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Native and alien floras in urban habitats: a comparison across 32 cities of central Europe

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ABSTRACT

Aim To determine relative effects of habitat type, climate and spatial pattern on species richness and composition of native and alien plant assemblages in central European cities.

Location Central Europe, Belgium and the Netherlands.

Methods The diversity of native and alien flora was analysed in 32 cities. In each city, plant species were recorded in seven 1-ha plots that represented seven urban habitat types with specific disturbance regimes. Plants were classified into native species, archaeophytes (introduced before AD 1500) and neophytes (introduced later). Two sets of explanatory variables were obtained for each city: climatic data and all-scale spatial variables generated by analysis of principal coordinates of neighbour matrices. For each group of species, the effect of habitat type, climate and spatial variables on variation in species composition was determined by variation partitioning. Responses of individual plant species to climatic variables were tested using a set of binomial regression models. Effects of climatic variables on the proportion of alien species were determined by linear regression.

Results In all cities, 562 native plant species, 188 archaeophytes and 386 neophytes were recorded. Proportions of alien species varied among urban habitats. The proportion of native species decreased with increasing range and mean annual temperature, and increased with increasing precipitation. In contrast, proportions of archaeophytes and neophytes increased with mean annual temperature. However, spatial pattern explained a larger proportion of variation in species composition of the urban flora than climate. Archaeophytes were more uniformly distributed across the studied cities than the native species and neophytes. Urban habitats rich in native species also tended to be rich in archaeophytes and neophytes.

Main conclusions Species richness and composition of central European urban floras are significantly affected by urban habitat types, climate and spatial pattern. Native species, archaeophytes and neophytes differ in their response to these factors.

Keywords

Archaeophytes, invasive species, neophytes, non-native plants, species richness, vascular plants.

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INTRODUCTION

Large cities harbour a greater proportion of alien plant species than their surroundings (Pyšek, 1998; Roy *et al.*, 1999; Kühn & Klotz, 2006; Pyšek *et al.*, 2010). For example, alien plant species make up about 40% of the total floras of central European cities, including approximately 15% of archaeophytes (pre-AD 1500 invaders) and 25% of neophytes (post-AD 1500 invaders; Pyšek, 1998). Two major mechanisms, disturbance associated with pulses of available nutrients (Davis *et al.*, 2000) and alien propagule pressure (Lonsdale, 1999), have been proposed as the main controlling factors of the level of plant invasion, and both of them are of high importance in cities. Firstly, cities are heterogeneous environments with mosaics of different habitats, many of them strongly disturbed and frequently enriched in nutrients. It has been repeatedly shown that strongly disturbed habitats in both urban and non-urban settings are more easily invaded than other habitats (Davis *et al.*, 2000; Chocholoušková & Pyšek, 2003; Celesti-Grapow *et al.*, 2006; Chytrý *et al.*, 2008b). Secondly, urban habitats are exposed to a high propagule pressure from alien plants, including both cultivated species and weeds. Many ornamental plants are grown in urban gardens, parks and residential areas, and some of them may eventually escape from cultivation and naturalize (Pyšek, 1998; Hanspach *et al.*, 2008; Loram *et al.*, 2008).

Besides disturbances, fluctuations in available resources and propagule pressure, the distribution of both alien and native plant species is significantly controlled by climate. In central Europe, the number of alien species and their proportion relative to the total flora is generally higher in warm and dry lowlands than in cooler and wetter areas (Pyšek *et al.*, 2002, 2005; Chytrý *et al.*, 2008a; Simonová & Lososová, 2008). However, little is known about the macroclimatic effects on alien floras in large cities because comparative studies of urban floras across large areas based on standardized sampling protocols are rare (but see Celesti-Grapow & Blasi, 1998; Loram *et al.*, 2008) and a few published meta-analyses used data from various sources which may not be directly comparable (Pyšek, 1998; La Sorte *et al.*, 2008; Ricotta *et al.*, 2009). Furthermore, like the native flora, the alien flora also has a distinct distribution pattern in Europe (Pyšek *et al.*, 2008), which means that variation in its species richness and composition cannot be explained solely by habitat qualities and climatic variables: the spatial pattern of the studied sites must be also taken into account. Cities are not distributed randomly. Their distribution is a result of historical and environmental factors such as bedrock type, landscape productivity, land-use history, development history or planning and management strategies (Kühn *et al.*, 2004). Urban environments share many characteristics that are absent in habitats of the surrounding landscape. Again, little is known about the relative effects of urban habitats and associated disturbance regimes, climate and spatial patterns of native and alien urban floras. These issues can only be satisfactorily resolved by obtaining data sets from plots across many cities, using standardized sampling protocols.

Here we used newly collected field data from 32 cities in central Europe to: (1) compare the level of invasion in urban habitats and cities located in different climatic regions of central Europe; (2) specify the relative importance of urban habitat types, climate and spatial pattern on the proportions and species composition of native and alien floras; and (3) quantify the relationships between the proportions of native and alien species in urban habitats. We distinguished between two groups of alien species that are known to have different habitat affinities (Pyšek *et al.*, 2005; Chytrý *et al.*, 2008b): archaeophytes (introduced before AD 1500) and neophytes (introduced after AD 1500; Pyšek *et al.*, 2002). We hypothesize that: (1) the proportion of alien species is higher in strongly disturbed urban habitats than those with moderate disturbance levels; (2) alien species richness is positively related to the richness of native species; (3) variation in the species composition of urban floras is related to urban habitat types, climate and the spatial pattern of the cities, but these factors affect native and alien species in different ways.

MATERIALS AND METHODS

Species data

We sampled the flora in 32 cities in Belgium, the Netherlands, Germany, Poland, the Czech Republic, Slovakia, Hungary, Slovenia, Austria and Switzerland (Table 1, Fig. 1). For simplicity, we call this region central Europe even though it exceeds the traditional delimitation of central Europe to the north-west. Each of these cities had more than 100,000 inhabitants. The cities were selected to represent different climatic regions of central Europe. We used climatic data obtained from the WorldClim data set (Hijmans *et al.*, 2005) to classify central Europe into regions on the basis of mean annual temperature higher or lower than 9 °C, difference between July and January mean temperatures higher or lower than 19 °C, and annual precipitation higher or lower than 700 mm. In the ArcGIS 8.3 geographical information system (ESRI, 2003), we overlaid these areas to obtain eight climatic regions. The thresholds given above are rounded medians from the climatic data obtained for about 50 large cities situated in the study area. In each climatic region, we selected four cities that, where possible, were not located very close to each other. The mean distance between pairs of cities within climatic regions was 250 km. This selection reduced correlations between climatic variables and helped to separate the effects of temperature and precipitation on urban biodiversity.

