MASARYK UNIVERSITY
FACULTY OF SCIENCE
DEPARTMENT OF BOTANY AND ZOOLOGY

Diversity of European urban vegetation

Ph.D. Dissertation

Natálie Čeplová

Supervisor: doc. RNDr. Zdeňka Lososová, Ph.D.

Brno 2016

Bibliographic Entry

Author:	Mgr. Natálie Čeplová Masaryk University, Faculty of Science, Department of Botany and Zoology
Title of Dissertation:	Diversity of European urban vegetation
Degree Programme:	Biology
Field of Study:	Botany
Supervisor:	doc. RNDr. Zdeňka Lososová, Ph.D. Masaryk University, Faculty of Science, Department of Botany and Zoology
Academic Year:	2016/2017
Number of Pages:	132
Key words:	Alpha diversity; archaeophytes; biological invasions; city; community assembly; competitiveness; dispersal strategy; Europe; invasive biology; native species; neophytes; niche preferences; non-native; phylogenetic community structure; propagule pressure; species traits; urban ecology; urban habitats; vascular plants

Bibliografický záznam

Autor:	Mgr. Natálie Čeplová Masarykova univerzita, Přírodovědecká fakulta, Ústav botaniky a zoologie
Název práce:	Diverzita vegetace evropských měst
Studijní program:	Biologie
Studijní obor:	Botanika
Školitel:	doc. RNDr. Zdeňka Lososová, Ph.D. Masarykova univerzita, Přírodovědecká fakulta, Ústav botaniky a zoologie
Akademický rok:	2016/2017
Počet stran:	132
Klíčová slova:	Alfa diverzita; archeofyty; biologické invaze; město; druhová skladba společenstva; konkurenceschopnost; strategie šíření; Evropa; invazní biologie; původní druhy; neofyty; stanovištní nároky druhu; nepůvodní; fylogenetická struktura společenstva; přísun diaspor; vlastnosti druhů; urbánní ekologie; cévnaté rostliny

Abstract

Urban areas are considered to be the important hotspots of plant biodiversity. Due to their high habitat heterogeneity and intense human impact they form a unique environment rich in plant species, both native and alien. Urban habitats differ in disturbance regimes, which act as a strong environmental filter determining plant community species composition. This is why plant communities in different urban habitats provide a suitable model for studying their role as starting points for the introduction of alien species and the effect of different disturbance regimes on species composition and phylogenetic diversity. Main aim of this Ph.D. thesis is (i) to determine the significance of introduction effort as a factor in woody plant naturalization in the urban environment, (ii) to explore the effect of the settlement size on plant species richness, composition and temperature requirements of resident plant communities, (iii) to explore how phylogenetic diversity varies across urban plant communities and whether the introduction of alien species changes the phylogenetic diversity of resident communities of native species, (iv) to test whether phylogeny can be used as a proxy for functional diversity in general and specifically for diversity in plant niche preferences, dispersal strategies and competitiveness-related traits.

We found a significant relationship between the number of planted individuals and the ability of woody species to spontaneously occur in the urban area. Temperate European native species, followed by neophytes originated from North America and Central-eastern Asia were observed to escape the most often from cultivations. 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 high proportion of neophytes that are dependent on constant input of propagules caused by human activities and also 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 with respect to temperature requirements is significantly more affected by local habitat conditions than by settlement size. Phylogenetic diversity of urban plant communities was lower than random. It varied with the disturbance regime in different urban habitats in all the species subsets, native species, archaeophytes and neophytes. Introduction of alien species reduced phylogenetic diversity of the urban plant communities. Low phylogenetic diversity of disturbed plant communities in urban habitats probably results from strong environmental filtering, which selects species from a limited number of lineages that have traits that enable them to survive in disturbed habitats. We found positive significant yet very weak relationships between phylogenetic diversity and overall functional diversity, and between phylogenetic diversity and diversity in both species dispersal strategies and competitiveness taken separately. The relationship between phylogenetic diversity and diversity in species niche preferences was not significant. Phylogenetic diversity is a weak proxy for functional diversity of urban plant communities.

Abstrakt

Města jsou považována za důležitá centra druhové bohatosti. Vzhledem k pestré mozaice stanovišť a intenzivní činnosti člověka tvoří jedinečné prostředí bohaté na rostlinné druhy, a to jak původní tak nepůvodní. Městské biotopy se liší režimem disturbancí, které působí jako silný environmentální filtr a ovlivňují tak druhové složení rostlinných společenstev. Rostlinná společenstva ve městech proto poskytují vhodný model pro studium vlivu disturbancí na druhové složení a fylogenetickou strukturu společenstva a pro studium významu měst pro šíření nepůvodních druhů do okolní krajiny. Hlavním cílem této práce je (i) stanovit význam frekvence vysazování jako faktoru při naturalizaci dřevin ve městech, (ii) prozkoumat vliv velikosti sídla na druhovou bohatost, druhové složení a teplotní požadavky rostlinných společenstev, (iii), prozkoumat jak se liší fylogenetická diverzita různých rostlinných společenstev ve městech a zda introdukce nepůvodních rostlinných druhů mění fylogenetickou diverzitu společenstev původních druhů, (iv) otestovat, zda fylogenetická struktura společenstva může být použita jako zástupná proměnná pro funkční diverzitu obecně a konkrétně pro diverzitu vlastností rostlin souvisejících se stanovištními nároky druhů, strategiemi šíření a mezidruhovou kompeticí.

