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Alien plant species do have a clear preference for different land uses within urban environments

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Abstract

Since neophytes can become invasive in the future, untangling their ecological preferences is of paramount importance, especially in urban areas where they represent a substantial proportion of the local flora. Studies exploring alien species assemblages in urban environments are however scarce. This study aims to unravel alien plant species preferences for five urban land uses (densely built-up areas, open built-up areas, industrial areas, broadleaved urban forests, and agricultural areas and small landscape elements). We took the city of Brussels as a model, in which we recorded all vascular species growing spontaneously in grid cells of 1 km^2. We tested two different ways of classifying the 1-km^2 cells: (1) We simply associated each cell with its dominant land cover; (2) We used a fuzzy approach for which the degree of association of a given cell to a given land cover depended on the proportion of that land cover within the cell. For both classification methods, we calculated the indicator species of the resulting land cover types based on alien species only. The crisp and fuzzy classifications identified 33 and 49 species, respectively, with a clear preference for some urban land use types (from a total of 129 alien plant species analyzed). Results showed that urban land use types having apparently similar environmental conditions can actually harbor different neophyte assemblages. Fine-tuning the categorization of urban environments in future ecological studies is therefore important for understanding spatial patterns of alien species occurrence.

Keywords Exotic plants · Neophytes · Indicator species · Brussels · Land use classification · Ellenberg's indicators

Introduction

The number of alien species increased over recent decades in Europe (Butchart et al. 2010), especially in urban areas where they represent on average 28% of the local flora (Aronson et al. 2014). Alien species are able to influence the functioning of ecosystems through their impacts on resident plant and animal communities, soil biota and nutrient concentrations (e.g. Vanderhoeven et al. 2005; Morales and Traveset 2009; Maurel et al. 2010; Pyšek et al. 2012; Downey and Richardson 2016). They may also be responsible for species extinction. For instance, five plant species recorded as extinct on the IUCN red list have exotic plant species listed as one of the causes of their extinction (IUCN 2015).

Cities impose strong environmental filters on the urban flora (Ricotta et al. 2009; Williams et al. 2009; Aronson et al. 2016). In spite of this, it has been demonstrated on several occasions that cities are species-rich (e.g. Kühn et al. 2004a). The affinity of several alien plant species towards urban areas has been shown previously. For instance, an urbanity scale ranging from urbanophilic to urbanophobic depending on the species' presence or absence in cities has been developed for 3659 taxa of the European flora (Klotz et al. 2002; Kühn et al. 2004b). However, if we want to improve our knowledge of the ecology of urbanophilous species we cannot consider the urban environment as a homogeneous entity but rather as a set

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of more or less distinct habitats, e.g. housing areas of different types and densities, transport infrastructures, industrial areas, cemeteries, parks, etc.

Very little published work on the distribution of aliens in cities has taken into account sub-categories of the urban environment. When considering several urban land-use types in a city of southern Korea, Zerbe et al. (2004) showed that rural residential areas and industrial areas harbor the highest proportions of non-native species. Preliminary work on the urban flora of Brussels city showed the positive relationship between densely built-up areas and the presence of aliens (Godefroid and Koedam 2007; Ricotta et al. 2010a). In a comparative study across 32 cities in central Europe, Lososová et al. (2012) found that the highest proportion of alien species was found in historical squares and boulevards, whereas very few aliens had been identified in parks. Similarly, in 45 Central European settlements, Čeplová et al. (2017) highlighted that the number of neophytes was higher in residential areas compared to settlement centers and older successional sites. These studies did not, however, focus on the requirements of individual species. This is unfortunate since a better understanding of the ecology of alien species can help to assess the risks to native biodiversity and implement mitigation measures (Polce et al. 2011).

If the ecological niche of some alien species is quite well described (e.g. Tiley et al. 1996; Phartyal et al. 2009; Godefroid and Koedam 2010; Chmura et al. 2013), it is because these are among the most invasive plants on earth, which calls for urgent research given the economic impact that these species have on their environment. The situation is quite different for those alien species which are not (yet) recorded as invasive. These can however become invasive after staying for decades in relatively low numbers (Crooks 2005) or under future climate warming scenarios (Ricotta et al. 2010b). It is therefore imperative to try to understand the ecological needs of as many exotic species as possible. In doing this, we cannot rely on the ecological data available for the area of origin of the species since they may behave differently in their native vs. introduced areas (Kudoh et al. 2007; Hierro et al. 2009; Beckmann et al. 2011).

This paper aims to fine-tune our knowledge of alien species preferences for different land uses within urban environments. To this end, we took the city of Brussels as a model, in which we recorded the flora in grid cells of 1 km^2. We tested two different ways of classifying the 1-km^2 cells in different urban environments: (1) We simply associated each cell with its dominant land cover; (2) We used a fuzzy approach for which the degree of association of a given cell to a given land cover depended on the proportion of that land cover within the cell. Next, for both classification methods we calculated the indicator species of the resulting land cover types based on alien species only. We believe that the proposed approach could help to identify indicator species of various urban environments among the alien flora.

