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Similar responses of native and alien floras in European cities to climate

Veronika Kalusová¹ | Natálie Čeplová^{1,2} | Milan Chytrý¹ | Jiří Danihelka^{1,3} | Pavel Dřevojan¹ | Karel Fajmon¹ | Ondřej Hájek¹ | Veronika Kalníková¹ | Pavel Novák¹ | Vladimír Řehořek¹ | Jakub Těšitel¹ | Lubomír Tichý¹ | Tamás Wirth⁴ | Zdeňka Lososová¹

¹Department of Botany and Zoology, Masaryk University, Brno, Czech Republic

²Department of Biology, Masaryk University, Brno, Czech Republic

³The Czech Academy of Sciences, Institute of Botany, Průhonice, Czech Republic

⁴Department of Ecology, University of Pécs, Pécs, Hungary

Correspondence

Veronika Kalusová, Department of Botany and Zoology, Masaryk University, Brno, Czech Republic.
Email: kalveron@tiscali.cz

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Abstract

Aim: Climate is an important factor controlling plant distributions. However, it is not yet fully understood how climate interacts with human impacts or whether the effects of these factors differ between native and alien species. Facing ongoing climate change and urbanization, we explore the effects of climate on plant species richness and composition across European cities.

Location: Sixty cities in Western, Central and Southern Europe.

Taxon: Vascular plants.

Methods: Species presence was recorded in seven habitats in each city. Large-scale climatic gradients were derived from 22 climatic variables using a partial principal component analysis that controlled for the effects of human population size and gross domestic product. The effects of climate and habitat type on the numbers of native and alien species were tested using linear mixed-effect models. The native and alien compositional variation across cities and habitats was analysed using principal component analysis with variation partitioning.

Results: The Mediterranean-to-temperate climatic gradient had a significant effect on species numbers across all habitats. The numbers of both native and alien species increased from the Mediterranean to temperate Europe. Within each city, the proportion of alien species decreased from highly urbanized to less urbanized habitats. Climate had a stronger effect on the composition of alien plants than on the composition of native plants. The native species composition especially changed from the Mediterranean to temperate cities and alien species composition also from oceanic to continental cities.

Main conclusions: Urban native and alien species richness follow the pattern found for the whole European flora. Based on this observation, we suggest that the future shift of warm and dry conditions from the Mediterranean to the north that is expected under global change scenarios could affect richness and change the composition of European urban floras. However, this shift would not necessarily alter the proportions of aliens.

KEYWORDS

alien species, invasion, macroclimate, native species, neophytes, plant species composition, species richness, urban habitats

1 | INTRODUCTION

A fundamental goal of ecological research is to understand the processes that control biological diversity and its shifts in response to environmental changes. Broad-scale variation in plant species diversity has been shown to be strongly correlated with climate across areas with diverse evolutionary histories and vegetation formations in different parts of the world (Currie et al., 2004; Francis & Currie, 2003; Gaston, 2000). Various climate-based mechanisms have been hypothesized to control geographical patterns of species diversity, including the effect of climatic constraints, such as temperature and drought, on plant physiology (Breckle, 2002; Normand et al., 2009; Pigott & Pigott, 1993; Woodward, 1987).

Globally, native plant species richness tends to decrease from the equator to the poles (Barthlott et al., 1999; Mittelbach et al., 2007) in response to climate, historical climatic changes, associated speciation and extinction processes, and other factors (Gaston, 2000; Hawkins et al., 2003; Rohde, 1992). In Europe, the species richness of both native and alien species has been shown to considerably differ between major biogeographical regions (Araújo, Thuiller, Williams, & Reginster, 2004; Lambdon et al., 2008). Continental-scale analyses revealed that the highest native plant richness occurs at the border between the Mediterranean and Central Europe (Ronk, Szava-Kovats, Zobel, & Pärtel, 2017) rather than in Mediterranean Europe, as would be expected from the global latitudinal trend. In contrast, alien plant species richness was shown to be highest in Northwestern and Central Europe and lowest in the Mediterranean and the Boreal zone (Ronk et al., 2017). However, patterns of species richness and composition in Europe also depend on other factors, and the factor gaining increasing importance is the anthropogenic impact (Araújo, 2003; Luck, 2007). Climate-related diversity patterns based on country-level species records therefore can be biased because the compared areas differ not only in climate but also in size, sampling intensity, human population density and human impact.

Previous comparative studies on European urban and rural areas have shown that cities usually have higher native and alien plant diversity than their surrounding areas (Kühn, Brandl, & Klotz, 2004; Wania, Kühn, & Klotz, 2006). Each city is a mosaic of urban habitats that developed under different human management regimes (frequency, intensity and type of disturbance) that determine the distribution and richness of native and alien plant species (Godefroid & Koedam, 2007; Lososová et al., 2011; Niemelä, 1999). However, local conditions in similar urban habitats that developed under similar human management regimes are comparable across cities (Rebele, 1994; Savard, Clergeau, & Mennechez, 2000). Knowledge on urban floras in climatically contrasting regions is therefore not only important for exploring differences in native and alien plant

diversity in urban areas compared to that in a broader landscape, but cities can also be advantageous for testing the effects of macroclimate. Despite their potential differences due to the various city size, socio-economic conditions and land use histories (Čeplová, Kalusová, & Lososová, 2017; Klotz, 1990; Pyšek, 1998), urban habitats provide a convenient set of sites with comparable local environmental conditions located across different macroclimatic areas. A previous study by Lososová et al. (2012a) showed that while urban habitats contribute to differences in plant richness and composition in within-city comparisons, the climate is very important in between-city comparisons. However, this and several other studies on European urban floras (e.g. Celesti-Grapow & Blasi, 1998; Lososová et al., 2011; Pyšek, 1998) covered a restricted range of European climates. It is therefore desirable to collect data on urban native and alien floras in a standardized way across extended geographical and climatic space. Studies based on such data are not only indicative of climate-related diversity patterns but are also important for forecasting biodiversity changes in the face of ongoing climate change that is coupled with increasing urbanization.