Potvrdili jsme významný vztah mezi počtem vysazených jedinců a schopností dřevin spontánně se šířit ve městě. Z výsadeb se nejčastěji šíří původní druhy mírného pásu Evropyé a dále nepůvodní druhy pocházející ze severní Ameriky a střední a východní Asie. Rostlinná společenstva ve velkých sídlech jsou obecně druhově bohatší než společenstva malých obcí. Tyto rozdíly se nejvíce pojevují v obytných čtvrtích. Se zvětšující se velikostí sídla roste i množství jak nově zavlečených nepůvodních druhů (neofytů) závislých na konstantním přísunu diaspor působením lidské činnosti tak druhů původních, přežívajících ve zbytcích polopřirozené vegetace. Naopak archeofyty jako homogenní skupina druhů s podobnými vlastnostmi jsou rozšířeny rovnoměrně napříč sídly všech velikostí. Nepotvrdili jsme vliv tepelného ostrova na druhové složení společenstev, což zřejmě znamená, že lokální stanovištní podmínky hrají ve formování společenstev větší roli než velikost sídla a s ní související vznik tepelného ostrova. Fylogenetická diverzita rostlinných společenstev ve studovaných městských společenstvech je nižší než náhodná. Její hodnota se mění s režimem disturbancí a to pro všechny studované skupiny druhů (původní druhy, archeofyty a neofyty). Introdukce nepůvodních druhů snižuje fylogenetickou diverzitu společenstev. Nízká fylogenetická diverzita disturbovaných rostlinných společenstev ve městech vzniká pravděpodobně v důsledku silného působení environmentálních filtrů, které umožňují usazení druhů pouze z omezeného počtu vývojových linií. Tyto druhy se vyznačují vlastnostmi, díky kterým přežívají na narušených stanovištích. Zjistili jsme, že vazba mezi fylogenetickou a celkovou funkční diverzitou městských rostlinných společenstev je ale velmi slabá, podobně jako vazba mezi fylogenetickou diverzitou a vlastnostmi navázanými na strategie šíření a mezidruhovou kompetici. Vztah mezi fylogenetickou diverzitou a vlastnostmi druhů souvisejících s jejich nároky na podmínky stanoviště nebyl statisticky významný. Fylogenetická diverzita je pouze slabým ukazatelem funkční diverzity městských rostlinných společenstev.

Acknowledgements
Poděkování

Děkuji

Zdeňce za příležitost vrátit se zpátky k botanice, podívat se na zajímavá místa a získat zkušenosti na zahraničních konferencích, za ochotu řešit všechny zádrhele a otázky (byť sebevíce triviální), za podporu při řešení jakéhokoliv problému a za čas, který mi v průběhu mého studia věnovala.

Verče za společnost v kanceláři, v terénu i jinde, za cenné rady z pozice zkušenějšího botanika a za ochotu převádět mé leckdy krkolomné věty do skutečné angličtiny.

Milanovi za pomoc s rukopisem mého prvního článku a za otázky, které mě vždycky posunuly v mém studiu o kus dál.

Lubošovi a Davidovi za pomoc s analýzami.

Ondrovi za přípravu map.

Všem z Ústavu botaniky a zoologie PřF a také z Katedry biologie PdF za přátelské a podpůrné prostředí.

Viktorovi za podporu a nekonečnou dávku tolerance a trpělivosti; Kryštofovi a Mikymu, že to se mnou těch pět a půl roku vydrželi.

Content

Author contributions to the papers presented in the Ph.D. Dissertation

Paper I

Čeplová N., Lososová Z. & Kalusová V. (submitted) Urban ornamental trees: a source of recent invaders? A case study from European city.

NČ, ZL and VK conceived the ideas; NČ and ZL analysed the data, NČ led the writing; all authors commented on the manuscript.

Paper II

Čeplová N., Kalusová V. & Lososová Z. (2017) Does the size of settlement matter? Effects of urban heat island, settlement size and habitat type on urban plant biodiversity. *Landscape and Urban Planning*, **159**, 15–22.

NČ, VK and ZL conceived the ideas; NČ and VK performed the field sampling; ZL provided data sets on large settlements, NČ performed the data analysis and wrote the manuscript, all authors commented on the manuscript.

Paper III

Čeplová N., Lososová Z., Zelený D., Chytrý M., Danihelka J., Fajmon K., Láníková D., Preislerová Z., Řehořek V. & Tichý L. (2015) Phylogenetic diversity of central-European urban plant communities: effects of alien species and habitat types. *Preslia*, **87**, 1–16.

NČ and ZL conceived the ideas and led the writing; ZL, MC, JD, KF, DL, ZP and LT collected data in the field; JD and VŘ revised the herbarium specimens; NČ and DZ analyzed the data; all authors commented on the manuscript.

Paper IV

Lososová Z., **Čeplová N.,** Chytrý M., Tichý L., Danihelka J., Fajmon K., Láníková D., Presilerová Z. & Řehořek V. (2016) Is phylogenetic diversity a good proxy for functional diversity of plant communities? A case study from urban habitats. *Journal of Vegetation Science*, **27**, 1036–1046.

ZL, MC conceived the ideas and led the writing; ZL, MC, JD, KF, DL, ZP and LT collected data in the field; JD and VŘ revised the herbarium specimens; NČ prepared the phylogenetic tree and analyzed the phylogenetic structure of plant communities; ZL performed the rest of analyses. All authors commented on the manuscript.

Introduction

Human settlements form a specific environment with unique inner conditions which strongly influence plant biodiversity (McKinney 2006). Urban environment is defined especially by human impact such as activities connected to trade, industry and human well-being. Cities are characterized by mosaic of specific habitats with high plant species diversity (Kühn & Klotz 2006). Human activities result in high propagule pressure and as a consequence to high proportion of alien species. Introduced species may then spread from settlements to surrounding landscape through natural dispersal (Hulme et al. 2008, Essl et al. 2015), where part of them became naturalized and even invasive.