Materials and methods

Study area

The area considered in the present study is the city of Brussels (50°48'N – 004°21′E; 161 km^2; 1.2 million inhabitants). It is characterized by a temperate climate with a mean annual temperature of 10.5 °C and a mean annual rainfall of 852 mm (data provided for the period 1981–2010 by the Belgian Royal Meteorological Institute). The mean annual temperature of the city has risen by 1.5 °C in the last 40 years (Godefroid 2011). From a structural point of view, the city appears as a succession of four concentric zones, from its business and historical center to the outlying suburbs (De Bruyn and Lannoy 1991 in IBGE-BIM 1995): (1) the core is dominated by commercial and administrative activities with a limited residential function; (2) the districts, constructed in the last century, are densely built-up; (3) the periphery, less densely built-up; and (4) the suburbs which can be considered as the maximum (or peak) demographic growth zone. This part of the city still keeps green areas. This structure is in line with the concentric zone model presented by Burgess (1925) introducing the complexity of urban land use.

Flora census

The city was divided in 189 grid cells of 1 km^2. However, in this study, only 159 cells which are included in the administrative limits of the city for at least 75% of their area were considered. Within each of these 1 km^2-cells, we recorded all spontaneous (growing naturally) species of the vascular flora between March and October during 3 years (1992–1994). With the exception of private gardens, the whole city area has been surveyed, including managed areas (e.g., road verges, parks, lawns), sometimes requiring a special permit (e.g. in the case of train stations or properties of the royal family). In order to avoid under-sampling because of the seasonal variation, each 1 km^2-cell was surveyed twice along the growing season (early spring and summer or early autumn). Upon each visit, the field survey was long enough to reach the point where it was difficult to add further species to the list.

Each species was then classified as alien or native, where alien species are defined according to Pyšek et al. (2004) as those introduced to the region as a result of human activities and successfully naturalized. Only alien species introduced after AD1500 were considered in this study. This date represents the discovery of the New World and the start of a period of radical change in human movement, commerce and industry.

Soil nutrient availability (N), soil reaction (R), soil moisture (F) and light (L) in each cell were estimated using Ellenberg's species indicator values (Ellenberg et al. 1991).

These indicator values have been widely applied to summarize the species' response to edaphic and climatic parameters in Central Europe (e.g. Diekmann 2003; Ewald 2003; Jansen et al. 2011). However, because the species' ecological requirements are not always constant, but vary widely from one region to another (Godefroid and Dana 2007), we used the re-calibrated Ellenberg's indicator values for the British Isles (Hill et al. 1999), which are phytogeographically closer to our study area. For each cell, representative Ellenberg's indicator values either for nutrient, reaction (pH), moisture or light were derived by averaging the corresponding indicator values for all species present in that cell (Godefroid and Koedam 2007).

Land use analysis

Land use types were extracted from the Biological Valuation Map (Brichau et al. 2000), which is a standardized field survey and evaluation of the biotic environment of Flanders and the Brussels Capital Region (scale 1:10,000). The polygons on the map were defined based on primary units such as the land use type (e.g. standing water, grassland, agricultural area, urban area), subunits embedded in the primary categories such as the vegetation type (e.g. mesophilic hay meadow, reed bed, oak-hornbeam forests) and small landscape elements (e.g. ditches, verges, tree alignments, hollow road) identified on the field and delineated with the help of aerial photographs. Using Arc View Spatial Analyst (ESRI 1996), we next calculated the proportion of land use types for each grid cell. For the analyses, we only focused on the most abundant land use types, some of them may have been aggregated compared to the original classification to increase the power of the analyses: densely build up (UD), open built up (UO), broadleaved urban forests (FOR), industrial areas (IND), and agricultural areas and small landscape elements (AGR). The last category results from the combination of three mapping units: (1) agricultural areas (cropland), (2) isolated farms in agricultural areas, and (3) small landscape elements (i.e. orchards, tree alignments of Canadian poplars, ditches and verges, line-shaped vegetation of field borders, and hollow roads). Given that this third mapping unit is essentially recorded in agricultural environments, we considered relevant to include it in our "AGR" land use type. The five land use types that we considered in this study cover on average 74.3% of the surface area of our grid cells (median: 79.6%). Among the land use types excluded from the analysis, the least rare are: main roads, railways, pastures and bushes (each of them covering less than 2% of the grid cell area). Moreover, the flora associated to large boulevards and railways could not be inventoried (a special permit is necessary and it was not granted for obvious safety reasons).

Statistical analyses

To test whether 1-km^2 cells with similar land uses are environmentally more similar than cells with different land uses, we used Mantel correlation between the pairwise Euclidean distances calculated from the land use composition within each cell and the corresponding Euclidean distances between the Ellenberg's indicator values of each cell. Next, to investigate the preference of alien species for different urban land uses, we used two different ways for classifying the 1-km^2 cells:

(1) Crisp classification. We associated each cell with its dominant land use among those previously identified (densely built-up, open built-up, broadleaved urban forests, industrial areas, and agricultural areas and small landscape elements). To validate the environmental distinctness of the land use types identified by the crisp classification, we performed a permutational multivariate analysis of variance (PERMANOVA) on the pairwise Euclidean distances between the Ellenberg's indicator values of each 1-km^2 cell (999 randomizations). PERMANOVA is a multivariate extension of the traditional analysis of variance (ANOVA), which is used for testing for significant difference between two or more groups of cells based on any distance measure of choice (Anderson 2001). All analyses were performed with the software PAST 3.17 (Hammer et al. 2001) freely available at: http://folk.uio.no/ohammer/past.

