereafter referred to as species.

Trait data

Information on biological traits for each recorded plant species were adopted from the LEDA database on the life-history traits of the North-West European flora (Kleyer et al. 2008; http://www.leda-traitbase.org). The biological traits included dispersal type (four categories), growth form (seven categories), plant canopy height (m), seed bank longevity (four categories), seed mass (mg), leaf dry matter content (LDMC, $mg.g^{-1}$) and specific leaf area (SLA, $mm^2.mg^{-1}$). For continuous variables, we calculated the averages of the values provided for each country in LEDA. Ecological indicator values were taken from the BiolFlor biological and ecological trait database of German flora (Klotz et al. 2002; Kühn et al. 2004) and included ecological life strategy according to Grime's classification (1979) and Ellenberg indicator values (Ellenberg et al. 1992) reflecting species' affinities to local environmental conditions. Although the indicators are not measurable functional traits per se, we nevertheless refer to their categorical values as trait states, for simplicity. Moreover, the trait states for one more distributional indicator, the immigration pathway to the urban areas, which had three possible states, were assigned by the authors following definitions from Jäger et al. (2008). In total, 4 continuous, 6 ordinal and 5 categorical plant traits were used, with the categorical traits having a total of 21 possible trait states. However, the Ellenberg indicator values, although formally corresponding to ordinal variables, behave as continuous variables when a sample contains more than 100 species (ter Braak and Barendregt 1986). Missing Ellenberg indicator values for species were replaced by mean values calculated across all species with the value. Complete data for all trait states were available for 648 species that were used in the analyses. The list of traits, along with the percentages of species for which measurements were available (continuous traits) or the percentages assigned to each trait state (categorical) for the whole data set can be seen in Table 2.

Data analysis

The estimation of the frequency of occurrence of plant species was performed at two levels. First, the presence of each species was summed across all plots regardless of city and habitat types, yielding what is hereafter called the *total frequency of*

Table 2 A list of traits and trait states (for traits treated as categorical variables) and their descriptions according to the LEDA database (Kleyer et al. 2008) and BiolFlor (Klotz et al. 2002; Kühn et al. 2004). For continuous variables, metric units are shown; cat = categorical, ord = ordinal variable. Proportions of species (N_{total} = 1065) having particular trait states are indicated; for categories proportions of species assigned to 0/1 are shown separately

Trait	Units	Trait state	Description	Proportion (%) of total species assigned to given category/other categories
Canopy height	m		Mean distance between ground and the highest photosynthetic tissue of plant	91.6
Dispersal type[a]	cat	autochory	Self-dispersal of seeds	45.1/38.4
		hemerochory	Dispersal by humans, both intentional and unintentional	23.8/59.6
		meteochory	Dispersal by wind or surface water currents	59.6/23.8
		zoochory	Dispersal by animals (incl. Adhesion, digestion and scatter-hoarding animals)	15.5/67.9
Ecological life strategy[a]	cat	C	Competitors: tree, shrubs and forbs with high competitive ability	14.5/71.7
		R	Ruderals: usually annuals producing many seeds easily colonizing pioneer habitats	52.1/34.1
		S	Stress-tolerators; plants with slow growth and adaptation to extreme environmental conditions	42.5/43.6
Ellenberg indicator value	1–9	light	Optimal light conditions for species	73.9
	1–9	temperature	Optimal temperature for species	60.0
	1–9	continentality	Optimal continentality for species	65.2
	1–12	moisture	Optimal soil moisture for species	69.0
	1–9	reaction	Optimal soil pH for species	56.6
	1–9	nutrients	Optimal soil fertility for species	67.9
Growth form[a]	cat	phanerophyte	Woody or evergreen perennials taller than >50 cm, with resting buds above ground	81.1/15.7
		liana	Plants germinating on the ground, keeping contact with soil and using other plants for support	93.7/3.1
		chamaephyte	Woody or evergreen perennials 25–50 cm tall with resting buds above ground	89.1/7.7
		hemicryptophyte	Biennial and perennial herbs with stems dying back in unfavourable seasons with resting buds on the soil surface	47.7/49.1
		hydrophyte	Submerged or floating aquatic herbs with resting buds under water surface	95.6/1.3
		therophyte	Annual herbs dying after seed production surviving unfavourable part of the year as seeds	66.2/30.6
		geophyte	Generally perennial herbs (some biennial) with resting buds underground on storage organs	87.3/9.6
Immigration pathway	cat	crop	Cultivated by humans for agricultural products	93.4/6.6
		ornamental	Cultivated by humans for decorative purposes	63.6/36.4
		weed	Non-cultivated species undesirably occurring in settings cultivated by humans	23.5/76.5
Leaf dry matter content (LDMC)	mg.g^{-1}		Ratio of dry leaf mass to fresh leaf mass, i.e., tissue density	69.6
Seed bank type	cat	long-term	Seeds persist in soil >5 years	29.7/35.8
		short-term	Seeds persist in soil 1–5 years	24.0/41.4
		transient	Seeds persist in soil <1 year	5.5/6.0
		present	Seeds persist in soil for unknown time	28.1/37.3
Seed mass	mg		Mean air-dried seed weight	78.6
Specific leaf area (SLA)	mm^2.mg^{-1}		Ratio of fresh leaf area to leaf dry mass	74.9

