Landscape and Urban Planning 159 (2017) 15–22

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research paper

# Effects of settlement size, urban heat island and habitat type on urban plant biodiversity

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## HIGHLIGHTS

- Detailed study on the effect of settlement size on urban plant diversity.
- Biodiversity change studied on specific habitat types with different disturbance regime.
- The effect of heat island on species temperature requirements determined by city size.

## ARTICLE INFO

*Article history:*
Received 7 March 2016
Received in revised form
27 September 2016
Accepted 1 November 2016

*Keywords:*
Alpha diversity
Archaeophytes
Central Europe
Native species
Neophytes
Urban habitats

## ABSTRACT

Urbanized areas with high habitat heterogeneity and intense human impact form unique environment which is surprisingly rich in plant species. We explore the effect of the settlement size on plant species richness, composition and temperature requirements of plant communities.

We studied three habitats with different disturbance regime in 45 Central European settlements of three different sizes. We sampled 1-ha plots in each habitat by recording all spontaneously occurring vascular plant species. We divided recorded species into groups according to their origin and residence time and according to their temperature requirements based on Ellenberg indicator values. We used ordination methods and ANOVA to detect that species communities in urban areas are generally more species rich in larger settlements than in small ones. These differences are mostly pronounced in residential areas. Increasing settlement size is significantly reflected by neophytes that are dependent on constant input of propagules caused by human activities and by native species that survive in remnants of semi-natural vegetation in urban environment. In contrast archaeophytes as a homogeneous group of species with similar traits are widespread equally through settlements of all sizes. We did not confirm the effect of urban heat island on species composition, indicating that species composition is significantly more affected by local habitat conditions than by urban size. Our results highlight the importance of urban size as important factor shaping biodiversity of native and alien plant communities in individual urban habitats and the important role of habitat mosaic for maintaining high species richness in city floras.



## 1. Introduction

Human settlements form a specific environment that is unique in its characteristics and intrinsic conditions, which strongly affect biodiversity (McKinney, 2006). The interior of each settlement is composed of a mosaic of numerous different habitats of various sizes. The resulting heterogeneity reflects different human activities, the diverse history of the area and various local conditions (Kühn & Klotz, 2006; Lososová et al., 2012a). Habitat heterogeneity (Kowarik, 1995; Kühn, Brandl, & Klotz, 2004) together with the high input of seeds that increases with the level of urbanization and the city size (Luck & Smallbone, 2011; Pyšek, 1998) lead to high plant species diversity in total urban floras (Deutschewitz, Lausch, Kühn, & Klotz, 2003; Klotz, 1990; Kühn et al., 2004; Stadler, Trefflich, Klotz, & Brandl, 2000).

From the perspective of island biogeography (MacArthur & Wilson, 1967), cities can be considered as a type of ecological island isolated from the other city islands by the surrounding landscape (Begon, Townsend, & Harper, 2006; Clergeau, Croci, & Jokimäki,

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http://dx.doi.org/10.1016/j.landurbplan.2016.11.004