Using indicator species analysis, we then identified the alien species that best characterize each land use type. Indicator species are defined according to Ricotta et al. (2015) as those species that are more common in a given group of 1-km^2 cells than expected from a random null model in which all cells have equal probability to host each species. Dealing with species presence and absence data, to determine if a given species is significantly associated with a target land use type, the observed number of presences of that species in the target group of cells was compared with a random null model in which the species occurrences are randomly permuted between all cells. For each group of cells, p-values were then calculated as the proportion of permutation-derived values of species presences that were as high or higher than the actual values (999 randomizations). As shown by Ricotta et al. (2015), the permutation of presence and absence data renders this test equivalent to more complex statistics for testing the species fidelity to a given group of sites (see e.g. Chytrý et al. 2002; De Cáceres and Legendre 2009).

(2) Fuzzy classification. We used a fuzzy approach for relaxing the traditional one-cell-one-class method in which each 1-km^2 cell is unambiguously assigned to a

single land use type. The principle behind this fuzzy classification is that, at this scale of analysis, the situation of one land use type being exactly right and all other types being equally and exactly wrong usually does not exist (Rocchini and Ricotta 2007). Conversely, there is a gradual change from membership to non-membership, such that the degree of association of a given cell to a given land cover type depends on the proportion of that land cover within the cell.

Accordingly, the observed number of occurrences $N_{i\tau}$ of a given species i for a target land use τ was calculated as:

$$N_{i\tau} = \sum_{k=1}^{M} p_{\tau k} \varepsilon_{ik} \quad (1)$$

where $p_{\tau k}$ is the proportion of land use τ in cell k ($k = 1, 2, ..., M$) and ε_{ik} takes the value of 1 if species i is present in cell k, otherwise it takes the value of zero.

The contribution of a species' presence to $N_{i\tau}$ is thus directly related to the proportion of land use τ in that cell. Therefore, cells with low values of $p_{\tau k}$ contribute less to $N_{i\tau}$ than cells with higher values of $p_{\tau k}$.

Like for the previous case, the observed number of occurrences of a given species $N_{i\tau}$ in each land use type was then compared with a null distribution obtained from 999 randomizations, in which the species occurrences are randomly permuted between all cells.

Results

The Mantel correlation highlighted a significant relationship between land use composition and the Ellenberg's indicator values ($R = 0.428$, $p < 0.001$, 999 randomizations). Therefore, cells with similar land use composition are also environmentally similar in terms of light, soil nutrient availability, soil reaction, and soil moisture.

Looking at the different methods for classifying the 1-km^2 cells, our results showed that:

(1) For the crisp classification, the permutational analysis of variance emphasized the environmental uniqueness of the five land use types in terms of the Ellenberg's indicators (overall $F = 33.78$, $p < 0.001$), meaning that the land use classification used for analyzing the urban flora of Brussels makes sense from an environmental point of view (Fig. 1 and Table 1). The alien species that were significantly associated with the five urban land use types are shown in Table 2. Among the 129 alien species used in this study, 33 had significant association with at least one land use type ($p < 0.05$, two-tailed test).

(2) Relaxing the mutually exclusive nature of the landscape classification in (1) and allowing for partial and multiple class membership of the 1-km^2 cells, the number of indicator species raised to 49 (Table 2), showing that the proposed fuzzy approach improves the flexibility of the species' association with a given land use type in a complex and stratified environment, such as the urban area of Brussels. The highest increment in the number of indicator species is shown by industrial and agricultural areas, which passed from 3 indicator species to 14 and from 4 to 11, respectively.

Open built areas support the largest number of neophytes (16 species common to both statistical approaches). This land use has the highest number of invasive species, including *Fallopia sachalinensis, Prunus serotina, Robinia pseudoacacia, Solidago canadensis* and *S. gigantea*. Conversely, very few species have been identified as indicators of densely built-up areas, i.e. *Buddleja davidii, Galinsoga ciliata, Matricaria discoidea, Phalaris canariensis* and *Mahonia aquifolium* (only with the Crisp classification).