Many emerging species are deliberately planted crops and ornamental plants. Spontaneous occurrence of these species is directly connected to the frequency of planting (Williamson 1996, 1999, Lockwood et al. 2005, Dehnen-Schmutz et al. 2007a, b, Hanspach et al. 2008). The more often is the species planted, the higher is probability of its spontaneous escape from cultivation. Whereas planted native species could easily spread from cultivations, they usually don’t have negative impact on diversity of adjacent habitats (Simberloff et al. 2012). On the contrary alien species would escape less likely but if they naturalized or become invasive, there is a higher probability of their impact on plant communities. Alien species often grow larger and more densely in their introduced range (Parker et al. 2013), so successfully established species might have a negative impact on plant biodiversity through competition. The probability of establishment and spontaneous spread of plant species also increases with the residence time. Species with longer residence time has usually larger area of the occurrence as well (Křivánek et al. 2005, Pyšek et al. 2014, 2015). The invasion process of introduced plant species is well described, but there is a lack of information about first steps of introduction including escape from cultivation and frequency of failures is rather scarce.

It has been demonstrated that proportion of alien plant species in urban floras increases with city size (Klotz 1990, Pyšek 1998), but our knowledge about differences in particular urban plant communities based on settlement size is rather theoretical. The settlement size is recognized as an important property directly connected to species richness and species composition in urban habitats. Habitat heterogeneity (Kowarik 1995, Kühn et al. 2004) together with high input of seeds increasing with the level of urbanization and the city size (Pyšek 1998, Luck & Smallbone 2011) lead to high plant species diversity in total urban floras (Klotz 1990, Stadler et al. 2000, Deutschewitz et al. 2003, Kühn et al. 2004). It is assumed that city size could affect not only total species number within the whole city but also species richness of individual habitats. Settlement size could also have different effect 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 (Pyšek 1998, Dunn & Heneghan 2011). 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 (Pyšek 1993, Kühn & Klotz 2006, Wania et al. 2006).

Large built-up areas of cities with impervious surfaces made of concrete, asphalt and paving, along with the heat and smog pollution, contribute to changed climatic conditions in settlements in comparison with the surrounding landscape. 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 et al. 2010). It is predicted that the species composition of the urban vegetation is influenced by UHI (Wittig & Durwen 1982, Wittig 2002, Knapp et al. 2009).

For our better understanding of community assembly processes, phylogenetic and functional diversity are considered as the additional important community properties. At a short temporal scale, disturbance is the key factor shaping not only species composition but also the phylogenetic diversity of plant communities (Brunbjerg et al. 2012). Strongly disturbed or early successional habitats tend to host phylogenetically clustered communities (with lower than random phylogenetic diversity), which change to overdispersed (with higher than random phylogenetic diversity) during the course of succession (Letcher 2010, Brunbjerg et al. 2012, Letcher et al. 2012). Disturbed habitats in urban environment contain many alien species (Lososová et al. 2012a) and it is unclear how they influence phylogenetic diversity. It is hypothesized that the phylogenetic structures of native and alien species differ because of their different origin and residence time (Ricotta et al. 2009). We suggest that most urban plant communities have a lower than random phylogenetic diversity, because of strong habitat filtering. This is supported by previous studies (Knapp et al. 2008, Ricotta et al. 2009), which show that floras of entire European and American cities are composed of a limited number of lineages. However, cities host mosaics of different habitats, each harbouring a specific group of species and each with a different proportion of aliens (Ricotta et al. 2010, Lososová et al. 2012a). Therefore the patterns of phylogenetic diversity of urban floras can be fully understood only if phylogenetic diversity is analysed for particular habitats.

It is often problematic to study the functional diversity of the urban plant communities, because of the lack of plant trait data, especially for alien species. In several studies phylogenetic diversity has been proposed as a proxy for functional diversity (Harvey & Pagel 1991, Prinzing et al. 2001, Webb et al. 2002, Kraft et al. 2007, Cavender-Bares et al. 2009). The use of this proxy is based on the assumption that the phylogenetic distance between species is proportional to the evolutionary time during which distinct traits and environmental preferences could have evolved, but this would be valid only if evolutionary processes were stationary (Diniz-Filho et al. 2010). It has been poorly tested to what extent can be phylogenetic diversity used to estimate functional diversity.

As plant communities in urban habitats are exposed to various disturbance regimes and intensities, we could expect that different sets of traits would have different importance for community assembly. Disturbances tend to promote plant communities with a broad interspecific variation in dispersal traits such as seed mass, dispersal vectors and soil seed bank type (Grime 2006). Thus, divergence in dispersal traits may reflect newly emerging communities after a strong disturbance. In contrast, convergence in dispersal traits may indicate a longer established community. Traits connected to species competitiveness (e.g. plant height, life span, specific leaf area and leaf dry matter content) are probably less important for colonizing newly created habitats, but they are more important for persistence of species within an established community. In undisturbed habitats, competition is expected to be strongest among species that are dissimilar in competitiveness traits. Competition will be asymmetric and stronger species will win, resulting in convergence in competitiveness traits. By contrast, in disturbed habitats, competition is expected to be more symmetric with fewer winners and losers, leading to divergence in competitiveness traits (Grime 2006; Gerhold et al. 2015). We expect that strongly disturbed urban habitats will harbour communities of species with similar niche preferences but relatively high variation in competitiveness traits. In contrast, less-disturbed habitats will support functionally and phylogenetically convergent communities with over-represented values of competitiveness traits due to the exclusion of phylogenetically related weaker competitors (Swenson et al. 2007; Narwani et al. 2013; Purschke et al. 2013).

Under the assumption that species traits are phylogenetically conserved, diversity in the subsets of traits representing niche preferences, dispersal strategy and competitiveness should be related to phylogenetic diversity (Prinzing et al. 2001, Cavender-Bares et al. 2009). However, this expectation has not been sufficiently tested with real data. Some studies have been performed on the relationships between phylogenetic and functional diversity for different subsets of traits (Silvertown et al. 2006, Cahill et al. 2008, Carboni et al. 2013, Perronne et al. 2014).