[a] Species with two or more trait states were included in all of them

species occurrence. Second, the presence of each species was summed across all plots assigned to a given habitat type regardless of city, yielding what is hereafter called the *habitat*

frequency of species occurrence. To assess which plant traits generally promote species occurrence in the urban environment, we used regression trees (Breiman et al. 1984; De'ath

and Fabricius 2000) with total frequency of species occurrence as the dependent variable, and species traits as explanatory variables. Similarly, to assess the relative importance of plant traits for success in urban habitat types with differing disturbance regimes, we used the same statistical technique to assess the relationships between the species traits and habitat frequency of species occurrence in each of seven urban habitats.

Use of regression trees is an appropriate exploratory method for the prediction of a continuous dependent variable using many explanatory variables (predictors), both continuous and categorical, with possible interactions (De'ath and Fabricius 2000). The dependent variable, total frequency of species occurrence or habitat frequency of species occurrence for each habitat type, was hierarchically dichotomously split into subsets. Gradual separation of the variable in the splits (nodes) was based on particular values of continuous predictors or categorical predictors (species traits). Splits were determined based on minimizing variation within and maximizing variation between resulting subsets (Breiman et al. 1984). A minimum membership of $n = 9$ was chosen for subsets, i.e., tree splitting would stop in order to ensure that a maximally split tree would have at least this number of members in each of its terminal nodes. Subsequently, the sequences of trees of decreasing size were calculated for dependent variables and the relative resubstitution errors were obtained as the residual sum of squares of every tree. Optimal tree size for each dependent variable was identified using ten-fold cross-validation to minimize the risk of tree overfitting. Thus, the data set was divided into ten random approximately equal subsamples. Trees of the specified sizes were computed ten times, each time leaving out one subsample to be used as a test sample for cross-validation. The CV (cross-validation) costs were then computed for each of the test samples and averaged for each tree size. To select the optimal tree, the SE = 1 rule was applied (Breiman et al. 1984), i.e., the smallest-sized tree whose CV cost did not excess the minimum tree CV cost plus 1 × the standard error was selected. The total variation (R^2) explained by the optimal tree in total frequency of species occurrence or habitat frequency of species occurrence was then calculated as 1- the resubstitution relative error for each optimal tree. For each node of the trees, surrogates were calculated as other explanatory variables that mimic the separation done by the predictor. Only those with an associated value >0.2 were considered further. Surrogates were used to detect alternative splits within the regression trees and reveal explanatory variables closely correlated with the predictor in a given split.