Discussion

Comparison between the crisp and fuzzy approaches

For the selected urban land use types, the crisp and fuzzy classifications identified 33 and 49 indicator species, respectively. The difference observed between both methods was mainly due to the higher number of indicators of industrial areas and agricultural areas and small landscape elements obtained when using a fuzzy algorithm. Conversely, those species identified as indicators of densely built-up areas, open built-up areas and urban forests were basically the same for both land use classifications. Previous theoretical work had shown that the classification performance obtained by crisp and fuzzy approaches was not statistically different (Jara and Acevedo-Crespo 2009). However, in the urban context of the present study, the identification of indicator species seems to be more efficient when using the fuzzy classification, at least for those land uses which do not dominate the urban matrix. By using a crisp classification, we assigned only one land use class to each grid cell, which is a simplified and somewhat distorted view of the urban complexity. Using a fuzzy approach allows for modelling gradients between categorical variables, thus decreasing the loss of information resulting from the crisp classification (Nickel and Schröder 2017). By taking into account the transition zones, the fuzzy approach probably better represents the mosaic of land uses that is so typical in urban areas. As a result, the 1-km cells used in this study are most likely better described in terms of

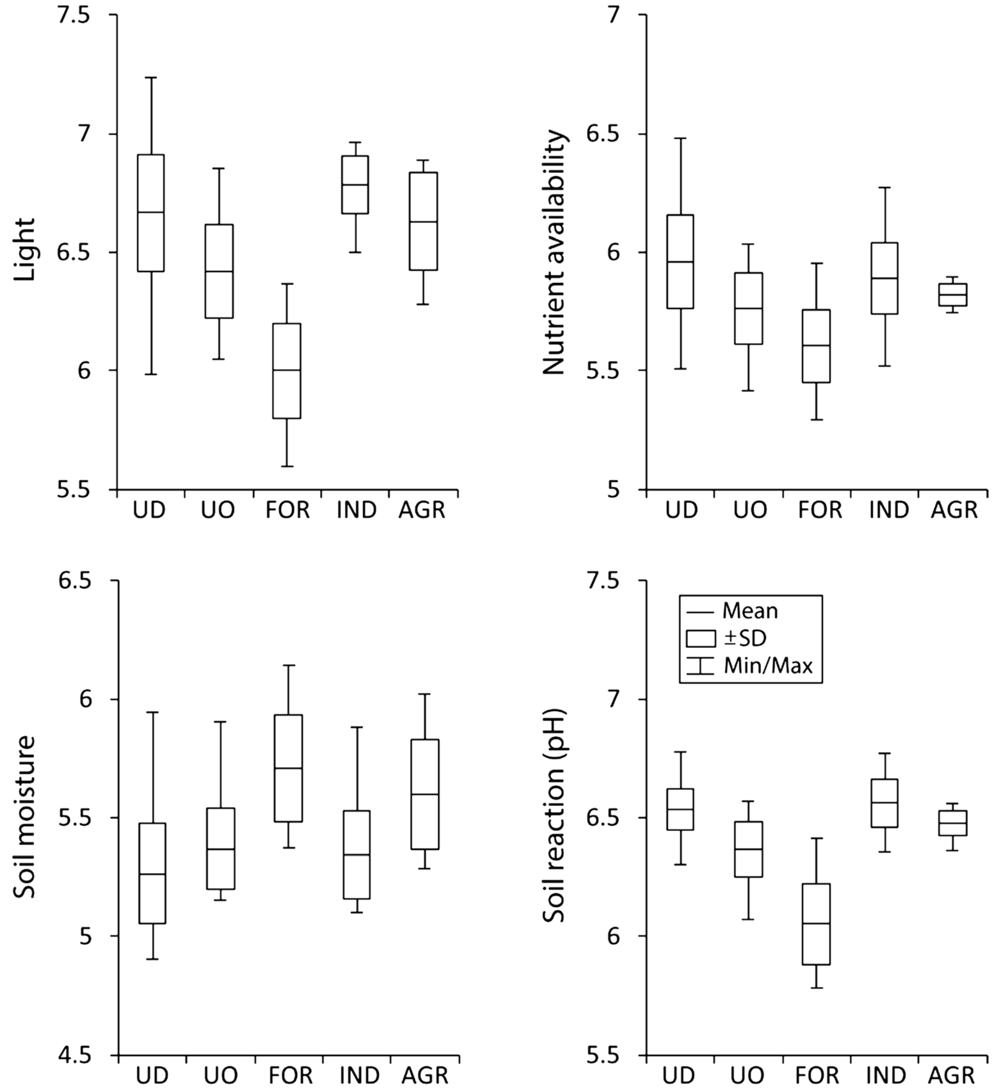

Fig. 1 Box plots of the Ellenberg's indicator values for the five crisp land use types used in this study. UD = densely built-up, UO = open built-up, FOR = broadleaved urban forests, IND = industrial areas, AGR = agricultural areas and small landscape elements

combinations of land uses, rather than as single land use. However, in order to increase the robustness of our results, we opted for a conservative approach and discuss below only indicator species that were significant in both approaches (crisp and fuzzy) which gave identical results for 28 taxa.