Recent climate change scenarios for the 21st century suggest increasing temperatures and drought across large parts of the European continent (IPCC, 2014). It is usually predicted that changes in climate will exacerbate plant invasions (Hulme, 2017) and have serious consequences for regional species diversity in Europe (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005; Thuiller, Richardson et al., 2005). Changes in climate are supposed to release the climatic restrictions on introduced alien plants that are now climatically constrained (Dullinger et al., 2017), leading to an increase in alien species numbers. The composition of alien floras will also change (O'Donnell et al., 2012). Indeed, the spread of alien species from Southern Europe to the north, which is supported by warmer and drier conditions at higher latitudes, has been documented (Walther et al., 2009). The results can be novel species interactions and consequent changes in local native diversity (Chytrý et al., 2012; Dawson, Jackson, House, Prentice, & Mace, 2011; Lososová et al., 2018). Usually, under climate change, native communities become more vulnerable to invasion as a consequence of increased environmental stress (Diez et al., 2012), and incoming alien species can decrease native species richness (Hulme, 2015). However, some experimental studies have also indicated that native species can benefit more from warmer or drier conditions than aliens (e.g. Buckland, Thompson, Hodgson, & Grime, 2001; Morecroft, Stokes, Taylor, & Morison, 2008). Therefore, it is still unclear whether the climate-induced spread will promote alien species disproportionately more than native species. If it did, then the level of invasion, which is expressed as the proportional representation of alien species (Chytrý, Maskell et al., 2008; Chytrý,

Jarošík et al., 2008; Richardson & Pyšek, 2006), would inevitably increase in the future solely due to the effect of climate change. In contrast, if alien and native European species responded to climate change in a similar way, an increase in the level of invasion would not necessarily occur as a result of climate change. These changes in climate will coincide with increasing urbanization of the landscape (United Nations, 2018). As they are places of frequent alien plant introduction (Dunn & Heneghan, 2011) and high alien richness (Kühn et al., 2004), urbanized areas can be subjected to most rapid climate-induced changes in invasion levels. Therefore, it is also important to determine whether climate-related causalities are the same for native and alien species occurrences in urban areas. The present-day patterns that are found in cities with warm and dry conditions can indicate how patterns of plant invasions in urban areas could change once such conditions shift to other European regions.

In this study, we examined urban plant species composition and richness across Western, Central and Southern Europe. We used a large data set that was collected following a standardized sampling protocol and consisted of species records from 420 plots in 60 European cities located in different biogeographical regions in order to cover a broad variation in macroclimatic conditions. We hypothesized the following: (a) climate-related native and alien richness patterns in cities across Europe are comparable to those found in the whole European flora and are consistent across different urban

habitats, and (b) the mean proportions of alien plant species across all habitats in a city, i.e. urban level of invasion, change along the climatic gradients in Europe. In other words, native and alien species richness responds differently to climatic gradients. (c) Differences among habitats within cities have a weaker effect on the composition of both native and alien floras than the climatic differences among cities.

2 | MATERIALS AND METHODS

2.1 | Species sampling in the field

We sampled plant species (presence/absence) in 60 cities with more than 100,000 inhabitants across Western, Central and Southern Europe (Figure 1). The cities were located in six biogeographical regions that were obtained by merging smaller regions from the Biogeographic Map of Europe (Rivas-Martínez, Penas, & Díaz, 2004), covering a considerable portion of European climate types:

1. Oceanic Western Europe (Ocean; 4 cities),
2. Central Europe (Central; 28 cities),
3. Continental Eastern Europe (Cont; 7 cities),
4. Submediterranean Europe (Submed; 7 cities),
5. Western Mediterranean Europe (MedW; 6 cities), and
6. Central and Eastern Mediterranean Europe (MedCE; 8 cities).