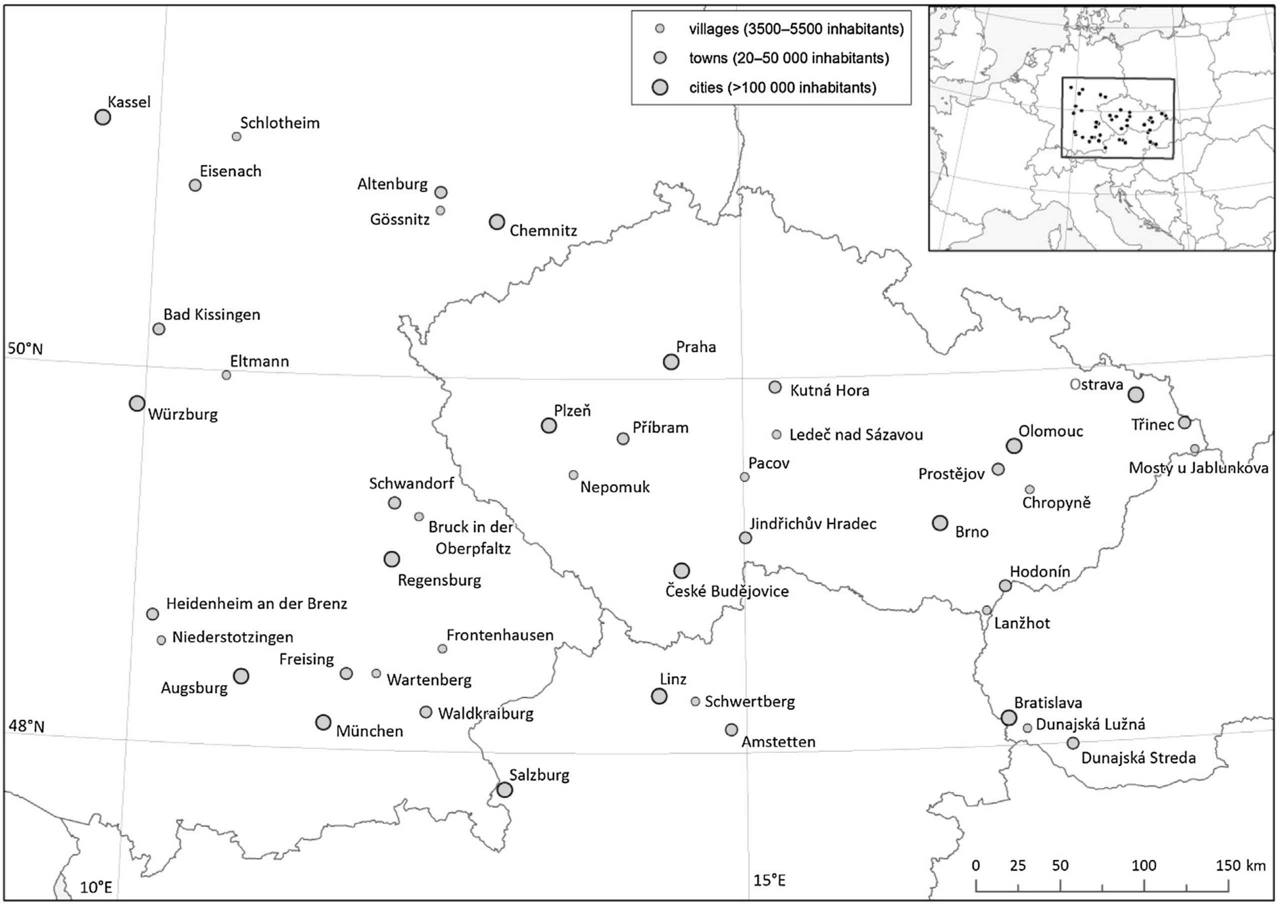


**Fig. 1.** Map of studied settlements.

2004; Davis and Glick, 1978; McGregor-Fors, Morales-Pérez, & Schondube, 2011). Because city islands are not completely isolated from the surrounding landscape, many generalists could be present both inside and outside the settlement, but it has been shown that the species-area relationship exists in both isolated as well as not completely isolated systems (MacArthur & Wilson, 1967; Preston, 1962; Williams, 1964). Previous studies have demonstrated that the total number of species on an island is a function of its area (Begon et al., 2006; Cain, 1938; Connor & McCoy, 1979; Rosenzweig, 1995). In human settlements as well, the total number of species increases with the city size (Pyšek, 1998), most likely due to the high number of different habitats in urban areas (Boecklen, 1986; McIntyre, 1995; Winter, Johnson, Shaffer, Donovan, & Svedarsky, 2006). It is assumed that the city size could affect not only the total species number within the city as a whole but also the species richness of individual habitats. The diversity of vegetation in isolated urban habitats depends on the balance between colonization and extinction (MacArthur and Wilson, 1967). We assume that in small cities, fewer patches of the same habitat type occur and that these patches are usually smaller than in large cities. This is why such habitats would host fewer species in smaller populations, which can be more prone to local extinction (Dupré & Ehrlén, 2002; Jackson & Sax, 2010; Tilman, 1994). Moreover, in urban habitats, colonization and extinction are also affected by human management (Marzluff et al., 2008). A similar pattern has been well-documented in urban bird communities (e.g., Garaffa, Filloy, & Bellocq, 2009; Jokimäki & Kaisanlahti-Jokimäki, 2003). There are practically no studies that have focused on the effect of city size on plant species richness in individual habitats. Large cities with a heterogeneous mosaic of habitat types, high traffic, industry and high population density could most likely host more plant species than small settlements on comparably sized plots in similar habitats due to the higher availability of dispersal vectors and types of seed sources.

The city size can also have different effects on species with distinct origin and residence time. For remnant populations of native species surviving in urban areas, a city of large size could mean greater isolation from populations growing in the surrounding rural landscape and therefore a reduced possibility of propagule input. This could lead to the local extinction of some species and therefore a reduction in their species richness. The opposite could be true for alien species. Their occurrence in urban areas is associated with human activities such as cargo traffic, planting and landscaping or trading activities (Dunn & Heneghan, 2011; Pyšek, 1998). As a consequence, a higher proportion of alien species can be found in the urban environment than in the surrounding rural landscape, as has been shown for several cities in Europe (Kühn & Klotz, 2006; Pyšek, 1993; Wania, Kühn, & Klotz, 2006). Because the proportion of alien plant species in urban floras increases with city size (Klotz, 1990; Pyšek, 1998), larger cities are considered to be an important source of alien species for their subsequent spread to smaller settlements and the surrounding landscape (Pyšek, 1998).