Table 1 Results of the permutational analysis of variance on pairwise Euclidean distances between the Ellenberg's indicator values of each 1-km^2 cell. The *p*-values of the pairwise comparisons of environmental differences between land use types are shown without adjustment for multiple testing (overall $F = 33.78$, $p < 0.001$, 999 randomizations). UD = densely built-up, UO = open built-up, FOR = broadleaved urban forests, IND = industrial areas, AGR = agricultural areas and small landscape elements

Land Use	UD	UO	FOR	IND	AGR
UD		$p < 0.001$	$p < 0.001$	$p = 0.073$	$p < 0.001$
UO	$F = 20.57$		$p < 0.001$	$p < 0.001$	$p < 0.001$
FOR	$F = 101.80$	$F = 38.01$		$p < 0.001$	$p < 0.001$
IND	$F = 2.29$	$F = 18.31$	$F = 74.48$		$p = 0.003$
AGR	$F = 8.88$	$F = 8.23$	$F = 32.49$	$F = 6.63$	

Preferences of alien species for specific urban land uses

From a total of 129 alien plant species analyzed, we identified 28 (common to both classification methods) with a clear preference for certain types of urban land uses. It therefore appears that more than a fifth of the species considered seem to have rather narrow ecological requirements allowing them to differentiate between densely or openly built areas, or industrial areas. Analyses of a large number of vegetation relevés from North-Eastern Germany already revealed that alien species show individualistic ecological preferences (Jansen et al. 2011), but this comparative study focused on 34 phytosociological classes without particular emphasis on urban ecosystems. Several studies compare environmental preferences of exotic and native species (e.g. Hulme 2009; Polce et al. 2011),

Table 2 Alien indicator species for the selected urban land use types obtained by comparing the actual number of presences of each species in a given land use type with a random null model in which the species occurrences are randomly permuted between all 1-km^2 cells ($p < 0.05$, 999 randomizations, two-tailed test). UD = densely built-up, UO = open built-up, FOR = broadleaved urban forests, IND = industrial areas, AGR = agricultural areas and small landscape elements

Indicator Species	Land Use Types									
	Crisp Classification					Fuzzy Classification				
	UD	UO	FOR	IND	AGR	UD	UO	FOR	IND	AGR
Acer platanoides		x					x			
Ailanthus altissima										x
Allium schoenoprasum		x					x			
Alnus incana			x					x		
Amaranthus blitum										x
Barbarea intermedia							x			
Barbarea stricta									x	
Berteroa incana				x					x	
Bidens frondosa									x	
Buddleja davidii	x					x			x	
Castanea sativa		x	x				x	x		
Conyza canadensis							x			
Cymbalaria muralis		x					x			
Digitaria sanguinalis									x	x
Euphorbia lathyris		x					x			
Fallopia sachalinensis		x					x			
Galega officinalis									x	
Galinsoga quadriradiata	x					x				
Impatiens glandulifera							x			
Impatiens parviflora			x					x		
Juncus tenuis			x					x		
Lepidium virginicum									x	
Ligustrum ovalifolium					x					x
Lolium multiflorum										x
Mahonia aquifolium	x									
Matricaria discoidea	x					x				
Mercurialis annua									x	
Mespilus germanica		x					x			
Oenothera biennis										x
Oenothera glazioviana									x	
Oenothera deflexa									x	
Pentaglottis sempervirens							x			x
Phalaris canariensis	x					x				
Potentilla intermedia									x	
Prunus serotina		x					x			x
Pseudofumaria lutea		x					x			
Quercus rubra			x					x		
Robinia pseudoacacia		x					x			
Sedum spurium		x					x			
Senecio inaequidens				x					x	
Sisymbrium altissimum				x					x	
Solidago canadensis		x					x			
Solidago gigantea		x					x			

Table 2 (continued)

Indicator Species	Land Use Types									
	Crisp Classification					Fuzzy Classification				
	UD	UO	FOR	IND	AGR	UD	UO	FOR	IND	AGR
Symphoricarpos albus		x					x			
Taxus baccata		x					x			
Trifolium hybridum					x					x
Veronica filiformis		x					x			x
Veronica persica		x			x					x
Vicia villosa									x	
Vinca major					x					
Total	5	18	5	3	4	4	21	5	14	11

but so far there is very little published work examining the ecological requirements of exotic species in an urban context, especially for non-invasive aliens.

We know from previous work that the presence of alien plants is positively correlated with anthropogenic disturbance (e.g. Roy et al. 1999; Zerbe et al. 2004; Godefroid and Koedam 2007; La Sorte et al. 2007; Polce et al. 2011; Aronson et al. 2015), but the present study contributes to fine-tune our knowledge of the ecology of these species. For instance, *Buddleja davidii* and *Pseudofumaria lutea* were known to be associated with urban land cover (Botham et al. 2009), while our analyses identified a preference for densely built-up areas for the former and open built-up areas for the latter. If environmental conditions are obviously very different between the urban matrix and forest islands or semi-natural remnants, the results shown here also highlight that densely and open built-up areas are perceived differently by a large number of exotic plant species. Studies exploring the influence of urban land use types on species assemblages are scarce. Some compare very different entities like tramlines, buildings, cemeteries and green areas (Sudnik-Wójcikowska and Galera, 2005), thus yielding expected results on plant species composition. Others present a list of diagnostic species for compact vs. open residential areas but do not focus particularly on aliens (Lososová et al. 2011). The few studies that have considered different urban land uses mainly focused on their β-diversity rather than on the ecological preferences of the constituting taxa. For instance, a recent study carried out in 45 Central European settlements showed that residential areas contain more exotic species than settlement centers (Čeplová et al. 2017). In a review of 32 European cities, Lososová et al. (2016) have recorded similar numbers of alien species in compact vs. open residential areas. These results, however, did not answer the question whether these environments harbor a specific flora.