Sampling was performed in 2007–09 from mid June to late August, i.e. during a period in which the floristic composition of the studied habitats was quite stable and records of species occurrence sampled on different dates were comparable. We avoided the spring period because the comparability of spring and summer records is limited due to spring annuals and geophytes that usually develop in March–May and disappear by early June.

In each city, we focused on seven types of urban habitat:

Table 1 Basic data on the 32 central European cities studied. The area and population for each city were obtained from Eurostat – Statistical Office of the European Commission (<http://epp.eurostat.ec.europa.eu>) and climate data from the WorldClim data set (Hijmans *et al.*, 2005).

City	Population	Pop. density (inhabitants km ⁻²)	Area (km ²)	Longitude	Latitude	Mean annual temperature (°C)	Annual precipitation (mm year ⁻¹)	Mean July–January temperature difference (°C)
Amsterdam, NL	762,000	4460	219	4°52' E	52°21' N	9.2	827	14.2
Antwerpen, BE	462,000	2260	205	4°25' E	51°12' N	10.1	812	15.2
Augsburg, DE	264,000	1790	147	10°53' E	48°22' N	8.5	868	19.1
Bern, CH	123,000	2390	52	7°27' E	46°57' N	8.5	957	17.9
Bratislava, SK	431,000	1170	368	17°07' E	48°08' N	9.8	705	21.3
Brno, CZ	405,000	1760	230	16°35' E	49°12' N	9.0	584	20.9
Budapest, HU	1,722,000	3240	525	19°03' E	47°30' N	11.2	627	22.3
Debrecen, HU	207,000	440	461	21°37' E	47°31' N	10.1	646	23.0
Freiburg, DE	222,000	1450	153	7°51' E	48°01' N	10.5	919	18.3
Genève, CH	186,000	11,730	16	6°07' E	46°12' N	10.1	975	18.7
Groningen, NL	188,000	2320	84	6°34' E	53°13' N	8.6	816	14.6
Halle, DE	232,000	1720	135	11°57' E	51°29' N	9.1	544	18.1
Hamburg, DE	1,769,000	2340	755	9°57' E	53°33' N	8.5	770	17.5
Chemnitz, DE	243,000	1100	221	12°55' E	50°50' N	7.9	644	18.8
Innsbruck, AT	119,000	1120	105	11°23' E	47°16' N	9.0	945	20.1
Kassel, DE	195,000	1820	107	9°29' E	51°18' N	9.1	726	17.6
Köln, DE	1,001,000	2470	405	6°56' E	50°55' N	10.1	820	16.6
Košice, SK	239,000	980	243	21°15' E	48°43' N	8.7	679	22.7
Kraków, PL	755,000	2310	327	19°55' E	50°04' N	8.2	722	21.6
Linz, AT	189,000	1970	96	14°17' E	48°17' N	9.2	900	20.6
Ljubljana, SI	280,000	1020	275	14°30' E	46°02' N	10.4	1312	20.6
Maribor, SI	113,000	760	148	15°39' E	46°33' N	9.5	1030	21.1
München, DE	1,330,000	4290	310	11°33' E	48°08' N	8.0	958	19.3
Oldenburg, DE	161,000	1570	103	8°12' E	53°08' N	8.8	796	15.7
Ostrava, CZ	337,000	1590	214	18°16' E	49°50' N	8.6	746	20.9
Praha, CZ	1,251,000	2520	496	14°23' E	50°05' N	8.9	560	19.7
Regensburg, DE	134,000	1670	81	12°06' E	49°00' N	8.4	709	20.2
Salzburg, AT	150,000	2290	66	13°02' E	47°48' N	8.9	1211	19.6
Stuttgart, DE	602,000	2900	207	9°10' E	48°46' N	9.3	732	17.9
Szczecin, PL	406,000	1350	301	14°33' E	53°25' N	8.6	591	19.5
Utrecht, NL	300,000	3070	99	5°07' E	52°05' N	9.3	829	14.5
Würzburg, DE	133,000	1520	88	9°55' E	49°46' N	9.6	658	18.9

1. Historical square in the city centre, usually with pre-19th-century houses and with more than 90% of paved or sealed area.
2. Boulevard with 19th-century houses, lines of trees, small lawns and more than 70% of paved or sealed area.
3. Residential area with a compact building pattern, consisting of family houses at least 50 years old and private gardens (garden cities).
4. Residential area with an open building pattern, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs.
5. City park with old deciduous trees (tree cover 10–50%) and frequently mown lawns.
6. Early successional, recently disturbed site with prevailing bare ground and sparse vegetation, usually in or around construction sites.
7. Mid-successional site abandoned for 5–15 years, dominated by perennial grassland with scattered shrubs and young trees.

Each habitat was sampled in 1-ha plots of square or rectangular shape; the latter was used in habitat patches narrower than 100 m. Due to the restricted access to private gardens in residential areas with a compact building pattern, 500 m of streets instead of a 1-ha plot were sampled in this habitat to record species occurring in accessible public areas and also those growing in private gardens which were visible from the street. In total, 224 plots (32 cities × 7 habitats) were sampled. At each site, all spontaneously occurring vascular plant species were recorded, including garden escapes and seedlings of spontaneously regenerating planted trees and shrubs. Deliberately planted individuals were not recorded. Taxonomy and nomenclature mainly followed Jäger & Werner (2005) and Jäger *et al.* (2008). We used species aggregates for some taxonomically intricate taxa or taxa frequently recorded as juvenile individuals that were difficult to identify. Species aggregates not defined in the above-mentioned floras were: *Cerastium tomentosum* agg.:

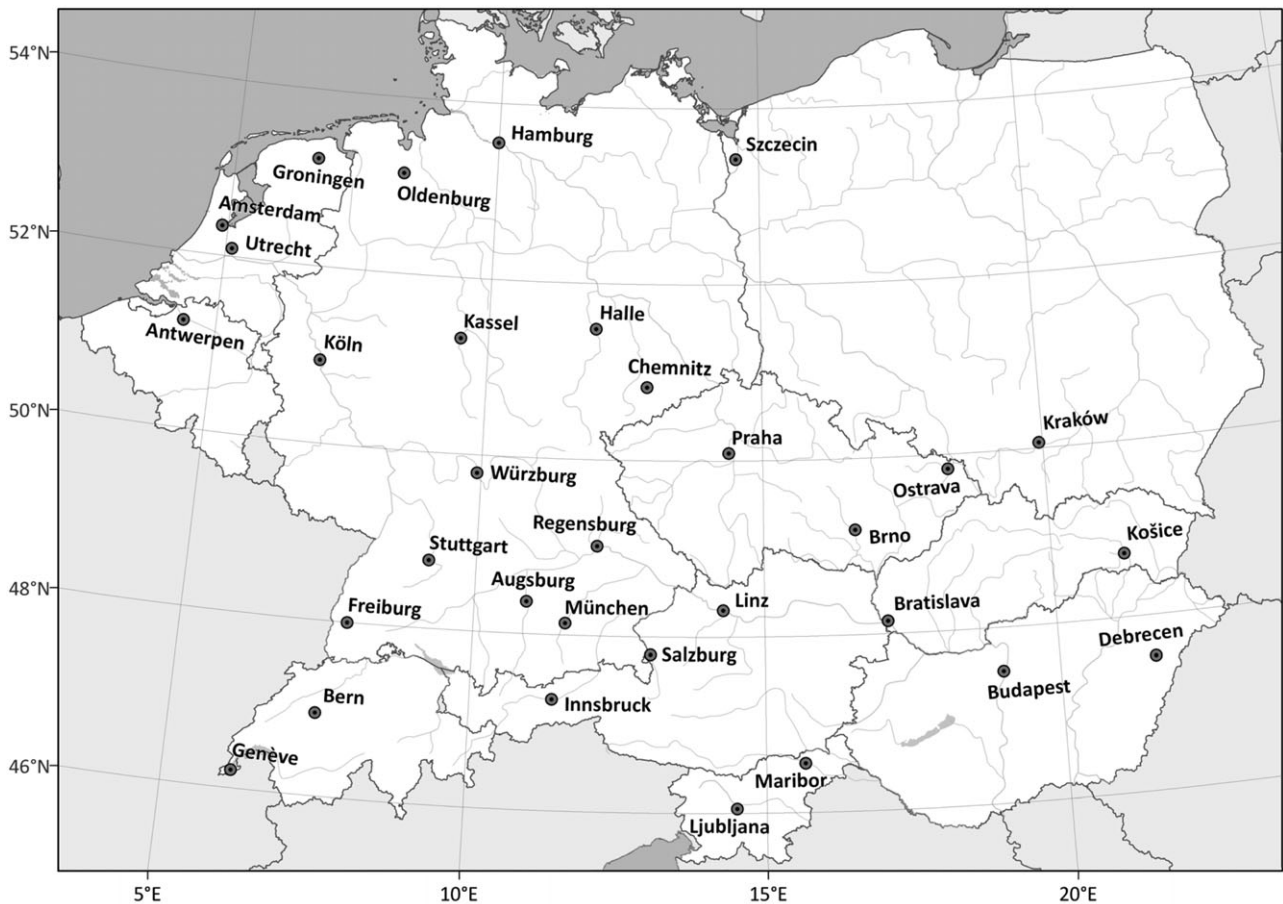


Figure 1 Map of the studied cities.

Cerastium biebersteinii and *C. tomentosum*; *Medicago sativa* agg.: *Medicago sativa* and *M. × varia*; *Oenothera biennis* agg.: *Oenothera biennis* agg. and *Oe. parviflora* agg.; *Parthenocissus quinquefolia* agg.: *Parthenocissus inserta* and *P. quinquefolia*.

The species were classified according to their status as native or alien, and the alien species were additionally divided according to their date of introduction into archaeophytes and neophytes. The classification followed the national lists of alien plants and specialized databases (Klotz *et al.*, 2002; Pyšek *et al.*, 2002; DAISIE, 2009). Species considered native in a part of a country were considered native in the whole country. Another attribute used was the geographical origin of alien species, which was mainly adopted from the BioFlor database (Klotz *et al.*, 2002). Four categories of species origin were recognized: Europe + western Asia, Asia (except its western part), the Americas and others. The last category included species from Africa, Australia and New Zealand, species of uncertain origin, hybrids and recent cultigens. The data set was edited using the program JUICE 9 (Tichý, 2002).

Data analysis

Patterns in species data were explored with respect to three groups of explanatory variables: habitat type, climatic data (for

each city: mean annual temperature, mean annual precipitation and annual temperature range, i.e. the difference between July and January mean temperatures) and spatial variables (for each city) generated by the analysis of principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2002). PCNMs are based on the calculation of principal coordinate analysis (PCoA) of a truncated pairwise geographical distance matrix between sampling sites (cities in our case). Firstly, a matrix of geographical distances between the sampled cities was truncated at a distance determined by the minimum spanning tree technique. This matrix was then analysed using a part of the 'Quick exploratory PCNM analysis' function (Borcard, 2008) in R, version 2.9.2 (R Development Core Team, 2010). The resulting 18 principal coordinates (spatial axes) with positive eigenvalues were used as explanatory variables representing the effect of spatial pattern in further analyses. These coordinates describe spatial structure of the data set across multiple scales. The spatial structure of our data set explained by 18 spatial principal coordinates is unrelated to variations in macroclimate. It is related to species dispersal ability and it could also be a result of other unmeasured factors such as different bedrock types, different land-use history and human management of the studied cities.

Ordination techniques were used to assess the effects of the explanatory variables on species composition. Firstly, for the

whole data set of 224 plots, a variation partitioning algorithm was applied to determine the net effects of climatic variables and urban habitat types separately for all species and for subsets of native species, archaeophytes and neophytes. Secondly, for the data set of total floras of the 32 cities (i.e. 32 lists of all species recorded cumulatively in seven plots of the same city), we applied the same procedure to determine the net effects of climate and space, also separately for all plant species, native species, archaeophytes and neophytes. The three above-mentioned climatic variables and 18 spatial axes were used. Redundancy analyses (RDA) with Hellinger transformation (Legendre & Gallagher, 2001) of the species data and the variation partitioning algorithm proposed by Peres-Neto *et al.* (2006) were used to balance the bias caused by different numbers of explanatory variables representing the climate and space. Significances of the net effects of climatic variables and urban habitat types (for individual plots) and of climatic and spatial variables (for cities) were tested by Monte Carlo tests with 999 permutations. These calculations were done using the 'vegan' 1.17-2 package (Oksanen *et al.*, 2010).