Main aims of the Ph.D. Dissertation

Paper I
Aim of the paper is to determine the influence of propagule pressure, origin of species and residence time on the risk that planted woody species would escape from cultivations. It is expected that probability of escaping increases with frequency of planting and that species with longer residence time or originated from climatically similar regions are more likely to escape.

Paper II
Aim of the paper is to explore the influence of the size of different settlement types (cities, towns and villages) on total species number, species richness and species composition in particular urban habitats. It is expected that number of native species decreases with settlement size and number of aliens increases. It is also predicted that species composition could be affected by urban heat island, where large settlements would host more thermophilous communities in comparison to the smaller ones.

Paper III
Aim of the paper is to test whether strong environmental filtering, caused especially by disturbances, decreases the phylogenetic diversity of urban plant communities. As urban plant communities contain a large proportion of alien species and their phylogenetic diversity is relatively low, the expectation is that the introduction of alien species decreases their phylogenetic diversity. As the origin and biogeographical history of plant species in the urban environments are diverse, the expectation is that native species and groups of alien species with different residence times have different phylogenetic diversities.

Paper IV
Aim of the paper is to test whether community phylogenetic diversity can be used as a proxy for functional diversity. It is hypothesized that phylogenetic diversity could be only a weak predictor of diversity of dispersal strategies and competitiveness traits among species in urban plant communities. In contrast, it is hypothesized that human preferences have much weaker effect on the relationship between species niche preferences and phylogeny, therefore phylogeny can be a good proxy for niche preferences.

Methods

Here follow summarized characteristics of data sets used and analyses applied. For detailed description see Methods/Materials and Methods chapters of each enclosed paper.

Paper I

The list of planted trees and shrubs was compiled based on information about planted individuals in public areas of the city Brno, Botanical garden of Masaryk University and Arboretum of Mendel University. Number of planted individuals in public area, i.e. the frequency of planted species, was used as a proxy for propagule pressure of planted species. From the floristic database of flora of Brno information about escaping woody species was obtained (http://www.sci.muni.cz/botany/vraticka/www/). The database includes information about presence of species in 113 grid cells of the size 1.1 × 1.5 km covering the whole urban area. Number of grid cells occupied by each woody species, i.e. the frequency of escaping species, was used to characterize the capacity of species to escape from cultivation.

The species were divided into groups according to their origin, residence time and invasive status following the information adopted from Pyšek et al. (2012) and from the regional floras. Based on the origin and residence time native species, archaeophytes (introduced before the discovery of America, ~ 1500 AD) and neophytes (after 1500 AD) were distinguished. Based on invasive status, archaeophytes and neophytes were further divided into three categories: casual species (species that do not form self-sustaining populations, their persistence depends on repeated introductions of propagules), naturalized species (form self-sustaining populations, their persistence does not depend on introduction of propagules), and invasive species (subset of naturalized species that produce large numbers of offspring and have potential to spread over long distances, for details see Pyšek et al. 2012). Species which were absent in the database of alien flora of the Czech Republic, but were planted in public area of Brno were recognized as known from cultivation.

Linear regressions were used to explain relationship between frequencies of planted and escaping species. All mentioned categorical variables (origin, residence time, invasive status) and one continuous variable (number of planted individuals) were used to assess which characteristics generally promote species escaping from cultivation in the city. Frequency of escaping species was related as dependent variable to the species characteristics as explanatory variables using regression tree (Breiman et al. 1984, De'ath & Fabricius 2000). The influence of categorical variables with high relative importance value, but not shown as predictors in the tree, were tested by t-tests.

Paper II

Data on the occurrence of vascular plant species were collected in central European settlements of three different sizes:

villages – small settlements with 3500–5500 inhabitants
towns – medium-sized settlements with 20–50 000 inhabitants
cities – large settlements with more than 100 000 inhabitants

Data sampling was carried from mid-June to late August in 15 settlements of each size. In each settlement three types of habitats with different disturbance regime were sampled:

settlement centre with total paved or sealed area > 90%
residential area with **compact** building pattern consisting of rows of family houses (older than 50 years) and private gardens
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. In total 135 plots (15 plots × 3 habitats × 3 settlement sizes) were sampled. Three types of sampled plots in cities are identical to plots used in dataset in Paper III and IV (square, residential area compact and older successional site called mid-successional site in Paper III and IV).

Recorded species were divided into groups according to their origin and residence time as native in Central Europe, archaeophytes and neophytes (Pyšek et al. 2012, DAISIE 2009).

Differences in species richness between plots with the same disturbance regime depending on the size of the settlements were tested by ANOVA and Tukey post hoc tests. To identify how the species composition changes depending on the settlement size, principal component analysis (PCA) was used across whole dataset. Differences in species composition for groups of plots with the same disturbance regime were tested using permutation multivariate analyses based on Bray-Curtis dissimilarities (PERMANOVA; Anderson et al. 2006).

To determine the effect of urban heat island on species composition, Ellenberg indicator values (EIV) for temperature were used. EIV reflects plants` affinities to local temperature conditions ranging from 1 to 9 (Ellenberg et al. 1992). Mean EIVs for temperature were calculated for each plot as a mean of EIV`s of species recorded in the plot. Differences in mean EIV for temperature between plots with the same disturbance regime depending on the size of the settlements were tested by ANOVA and Tukey post hoc tests.