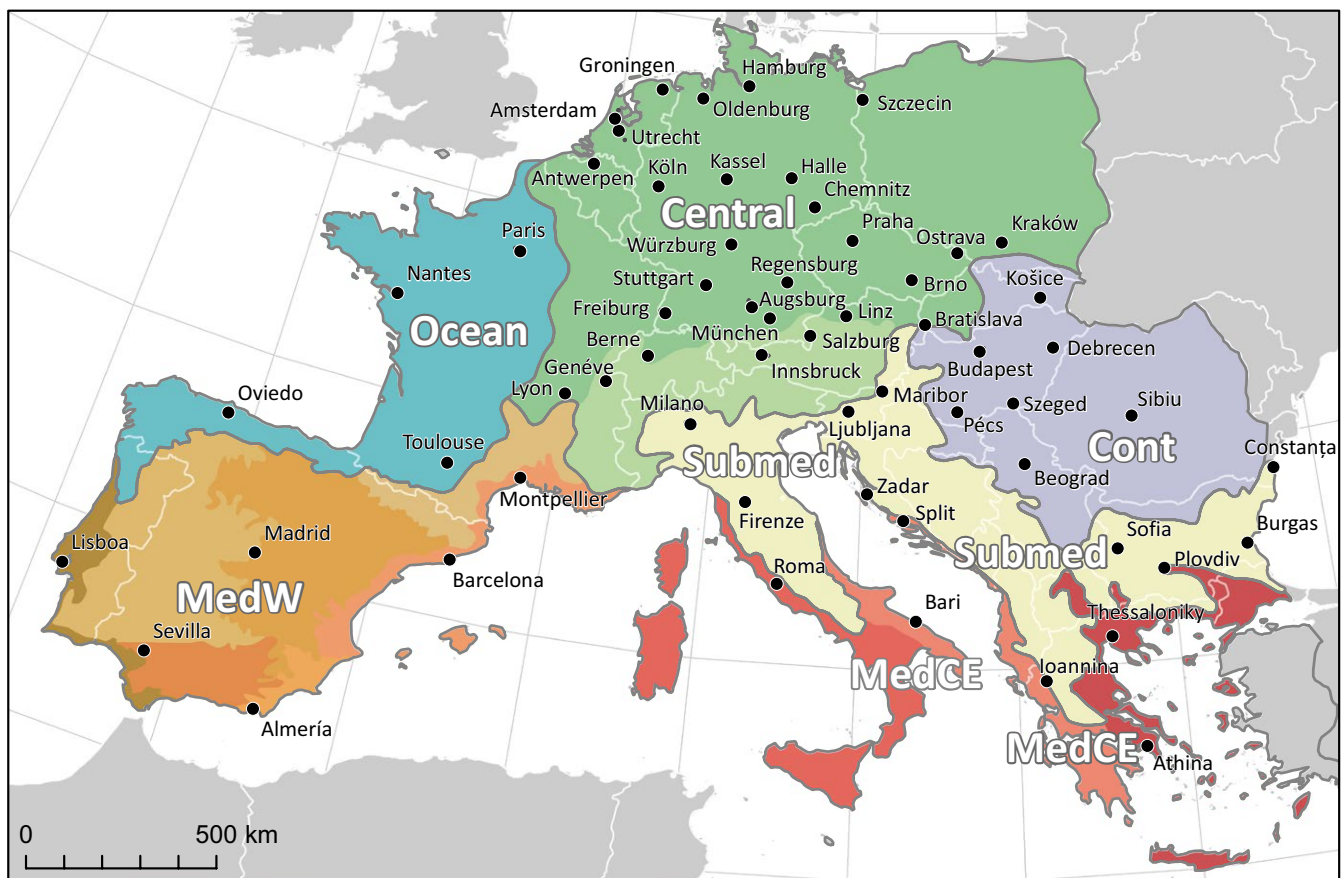


FIGURE 1 European cities sampled in this study within biogeographical regions (See Materials and Methods for abbreviations)

Sampling was performed from 2009 to 2015 using a standardized protocol (see Lososová et al., 2011 for details). The presence of all spontaneously established vascular plants (disregarding plants that had obviously been intentionally planted by humans) was recorded in seven 1-ha plots within each city. Ornamentals and crops were considered spontaneously established only if they were found outside their usual places of plantation. The locations of sampling plots were selected before the fieldwork began using aerial photographs in order to represent seven distinct urban habitat types (hereafter called habitats) that were used as a proxy for various management regimes that occur within cities:

1. Historical central square with pre-19th-century houses and paved or sealed areas >90% (hereafter called Square),
2. Boulevard built in the 19th century with lines of trees, small lawns and paved or sealed area <70% (Boulevard),
3. Residential area with a compact building pattern, including rows of family houses and private gardens (garden cities), that was at least 30 years old (ResComp),
4. Residential area with an open building pattern, including housing estates with blocks of flats built in the 1960s–1980s, with scattered trees (ResOpen),
5. City park with old deciduous trees (tree cover 10%–50%) and regularly mown grassland (Park),
6. Early successional site that was recently disturbed and had large areas of bare ground and vegetation cover <20% (EarlySuc),
7. Mid-successional unmanaged site on the periphery of the city that had been abandoned for 5–15 years and was dominated by herbaceous vegetation with scattered shrubs (MidSuc).

The taxonomy and nomenclature of the vascular plant taxa (hereafter called species) followed the Euro+Med PlantBase (2006–2018, www.emplantbase.org). The two groups of plant species were distinguished based on the Euro+Med PlantBase according to their introduction status: (a) native species included all species native to any region of Europe and merged with archaeophytes, i.e. species introduced to European countries before 1500 AD and (b) neophytes, i.e. species introduced to European countries after 1500 AD (Pyšek et al., 2004). Although some archaeophytes are native to some parts of Europe and alien in other parts of the continent, we merged archaeophytes with native species because it is unknown whether many species are native or archaeophytes in certain regions of Southern Europe. Neophytes included both the species with their native range in some part of Europe and those that came from outside Europe. Within-European neophytes had low frequencies in the plots; therefore, all neophytes were analysed together, and they are hereafter referred to as alien species.

2.2 | Climatic data and identification of the main climatic gradients

To assess the effect of climate on the richness and composition of native and alien plant species in cities, we used 22 macroclimatic variables that were derived from the interpolated climate station

data at a 5-min pixel resolution from WorldClim (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and the Global Aridity and PET Database (<http://www.cgiar-csi.org/data/global-aridity-and-pet-database>; Zomer et al., 2007; Zomer, Trabucco, Bossio, van Straaten, & Verchot, 2008). We extracted the values of these variables for each sampled plot based on its geographical coordinates using ArcGIS 8.3 (ESRI, 2003). The climatic variables for each city were calculated as means of values obtained in particular plots located within the city. We also obtained two socio-economic characteristics for each city: number of inhabitants and gross domestic product per capita (GDP; €/yr in 2017) from Eurostat (2018). These factors were shown to be good representatives of propagule pressure and human disturbance in previous studies on European plant invasions (e.g. Dalmazzone, 2002). To derive the main climatic gradients in Europe, a partial principal component analysis (pPCA) was calculated with the matrix of mean values of all climatic variables to characterize that main climatic differences among cities. The numbers of inhabitants and GDP values were applied as covariates to remove their effect on the obtained climatic gradients because socio-economic differences among cities can create a similar geographical pattern as climatic differences. As a reference, we also repeated this analysis (and subsequent analyses of species richness) without considering any socio-economic covariates and present this in Supporting Information, the discrepancies between both richness analyses indicate the effect of socio-economic differences hidden under climatic gradients. Log transformations were applied for variables with a skewed distribution, and all variables were centred and divided by the standard deviation prior to the analysis. The pPCA was performed using the function *rda* from the package 'vegan' version 2.4 (Oksanen et al., 2017) in R, version 3.5.0 (R Core Team, 2018). The scores of the cities on the first, second and third pPCA axes, which together accounted for 70.4% of the variance in the climatic data (an additional 14.5% was attributed to the covariates), were extracted to represent the main climatic gradients in the data set.

2.3 | Species richness analysis

The effects of the three climatic gradients expressed as pPCA axes, urban habitats and their interaction on species richness and the ratio between native and alien species were tested using a linear mixed-effect model (LMM). The model contained square root-transformed species richness as a response variable, and pPCA axes, habitats, species introduction status and all their interactions as fixed-effect predictors. Its random effect structure consisted of introduction status nested within the habitat, which was further nested within the cities to account for the split-plot structure of the data. A full model containing all possible predictors and their interactions was fitted first. Non-significant fixed-effect terms were subsequently removed to obtain a minimum adequate model. The significant effects of environmental predictors in this model indicate the effects on total species richness irrespective of species introduction status, while the differential trends in the native:alien ratio are indicated by significant interactions between environmental predictors and the

species introduction status. Two- and three-way interactions of predictors were tested, but three-way interactions were not significant and are not shown. The LMM was constructed using function *lme*, package 'nlme' version 3.1 (Pinheiro, Bates, & DebRoy, 2018) in R.

To graphically illustrate the significant trends that were revealed by the LMM, we computed mean values of species richness (or proportion of alien species) at the appropriate level of the hierarchically nested random structure of the model. These values were plotted against the significant climatic gradients (ordination scores of cities) in a scatter plot (with a regression line based on ordinary least-square regression) or displayed in a boxplot illustrating differences between habitats.