Proportions of species are not independent of each other but add up to one. An increase of one status group will therefore inevitably lead to the decrease of at least one other group (the so-called unit sum constraint; Aitchison, 1982). In order to overcome this problem, we used a multinomial approach based on log-ratios of proportions, i.e. replacing the observed proportions with the logarithms of ratios of proportions. Log-ratios have some desirable properties, most importantly the invariance property, which ensures that the choice of numerator and denominator in forming the ratios is unimportant (Kühn *et al.*, 2006). The calculations were performed using the 'vglm' function in the 'VGAM' 0.8-1 package (Yee, 2010) of R, with multinomial family and the proportion of native species as common denominator.

Furthermore, we related the presence/absence of each species in the studied cities (response variable) to climatic data (explanatory variable) using a set of generalized linear models with binomial distribution and logit link function to determine which species responded to individual climatic variables. This analysis was calculated in JUICE 9 (Tichý, 2002) and the 'stats' package of R.

Correlation coefficients, one-way ANOVA and linear regressions between the proportions of native species, archaeophytes and neophytes, and climatic variables, were calculated using STATISTICA 9 (StatSoft Inc., 2010).

RESULTS

Among the 1180 plant taxa (including species and species aggregates) recorded in all of the studied cities, there were 562 (48%) native species, 188 (16%) archaeophytes, 386 (33%) neophytes and 44 taxa identified only to the genus level that could not be assigned to any species group. The most frequent taxa in almost all habitats of each city were the European natives *Poa annua*,

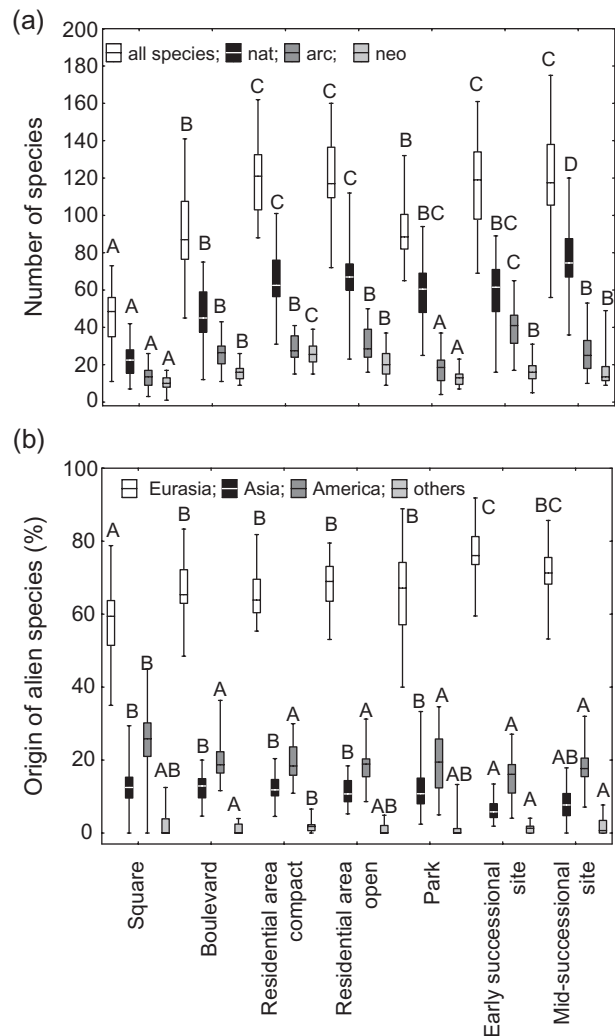


Figure 2 Numbers of native species (nat), archaeophytes (arc) and neophytes (neo) in different urban habitat types (a) and proportion of alien species with different geographical origin (b). Boxes and whiskers include 25–75% and min/max values, respectively. Horizontal lines indicate the medians. The same letters indicate homogeneous groups of habitat types according to the Tukey post-hoc test at $P < 0.05$.

Polygonum aviculare agg. and *Taraxacum* sect. *Ruderalia*. The most frequent alien species were the archaeophytes *Capsella bursa-pastoris*, *Plantago major* and *Sonchus oleraceus*. The most common neophytes were *Conyza canadensis* and *Erigeron annuus*. Individual 1-ha plots in different urban habitats contained 11–175 (mean 101) plant species, including on average 56% native species, 26% archaeophytes and 17% neophytes. The mean proportion of native species varied from 48% in city squares to 65% in city parks, whereas the proportion of archaeophytes was lowest (20%) in city parks and highest (35%) at early successional sites. The lowest proportion of neophytes (14%) was in mid-successional sites and the highest proportions (22%) were in residential areas with a compact building pattern and on historical squares in city centres (Fig. 2a).

Table 2 Relationships between the numbers of native species (nat), archaeophytes (arc) and neophytes (neo) observed in urban habitats of 32 central European cities. Pearson's correlation coefficients are shown.

	All habitats	Square	Boulevard	Residential area compact	Residential area open	Park	Early successional site	Mid-successional site
Nat versus arc	0.31***	0.35	0.43*	-0.18	0.08	-0.27	0.18	0.04
Nat versus neo	0.39***	0.50**	0.28	0.34	0.11	-0.16	0.39*	0.14
Nat versus (arc + neo)	0.39***	0.43*	0.46**	0.08	0.11	-0.27	0.30	0.09
(Nat + arc) versus neo	0.51***	0.72***	0.32	0.35	0.27	0.00	0.50**	0.46**
Arc versus neo	0.49***	0.75***	0.26	0.03	0.38*	0.35*	0.41*	0.71**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; coefficients without asterisks are not significant.