Large built-up urban areas with impervious surfaces made of concrete, asphalt and pavement, along with heat and smog pollution, contribute to changed climatic conditions in settlements in comparison with the surrounding landscape. The so-called urban heat island (UHI; Landsberg, 1981; Oke, 1982) is manifested by higher temperatures measured in urban areas and is highly pronounced in large settlements (Gaston, Davies, & Edmondson, 2010). It is predicted that the species composition of urban vegetation is influenced by the UHI (Knapp et al., 2009; Wittig, 2002; Wittig & Durwen, 1982). Schmidt, Poppendieck and Jensen (2014) demonstrated the effect of the UHI in the city of Hamburg, where a higher proportion of thermophilous species was found in city centres compared to rural areas. Therefore, in the same habitat type, it is likely that smaller settlements with a less pronounced UHI would contain fewer thermophilous species than large settlements. As far as we know, this generally assumed hypothesis has never been tested.

Settlement size is recognized as an important property directly connected to the species richness and species composition of urban habitats. The aim of this study is to explore the influence of the size of different settlement types (cities, towns and villages) on the total species number, the species richness of groups of species with different origin and residence time and the species composition. It is expected that the number of native species decreases with the settlement size and that the number of aliens increases. It is also predicted that the species composition could be affected by the UHI, where large settlements would host more thermophilous communities in comparison to those that are smaller. To test these predictions, we studied the species composition of three different types of habitats with various disturbance regimes in settlements located in Central Europe.

## 2. Materials and methods

Data on the occurrence of vascular plant species were collected in German, Czech, Austrian, and Slovak settlements of three different sizes: (i) small settlements (villages) with 3500–5500 inhabitants, (ii) medium-sized settlements (towns) with 20–50,000 inhabitants, and (iii) large settlements (cities) with more than 100,000 inhabitants, considering 15 settlements of each size (Fig. 1). All settlements are located in areas with comparable climatic conditions (see Lososová et al., 2011), and the influence of climate on the species composition of the plant communities in cities of different sizes is therefore negligible. Sampling was carried out between the years 2007–2009 and 2012–2014 from mid-June to late August. In each settlement, three types of habitats with different disturbance regimes were sampled: (i) settlement centre with a total paved or sealed area of >90%, (ii) residential area with a compact building pattern consisting of rows of family houses (older than 50 years) and private gardens, (iii) older successional site abandoned for 5–15 years dominated by perennial grassland with scattered shrubs and young trees. One plot of 1-ha size was sampled in each type of habitat in each settlement by recording all spontaneously occurring vascular plant species, including garden escapes and spontaneously regenerating trees and shrubs. Planted species were not recorded. The time spent in one plot was between 1 and 2 h.

The taxonomy and nomenclature of the recorded taxa mainly followed Jäger and Werner (2005) and Jäger, Ebel, Hanelt and Müller (2008). Taxa that were difficult to identify due to their affiliation with small and taxonomically similar groups of species or that were frequently found as juveniles were aggregated into higher taxonomical levels referred to as aggregates. The species aggregates not defined in the above-mentioned floras were *Cerastium tomentosum* agg.: *Cerastium biebersteinii* and *C. tomentosum*; *Medicago sativa* agg.: *Medicago sativa* and *M.* × *varia*; *Oenothera biennis* agg.: *Oenothera biennis* and *Oenothera parviflora*; and *Parthenocissus quinquefolia* agg.: *Parthenocissus inserta* and *P. quinquefolia*.

The recorded species were divided into groups according to their origin and residence time as native to Central Europe, archaeophytes (non-native, introduced before 1500 AD), and neophytes (non-native, introduced after 1500 AD; DAISIE, 2009; Pyšek et al., 2012).