2.4 | Species composition analysis

The data on species presence/absence in plots were transformed by Hellinger transformation (Legendre & Gallagher, 2001). To compare the similarity in native and alien plant species compositions among cities and different urban habitats, a transformation-based principal component analysis (tbPCA) was computed on plot-by-species matrices of native and alien species separately. The PCA function from the package 'vegan' version 2.4 (Oksanen et al., 2017) in R was used. The scores of each plot on the first and second PCA axes were mapped using ArcGIS 8.3 to reveal the patterns in native and alien species composition of cities across Europe. A variation partitioning algorithm using transformation-based redundancy analysis (tbrDA; Peres-Neto, Legendre, Dray, & Borcard, 2006) was separately applied to the plot-by-species matrices of native and alien species. The net effects of climate (three main climatic gradients that were derived from the pPCA) and urban habitats on the species composition of both groups were calculated. The net effects of each of three climatic gradients were separated, and the shared variation between climate and urban habitats was computed. This algorithm balances the bias caused by the different number of explanatory variables characterizing climate and habitats. The significance of the net effect of each variable was tested using the Monte Carlo test under a reduced model with 999 permutations. Variation partitioning was computed using the function *varpart* and tested by ANOVA from the package 'vegan' version 2.4 (Oksanen et al., 2017) in R.

3 | RESULTS

3.1 | Patterns and drivers of native and alien urban species richness

In total, 2017 species were recorded across all 420 plots in the 60 cities. Of all species, 505 species were identified as being alien to Europe, including 365 aliens of extra-European origin and 140 aliens that were native in some parts of the European continent.

The ordination of mean values of the climatic characteristics (Appendix S1 in Supporting Information, Figure S1a, b) revealed three main climatic gradients across the studied European cities. The first axis (pPC1; Figure S1a) represented

the Mediterranean-to-temperate climatic gradient in Europe. The low precipitation in the warmest quarter and the driest month of the year at the left end of the axis indicated the summer drought characteristic of the Mediterranean climate. The high annual mean temperature and mean temperature of the coldest quarter of the year also correspond to this warm climate type. The cities with low ordination scores (Mediterranean part of the gradient) included Almería, Sevilla, Lisboa and Athina in Southern Europe, whereas cities with the highest scores (temperate part) included Kraków, Szczecin and Ostrava in Central Europe. The ordination scores of all cities on the pPCA axes are available in Appendix S1, Table S1, and the climatic correlates of these axes are shown in Appendix S1, Table S2. The second axis (pPC2; Figure S1a) corresponded to the gradient of increasing precipitation. The cities with low scores (dry conditions) included Almería in southern Spain and Constanța in eastern Romania. The cities with high scores (wet conditions) included Ljubljana, Salzburg and Milano, which are all located around the Alps. The third axis (pPC3; Figure S1b) reflected the oceanic-to-continental gradient across Europe, i.e. increasing temperature range and increasing drought stress towards the east. The cities with low scores (oceanic) included Oviedo, Nantes, Amsterdam or Antwerpen in Western Europe, whereas those with high scores (continental) included Bratislava, Innsbruck, Praha, Sibiu and Szeged in Central and Eastern Europe.

The LMM analysis revealed a significant positive effect of the city position on the Mediterranean-to-temperate gradient (pPC1 scores) on the numbers of all plant species in the plots (Table 1; Figure 2). This effect was consistent between native and alien species and independent of urban habitats, as indicated by the non-significance of the interaction terms. The precipitation gradient (pPC2 scores) showed a significant interaction with species introduction status, indicating a higher proportion of native species in cities with high precipitation than in cities with low precipitation ($t_{412} = 2.93$, $p = 0.004$). However, this pattern was strongly affected by the single city of Almería, which was an outlier with extremely low precipitation, as showed in the re-analysis of the data excluding this city effect (see Appendix S2, Table S3). The effect of the interaction between the precipitation gradient and habitat on the number of all species was also significant, but its significance was rather marginal and was also partly influenced by the climatic extremity of Almería; no clearly interpretable pattern was observed. The oceanic-to-continental gradient (pPC3 scores) had no significant effect on the numbers of native and alien species in the plots (habitats). However, when the Oceanic and Continental Eastern biogeographical regions were compared, the cities in Continental Eastern Europe had significantly higher numbers and proportions of alien species than those in Oceanic Europe (alien numbers: $t_{90,72} = 4.14$, $p < 0.001$; alien proportions: $t_{106,33} = 4.15$, $p < 0.001$). Similarly, we found an increase in the alien proportion along the oceanic-to-continental gradient (PC3 axis), when the LMM was recalculated with axes derived from the principal component analysis without considering the effects of the number of inhabitants and GDP as covariates (see Appendix S2, Table S4).

Within cities, urban habitats significantly affected the number of all species in the plots, and there was also a significant interaction between habitat and species introduction status (Table 1). The latter result means that the proportional representation of aliens significantly differed among urban habitats (Figure 3). The proportion

TABLE 1 Analysis of variance of the linear mixed-effect model testing the main effects of climatic gradients represented by the score of the city on the first three axes of a partial principal component analysis (pPC1, pPC2 and pPC3), urban habitats and species status (native vs alien) and their two-way interactions on species numbers in 1-ha plots ($n = 420$) that were sampled across European cities

Main effects and interactions	df effect, df error	F	p
pPC1	1, 56	13.856	0.001
pPC2	1, 56	2.036	n.s.
pPC3	1, 56	1.235	n.s.
Habitats	6, 336	73.676	<0.001
Native vs alien status	1, 392	7027.890	<0.001
pPC1:habitats	6, 336	1.471	n.s.
pPC2:habitats	6, 336	2.693	0.014
pPC3:habitats	6, 336	1.308	n.s.
pPC1:native vs alien status	1, 392	0.513	n.s.
pPC2:native vs alien status	1, 392	8.683	0.003
pPC3:native vs alien status	1, 392	2.653	n.s.
Habitats: native vs alien status	6, 392	56.548	<0.001

Notes. The model structure implies that the main effects indicate effects on species number irrespective of the species introduction status, while the terms containing interaction between the species status and other predictors indicate trends in native:alien species ratios. n.s., non-significant, three-way interactions were also tested but were not significant and are not shown.

of alien species showed a decreasing trend from highly urbanized habitats, such as squares, boulevards and residential areas, to less urbanized habitats, including successional plots of different ages.