Every explanatory variable in each regression trees received a relative importance value on a scale of 0 to 100. The relative importance was calculated as the sum of resubstitution relative errors of given explanatory variable over all nodes of the optimal tree relative to the highest sum found for any explanatory variable there (which would be

assigned 100). The influence of traits with high relative importance value, but not shown as predictors or surrogates in optimal trees, was tested by Pearson's correlation (continuous variables) and t-tests (categorical variables). All analyses were performed in Statistica 12 (http://www.statsoft.com).

Results

Plant species most frequently occurring across all plots and their frequencies of occurrence in urban habitat types are listed in Table 3. The most frequently recorded taxa within the data set were *Taraxacum* sect. *Ruderalia*, *Plantago major + uliginosa* and *Polygonum aviculare* agg., showing similarly high frequency of occurrence in all the urban habitat types, whereas e.g. *Stellaria media* agg. was recorded more often in city centres (squares and boulevards), *Trifolium repens* had more frequent occurrence in residential areas and city parks and *Urtica dioica* was found more often in longer-abandoned mid-successional sites.

The optimal regression trees relating total frequency of species occurrence to their traits (Fig. 1) explained 81.21 % of variance. The most frequent species in cities regardless of habitat types were those with short-term persistent seed banks consisting of seeds with low seed mass, the majority of them recognized as weeds. Of these, the ones requiring nutrient-rich soil or mesic or slightly dry conditions were noticeably more frequent than species needing wet or very dry or acid or nutrient-poor soils as well as species with high LDMC values. The other regression trees explaining frequencies of species occurrence in particular habitat types are not shown and can be found in Online Resource 1.

The species most frequent at historical city squares needed high nutrient levels (> 5.7) and had low seed mass (≤ 0.8 mg). In addition to them, R-strategists shorter than 0.6 m with SLA ≤ 23.4 mm^2.mg^{-1}, producing short-term soil banks and preferring mesic to dry soils were common there. For boulevards, the optimal regression tree has the same topology of nodes and predictors with identical splitting values as the optimal tree for total frequency of species. Thus, the most frequent species of boulevards shared the same traits as species successful in cities generally. In residential areas with a compact building pattern, the most frequently recorded species included nutrient demanding weedy plants (> 4.5) preferring drier to mesic conditions (3.5–6.5) with short-term soil seed banks and low seed mass (< 3.2 mg). However, species used as ornamentals with long-term seed banks were also found often. Residential areas with an open building pattern were occupied mostly by weeds with seed mass < 2.6 mg forming long-term persistent seed banks. Among them, nutrient-demanding species of mesic soils characterized by R- and C-strategies were the most common. For the city parks, two groups of frequently occurring species were revealed. The first

Table 3 Plant taxa with the highest total frequencies of occurrence in terms of the sum of all plots occupied, showing also the total numbers of plots they occurred in within each habitat type. Early-suc = early successional site, Mid-suc = mid-successional site

Species	All plots	City square	Boulevard	Residential area compact	Residential area open	City park	Early-suc site	Mid-suc site
Taraxacum sect. *Ruderalia*	212	31	32	32	32	31	29	25
Plantago major + uliginosa	203	31	31	29	28	29	28	27
Polygonum aviculare agg.	201	28	32	31	32	29	31	18
Lolium perenne	200	26	30	30	32	32	29	21
Poa annua	194	32	32	31	31	29	25	14
Conyza canadensis	193	29	31	31	30	20	29	23
Capsella bursa-pastoris	184	28	30	26	31	23	29	17
Trifolium repens	184	18	27	29	29	32	25	24
Elytrigia repens	178	9	27	28	28	25	32	29
Sonchus oleraceus	175	29	32	31	29	21	25	8
Medicago lupulina	174	13	25	26	29	24	30	27
Plantago lanceolata	174	11	26	27	29	24	26	31
Chenopodium album agg.	173	21	30	26	27	18	31	20
Stellaria media agg.	172	31	31	30	27	28	19	6
Urtica dioica	170	15	20	26	26	28	24	31

group comprised phanerophytes with the preference for rather fertile soils, with long-term persistent seed banks of larger seeds (seed mass > 3.2 mg) and often planted as ornamentals (but spontaneously regenerated) in the plots. The second group consisted of the other nutrient-demanding species, i.e., those with lower seed mass and broad moisture preferences except for very wet conditions.