Paper III and IV – data sampling and phylogenetic tree construction

Data on the occurrence of vascular species of plants were collected in 32 cities, each with more than 100 000 inhabitants, in central and north-western Europe, from mid June to late August. Seven habitats subject to different regimes of disturbance were sampled in each city:

> **Square** – a square in the historical city centre, usually with pre-19th century houses and with more than 90% of its area paved or sealed.
> **Boulevard** – a broad street with 19th century houses, lines of trees, small lawns, and more than 70% of its area paved or sealed.
> **Residential area compact** – residential area with a compact building pattern, consisting of family houses at least 50 years old and private gardens.
> **Residential area open** – residential area with an open building pattern, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs.
> **Park** – urban park with old deciduous trees covering 20–50% of the area and frequently mown lawns.
> **Early successional site** – recently disturbed site with prevailing bare ground and vegetation cover less than 20%, usually in or around construction sites.
> **Mid-successional site** – site abandoned for 5–15 years, dominated by perennial grassland with scattered shrubs and young trees.

Similarly to sampling protocol used in Paper II one plot of 1-ha size was sampled in each type of habitat in each city by recording all spontaneously occurring species of vascular plants. In total 224 plots (32 cities × 7 habitats) were sampled.

All species of plants recorded were classified into groups according to their origin, as native or alien (non-native) in central Europe. Alien species were further divided according to their residence time into archaeophytes and neophytes (Pyšek et al. 2002) using the national lists of alien species and specialized databases were used for this classification (Klotz et al. 2002, Pyšek et al. 2002, DAISIE 2009, http://www.europe-aliens.org).

The phylogenetic tree was constructed for the cumulative list of species spontaneously occurring in the sampled plots. The tree was constructed using the online tool *Phylomatic* (Webb & Donoghue 2005; http://phylodiversity.net/phylomatic/) based on the phylogenetic information provided by Davies et al. (2004) and Bremer et al. (2009). Node ages were assigned according to *Time Tree* (Hedges et al. 2006, Hedges & Kumar 2009; http://www.timetree.org/) and Wikström et al. (2001). Branch lengths were calculated using Phylocom algorithm *bladj*.

Paper III – statistical analysis

Following version of average phylogenetic distinctiveness index (*avpd*; Warwick & Clarke 1998) was used to describe the phylogenetic diversity of communities:

$$avpd = \sum_{i>j} Br_{ij} / \frac{S(S-1)}{2}$$

where Br_{ij} is the summed length of branches connecting species i and j ($i \neq j$), and S is the total number of species ($i, j = 1, 2, \ldots, S$). *Avpd* indicates mean phylogenetic distance separating two species in a community. Lower values of *avpd* indicate that species in the community tend to be more closely related (they are located on nearby branches of the phylogenetic tree).

Two different null models (with and without including species frequency), which correspond to a random distribution of species on the phylogenetic tree, were calculated to test if the phylogenetic diversity recorded for each plot significantly differs from the phylogenetic diversity of a plot with random species composition. Values significantly lower than random indicate a phylogenetically clustered community structure, while those significantly higher than random indicate an overdispersed structure.

The null distribution of random *avpd* was generated using 999 permutations for both null models, and significance was determined using a two-tailed test by comparing a reference value of *avpd* (calculated from real data) with the generated null distribution.

These analyses were calculated for each plot sampled. Further calculations were performed separately for native species, archaeophytes and neophytes occurring in each plot to determine the effect of urban habitats (and associated disturbance regimes) on groups of species with different residence times. *Avpd* values and null models were calculated using the R program, version 2.14 (R Core Team 2014), using the package *picante* (Kembel et al. 2010). The relationship between the phylogenetic diversity of communities and the proportion of alien species was tested using linear regressions.

Paper IV – plant functional data and statistical analysis

For each species the information about its niche preferences and life-history traits was compiled. Niche preferences were characterized by Ellenberg indicator values (Ellenberg et al. 1992) for light, temperature, continentality, moisture, soil reaction and nutrients, Grime's (1979) life-history strategy categories (competitive, stress-tolerant and ruderal) and categories according to species immigration pathways to the urban habitats (ornamental plants escaping from cultivation, crops escaping from cultivation and non-cultivated species). The life-history traits comprised mean plant height at maturity (m), specific leaf area (SLA; $mm^2 \cdot mg^{-1}$), leaf dry matter content (LDMC; mg

· g^{-1}), life form, dispersal type, seed mass (mg) and seed bank type. The trait information was obtained from the LEDA database (Kleyer et al. 2008). All these characteristics are further referred to as "traits".

The K statistic of the phylogenetic signal (Blomberg et al. 2003) was calculated for each trait based on the variance of phylogenetically independent contrasts. To determine if phylogenetic signal is statistically significant, the variance of contrasts for the real data was compared with the values obtained after the trait data were randomly permuted 999 times across the tips of the phylogenetic tree.

Functional diversity and phylogenetic diversity of each plot was measured using the mean pairwise distance of all possible species pairs (*mpd*; Pavoine & Bonsall 2011). In addition to *mpd*, phylogenetic diversity using the mean nearest taxon distance (*mntd*; Webb et al. 2002) was calculated. *Mpd* calculates mean phylogenetic distance between all species pairs for each community, whereas *mntd* measures the mean phylogenetic distance between each species and its phylogenetically nearest neighbour in the community.

Standardized effect size (*ses*), which is independent of species richness (Pavoine & Bonsall 2011) was calculated to quantify the difference between the observed diversity measure and the distribution of the diversity measure for 999 random-permutation-based communities with constant species richness. *Ses* was calculated as (observed diversity – mean of randomized diversity)/standard deviation of randomized diversity. Negative or positive values of *ses* indicate lower or higher diversity than random, respectively. For all randomization tests all species recorded across all cities were used. For each plot, the community-level weighted means of trait values were computed to identify functional composition of individual communities.