3.2 | Patterns and drivers of native and alien urban species composition

Variation partitioning revealed that the native plant species composition in the plots was slightly more influenced by the differences among urban habitats than by the climatic differences among cities, whereas for the alien species composition in the plots, the climate was much more important than habitats (Table 2). When the climatic gradients were analysed separately, the species composition of both the native and alien species in the plots mostly varied along the Mediterranean-to-temperate gradient (pPC1), followed by the continental-to-oceanic gradient (pPC3). The alien species composition compared to the native species composition was, therefore, more similar among urban habitats within each city and varied more across cities in different parts of the climatic gradients across Europe. No shared variation was found between the effects of climate and urban habitats for both native and alien species.

The scores of the plots on the first axis of the tbPCAs, which were calculated separately for native and alien species on plot-by-species matrices, were projected onto the map of Europe (Figure 4a,b). A coincident shift in species composition in the plots from the south to the north was found for native and alien species. The cities in Mediterranean Europe clearly differed in their native species composition from the rest of Europe. The habitats in the Mediterranean cities included Southern European species such as *Erodium malacoides* and *Sonchus tenerrimus* (for other species characterizing the gradient see Appendix S3, Table S5). The cities across the Submediterranean and continental regions had similar species compositions (yellow and bright green) but were clearly separated

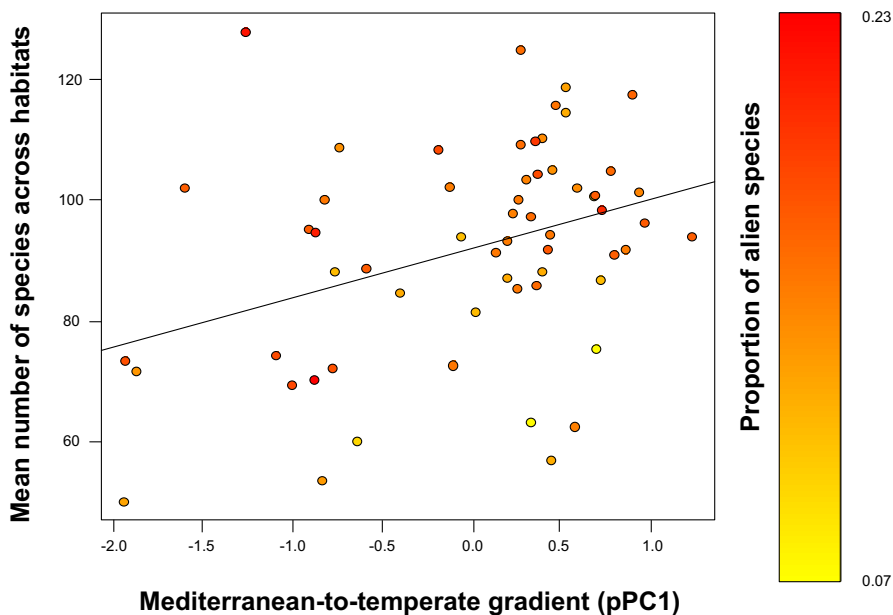


FIGURE 2 The relationship between the mean number of all plant species per city (across all habitats) and the city scores on the first axis of the partial principal component analysis (pPC1) representing the position on the Mediterranean (negative values) to temperate (positive values) climatic gradient in Europe. The mean proportion of alien species in a city is indicated by the colour scale. Regression summary: $R^2 = 0.13$, $F_{1,58} = 8.70$, $p = 0.005$



from the Mediterranean as well as Central European cities with a temperate climate (prevailing dark blue). The Central European cities hosted common Eurasian and circumpolar species such as *Achillea millefolium* agg., *Ranunculus repens* and *Urtica dioica*. Regarding habitats, the city squares in Northwestern and Central Europe were often similar to those in Submediterranean cities (Figure 4a). The composition of alien species in cities also changed from the Mediterranean to Central Europe (Figure 4b). The Mediterranean cities were characterized by Australian and South American alien species such as

TABLE 2 Proportion (%) of the total variation in the native and alien species composition of 1-ha plots ($n = 420$) across 60 cities that is explained by the net effect of the ordination scores on pPC1, pPC2 and pPC3 representing the Mediterranean-to-temperate climatic gradient, precipitation gradient and continental-to-oceanic gradient, all three climatic gradients together and urban habitats

	Variation explained (%)	
	Native species	Alien species
Climate	5.88***	5.59***
pPC1	4.61***	4.13***
pPC2	0.55***	0.43***
pPC3	0.89***	1.12***
Habitats	6.65***	3.03***

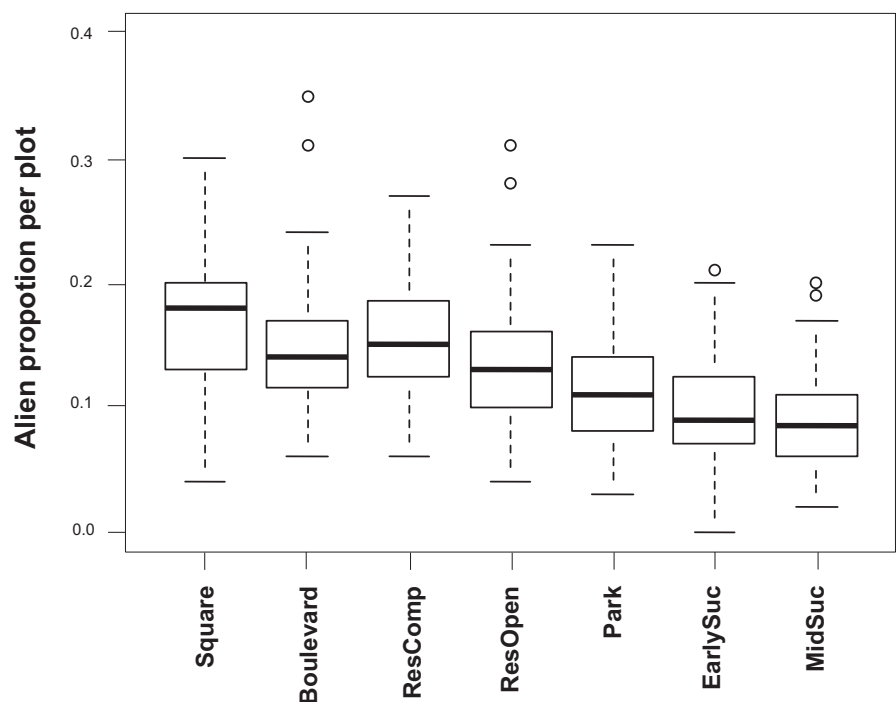
Notes. A redundancy analysis (tbRDA) with adjusted values of R^2 was used to balance the difference in the number of climatic variables and habitats as explanatory variables.