Most of the alien species found in the studied cities were of European and western Asian origins (e.g. *Euphorbia peplus*, *Geranium pusillum* and *Hordeum murinum*). These species grew in all of the studied urban habitats. The highest proportion of American neophytes was found in historical squares (26%); still, Eurasian species were the most specious group in this habitat. In other habitat types, the proportions of American neophytes varied between 15 and 18%. A large group of alien species came from Asia. These species (e.g. *Ailanthus altissima*, *Duchesnea indica* and *Oxalis corniculata*) accounted for about 12% of the species in all urban habitats except both types of successional sites, where they were less numerous. Alien species from other continents (e.g. *Citrullus lanatus* and *Lobelia erinus*, both from Africa) were rare in all urban habitats, representing on average about 2% of species (Fig. 2b).

Generally, there were positive or non-significant but no negative relationships between the richness of native species and both groups of aliens (Table 2). Archaeophyte and neophyte richness were positively correlated across all of the studied habitats. A positive relationship between native species richness and the richness of at least one group of aliens was revealed for both types of highly urbanized habitats, the historical squares and boulevards, and for early successional sites. Other relationships between native and alien species richness were not significant.

Both urban habitat types and climatic variables had significant effects on species composition for all groups of plant species (Fig. 3). There was no shared variation explained jointly by these two groups of predictors. Habitat types explained a higher proportion of the total variation than climate. Climate was relatively more important for neophytes than for the other groups.

For cumulative species lists of each city, spatial variables had a highly significant effect on the composition of all species groups, but the net effect of climate (after removing the shared effect of climatic and spatial variables) was not significant. A considerable amount of variation was shared between space and climate (Fig. 4). In spite of the weak net effect of climate on total species composition, some species did respond to changes in spatially structured climatic variables (Table 3). Of these, most (117) responded to the differences between July and January temperatures, whilst a lower number (35) responded to mean annual temperature (see Appendix S1 in Supporting Information for details).

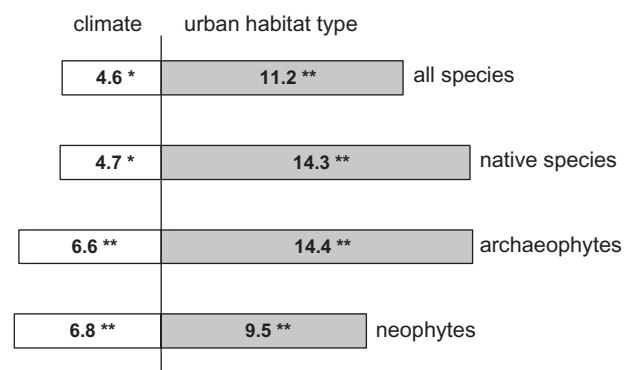


Figure 3 Percentage variation in species composition explained by the effects of climate and urban habitat types. Percentage variation explained by either climate or urban habitat type in redundancy analyses (RDA) is indicated. No shared effects were detected. The values were adjusted to balance the bias caused by a higher number of explanatory variables for habitat type than for climate. * $P < 0.05$; ** $P < 0.01$.

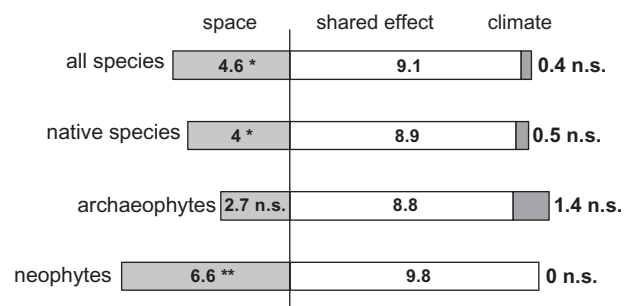


Figure 4 Percentage variation in species composition for all species and the different groups of species found in all plots in each city explained by the effects of space and climate, and the shared effect of both. Eighteen principal coordinates of neighbour matrices (PCNM) with positive eigenvalues were used as spatial variables. The percentage variation explained by either spatial variables or climate in redundancy analyses (RDA) is indicated; these values were adjusted to balance the bias caused by the lower number of explanatory variables used for climate than for space. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$.

Table 3 Numbers and percentages of species that responded significantly to individual climatic variables in generalized linear models (based on merged lists of the species recorded in seven habitats in each of 32 cities). See Appendix 1 for information on individual species.

	Native species	Archaeophytes	Neophytes
Number of species	562	188	386
Difference between July and January mean temperature			
No. (%) of species responding to the factor	57 (10.1%)	27 (14.4%)	33 (8.6%)
No. (%) of positively responding species	26 (4.6%)	18 (9.6%)	14 (3.6%)
No. (%) of negatively responding species	31 (5.5%)	9 (4.8%)	19 (4.9%)
Mean annual temperature			
No. (%) of species responding to the factor	17 (3.2%)	9 (4.8%)	9 (2.3%)
No. (%) of positively responding species	2 (0.4%)	8 (4.3%)	6 (1.6%)
No. (%) of negatively responding species	15 (2.8%)	1 (0.5%)	3 (0.8%)
Annual precipitation			
No. (%) of species responding to the factor	36 (6.4%)	19 (10.1%)	17 (4.4%)
No. (%) of positively responding species	29 (5.2%)	9 (4.8%)	14 (3.6%)
No. (%) of negatively responding species	7 (1.2%)	10 (5.3%)	3 (0.8%)

Table 4 Multinomial regression on log-ratios for the proportions of archaeophytes and neophytes. This regression breaks the unit sum constraint of compositional data (proportional data adding up to 1). Log(no. of archaeophyte species/no. of native species) and log(no. of neophyte species/no. of native species) in central European cities are explained by the difference between mean July and mean January temperatures (Δ Temperature), mean annual temperature and annual precipitation sum.