Linear regressions were used to quantify the relationship between functional and phylogenetic diversity. The differences in taxonomic, functional and phylogenetic diversities were compared among urban habitat types. The differences in functional diversity among plots belonging to the same habitat type were tested using ANOVA with Tukey post-hoc tests.

Spearman correlation coefficients were used to characterize the importances of individual community-level weighted means of trait values for functional diversity of the target community.

Main results

Paper I

We found positive relationship between the frequency of planting of individuals of trees and shrubs and the relative frequency of spontaneously escaping woody plant species. Although only 15% of all planted woody taxa was recognized as spontaneously growing in urban areas, the ability of woody species to spontaneously escape from cultivation in urban area is significantly higher when the species is more frequently planted. This relationship was found also for groups of native and alien species separately.

The tendency for spontaneous occurring of woody species differs in accordance to their origin and residence time. The highest potential for species escaping in the urban area was observed for native European species, followed by North American species and species originated from Central-eastern Asia. Species from these regions were in the same time also the most commonly planted woody species in the city.

Paper II

We proved that settlement size is an important factor which shape species richness and species composition of urban plant communities. We found that species communities in urban areas are generally more species rich in larger settlements than in small ones. Total number of all species was the highest in cities as well as total number of native species and neophytes. Total number of archaeophytes was almost the same in all sizes of settlements studied.

Taking habitat types separately, the total number of species in settlement centres did not vary according to the settlement size. For residential areas and older successional sites, higher total number of species was found in the cities in comparison with smaller settlements (towns and villages). The same pattern was found for native species. Number of archaeophytes did differ neither according to the settlement size, nor according to the habitat type. The total number of neophytes in settlement centres and older successional sites did not vary according to settlement size, but total number of neophytes in residential areas increased with the settlement size from villages to cities.

Species composition differs significantly among habitat types regardless different settlement sizes. City centres are generally more homogeneous compared to the other habitat types. We also found differences in species composition between villages and cities within the same habitat type.

We did not confirm the effect of urban heat island on species composition, no differences in mean EIV for temperature comparing settlement sizes were found.

Regardless settlement sizes, centres were characterized by higher EIV for temperature than older successional sites. Settlement size showed no effect on the difference.

Paper III

We proved that phylogenetic diversity of plant communities in urban habitats is often lower than random. It varies according to the disturbance regime in all the species groups with different residence time (native species, archaeophytes and neophytes).

Two different null models used showed a slightly different results. Using the first null model (disregarding species frequencies) the phylogenetic structures of plant communities in particular urban habitats were clustered in most cases. When the subsets of species according to their residence time were taken separately, phylogenetic diversity was mostly lower than random as well, only with small differences between particular habitats. Using the second null model (considering species frequencies) phylogenetic structure of plant communities in all studied urban habitats and also for species groups with different residence time was more often random.

Phylogenetic diversity of all types of studied communities (their *avpd* values) increased with increasing proportion of native species. The opposite trend was found for archaeophytes and neophytes.

Paper IV

Both phylogenetic diversity indices (*mpd, mntd*) were weakly positively significantly related to the functional diversity index. Significance was slightly weaker or none when individual trait groups were considered separately. Both phylogenetic indices predicted the variation in traits indicating dispersal strategy and competitiveness of plant species in urban habitats very poorly, and neither could predict the variation in species niche preferences or traits that indicate these preferences. The variation explained by phylogeny was very low for dispersal strategy and for competitiveness. We found almost no relationships between functional and phylogenetic diversity indices in the analyses within individual urban habitats.

In all urban habitats, functional diversity was lower than random, which means that all the studied plant communities were functionally more or less convergent. The highest degree of convergence was at successional sites. Convergence also appeared in all habitats for the trait subsets representing niche preferences and dispersal strategies, while both convergence and divergence were found for the subset of traits related to species competitiveness. The highest values of functional diversity in competitiveness-related traits were found in both types of residential areas and in urban parks.

Traits used in the analyses varied widely in their degree of associated phylogenetic signal. The strongest phylogenetic signals were found for the phanerophyte life form and for plant height, i.e. traits responsible for species competitiveness. Very weak phylogenetic signals were found for niche preferences and dispersal strategies. Species planting as crops and presence of persistent soil seed banks were not related to phylogeny. Functionally diverse urban plant communities were characterized by spontaneously occurring ornamental plants with high temperature requirements. Species in these communities tended to be relatively tall, and often phanerophytes, chamaephytes, or therophytes with ruderal life-history strategy. The prevailing dispersal type was by humans and the seed bank was short-term persistent or long-term persistent. In contrast, functionally homogeneous communities were composed mainly of spontaneously occurring hemicryptophytes or geophytes, which prefer humid conditions with abundant light. They were mainly competitors with high LDMC values, dispersed through zoochory and with transient soil seed banks.

Discussion and conclusions

Urban ornamental trees as a source of recent invaders

Most alien species are usually noticed after their successful establishment, spread and possible impact in affected habitats. In present study we tried to fill the gap in our knowledge about the first step in invasion process – escape and initial establishment of woody plant species. As many alien woody species are planted in the city parks and gardens, although most of them never escape, they may pose a potential risk for the native vegetation.

The presented results show that spontaneous escape from cultivation could be an effective pathway for introduction of woody plant species. It has previously been shown that the importance of this pathway in time could even become more important as showed when considered the effect of horticultural industry on invasive process in Britain (Dehnen-Schmutz et al. 2007a, b). The probability of escaping of planted ornamental woody species from cultivation increased with the propagule pressure, which is a strongly significant explanatory factor for native species and less important but still significant for alien species. Such results are in accordance with data coming from East Australian cities (Mulvaney 2001). Alien species success is closely related to the residence time (Pyšek & Jarošík 2005, Pyšek et al. 2015). Among planted woody species, archaeophytes that had a longer time to establish in a new region (Pyšek et al. 2015) are more likely to escape than neophytes. Most commonly planted alien species in Brno originated from North America and Central-eastern Asia, thus human preferences show a bias towards species from climatically similar regions. Such species probably better withstand cultivation due to their adaptations to similar environmental conditions (Dehnen-Schmutz 2007b) and therefore they can have higher probability of escaping to surroundings.