The significance of the explanatory variables was tested using the Monte Carlo test with 999 permutations, *** $p < 0.001$. No variance was shared between climate and habitats for the native and alien species. The effect of climate also includes the variation shared between pPC1, pPC2 and pPC3.

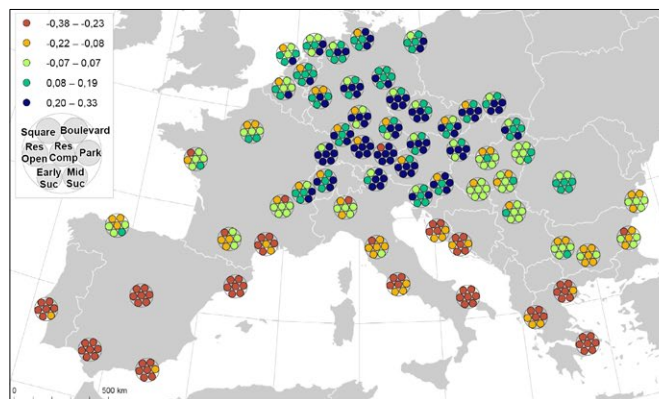
Dichondra micrantha and *Symphytotrichum squamatum*, whereas the cities in the temperate climate usually contained mainly North American species such as *Erigeron annuus*, *E. canadensis*, *Matricaria discoidea* and *Solidago canadensis*.

The scores of the second tbPCA axis that were calculated separately for native and alien species revealed differences in the response of native and alien species composition in cities. The native species composition (Figure 4c) changed slightly from Northwestern to Southeastern Europe. However, especially in Northwestern, Central and Western to Central Southern Europe, the scores of the plots varied more within cities than among cities. The plots on the one side of the gradient (orange and yellow) were mostly from squares, boulevards and residential areas, whereas the plots on the opposite side (green and dark blue) were mostly from both types of successional sites. Along the second axis of the tbPCA, the native species life-forms varied from short annuals and perennials that are tolerant to trampling at one end (e.g. *Ochlopoa annua*, *Plantago major*, *Sagina procumbens* and *Stellaria media*) to tall native biennials and perennials that are typical of irregularly disturbed sites at the other end (e.g. *Cichorium intybus*, *Daucus carota* and *Rumex crispus*), indicating differences in habitats rather than in climate. The type of urban habitat was therefore more important for the native species composition than for the alien species composition, which was consistent with the results of variation partitioning (Table 2). For the alien species composition, the scores on the second tbPCA axis clearly revealed that the second most important geographical gradient was from Western (dark green and blue) to Eastern Europe (yellow to orange). This shift is most likely affected by the oceanic-to-continental climatic gradient (Figure 4d). South African, South American and Southeast Asian species such as *Buddleja davidii*, *Erigeron bonariensis* and *Senecio inaequidens* were typical of the oceanic climate, whereas

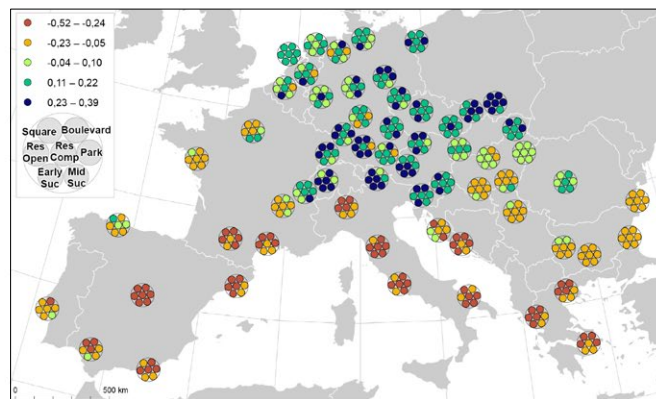
FIGURE 3 The proportion of alien to all plant species in 1-ha plots in seven urban habitats across all European cities ($n = 420$). The median (lines), interquartile range (25%–75% of values, boxes), ± 1.5 times the interquartile range (whiskers) and outliers (circles) are shown. ResComp–Residential area with compact building pattern, ResOpen–Residential area with open building pattern, EarlySuc–Early successional site, MidSuc–Mid-successional site