	Coefficient	SE	<i>t</i> -value	Level of significance
Intercept: log(archaeophytes/natives)	-2.688	0.36	-7.4	***
Intercept: log(neophytes/natives)	-2.642	0.38	-6.9	***
Δ Temperature: log(archaeophytes/natives)	0.031	0.01	2.8	**
Δ Temperature: log(neophytes/natives)	-0.003	0.01	-0.3	n.s.
Temperature: log(archaeophytes/natives)	0.183	0.03	5.5	***
Temperature: log(neophytes/natives)	0.195	0.04	5.5	***
Precipitation: log(archaeophytes/natives)	-0.0005	0.0002	-3.2	**
Precipitation: log(neophytes/natives)	-0.00007	0.0001	-0.5	n.s.

n.s., not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

There was a clear effect of climatic variables on the proportions of native species, archaeophytes and neophytes (Fig. 5). The effects of mean annual temperature and the difference between summer and winter temperatures were significantly positive and those of annual precipitation were significantly negative on the log-ratios of archaeophytes over natives. For the log-ratios of neophytes over natives, the only significant relationship was positive for mean annual temperature. This means that increasing annual temperature and difference between July and January mean temperatures increased the proportion of archaeophytes (and consequently decreased the proportion of native species), while precipitation had the opposite effect. The proportion of neophytes increased with annual temperature. This was true for the multiple variable model calculated for both groups of alien species (Table 4), as well as for the single-variable models with just one climatic variable used as a predictor (detailed results not shown). After partialling out the spatial effects, mean annual temperature and difference between summer and winter temperatures remained significant, but there was no net effect of precipitation on the proportion of individual species groups.

DISCUSSION

To the best of our knowledge, this is the first study using a standardized sample of field plots related to different urban habitats across such a large geographical area. Even though we only sampled a small fraction of the complete city flora in seven 1-ha plots per city, we found almost the same proportion of archaeophytes (16%) and a higher proportion of neophytes (33%) than Pyšek (1998) did for the entire flora of central European cities (15 and 25%, respectively). This is surprising, because large areas typically contain a larger proportion of aliens than small areas such as 1-ha plots (Chytrý *et al.*, 2005; Hulme, 2008). The differences in proportions of alien species may be due to the fact that complete urban species lists often include species from semi-natural habitats preserved in large cities, often protected as nature reserves. Such habitats harbour many native species otherwise absent from human-made habitats, which may increase the proportion of this species group. However we sampled mainly habitats strongly influenced or created by humans. Indeed, such high proportions of archaeophytes or neophytes are hardly found in European non-urban habitats except in some arable fields (Chytrý *et al.*, 2005,

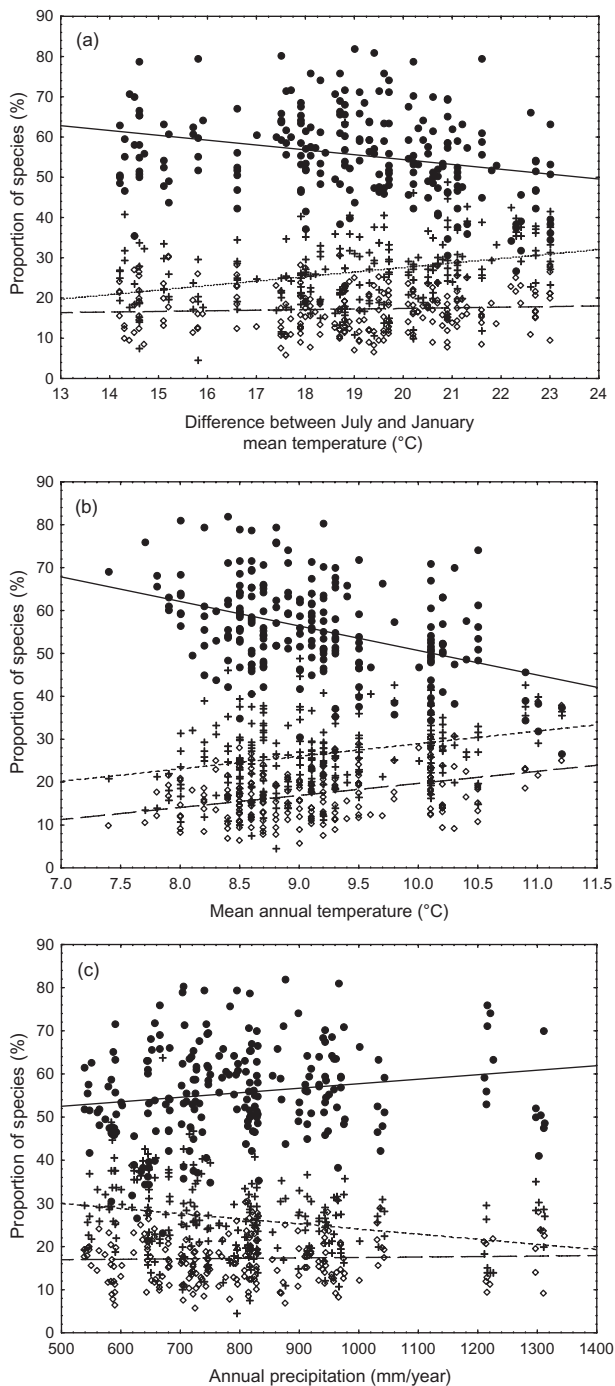


Figure 5 Relationships between the percentage proportions of native species, archaeophytes and neophytes, and individual climatic variables. Lines indicate trends of changing percentages of species belonging to particular groups along the climatic variables. See Table 4 for the statistics. ● solid line, native species; + dotted line, archaeophytes; ◇ dashed line, neophytes.

2008a,b; Simonová & Lososová, 2008). It could be argued that comparisons with published lists of the total city floras could be affected by the absence of some spring annuals or geophytes in our data, especially in view of the fact that some aliens have an earlier or later phenology than the majority of native

species (Pyšek *et al.*, 2003b). Nevertheless, we believe that this hardly affected our results because unlike in southern Europe (Celesti-Grapow *et al.*, 2003; Godoy *et al.*, 2009), spring species that are invisible in summer are relatively few in central Europe.

Our results indicate that urban habitat types and the specific disturbance regimes associated with each of them strongly affect species composition (Celesti-Grapow *et al.*, 2006; Godefroid & Koedam, 2007; Lososová *et al.*, 2011). Despite high percentages of alien species, widespread generalist native species are still the most common component of the studied urban floras of central Europe, similar to cities in Britain (Roy *et al.*, 1999) and northern Europe (Melander *et al.*, 2009). In our data, the highest proportion of alien species was found in historical squares and boulevards, both situated in city centres, which is also in accordance with case studies from single cities (Chocholoušková & Pyšek, 2003; Celesti-Grapow *et al.*, 2006; Godefroid & Koedam, 2007; Ricotta *et al.*, 2010).