Early successional sites were occupied mostly by small weedy species (height ≤ 0.43 m) with short-term or transient bank of light seeds (< 2.5 mg). They comprised both, R- and/or C-strategists, with Ellenberg indicator values showing broad preferences for nutrient content (> 3.5), alkaline soils (> 6.3) and avoidance of very wet conditions. The ideal regression tree explaining frequency of occurrence in mid-successional sites showed the most complex structure. In brief, one successful group of species consisted of small R-strategists (≤ 0.33 m), of which those with short-term seed banks and cultivated as crops occurred the most often. Another relatively frequent group included taller C- and/or R-strategists with short-term seed bank, with either low seed mass (≤ 3.2 mg), in the case of geophytes and hemicryptophytes or heavy seeds (> 33.9) in the case of phanerophytes. No clear trend of species

Fig. 1 Regression tree explaining total frequencies of species occurrence across all plots in relationship to species traits. Each node is characterized by mean ± SD of the total frequency of species included and N representing the number of species included at the node. Predictors and their splitting criteria are in black; surrogates splitting the data set most similarly to the predictor are shown in grey; LDMC = leaf dry matter content. Total variation explained: R^2 = 81.21 %
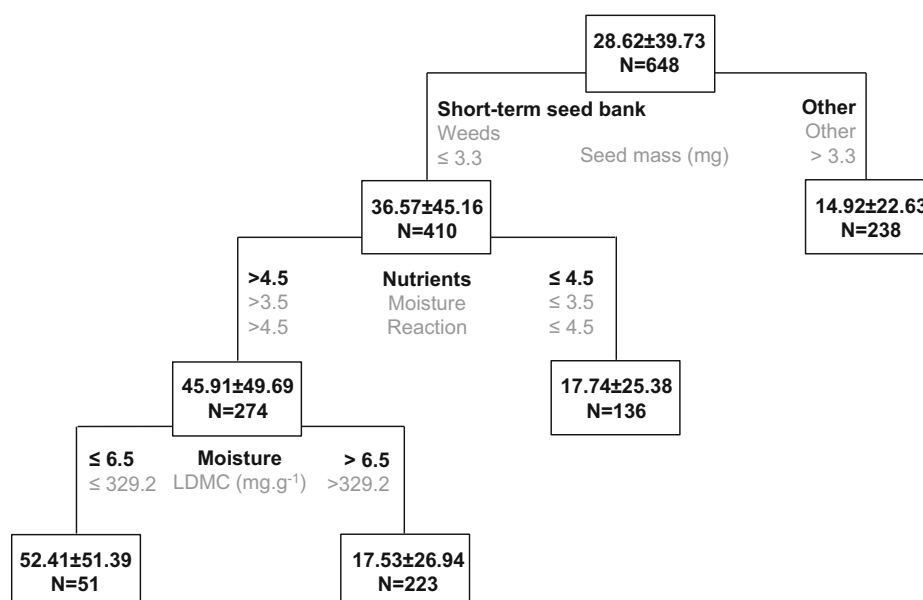
preferences to environmental conditions was revealed, in contrast to the other urban habitat types.

Comparing the importance of species traits across all nodes of optimal regression trees reveals four main traits (or in the case of Ellenberg indicator values, groups of traits) generally influencing frequency of species occurrence in the studied urban habitat types (Table 4). The first is dispersal type: hemerochory increases the frequency of species occurrence across habitat types inside cities, with meteochory co-acting with it in promoting species at mid-successional sites on the edges of cities ($t = -5.45$, $P < 0.001$). Second is ecological life strategy, as across all urban habitats, species not having the S-strategy were the most frequent. The third is the group of Ellenberg indicator values, as nutrient-demanding species of

Table 4 Relative importance on a scale from 0 to 100 of species traits in explaining the total frequencies of species occurrences across all plots and the frequencies of species occurrences within each urban habitat type. Early-suc = early successional site, Mid-suc = mid-successional site