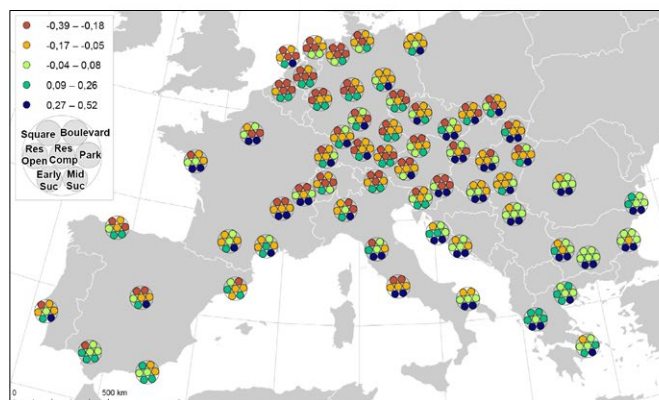
(a) Native species, Axis 1



(b) Alien species, Axis 1



(c) Native species, Axis 2



(d) Alien species, Axis 2

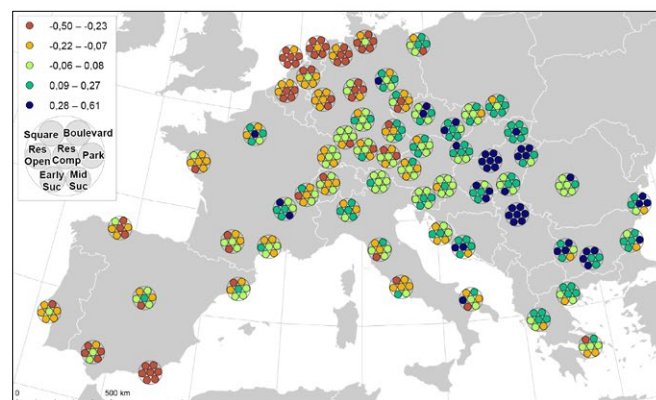


FIGURE 4 Maps with projections of the principal component analysis (PCA) scores of 420 sample plots in 60 European cities on the first (a, b) and second (c, d) tbPCA axes based on a species-by-plot matrix for native (a, c) and alien (b, d) plant species composition. The increasing score values along the two most important environmental gradients (PC1 and PC2 axes) are indicated by colour scales. Each point in a given city is one sampling plot, and its position indicates a habitat. Eigenvalues of PCA axes for native species: PC1 = 0.054, PC2 = 0.035, and for alien species: PC1 = 0.066, PC2 = 0.035. Total inertia_{native} = 0.693; total inertia_{alien} = 0.824

Asian and North American species such as *Acer negundo*, *Ailanthus altissima*, *Amaranthus retroflexus* and *Erigeron annuus* were often recorded in continental cities.

4 | DISCUSSION

4.1 | Species richness of native and alien species among cities

Although particular urban habitats host different numbers of native and alien species, both native and alien richness consistently decreased from cities in Central Europe to cities in Mediterranean Europe in all habitats. The level of plant species invasion, which was defined as the proportion of alien species averaged across the seven sampled habitats within each city, therefore did not show any significant change along the Mediterranean-to-temperate climatic gradient. Our result is in accordance with those from the studies of Kalwij, Robertson, Ronk, Zobel, and Pärtel (2014) and Ronk et al. (2017), which were based on grid atlas data on the whole (not only urban) flora, and they found the same decreasing trend in both native and

alien species richness from Central to Southern Europe. The observed differences in alien species richness among broader regions were attributed, in addition to climatic factors, to land use heterogeneity, human population density and human disturbance (Lambdon et al., 2008; Ronk et al., 2017). Population size influencing the propagule pressure and disturbances affects total species numbers and proportions in urban floras (e.g. Čeplová et al., 2017). In our study, however, the confounding effects of the number of inhabitants and GDP (i.e. correlates of propagule pressure; Dalmazzone, 2002) were excluded from the main analysis. This step ensured that there are no hidden effects of socio-economic differences among cities along climatic gradients that are shared with the effect of climate on urban species richness (compare Table 1 with Table S4). Sampling was performed in the same set of urban habitats in each city to keep the disturbance regimes as comparable as possible. Therefore, the similarity of the alien species response to that of native species provides evidence that alien species richness in Europe is similarly limited by climates like that of native species.

For many native European species, cold temperatures determine the upper latitudinal distribution limit in the north, and drought



stress determines the lower latitudinal limit in the south (Normand et al., 2009; Whittaker, Nogués-Bravo, & Araújo, 2007) through reproductive failure, growth reduction or higher mortality of individuals (Breckle, 2002; Pigott & Pigott, 1993; Woodward, 1987). The climatic conditions in areas of introduction should also meet at least the basic requirements of the incoming aliens for them to become established (Hulme, 2009; Kleidon & Mooney, 2000). In our data, alien species richness decreased from Central European to Mediterranean cities, in which dry summers probably prevent the occurrence of many alien species. The highest numbers of alien species can be expected in more northern regions where moist conditions together with moderate temperatures prevail (Polce et al., 2011). Native and alien species richness should also decrease towards Northern Europe due to the limitation by cold temperatures, as observed by Ronk et al. (2017). Several studies on urban floras indeed showed that low winter temperatures, which are connected with a short growing season, negatively affect urban species richness (Aronson et al., 2014; Jenerette et al., 2016). However, our study did not cover boreal and arctic parts of Europe, and thus, the decrease in native and alien species richness in the northern regions could not be detected.

According to the previous findings of Ronk et al. (2017), an increase in alien species richness can also be expected towards oceanic Northwestern Europe. Dullinger et al. (2017) suggested that oceanic Europe with mild winters and wet summers, which reduce frost and drought stress, could be suitable for more alien species to establish than continental Europe with its winter frosts and summer droughts. However, in our study, native and alien richness did not show the response to the continental-to-oceanic gradient when the confounding effects of population size and GDP were removed. The analysis with the effects of population size and GDP included (Table S4) showed a decrease in alien richness towards oceanic Europe, which is in contrast to the results of Ronk et al. (2017). The discrepancy in both of our analyses indicates that the expected response of urban alien richness to climatic continentality can in fact be conditioned by socio-economic differences among cities, which have a similar geographical pattern as climate. The reason for the opposite trend in alien richness in our study can be that individual countries differ in their policies or norms that influence the management of urban areas, and these differences partly depend on the socio-economic situation. A higher quality of public green services can result in more intense eradication of spontaneously established plants in cities of Northwestern Europe than in cities of eastern Central Europe. Another factor that can contribute to the higher alien richness in continental cities can be the urban heat island effect (UHI). For example, heath-absorbing surfaces covering large areas in city centres can locally mitigate the negative influence of low winter temperatures in continental areas (Gaston, Davies, & Edmondson, 2010) and enable the successful establishment of alien species originating from warm regions of the world, such as *Amaranthus deflexus*, in a continental climate (Appendix S3, Table S5). However, such mesoclimatic effects were not detectable in our study as it was designed to show the effects of macroclimatic gradients.

4.2 | Species composition of native and alien species among cities

The alien species composition in cities was generally less influenced by climate and urban habitats than native species composition, which could simply be because alien species had lower numbers in urban floras than did natives. However, the alien species composition clearly varied more along climatic gradients than among habitats, whereas the native species composition changed more between habitats than with the climate. No shared effect was found between climate and habitats. The pattern for native species is in accordance with that in a previous study analysing a shorter gradient from Northwestern to Central Europe (Lososová et al., 2012a); however, unlike a previous study, we analysed native species and archaeophytes together. Unfortunately, archaeophyte lists are not available for all countries, especially those in Southeastern Europe. The number of natives in cities was thus increased by the addition of archaeophytes, but we do not assume that this could have an important effect on the response of native richness because natives are usually much more numerous in urban floras than are archaeophytes (Lososová et al., 2012a). Merging these two groups could potentially lead to a slight decrease in the amount of native variation that would be attributable to climate because archaeophytes tend to homogenize urban floras in between-city comparisons (Lososová et al., 2012b). However, the higher importance of the effect of urban habitat compared to that of climate for the native species composition shown in our study agrees with the results of previous studies analysing native and archaeophytes separately (Lososová et al., 2012a; Lososová et al., 2012b).