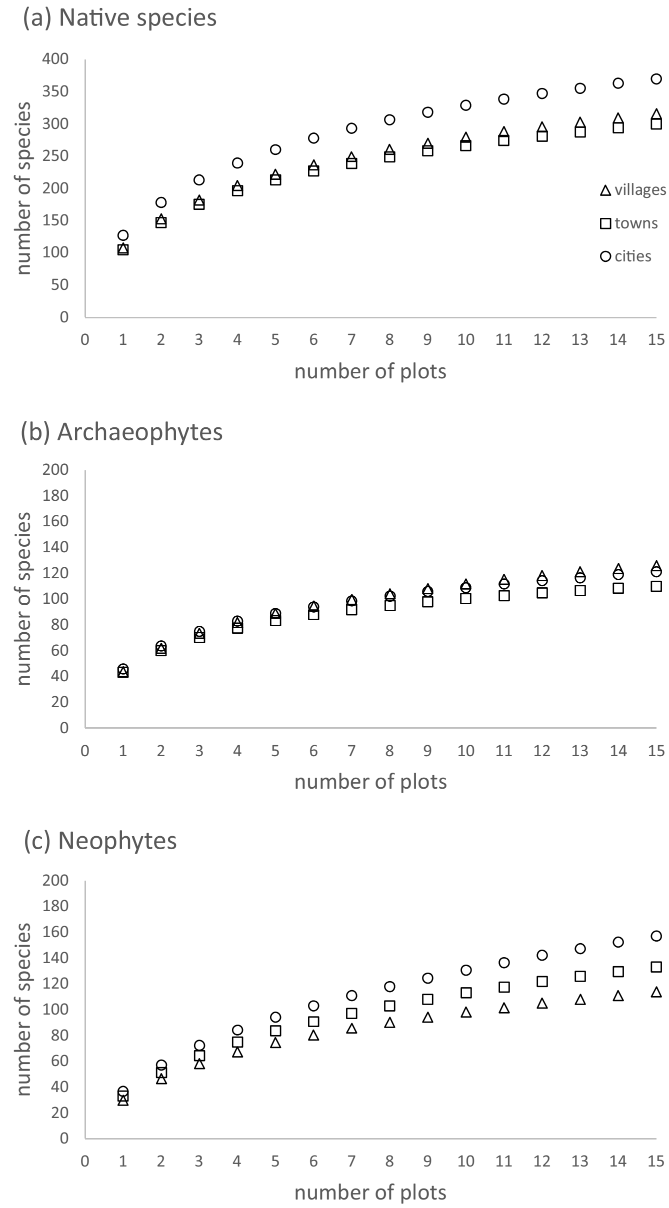


**Fig. 2.** Sample-based rarefaction curves showing accumulation of species across plots in settlements of different sizes calculated for groups of species with different origin and residence time (native species, archaeophytes and neophytes).

To show the accumulation of species across the plots in settlements of different sizes, sample-based rarefaction curves (Gotelli & Colwell, 2001) calculated according to the analytical formula published by Colwell, Mao and Chang (2004) were used to compare the species richness of the studied species groups (native species, archaeophytes, neophytes). This calculation was performed using the JUICE program, version 7 (Tichý, 2002).

The differences in species richness among habitat types depending on the size of the settlements were tested by ANOVA. The mean species richness values for the different habitat types and settlement sizes were compared by post hoc multiple comparisons by applying the Tukey test. This test compares pairs of all studied groups and identifies those with similar differences that are merged into homogeneous groups. The ANOVA and Tukey post hoc tests were conducted using Statistica 12 software (http://www.statsoft.com). To identify how the species composition changes depending on the settlement size, principal component analysis (PCA) was used across the full dataset using Canoco for Windows 4.5 (ter Braak