	All plots	City square	Boulevard	Residential area compact	Residential area open	City park	Early-suc site	Mid-suc site
Canopy height	30	63	24	43	23	100	40	100
Dispersal types								
Autochory	14	14	18	5	25	5	7	12
Hemerochory	77	52	79	63	53	34	75	53
Meteorochory	16	8	9	12	7	22	29	73
Zoochory	32	17	33	17	33	37	33	55
Ecological life strategy								
C	8	19	1	1	6	33	1	47
R	1	29	22	5	3	7	11	51
S	99	40	84	34	72	11	100	84
Ellenberg indicator values								
Light	18	24	16	19	14	69	31	65
Temperature	22	14	22	19	16	57	16	58
Continentality	36	23	36	35	33	36	59	51
Moisture	92	50	100	100	80	87	72	80
Reaction	59	14	49	34	39	52	72	76
Nutrients	100	43	98	45	100	63	76	53
Growth form								
Phanerophyte	6	2	1	7	10	30	16	35
Liana	5	1	3	3	1	4	9	39
Chamaephyte	22	26	23	49	10	54	34	36
Hemicryptophyte	0	14	1	0	1	21	2	29
Hydrophyte	20	6	16	19	8	21	5	10
Therophyte	2	47	19	0	2	32	25	72
Geophyte	3	6	1	2	4	4	1	48
Introduction mode								
Ornamental	17	18	35	4	16	18	40	11
Crop	2	2	1	2	0	2	3	19
Weed	12	8	12	11	4	39	13	24
LDMC	34	38	63	39	19	46	32	100
Seed bank type								
Long-term	51	52	49	57	40	63	56	62
Short-term	79	62	69	69	65	88	86	68
Transient	21	5	7	8	30	26	48	78
Present	16	4	12	21	16	40	17	33
Seedmass	22	100	40	29	20	44	62	50
SLA	23	33	40	31	26	56	29	57

roughly mesic conditions were the most successful; moreover, in both successional types of sites, species frequency also increased with their preference for higher soil reaction ($r_{s\ early}$ $_{successional}$ = 0.07, P = 0.02; $r_{s\ mid-successional}$ = 0.07, P = 0.04). The last is seed bank type, species with short-term seed banks are generally more frequent; however, in parks and mid-successional sites, species with short-term and long-term seed banks are similarly common (t_{park} = −5.59, P < 0.001; $t_{mid-successional}$ = 6,21, P < 0.001). Low seed mass often served as a surrogate for short-term seed bank, but also showed high importance independently of this effect in the particular cases of historical city squares and early successional sites. Other traits were also important in particular urban habitat types. Thus, the frequency of species with higher LDMC was greater in mid-successional sites (r_s = 0.09, P = 0.005). The effects of canopy height differed depending upon habitat type, as increasing height was associated with decreased species frequency in city squares, (r_s = 0.08, P = 0.006), whereas in city parks, it was a associated with increased species frequency (r_s = 0.09; P = 0.003).

Discussion

This study showed that particular plant functional traits and niche requirements favour plant species in urban environments. Generally, the most important features of widespread species in the studied cities were spread by human activities, use of R and/or C-strategy, preferences for drier to mesic conditions and moderately to high fertile soils, and use of short-term seed banks usually consisting of small seeds. Plant species underrepresented in the cities were stress-tolerators inhabiting dry, acidic, nutrient-poor or waterlogged conditions. It has previously been shown (Lososová et al. 2012) that species overrepresented in urban floras are usually widespread generalists that are common components of non-urban habitat types in the landscape (Hill et al. 2002), but which can pass through filters imposed by particular conditions of the urban environment from the regional species pools. Despite the strong filtering that is thought to result in generally low urban functional diversity, i.e., low variation in traits among urban species (Knapp et al. 2008b; Ricotta et al. 2008; Lososová et al. 2016), our results detected differences in some traits or their states among particular urban habitats.