An important message from this study is that several neophytes are more likely to be found in particular urban land use types. This indicates that environmental filters select a specific set of exotic species with similar requirements. Processes driving urban plant life are complex (Williams et al. 2009), ranging from soil compaction, eutrophication and pollution to enhanced dispersal, habitat fragmentation, high disturbance regime or urban heat island (e.g. Sukopp and Werner 1983; Pouyat et al. 1997; Godefroid and Koedam 2003). The combination of these processes likely explain the preference expressed by some exotic species for a particular type of urban land use. According to Lososová et al. (2011), species assemblages in urban areas are primarily dependent on the habitat type. Even within the same habitat, soil conditions can vary (e.g. texture or pH), leading to the presence of a very specific flora. In urban wasteland, Godefroid et al. (2007) have shown for example that different kinds of anthropogenic substrates (i.e. sand, pebbles, concrete, rubble) significantly influenced the presence and abundance of several ruderal species, including aliens. In a mid-sized city in the Czech Republic, Štajerová et al. (2017) found that the proportion of built-up areas was the most important predictor of the occurrence of invasive neophytes.

There are several features differentiating densely built-up areas from open built-up areas. For instance, the proportion of impervious surface is much higher in the former compared to the latter. Asphalt, concrete, and pavement generate high temperatures, contributing to the so-called urban heat island (Sukopp and Werner 1983), implying that plants must be pre-adapted to a warmer microclimate to survive. This has been confirmed for instance by Schmidt et al. (2014) who detected a higher proportion of thermophilous species in the center of the city of Hamburg. In these areas, plants grow in pavement cracks, on old house walls, or in wasteland (e.g. *Buddleja davidii*). These conditions also require adaptation to compacted substrates. On the other hand, open built-up areas are characterized by the presence of gardens, whose vegetation (particularly woody) generates a cooler and wetter microclimate than in densely built-up areas. This difference in microclimate inevitably has an effect on the floristic composition in these urban land use types, with indicator species like *Acer platanoides* or *Prunus serotina*.

According to the mean Ellenberg indicator values calculated for the five land use types used in this study, densely built-up areas were characterized by a higher light availability, soil nutrients, soil pH, and a lower soil moisture compared to open built-up areas. This is in agreement with previous studies showing that the most anthropized parts of cities are generally dry (Grimm et al. 2008), unshaded (Chocholouskova and Pyšek, 2003) and dominated by building materials, which tend to be strongly alkaline (Sukopp and Starfinger 1999). Interestingly, environmental conditions, as inferred by the Ellenberg values, for densely built-up areas and industrial areas were found to be the same. We however have identified specific indicator species for these two land use types. *Senecio inaequidens, Berteroa incana* and *Sisymbrium altissimum* were characteristic of industrial areas. The latter two are called urbanoneutral (i.e. having no preference for urban or non-urban areas) by Klotz et al. (2002). Industrial areas are characterized by trading activities involving the transport of goods and by a lower maintenance intensity than in densely built-up areas. These conditions increase seed dispersal opportunities and facilitate the establishment of alien species, especially those that require a lower disturbance regime than in densely built-up areas.

Disturbance regime has been reported as one of the main drivers of species composition in urban environments (Čeplová et al. 2017). In the present study, those species associated with densely built-up areas are actually typical of areas with high levels of disturbance, e.g. *Buddleja davidii, Galinsoga quadriradiata, Matricaria discoidea* and *Phalaris canariensis*. Most of them are listed as urbanophilic species (i.e. restricted to urban settlements) by Klotz et al. (2002). Regarding the species identified as indicators for open built-up areas, they have been allocated to several categories in the urbanity scale of Klotz et al. (2002), the majority being urbanoneutral (e.g. *Acer platanoides, Fallopia sachalinensis, Robinia pseudoacacia, Solidago canadensis, Symphoricarpos albus*) or moderately urbanophobic, i.e. restricted to non-urban areas (e.g. *Mespilus germanica, Prunus serotina, Solidago gigantea, Taxus baccata*). Our results are therefore mostly in line with the urbanity scale of Klotz et al. (2002).

Conclusions

Our analyses have shown that examining alien species presence in different urban land use types may interestingly reveal additional information compared to previous work, suggesting that cities should not be seen as homogeneous entities. In this study, we have demonstrated that fine-tuning the categorization of urban land use types is important for understanding spatial patterns of alien species occurrence. Some urban land use types actually have a different ecological signature for several exotic species. Future research aiming at understanding patterns of establishment or dispersal of non-native plant species within cities should therefore take into account the fact that each urban land use type represents a very specific environment. More studies are also needed on the mechanisms through which urban land use influences the establishment of alien species, especially for those that are not (yet) invasive and have received far less attention so far. Neophytes are relatively recent newcomers whose ecological requirements in their synanthropic range are not yet fully understood. Since they could become invasive in the future, identifying what particular species are associated with which land use types is of paramount importance.