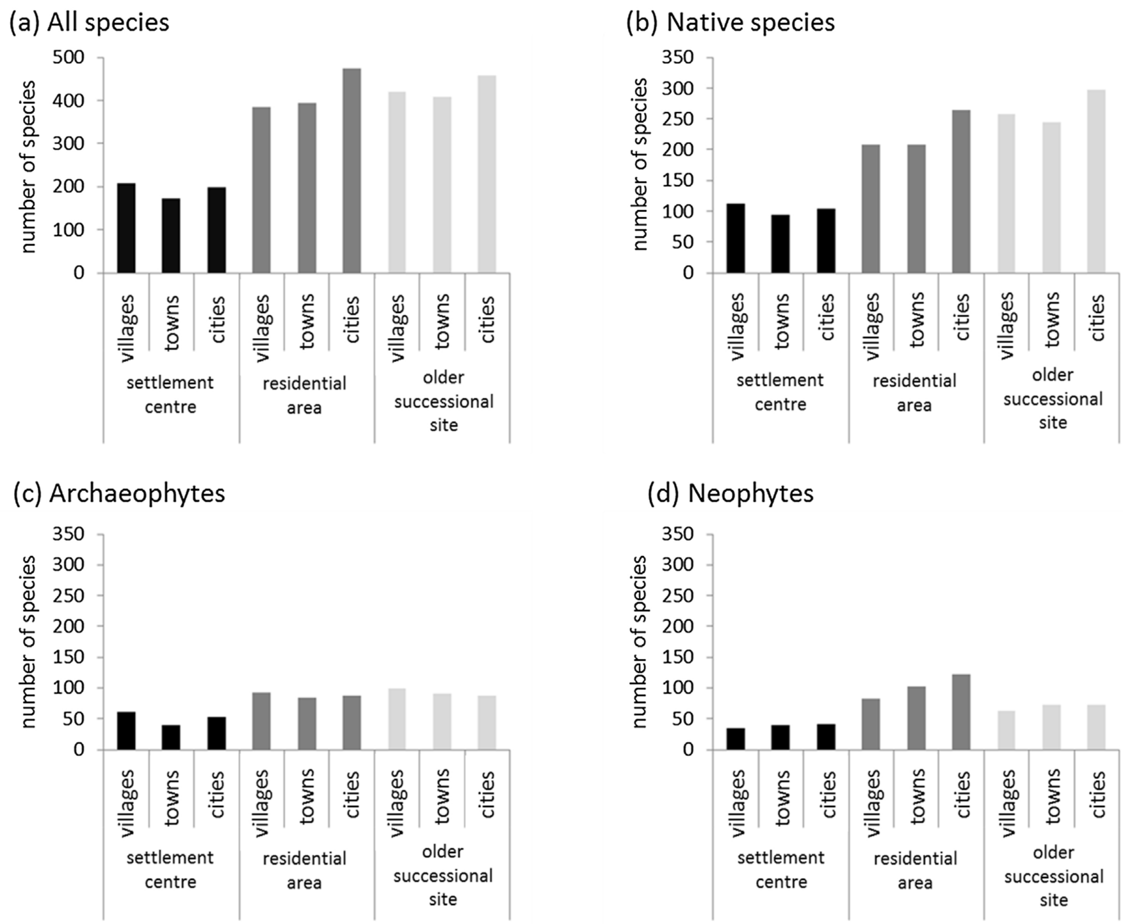


**Fig. 3.** Total number of species recorded in three settlement sizes studied (villages, towns, cities) and three habitat types (settlement centre, residential area, older successional site).

& Šmilauer, 2002). The differences in species composition among groups of plots with the same disturbance regime were tested using permutation multivariate analyses based on Bray-Curtis dissimilarities (PERMANOVA; Anderson, Ellingsen, & McArdle, 2006). The significance was tested using 9999 permutations. The differences in species composition among plots with the same disturbance regime depending on the size of the settlements were tested with the PRIMER-E program using the PERMDISP function, module PERMANOVA+ (Clarke & Gorley, 2006).

To determine the effect of the UHI on the species composition, Ellenberg indicator values (EIVs) for temperature were used. The EIV reflects a plant's affinity to the local temperature conditions and ranges from 1 to 9, where 1 is assigned to plants that are resistant to low temperatures (alpine plants), and 9 is assigned to plants with high demands for temperature (Mediterranean plants; Ellenberg, Weber, Düll, Wirth, & Werner, 2001). There were missing data for 207 species, but these were mainly neophytes with rare occurrence. Values for approximately 90% of the species were available for each plot. The mean EIVs for temperature were calculated for each plot as the mean of the EIVs of the species recorded in the plot. The differences in the mean EIV for temperature among plots with the same disturbance regime depending on the size of the settlements were tested by ANOVA and Tukey post hoc tests using Statistica 12 software (http://www.statsoft.com).

**Table 1**
Total number of species found across all studied habitats.

| | native species | archaeophytes | neophytes | all species |
|---|---|---|---|---|
| villages | 316 | 126 | 114 | 556 |
| towns | 300 | 110 | 133 | 543 |
| cities | 370 | 121 | 157 | 648 |

## 3. Results

A total of 835 species, of which 459 were native, 151 were archaeophytes and 225 were neophytes were found. The total number of all species was highest in cities as well as the total number of native species and neophytes. The total number of archaeophytes was roughly the same in settlements of all sizes (Table 1).

For the native species, the rarefaction curves clearly show that the number of recorded species increases more steeply with the number of plots sampled for cities than for smaller settlements, and no difference was detected between towns and villages (Fig. 2a). For archaeophytes, no differences were found among settlements of all sizes (Fig. 2b). For neophytes, the number of recorded species increases the most steeply for cities followed by towns and then by villages (Fig. 2c).

When considering the habitat types separately, the total number of species in the settlement centres did not vary according to the settlement size. For the residential areas and older successional sites, a higher total number of species was found only in the cities, whereas the total number of species in the villages and towns did not differ (Fig. 3a). The same pattern was found for native species (Fig. 3b). The total number of archaeophytes did not differ according to neither the settlement size nor the habitat type (Fig. 3c). The total number of neophytes in settlement centres and older succes-