Because of low connectivity of habitats within built-up areas, long-dispersal ability can promote plant frequency in the urban environment (Gilbert 1989). Human activities can serve as vectors, providing this ability, and indeed, hemerochory has been shown to be frequent among urban species (Knapp et al. 2008a; Knapp et al. 2010; Lososová et al. 2016). This human-mediated dispersal was also shown in the present study by the high frequency of weed and ornamental species in our data set.

In contrast to hemerochory, although animal-dispersed species have been reported as common in other studies of urban species (Knapp et al. 2008a; Knapp et al. 2010), they were not so pronounced in our data set, although they showed some importance in city parks, residential areas and both types of successional sites. The difference between our findings and those from the other studies could be due to the difficult distinction between these two dispersal types. Species with adhesive propagules are spread by wild and domestic animals as well as humans and vehicles (von der Lippe and Kowarik 2007, 2008); similarly, woody species with colourful fruits are not only dispersed by birds, but can be also be preferentially planted by gardeners (Knapp et al. 2010).

The low importance of meteochory, including wind dispersal found in the city interior, is in accordance with previous studies (Knapp et al. 2010; Williams et al. 2015). This can be attributable to relatively windless conditions in densely built-up areas, where propagules are not able to fly over barriers (Kuttler 1993). In contrast, at our mid-successional sites, wind-dispersed species were more common. Plants can probably profit from such habitat on the city outskirts that is usually open to the surrounding landscape, and thus more exposed to wind. Additionally, compared to intensively managed habitats in the city interior, the importance of ornamental species was lower at the outskirts, resulting in a higher proportion of the species occurring there that rely on long-distance dispersal.

As mentioned above, the isolation of patches within the city matrix results in the need for long-distance dispersal. Because the potential for wind dispersal is limited there, the effective dispersal of urban species can be promoted by low seed mass, which can facilitate dispersal despite of low wind speeds such as encountered in cities (Gilbert 1989). Additionally, small-seeded plants produce seeds in high numbers (Thompson et al. 1993; Leishman et al. 2000), and more seeds mean greater colonization potential (Lake and Leishman 2004; Šerá and Šerý 2004). We suggest that in cities, both mechanisms might enable small seeded plants to more effectively reach suitable habitat patches.

In the present study, the predominance of small-seeded species was manifested the most in the city squares, which are isolated in space. Small seeds are more likely to reach them and also probably be released into cracks and crevices of paved surfaces. The second habitat type with high importance of low seed mass was the early successional sites. They are also isolated, but temporally rather than spatially due to disturbance such as construction work that destroys vegetation and creates temporarily open ground for new colonization. Production of small seeds leading to large reproductive capacity corresponds to the R-strategy of Grime (1979) and thus correlates with the adaptation of species to disturbance. However, in our data we are not able to distinguish whether small seeds are favoured because of a dispersal advantage

reaching spatial isolated habitat or because their rapid life cycles make them better able to take advantage of habitat temporal availability between disturbances. Indeed, small seeds were highly correlated with short-term seed banks in our analyses. Seeds that sometimes germinate after dispersal and sometimes contribute to a soil seed bank (Thompson and Grime 1979) can also be advantageous in disturbed environment as shown by Kleyer (2002). In this case, the species can quickly colonize temporarily bare ground and also form a reserve in the soil seed bank that would be available when disturbance occurs a short time later. Higher seed mass and long-term seed banks were shown to be important in city parks, residential areas with an open building pattern and mid-successional sites that have longer-lasting undisturbed patches where late successional species such as phanerophytes can establish (Prach et al. 2001).

For urbanized areas, strong underrepresentation of stress-tolerators has been reported, and species growing in extreme pH and infertile soils are rare (e.g. Landolt 2000; Thompson and McCarthy 2008; Williams et al. 2015). This trend probably reflects both human preference for sites with fertile soils for settlements and a decrease in low-nutrient, often acid habitats within them due to aerial depositions (Preston 2000).

There is also within-habitat heterogeneity in urban habitats, such that patches of vegetation are kept at an early successional stage by mowing, trampling or herbicide use (Niemelä et al. 2009). This can promote co-existence of C- and R-strategists at the expense of S-strategists incapable of withstanding disturbance and competition (Grime 1979; Hill et al. 2002) which would was the pattern we found for parks, residential areas and successional sites.