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References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmas JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pyšek P, Siebert S, Sushinsky J, Werner P, Winter M (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc R Soc B 281(1780):20133330

Aronson MFJ, Handel SN, La Puma IP, Clemants SE (2015) Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. Urban Ecosyst 18:31–45

Aronson MF, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, La Sorte FA, Williams NS, Zipperer W (2016) Hierarchical filters determine community assembly of urban species pools. Ecology 97:2952–2963

Beckmann M, Bruelheide H, Erfmeier A (2011) Germination responses of three grassland species differ between native and invasive origins. Ecol Res 26:763–771

Botham MS, Rothery P, Hulme PE, Hill MO, Preston CD, Roy DB (2009) Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. Divers Distrib 15: 338–345

Brichau I, Ameeuw G, Gryseels M, Paelinckx D (2000) Biologische Waarderingskaart, versie 2. Kaartbladen 31–39. Mededelingen van het Instituut voor Natuurbehoud 15. IN/BIM, Brussels

Burgess EW (1925) The growth of the City: an introduction to a research project. In: Park RE, Burgess EW, McKenzie RD (eds) The City. The University of Chicago Press, Chicago, pp 47–62

Butchart SH, Walpole M, Collen B, van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Čeplová N, Kalusová V, Lososová Z (2017) Effects of settlement size, urban heat island and habitat type on urban plant biodiversity. Landsc Urban Plan 159:15–22

Chmura D, Nejfeld P, Borowska M, Woźniak G, Nowak T, Tokarska-Guzik B (2013) The importance of land use type in Fallopia (Reynoutria) japonica invasion in the suburban environment. Pol J Ecol 61:379–384

Chocholouskova Z, Pyšek P (2003) Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzen. Flora 198:366–376

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. J Veg Sci 13:79–90

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience 12:316–329

De Bruyn R, Lannoy W (1991) Migrations dans l'agglomération bruxelloise 1980-1990. Ministère de la Région de Bruxelles-Capitale, Bruxelles

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574

Diekmann M (2003) Species indicator values as an important tool in applied plant ecology –a review. Basic Appl Ecol 4:493–506

Downey PO, Richardson DM (2016) Alien plant invasions and native plant extinctions: a six-threshold framework. AoB PLANTS 8: plw047. https://doi.org/10.1093/aobpla/plw047

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot 18:1–248

ESRI (1996) ArcView spatial analyst. Advanced spatial analysis using raster and vector data. Environmental Systems Research Institute, Redlands

Ewald J (2003) The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés. Basic Appl Ecol 4:507–513

Godefroid S (2011) Brussels. In: Kelcey JG, Müller N (eds) Plants and habitats of European cities. Springer, New York, pp 131–170

Godefroid S, Dana ED (2007) Can Ellenberg's indicator values for Mediterranean plants be used outside their region of definition? J Biogeogr 34:62–68

Godefroid S, Koedam N (2003) How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? Glob Ecol Biogeogr 12:287–298

Godefroid S, Koedam N (2007) Urban plant species patterns are highly driven by density and function of built-up areas. Landsc Ecol 22: 1227–1239

Godefroid S, Koedam N (2010) Comparative ecology and coexistence of introduced and native congeneric forest herbs: *Impatiens parviflora* and *I. noli-tangere*. Plant Ecol Evol 143:119–127

Godefroid S, Monbaliu D, Koedam N (2007) The role of soil and microclimate variables in the distribution patterns of urban wasteland flora. Landsc Urban Plan 80:45–55

Grimm NB, Faeth SH, Golubiewski NE, Redman CR, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):9

Hierro JL, Eren O, Khetsuriani L, Diaconu A, Török K, Montesinos D, Andonian K, Kikodze D, Janoian L, Villarreal D, Estanga-Mollica ME, Callaway RM (2009) Germination responses of an invasive species in native and non-native ranges. Oikos 118:529–539

Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) Ellenberg's indicator values for British plants. ECOFACT vol. 2, technical annex. Institute of Terrestrial Ecology, Huntingdon

Hulme PE (2009) Relative roles of life-form, land use and climate in recent dynamics of alien plant distributions in the British Isles. Weed Res 49:19–28

IBGE-BIM (1995) Report on the state of the environment in the Brussels Capital Region (in French and Dutch). Les Cahiers de l'IBGE n°9. IBGE-BIM, Brussels

IUCN (2015) The IUCN red list of threatened species. IUCN, Gland, www.iucnredlist.org. Accessed 8 December 2017

Jansen F, Ewald J, Zerbe S (2011) Ecological preferences of alien plant species in north-eastern Germany. Biol Invasions 13:2691–2701

Jara JL, Acevedo-Crespo R (2009) Crisp classifiers vs. fuzzy classifiers: a statistical study. In: Kolehmainen M, Toivanen P, Beliczynski B (eds) Adaptive and Natural Computing Algorithms. 9th International Conference, ICANNGA 2009 Kuopio, Finland, April 23–25, 2009, Springer-Verlag, Berlin, pp 440–447