In contrast to the Central European study of Lososová et al. (2012a), our data set from the long climatic gradient across Europe showed that the alien species composition in the cities was most strongly affected by climate and less so by the type of urban habitat. High variation in alien species composition can be caused by both climate and stochasticity in alien species introduction. Incoming alien species are filtered according to their climatic tolerance (Thuiller, Araújo, & Lavorel, 2004; Thuiller, Lavorel et al., 2005; Thuiller, Richardson et al., 2005), but their occurrence also depends on accidental transport of propagules (Lockwood, Cassey, & Blackburn, 2005) and human preferences for traded and cultivated plants (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007; Niinemets & Peñuelas, 2008). Thus, some aliens, especially neophytes, can be absent from particular region despite suitable climatic conditions (Essl et al., 2011). With climate change, shifts in the composition of European alien urban floras can be expected when climatically constrained alien species move to suitable climatic conditions (Walther et al., 2009). Within the cities of the same climatic region, alien species probably prefer sites where their establishment is facilitated by disturbance (Davis, Grime, & Thompson, 2000; Kowarik, 1995) regardless of the specific habitat type. Additionally, many of alien species can be habitat generalists, which contribute to the lower importance of habitats in our analysis of alien species composition of European cities.

4.3 | Differences among habitats within cities

The patterns of the native and alien species richness among habitats within cities did not significantly differ. Our results showed that native species richness increased with decreasing disturbance and increasing space for plant growth from heavily urbanized habitats in the city centres to the less urbanized habitats, with the lowest native species richness on city squares and boulevards and the highest in both types of successional sites. This result is in accordance with previous findings from shorter climatic gradients or similar habitats (e.g. Celestigrapow, Pyšek, & Jarošík, 2006; Lososová et al., 2011, 2012a; Zerbe, Maurer, Schmitz, & Sukopp, 2003). Alien species richness peaked in city squares and residential areas that contained many ornamental species that had escaped from flower beds and private gardens and many weedy alien species. Indeed, gardening activities are shown to be one of the most important sources of alien plants in urban floras (Smith, Thompson, Hodgson, Warren, & Gaston, 2006). New alien species often first emerge in cities (Dunn & Heneghan, 2011) and then spread to the surrounding landscape (Essl et al., 2015; Kühn & Klotz, 2006; Wania et al., 2006), which can also be indicated by the increasing alien richness towards city centres. In contrast, habitats at the city margins can be substantially enriched by native species from the surroundings (Werner, 2011), and this influence slowly diminishes towards the city centres. This effect is clearly documented by the native species composition in the successional sites, which were usually found in marginal parts of the cities, and their native composition differed from that in the other urban habitats in all the studied European regions. The specific effect of some urban habitats on native species composition was also apparent when city squares were compared across Europe. Their native species composition in Northwestern and Central Europe was similar to that of more southern cities. This result could be a consequence of heat-absorbing surfaces such as asphalt and concrete that support thermophilous and drought-adapted species even at higher latitudes (Schmidt, Poppendieck, & Jensen, 2014).

4.4 | Urban floras and future climate change

In the context of ongoing climatic change and urbanization, the trends in the native and alien richness that were analysed across cities in European regions with contrasting climates indicate how the richness and levels of invasion of urban flora could change with the predicted future changes in climate. In the regions where climate change brings some Mediterranean features such as summer drought periods, both native and alien species richness may decrease. In contrast, current colder regions may become warmer and become similar to the current climates in Submediterranean or Central Europe, which may result in an increase in both native and alien species richness. However, our study also indicates that the proportional representation of aliens in urban floras might not markedly change due to climate change, because alien and native species, as whole groups, similarly respond to climate. However, the future projections based on the current native and alien richness patterns have several limitations. First, our results refer to

changes in European urban areas only because cities have specific conditions for their flora that are different from those in the surrounding landscape. Second, the prediction of the changes is based on the current composition of urban floras with alien species that are already present and assumes that shifts in the distribution ranges of alien species will be based on their climatic tolerance (Lososová et al., 2018). However, climate change can also support the arrival of new alien species, naturalization of currently climatically constrained ornamentals (Dullinger et al., 2017), change preferences in planted crops (Howden et al., 2007) or increase the risk of hybridization of alien plants with native congeners when climatically suitable ranges overlap (Klonner et al., 2017). All of these processes, in addition to climate, can influence the resulting levels of invasion. Urban areas as recipients and sources of many alien species will rapidly experience such changes (Nobis, Jaeger, & Zimmermann, 2009). Therefore, disentangling the effects of various factors on urban flora richness and composition can be very important for understanding the processes of global change.

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DATA ACCESSIBILITY

All climatic GIS layers used for this study are available at www.worldclim.org and <http://www.cgiar-csi.org/data/global-aridity-and-pet-database>. Species data can be obtained upon request from the last author.

ORCID

Veronika Kalusová  <https://orcid.org/0000-0002-4270-321X>
 Natálie Čeplová  <https://orcid.org/0000-0002-8796-654X>
 Milan Chytrý  <https://orcid.org/0000-0002-8122-3075>
 Jiří Danihelka  <https://orcid.org/0000-0002-2640-7867>
 Pavel Dřevojan  <https://orcid.org/0000-0003-0802-3509>
 Veronika Kalníková  <https://orcid.org/0000-0003-2361-0816>
 Pavel Novák  <https://orcid.org/0000-0002-3758-5757>
 Jakub Těšitel  <https://orcid.org/0000-0003-3793-3704>
 Lubomír Tichý  <https://orcid.org/0000-0001-8400-7741>
 Tamás Wirth  <https://orcid.org/0000-0001-8008-4782>
 Zdeňka Lososová  <https://orcid.org/0000-0001-9152-7462>

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BIOSKETCHES

Veronika Kalusová is a researcher at Masaryk University, Brno, Czech Republic. Her research is focused on plant invasion patterns at different scales and on urban vegetation.

The project was led by **Zdeňka Lososová**, an associate professor of Botany at Masaryk University with an interest in urban ecology and plant diversity patterns.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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