Habitat loss is likely to cause rarity of wetland species because during the development of cities, water bodies and wetlands were often destroyed and natural streams channelized and rerouted underground (Sukopp and Starfinger 1999). This could underlie the low frequency with which we found species with very high Ellenberg indicator values for moisture. Additionally, despite the often emphasized inference that warmer and drier climate of cities results in the prevalence of drought-tolerant species (Williams et al. 2015), we found a broader tolerance of species to soil moisture ranging from dry-mesic to mesic conditions. Such a pattern can reflect between-habitat heterogeneity, with shady habitats such as parks and gardens in residential areas providing a mild mesoclimate compared to sealed and exposed surfaces in the centres (Knapp et al. 2010).

Several studies have reported the prevalence of species of alkaline soils (Knapp et al. 2009; Williams et al. 2015). In our data set, affinity for higher pH was habitat-specific. Frequent occurrence of species preferring alkaline soils was found only in successional sites, often including those where debris such as concrete and mortar had been dumped. Whereas our findings regarding habitat moisture and pH conditions differ in

some ways from those of other studies, our results with respect to nutrient-level preferences are fully accord with previous findings (Wittig and Durwen 1982; Landolt 2000; Preston 2000; Chocholoušková and Pyšek 2003; Knapp et al. 2009). in that they clearly show urban species to be generally nutrient-demanding.

According to our results, species growth form is in general of minor importance, which can also reflect habitat heterogeneity in which different forms exist within the city matrix depending on the habitat disturbance regime. Some studies have reported greater representation of therophytes in strongly disturbed areas (Sudnik-Wójcikowska and Galera 2005; Knapp et al. 2008a) or of woody life forms due to garden escapes (Godefroid and Koedam 2007). This was to some extent showed by the canopy height important in city squares, where low therophytes that tolerate trampling dominated (e.g., *Poa annua*, *Polygonum aviculare* agg., *Eragrostis minor*). In city parks and mid-successional sites, recent escapes of planted (i.e., seedlings only) as well as spontaneously occurring adult phanerophytes (*Acer* ssp., *Fraxinus excelsior*, *Robinia pseudacacia*) also increased the importance of canopy height. Specific leaf area did not showed any clear trend across or within habitats despite findings from other studies in urban areas that have showed higher SLA of urban plants, favouring competitive abilities in high N soil content (Díaz et al. 1999; Knapp et al. 2008a).

We did find high leaf dry matter content to be characteristic of species generally less frequently occurring in the studied cities. High LDMC indicates sclerophylly, a slow growth rate and adaptation to unproductive, rarely disturbed environments (Cornelissen et al. 2003). Thus, species with low LDMC values would likely be handicapped by adaptations to conditions that are rare within urban areas and outcompeted by species better adapted to nutrient-rich disturbed sites.

Conclusions

In this study, we examined the effect of plant species functional traits and ecological indicators on the frequency of species occurrence in selected urban habitats. Dispersal type, life-ecology strategy, soil nutrient and moisture condition preferences and soil seed bank characteristics were found to be traits that had generally important influences on frequency of species occurrence. However, several cases of habitat-specific responses were also revealed, indicating that to better understand plant traits patterns in urban floras it is necessary to account for habitat heterogeneity of cities.

In large cities situated across a substantial part of temperate Europe, we assessed habitat types along a disturbance gradient from the centres to the outskirts of the cities, and therefore believe that our data set is representative of urban areas in that region. Our results demonstrated that urbanization strongly

disfavours species that are typically associated with low resource levels or extreme pH and moisture conditions or are weak competitors. For this reason we suggest including the conservation of such species as management priorities for urbanized areas to prevent regional extinctions and maintain diversity there. In the future, studies comparing urban habitat types in cities in different biogeographical regions or along disturbance gradients having different value ranges can further enhance our knowledge of the effects of urbanization on species occurrence.

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