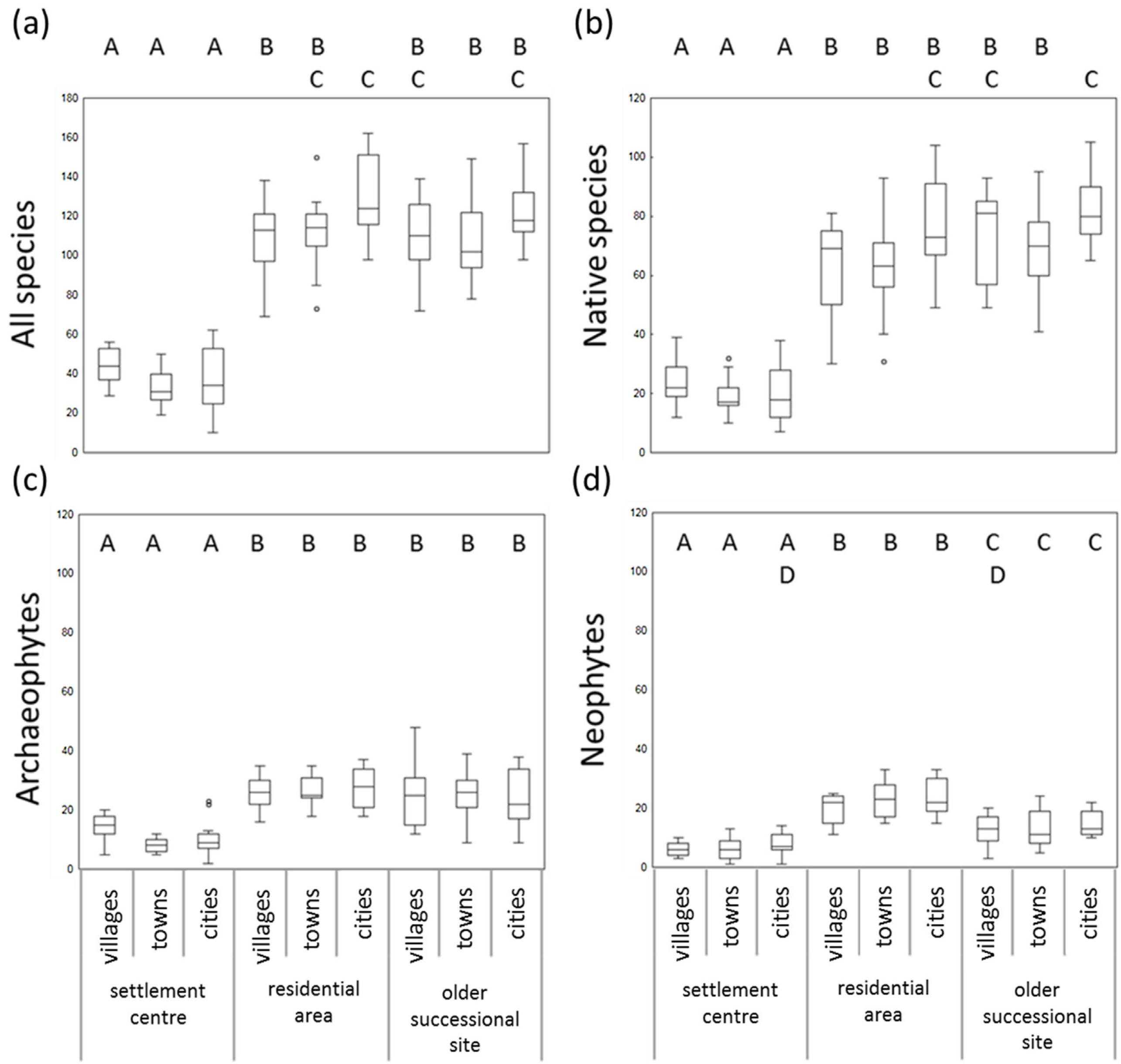


**Fig. 4.** Species richness recorded in three settlement sizes studied (villages, towns, cities) and three habitat types (settlement centre, residential area, older successional site). Boxes and whiskers indicate medians, 25–75% quantiles, non-outlier range, and outliers. Same letters indicate homogeneous groups of habitat types according to ANOVA followed by Tukey post-hoc tests at $p < 0.05$.

sional sites did not vary according to the settlement size, but the total number of neophytes in residential areas increased with the settlement size from villages to cities (Fig. 3d).

No differences in species richness of all species, native species, archaeophytes and neophytes in settlement centres were found comparing cities, towns and villages (Fig. 4). In residential areas, the species richness differed significantly for all species between the villages and cities (Fig. 4a). The species richness of native species as well as of archaeophytes and neophytes significantly differed among habitats but not among the settlements of different sizes.

The results of the PCA analysis indicate that the species composition differs significantly among the habitat types regardless of the settlement size, with city centres being more homogeneous compared to the other habitat types (Fig. 5). The results of the PERMANOVA show differences in the species composition between the villages and cities for all three habitat types. Significant differences were also found between villages and towns for centres and between towns and cities for older successional sites (Table 2).

No differences in the mean EIV for temperature were found when comparing settlements of different sizes. Regardless of the settlement size, centres were characterized by higher EIVs for temperature than older successional sites; however, settlement size showed no effect on the difference (Fig. 6).

## 4. Discussion

We confirmed that species assemblages in urban areas are generally more species-rich in larger settlements than in smaller settlements. This was already confirmed for entire city floras by Pyšek (1998). We did not study full urban floras, having focused instead on only selected habitats, but the result for species summed up across the studied habitats was nevertheless the same. Such results are in accordance with expectations based on the theory

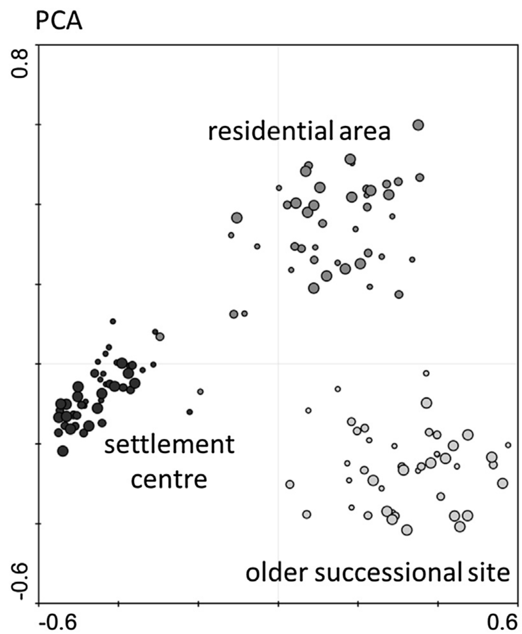


**Fig. 5.** PCA ordination plot of all studied sites shows clustering of habitat types across different settlement sizes. The size of the settlement corresponds to the size of the symbol.