Klotz S, Kühn I, Durka W (2002) BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde 38:1–334

Kudoh H, Nakayama M, Lihova J, Marhold K (2007) Does invasion involve alternation of germination requirements? A comparative study between native and introduced strains of an annual Brassicaceae, Cardamine hirsuta. Ecol Res 22:869–875

Kühn I, Brandl R, Klotz S (2004a) The flora of German cities is naturally species rich. Evol Ecol Res 6:749–764

Kühn I, Durka W, Klotz S (2004b) BiolFlor - a new plant-trait database as a tool for plant invasion ecology. Divers Distrib 10:363–365

La Sorte FA, McKinney ML, Pyšek P (2007) Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. Glob Chang Biol 13:913–921

Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Kühn I, Láníková D, Otýpková Z, Řehořek V (2012) Native and alien floras in urban habitats: a comparison across 32 cities of Central Europe. Glob Ecol Biogeogr 21:545–555

Lososová Z, Chytrý M, Danihelka J, Tichý L, Ricotta C (2016) Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences. J Veg Sci 27:452–459

Lososová Z, Horsák M, Chytrý M, Čejka T, Danihelka J, Fajmon K, Hájek O, Juřičková L, Kintrová K, Láníková D, Otýpková Z, Řehořek V, Tichý L (2011) Diversity of central European urban biota: effects of human-made habitat types on plants and land snails. J Biogeogr 38:1152–1163

Maurel N, Salmon S, Ponge JF, Machon N, Moret J, Muratet A (2010) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? Biol Invasions 12:1709–1719

Morales CL, Traveset A (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecol Lett 12:716–728

Nickel S, Schröder W (2017) Fuzzy modelling and mapping soil moisture for observed periods and climate scenarios. An alternative for dynamic modelling at the national and regional scale?. Ann For Sci https://doi.org/10.1007/s13595-017-0667-5

Phartyal S, Godefroid S, Koedam N (2009) Seed development and germination eco-physiology of the invasive tree *Prunus serotina* (Rosaceae) in a temperate forest in Western Europe. Plant Ecol 204:285–294

Polce C, Kunin WE, Biesmeijer JC, Dauber J, Phillips OL (2011) The ALARM field site network. Alien and native plants show contrasting responses to climate and land use in Europe. Glob Ecol Biogeogr 20:367–379

Pouyat RV, McDonnell MJ, Pickett STA (1997) Litter decomposition and nitrogen mineralization in oak stands along an urban–rural land use gradient. Urban Ecosyst 1:117–131

Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Chang Biol 18:1725–1737

Ricotta C, La Sorte FA, Pyšek P, Rapson GL, Celesti-Grapow L, Thompson K (2009) Phyloecology of urban alien floras. J Ecol 97:1243–1251

Ricotta C, Godefroid S, Rocchini D (2010a) Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. Biol Invasions 12:233–240

Ricotta C, Godefroid S, Rocchini D (2010b) Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. Divers Distrib 16:655–662

Ricotta C, Carboni M, Acosta ATR (2015) Let the concept of indicator species be functional! J Veg Sci 26:839–847

Rocchini D, Ricotta C (2007) Are landscapes as crisp as we may think? Ecol Model 204:535–539

Roy DB, Hill MO, Rothery P (1999) Effects of urban land cover on the local species pool in Britain. Ecography 22:507–515

Schmidt KJ, Poppendieck H-H, Jensen K (2014) Effects of urban structure on plant species richness in a large European city. Urban Ecosyst 17:427–444

Štajerová K, Šmilauer P, Brůna J, Pyšek P (2017) Distribution of invasive plants in urban environment is strongly spatially structured. Landsc Ecol 32:681–692

Sudnik-Wójcikowska B, Galera H (2005) Floristic differences in some anthropogenic habitats in Warsaw. Ann Bot Fenn 42:185–193

Sukopp H, Starfinger U (1999) Disturbance in urban ecosystems. In: Walker LR (ed) Ecosystems of disturbed ground, vol 16. Elsevier, Amsterdam, pp 397–412

Sukopp H, Werner P (1983) Urban environments and vegetation. In: Holzner W, Werger MJA, Ikusima I (eds) Man's impact on vegetation. Dr.WJunk Academic Publisher, The Hague, pp 247–260

Tiley GED, Dodd FS, Wade PM (1996) Heracleum mantegazzianum Sommier & Levier. J Ecol 84:297–319

Vanderhoeven S, Dassonville N, Meerts P (2005) Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. Plant Soil 275:169–179

Williams NSG, Schwartz MW, Vesk PA, McCarthy MA, Hahs AK, Clemants SE, Corlett RT, Duncan RP, Norton BA, Thompson K, McDonnell MJ (2009) A conceptual framework for predicting the effects of urban environments on floras. J Ecol 97:4–9

Zerbe S, Choi IK, Kowarik I (2004) Characteristics and habitats of non-native plant species in the city of Chonju, southern Korea. Ecol Res 19:91–98