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

Urban floras are generally more species rich in larger settlements than in the small ones (Pyšek 1998). We confirmed that this is true also for plant communities of studied urban habitats. When recorded species were divided into groups according to their origin and residence time, we found that higher number of species in large cities is caused by predominance of native species and neophytes. Archaeophytes did not contribute to this phenomenon. As has previously been demonstrated by Lososová et al. (2012b) essentially the same archaeophytes are equivalently distributed throughout all anthropogenic habitats. Higher number of neophytes in urban habitats of large cities was expected due to their higher input of propagules dependent on human activities which are generally more pronounced in large settlements (Zerbe et al. 2003). Despite native species are generally expected to be outcompete by neophytes in floras of highly disturbed urban areas (Pyšek 1998), we validated the opposite trend, similarly to Deutschewitz et al. (2003), who found no causal relationship between native and alien species richness at the regional scale in Germany. It is assumed that native and alien plant species are similarly affected by the same environmental conditions (Davis et al. 2000, Levine 2000). Moreover native species probably could 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 as neophytes (Duhme & Pauleit 1998, Deutschewitz et al. 2003). Differences in numbers of native species, archaeophytes and neophytes are less pronounced when habitat types are evaluated separately.

The lowest species richness across all settlement sizes was found in settlement centres with intense and regular disturbances as was showed also by Lososová et al. (2011). 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 (e.g. Blair & Launer 1997, Niemelä et al. 2002, Zerbe et al. 2003, Celesti-Grapow et al. 2006). The differences in species richness between settlements of different sizes within the same habitat were confirmed in residential areas, where numbers of species per plot were significantly lower in villages compared to cities probably because of more intense planting activities in the cities.

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

We did not confirm differences in species composition of different settlement sizes regarding to urban heat island effect. The trend in the occurrence of thermophilous species was nevertheless found comparing habitat types. Assuming that older successional sites are usually located on the 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 (McKinney 2002, Schmidt et al. 2014). We suppose that thermophilous assemblages occurring in centres of villages, where the presence of the heat island is not expected, may be caused by heat capacity of the surface made of asphalt or paving. These surfaces are easily heated in summer and this local overheating could affect species composition similarly to urban heat island.

Phylogenetic diversity of central European urban plant communities

We confirmed our hypothesis that phylogenetic diversity of central European urban plant communities tend to be smaller than random. Our analyses confirmed the results of previous studies that showed that the floras of Rome and Brussels were phylogenetically clustered (Ricotta et al. 2008, 2012). We demonstrated that phylogenetic clustering also occurs within individual habitats. Nevertheless, we did not find any clear evidence that disturbance regime affects the phylogenetic diversity of urban plant communities. Less disturbed habitats, such as mid-successional stages or park grasslands were clustered to a similar degree as the heavily disturbed sites in city centres. We found no clear trend related to the level of disturbance, which is similar to the findings for household yard flora in the Minneapolis-Saint Paul metropolitan area in Minnesota (Knapp et al. 2012), where phylogenies of particular urban habitats were clustered and differences among fine-scale sites had no significant effect on phylogenetic diversity. We suggest that the main reason for generally low phylogenetic diversity recorded for urban plant communities is environmental filtering at the level of the whole city (e.g. Knapp et al. 2008, Ricotta et al. 2008, 2009). In cities, abiotic conditions such as climate, together with constraints on dispersal and competition, are supplemented by human-induced factors such as disturbance, soil degradation or application of chemicals (Hobbs et al. 2006, Knapp et al. 2012). These factors favour sets of ecologically similar species, which are often phylogenetically related.

We found that introduction of alien species decreases phylogenetic diversity of urban plant communities. The relationship between the proportion of alien species and phylogenetic diversity has only previously been studied for broadly defined types of vegetation (Winter et al. 2009, Gerhold et al. 2011) or small areas (Cadotte et al. 2010). These studies indicate that introduction of alien species is associated with a decrease in phylogenetic diversity, i.e. communities with a high proportion of aliens are significantly more clustered. Moreover, Ricotta et al. (2010) show that the more alien species there are in a community the lower its phylogenetic diversity. We studied communities in habitats with a large proportion of alien species and subject to strong human impact, and our results show the same pattern.

Although increasing phylogenetic clustering of urban plant communities is caused by both groups of alien species, it is stronger in the case of archaeophytes than neophytes. Many widespread and common archaeophytes are associated with human activities and (pre)adapted to habitats affected by disturbance (Pyšek et al. 2002) and usually increase the phylogenetic similarity of plant communities in urban habitats (Ricotta et al. 2009, 2012, Knapp et al. 2012). In contrast, neophytes are still being introduced and come from a broad spectrum of geographic regions (Pyšek et al. 2002).

Many of these species are rather scarce and their occurrences are often casual, as they have not had enough time to colonize the whole range of possible habitats (Gassó et al. 2010) thus they do not affect the phylogenetic diversity of communities so much. Their occurrences are more dependent on their propagule pressure and less on environmental filtering than those of archaeophytes (Chytrý et al. 2008).

Phylogenetic diversity as a proxy for functional diversity of plant communities

The results of our study suggest that the relationship between phylogenetic and functional diversity is very weak for European urban plant communities. It becomes even weaker when assessed for subsets of traits. Such results are in accordance with some previous studies (Kraft et al. 2007, Bernard-Verdier et al. 2013, Carboni et al. 2013, Pavoine et al. 2013). Our analyses only slightly support the general expectation of ecological similarity among closely related species (Harvey & Pagel 1991, Prinzing et al. 2001, Webb et al. 2002, Kraft et al. 2007).