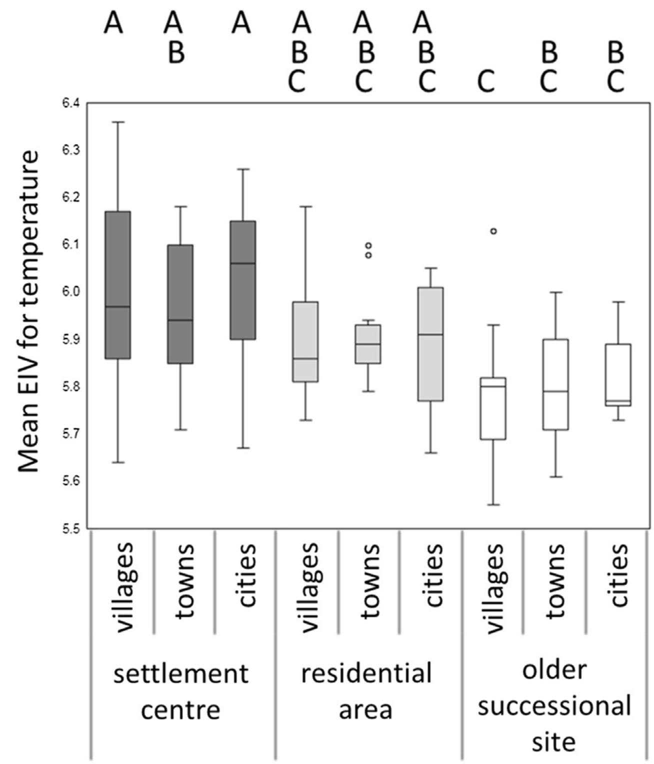


**Fig. 6.** Mean Ellenberg indicator values (EIV) for temperature for each plot. Boxes and whiskers indicate medians, 25–75% quantiles, non-outlier range, and outliers. Same letters indicate homogeneous groups of habitat types according to ANOVA followed by Tukey post-hoc tests at $p < 0.05$.

**Table 2**
Differences in species composition among studied habitats tested by PERMANOVA indicated by *p*-values. Differences between clusters represented by different settlement size were tested for each habitat separately. Significant differences between pairs of settlement sizes are indicated by * at significance level $p < 0.05$.

| Habitat type | villages | towns |
|---|---|---|
| Settlement centre | | |
| villages | | |
| towns | 0.016* | |
| cities | 0.014* | 0.472 |
| Residential area | | |
| villages | | |
| towns | 0.738 | |
| cities | 0.022* | 0.135 |
| Older successional site | | |
| villages | | |
| towns | 0.409 | |
| cities | 0.039* | 0.033* |

of island biogeography (MacArthur & Wilson, 1967). When the recorded species were divided into groups according to their origin and residence time, we found that the higher number of species in large cities is caused by a predominance of native species and neophytes. Archaeophytes did not contribute to this phenomenon, most likely because this is a relatively small group of species with a narrow range of traits, which enables them to grow in disturbed sites. The same archaeophytes are thus equivalently distributed throughout all anthropogenic habitats (Lososová et al., 2012b). A higher number of neophytes was expected due to the higher input of propagules caused by human activities such as cargo traffic, gardening and trading activities, which are generally more pronounced in large settlements (Zerbe, Maurer, Schmitz, & Sukopp, 2003). Although native species are generally expected to be outcompeted by neophytes in the floras of highly disturbed urban areas (Pyšek, 1998), we validated the opposite trend, similarly to Deutschewitz et al. (2003), who also found no causal relationship between the native and alien species richness at the regional scale in Germany. One explanation could be that native and alien plant species are similarly affected by the same environmental conditions (Davis, Grime, & Thompson, 2000; Levine, 2000). Moreover, native species can most likely spread to urban areas not only from their rural surroundings but also from remnants of semi-natural vegetation in the interior of the settlements (Aronson et al., 2014), and they are dispersed by human activities similarly to neophytes (Deutschewitz et al., 2003; Duhme & Pauleit, 1998). In addition, human activities form a number of different habitats in cities, such as gardens, parks, cemeteries and abandoned ruderal areas, and this habitat heterogeneity is responsible for the high species richness of alien as well as native species (Ernst et al., 2000; Stadler et al., 2000).