City parks and mid-successional sites were the two urban habitats with the highest proportions of native species. Lososová *et al.* (2011) showed that parks are habitats with low alpha and gamma diversity, whereas mid-successional sites are rich in species. However, the present study revealed that the low number of species in parks is due to the low number of aliens rather than native species. Indeed, parks are suitable habitats for a large group of native plant species. A mosaic of tree, shrub and lawn vegetation also provides opportunities for many animal species (Clergeau *et al.*, 2001). In this context, parks increase the diversity of central European urban biota.

Although archaeophytes were less numerous than neophytes in our cumulative species list, they were represented by a higher proportion in each of the studied habitats. This indicates that individual species of archaeophytes are on average more common than neophyte species. The highest proportion of archaeophytes was recorded at early successional sites (35%). Most of the archaeophytes (66%) in our data set were annual species able to persist in frequently disturbed habitats. Similarly, Pyšek *et al.* (2003a) observed that annuals make up 58% of archaeophytes but only 39% of neophytes in the Czech flora. In our data set, there were only 29% of annual species among the neophytes. This pattern may have resulted from the immigration and introduction history of these species. Archaeophytes have been exposed to frequent disturbances since the Neolithic, when they migrated to new areas with the first farmers and became established in regularly disturbed habitats such as arable land (Pyšek & Jarošík, 2005). Neophytes growing in cities are a much more diverse group of species (La Sorte *et al.*, 2008; Ricotta *et al.*, 2009). The diversity of life-forms enables neophytes to colonize various urban habitats. The distribution of neophytes in cities is less affected by differences in land use than that of the other species groups (Fig. 3), and therefore it is less predictable. Similar results were found for the occurrences of neophytes in human-made (Simonová & Lososová, 2008) and other habitats (Chytrý *et al.*, 2008a). These species were introduced relatively recently, therefore their adaptation to individual habitats in the non-native

range is still proceeding (Pyšek *et al.*, 2005; Celesti-Grapow *et al.*, 2006). In contrast, the majority of archaeophytes became naturalized in central Europe long ago; their distribution, like the distribution of native species, is much more limited by differences between habitats than by climate (Fig. 3). However, the generally weaker effect of climate than of habitats on both native species and the two groups of aliens reflects the limited importance of climatic variation within central Europe, even though the studied cities were located along a transect more than 1200 km long from the oceanic Netherlands to continental Hungary. The opposite pattern was documented from a north–south transect across Italy, covering the transition from central European to a Mediterranean climate, along which the floras of five cities were more affected by climate than by differences among urban habitats (Celesti-Grapow & Blasi, 1998).

We found a positive relationship between the numbers of native and alien species both for the merged flora from different habitats within the same city and for most of the studied habitats that were analysed separately (Table 2). Significant correlations were revealed both for the strongly disturbed, species-poor habitats in the city centres and for the species-rich early and mid-successional sites, often located on city peripheries. This pattern is consistent with simulation studies based on a null model of community invasibility, which showed that a positive relationship between numbers of native and alien species prevails in large areas, whereas the opposite relationship is associated with small plots that accommodate a few individual plants (Fridley *et al.*, 2004). Obviously 1-ha plots are already too large for negative relationships to occur; indeed, positive relationships were found to prevail in much smaller plots (Chytrý *et al.*, 2005).

Our study demonstrated that besides the climatic control of native and alien species assemblages, there is a significant spatial pattern in the large-scale distribution of urban plant species which is unrelated to variations in the macroclimate. The spatial pattern reported in our results was related to many unmeasured factors: besides species dispersal ability, it could have resulted from environmental and historical factors, such as bedrock types or history of land use and human management of the studied cities. Most neophytes are still spreading across Europe (Williamson *et al.*, 2009), therefore individual species can be quite common in some parts of the continent and absent elsewhere, but their climatic niche is only partly filled. Thus, these species are not in equilibrium with climate: the variation in neophyte distribution explained by the spatial pattern of these cities, but not by climate, is higher than in native species and archaeophytes. However, the net effect of spatial pattern is still significant for native species, although it is weaker than for neophytes. This probably reflects the fact that native species are constrained by their geographical ranges. In contrast, the net effect of spatial pattern is not significant for archaeophytes in central European cities. It is probable that many of these species used their long residence time of several centuries or millennia in central Europe to fill their potential range and find suitable habitats within this range (Pyšek & Jarošík, 2005). The occurrence of many of

them might be determined more by the availability of suitable disturbed habitats than by climate. Therefore, they tended to have a more uniform distribution across the studied cities than the native species and neophytes.

We identified clear patterns in the proportions of alien and native species along the climatic gradients. Increasing mean annual temperature was correlated with increasing proportions of both groups of alien species, while the increasing difference between summer and winter temperatures was associated with an increasing proportion of archaeophytes. This is consistent with other, more regional, European studies, in which both archaeophytes and neophytes were shown to occur more frequently in warmer areas at low elevations than in cooler highlands (Roy *et al.*, 1999; Pyšek *et al.*, 2005; Chytrý *et al.*, 2008a; Simonová & Lososová, 2008). They were also shown to have a greater representation in habitats of subcontinental Europe than those of oceanic Europe (Chytrý *et al.*, 2008b). For archaeophytes, this pattern reflects their origin in warm regions of southern Europe and the Middle East (Pyšek *et al.*, 2002). The high levels of invasion by neophytes in the warm and dry lowlands of central Europe have often partly been explained by the higher densities of human populations in the lowlands and partly by the high temperature requirements of neophytes, although other mechanisms may be involved as well.

In conclusion, we showed that variations in the species composition of central European native and alien urban flora is mainly related to differences between the studied habitats and less so, but still significantly, to variations in the spatial pattern of the studied cities and their climates. Our results are representative of central Europe, but they may be specific to this particular region. Further research is therefore needed to obtain comparative data from other regions with different genesis of their native and alien floras, and different human settlement histories.

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REFERENCES

- Aitchison, J. (1982) The statistical analysis of compositional data. *Journal of the Royal Statistical Society, Series B – Methodological*, **44**, 139–177.
- Borcard, D. (2008) *Quick exploratory PCNM analysis*. Available at: <http://www.bio.umontreal.ca/legendre/indexEn.html#R> Functions (accessed 21 April 2010).

- Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.
- Celesti-Grapow, L. & Blasi, C. (1998) A comparison of the urban flora of different phytoclimatic regions in Italy. *Global Ecology and Biogeography Letters*, **7**, 367–378.
- Celesti-Grapow, L., Di Marzio, P. & Blasi, C. (2003) Temporal niche separation of the alien flora of Rome. *Plant invasions: ecological threats and management solutions* (ed. by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade and M. Williamson), pp. 101–111. Backhuys Publishers, Amsterdam, Netherlands.
- Celesti-Grapow, L., Pyšek, P., Jarošík, V. & Blasi, C. (2006) Determinants of native and alien species richness in the urban flora of Rome. *Diversity and Distributions*, **12**, 490–501.
- Chocholoušková, Z. & Pyšek, P. (2003) Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzeň. *Flora*, **198**, 366–376.
- Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, **77**, 339–354.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. & Danihelka, J. (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541–1553.
- Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. & Smart, S.M. (2008b) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.
- Clergeau, P., Jokimäki, J. & Savard, J.-P.L. (2001) Are urban bird communities influenced by the bird diversity of adjacent landscapes? *Journal of Applied Ecology*, **38**, 1122–1134.
- DAISIE (2009) *European invasive alien species gateway*. Available at: <http://www.europe-aliens.org> (accessed 1 April 2009).
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- ESRI (2003) *ArcGIS 8.3*. Available at: <http://www.esri.com> (accessed 1 April 2009).
- Fridley, J.D., Brown, R.L. & Bruno, J.E. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, **86**, 1848–1855.
- Godefroid, S. & Koedam, N. (2007) Urban plant species patterns are highly driven by density and function of built-up areas. *Landscape Ecology*, **22**, 1227–1239.
- Godoy, O., Richardson, D., Valladares, F. & Castro-Díez, P. (2009) Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, **103**, 485–494.
- Hanspach, J., Kühn, I., Pyšek, P., Boos, E. & Klotz, S. (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 241–250.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hulme, P.E. (2008) Contrasting alien and native plant species–area relationships: the importance of spatial grain and extent. *Global Ecology and Biogeography*, **17**, 641–647.
- Jäger, E.J. & Werner, K. (eds) (2005) *Exkursionsflora von Deutschland. Band 4. Gefäßpflanzen: Kritischer Band*, 10th edn. Spektrum Akademischer Verlag, Elsevier, Munich, Germany.
- Jäger, E.J., Ebel, F., Hanelt, P. & Müller, G.K. (eds) (2008) *Exkursionsflora von Deutschland. Band 5. Krautige Zier- und Nutzpflanzen*. Spektrum Akademischer Verlag, Springer-Verlag, Berlin, Germany.
- Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde*, **38**, 1–334.
- Kühn, I. & Klotz, S. (2006) Urbanisation and homogenization – comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.
- Kühn, I., Brandl, R. & Klotz, S. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.
- Kühn, I., Bierman, S.M., Durka, W. & Klotz, S. (2006) Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *New Phytologist*, **172**, 127–139.
- La Sorte, F., McKinney, M.L., Pyšek, P., Klotz, S., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2008) Distance decay of similarity among European urban floras: the impact of anthropogenic activities on β diversity. *Global Ecology and Biogeography*, **17**, 363–371.
- Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.
- Lonsdale, M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Loram, A., Thompson, K., Warren, P.H. & Gaston, K.J. (2008) Urban domestic gardens (XII): the richness and composition of the flora in five UK cities. *Journal of Vegetation Science*, **19**, 321–330.
- Lososová, Z., Horsák, M., Chytrý, M., Čejka, T., Danihelka, J., Fajmon, K., Hájek, O., Juričková, L., Kintrová, K., Láníková, D., Otýpková, Z., Řehořek, V. & Tichý, L. (2011) Diversity of Central European urban biota: effect of human-made habitat types on plants and snails. *Journal of Biogeography*, **38**, 1152–1163.
- Melander, B., Holst, N., Grundy, A.C., Kempenaar, C., Riemens, M.M., Verschwele, A. & Hansson, D. (2009) Weed occurrence on pavements in five North European towns. *Weed Research*, **49**, 516–525.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2010) *Vegan: community ecology package*. Version 1.17–2. Available at: <http://vegan.r-forge.r-project.org> (accessed 21 April 2010).

- Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.
- Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
- Pyšek, P. & Jarošík, V. (2005) Residence time determines the distribution of alien plants. *Invasive plants: ecological and agricultural aspects* (ed. by Inderjit), pp. 77–96. Birkhäuser Verlag, Basel, Switzerland.
- Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
- Pyšek, P., Sádlo, J. & Mandák, B. (2003a) Alien flora of the Czech Republic, its composition, structure and history. *Plant invasions: ecological threats and management solutions* (ed. by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade and M. Williamson), pp. 113–130. Backhuys Publishers, Amsterdam, Netherlands.
- Pyšek, P., Sádlo, J., Mandák, B. & Jarošík, V. (2003b) Czech alien flora and the historical pattern of its formation: what came first to Central Europe? *Oecologia*, **135**, 122–130.
- Pyšek, P., Jarošík, V., Chytrý, M., Kropáč, Z., Tichý, L. & Wild, J. (2005) Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. *Ecology*, **86**, 772–785.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z. & Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, **23**, 237–244.
- Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., Gassó, N., Kenis, M., Lambdon, P.W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M. & Hulme, P. (2010) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography*, **19**, 317–331.
- R Development Core Team (2010) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org> (accessed 1 April 2009).
- Ricotta, C., La Sorte, F.A., Pyšek, P., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.
- Ricotta, C., Godefroid, S. & Rocchini, D. (2010) Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. *Biological Invasions*, **12**, 233–240.
- Roy, D.B., Hill, M.O. & Rothery, P. (1999) Effects of urban land cover on the local species pool in Britain. *Ecography*, **22**, 507–515.
- Simonová, D. & Lososová, Z. (2008) Which factors determine plant invasions in man made habitats in the Czech Republic? *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 89–100.
- Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, **13**, 451–453.
- Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., Stout, J. & Pyšek, P. (2009) The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*, **15**, 158–166.
- Yee, T.W. (2010) The VGAM package for categorical data analysis. *Journal of Statistical Software*, **32**, 1–34. Available at: <http://www.jstatsoft.org/v32/i10> (accessed 6 October 2010).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Lists of species that significantly respond to climatic variables.

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BIOSKETCH

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