The differences in the numbers of native species, archaeophytes and neophytes are less pronounced when the habitat types are evaluated separately. We confirmed differences in species richness only for residential areas, where the number of species per plot was significantly lower in villages compared to cities most likely because of more intense planting activities, which leads to a higher probability of escaping from cultivation (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007). The lowest species richness across all settlement sizes was found in settlement centres with intense and regular disturbances, as was also shown by Lososová et al. (2011). In other habitat types, the species richness was higher because of irregular and less strong disturbances. This corresponds with the intermediate disturbance hypothesis (Conell, 1978; Hobbs & Huenneke, 1992), which assumes that disturbances of moderate intensity positively affect species diversity, which was demonstrated for the urban environment by Zerbe et al. (2003). Our results confirm the previously documented pattern that species richness increases from city squares and boulevards to less urbanized habitats found in residential areas and on urban peripheries. This pattern has been shown for various taxa including birds, butterflies, carabid beetles and plants (Blair & Launer, 1997; Celesti-Grapow, Pyšek, & Jarošík, 2006; Niemelä et al., 2002; Zerbe et al., 2003).

Therefore, the species composition in urban habitats is primarily dependent on the habitat type (Lososová et al., 2011). The differences in species composition in settlement centres are smaller than those in residential areas and older successional sites, indicating homogeneity in the plant communities of city centres. These areas are subject to strong environmental filtering, especially from the disturbance regime, which is most likely similar for the habitat type as a whole (McKinney, 2006). Our results thus detected a low level of species turnover in city centres compared to residential areas and mid-successional plots, suggesting a more homogenized species pool or saturation from the regional pool compared to the more diverse plots in the other studied habitats. Plants occur in cracks in the asphalt, in gaps between the tiles, in flower pots, or in regularly mown small lawns. These are most commonly perennials adapted to trampling such as *Plantago major* and *Sagina procumbens* or seedlings of wind dispersed tree species e.g., *Populus* sp. and *Salix* sp.

We also found differences in the species composition in the same habitats when comparing settlements of different sizes. The species composition in all three habitat types differed between villages and cities, as was expected. The species composition in villages is strongly affected by the surrounding landscape due to their small size and the consequently weak isolation of habitats from natural or semi-natural vegetation (Pyšek, 1998). In contrast, species assemblages in large cities isolated from the rural landscape are much more dependent on propagule input caused by human activities, and their species composition is therefore depleted compared to that of villages. Middle-sized towns are somewhere in between these two extremes; their species assemblages are sometimes similar to those of small villages and sometimes more similar to those of cities. This is most likely due to the different histories, geographic locations and urban structures of individual towns.

However, it was expected that the UHI (Landsberg, 1981; Oke, 1982) could be strongly pronounced in large cities and that their species assemblages would therefore contain more thermophilous species, especially in habitats situated in the centres of large cities (Schmidt et al., 2014). We did not confirm differences in the species composition in settlements of different sizes in accordance with the UHI. The trend in the occurrence of thermophilous species was nevertheless found when comparing habitat types. Assuming that older successional sites are usually located on settlement edges, settlement centres in the middle, and residential areas in the transitional zone between them, we found that species assemblages tended to be more thermophilous from the edges to centres regardless of the settlement size. Such findings are in accordance with previous studies (Schmidt et al., 2014; McKinney, 2002). We suppose that thermophilous assemblages occurring in the centres of villages, where no UHI is expected to occur, may be caused by the heat-absorbing capacity of the surfaces made of asphalt or pavement. These surfaces are easily heated in summer, and this local overheating could affect the species composition similarly to the UHI. We are aware of the fact that species requirements for temperature based on Ellenberg indicator values are not known for all of the species that occurred in the studied plots. An especially high number of ornamental plants, whose occurrence depends on repeated introduction by humans, could slightly change the characteristics of species assemblages in residential areas, but we believe that the resulting pattern would most likely be similar with this large dataset containing more than eight hundred plant species.

## 5. Conclusions

Human settlements form a unique environment with high plant species diversity. Understanding the patterns of plant species diversity is an important challenge. We showed that settlement size is an important factor that shapes not only the species richness of native species and aliens but also the species composition of urban plant communities. Although the disturbance regime and the correspondingly created habitat type are still the major factors forming species assemblages, the species composition significantly differs between small and large settlements. Despite the general assumptions that the urban heat island affects the species composition, we have found that the occurrence of thermophilous species is more affected by the habitat type than the settlement size, which determines the presence of urban heat island. These results showing factors affecting biodiversity on the habitat scale are important for sustainable urban planning and biodiversity conservation.

## Acknowledgements

We thank Milan Chytrý, Jiří Danihelka, Karel Fajmon, Deana Láníková, Zdenka Preislerová, Vladimír Řehořek, Lubomír Tichý and Stanislav Němejc for their help in the field, and Ondřej Hájek for map preparation. This work was supported by the Czech Science Foundation (project 14-10723S).

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