Strong phylogenetic signal in traits is necessary to predict functional diversity from phylogenetic diversity (Swenson & Enquist 2009). We found no relationship between phylogenetic diversity and traits related to niche preferences or dispersal traits, and only a very weak relationship between phylogenetic diversity and traits determining competitiveness. Traits related to niche preferences are expected to show different evolutionary patterns than traits determining competitiveness, because coexisting species must evolve similarities in the former and differences in the latter (Silvertown et al. 2006, Cavender-Bares et al. 2009, but see Mayfield & Levine 2010, Kraft et al. 2015). In accordance with this expectation, we obtained different evolutionary patterns for niche preferences and competitiveness traits. However, we detected an opposite pattern in which closely related species do not share similar niche preferences, whereas they do have similar traits connected with competitiveness.

We observed low functional diversity within all the studied urban communities and very low variation in functional diversity among communities. This contrasts with the high variation in species richness among urban habitats (Lososová et al. 2011) and could imply that the whole urban floras are under strong human-induced and environmental filters (Knapp et al. 2008, Ricotta et al. 2008, 2009, 2012). Our findings indicate that strong human-induced and environmental filtering in urban habitats causes very low variation in species niche preferences. The detected variation in this part of functional diversity is unrelated to phylogeny. Our results obtained for niche preferences thus support the idea that phylogenetic diversity cannot be used as a proxy for functional diversity (Emerson & Gillespie 2008, Bernard-Verdier et al. 2013, Carboni et al. 2013, Mason et al. 2013).

We proved that traits responsible for niche preferences are less phylogenetically conserved than traits related to competitiveness. These results differ from previous studies of semi-natural grasslands (Cahill et al. 2008) or simulated data (Kraft et al. 2007) that demonstrated the opposite effect. Therefore in urban vegetation phylogenetic diversity reflects the variability in competitiveness better than the variability in species niche preferences or dispersal strategies.

Individual urban habitat types differ in the phylogenetic and functional diversity of their plant communities, but the diversity values are very low, suggesting the importance of environmental and human-induced filtering at the scale of the whole urban flora (e.g. Knapp et al. 2008, 2012, Ricotta et al. 2008, 2009).

References

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**, 683–693.

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., 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. *Proceedings of the Royal Society B*, **281**, 20133330.

Bernard-Verdier, M., Flores, O., Navas, M.L. & Garnier E. (2013) Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *Journal of Vegetation Science*, **24**, 877–889.

Blair, R.B., & Launer, A.E. (1997) Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological Conservation*, **80**, 113–125.

Blomberg, S.P., Garland, T. Jr. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution,* **57**, 717–745.

Breiman, L., Friedman, J. H., Olshen, R. A. & Stone, C.G. (1984) *Classification and regression trees*. Wadsworth International Group, Belmont.

Bremer, B., Bremer, K., Chase, M. V., Fay, M. F., Reveal, J. L., Soltis, D. E., Soltis, P. S., Stevens, P. F., Anderberg, A. A., Moore, M. J., Olmstead, R. G., Rudall, P. J., Sytsmar, J., Tank, D. C., Wurdack, K., Xiang, J. Q. Y., Zmarzty, S. & Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Brunbjerg, A. K., Borchsenius, F., Eiserhardt, W. L., Ejrnæs, R. & Svenning, J.-C. (2012) Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science*, **23**, 1082–1094.

Cadotte, M. W., Borer, E. T., Seabloom, E. W., Cavender-Bares, J., Harpole, W. S., Cleland, E. & Davies, K. F. (2010) Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in Northern California. *Diversity and Distributions*, **16**, 892–901.

Cahill, J. F., Kembel, S. W., Lamb, E. G & Keddy, P. A. (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology Evolution and Systematics*, **10**, 41–50.

Carboni, M., Acosta, A. T. R. & Ricotta, C. (2013) Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? *Journal of Vegetation Sciences*, **24**, 932–941.

Cavender-Bares, J., Kozak, J. K. H., Fine, P. V. A. & Kembel, S. W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Celesti-Grapow, L., Pyšek, P., & Jarošík, V., (2006) Determinants of native and alien species richness in the urban flora of Rome. *Diversity and Distributions*, **12**, 490–501.

Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. & Danihelka, J. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541–1553.

DAISIE (Eds.) (2009) *Handbook of alien species in Europe*. Berlin, Springer.

Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the USA*, 101, 1904–1909.

Davis, M. A., Grime, J. P., & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

De'ath, G. & Fabricius, K. E. (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, **81,** 3178–3192.

Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M. (2007a) A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, **13**, 527–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M. (2007b) The horticultural trade and ornamental plant invasion in Britain. *Conservation Biology*, **21**, 224–231.

Deutschewitz, K., Lausch, A., Kühn, I., & Klotz, S. (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12**, 299–311.

Diniz-Filho, J. A. F., Terribile, L. C., Cruz, M. J. R. d. & Vieira, L. C. G. (2010) Hidden patterns of phylogenetic non-stationarity overwhelm comparative analyses of niche conservatism and divergence. *Global Ecology and Biogeography*, **19**, 916–926.
Duhme, F., & Pauleit, S. (1998) Some examples of different landscape systems and their biodiversity potential. *Landscape and Urban Planning*, **41**, 249–261.
Dunn, C. P., & Heneghan, L. (2011) Composition and diversity of urban vegetation. *Urban Ecology: Patterns, Processes, and Applications* (ed. by Niemelä, J., Breuste, J. H., Elmqvist, T., Guntenspregen, G., James, P. & McIntyre, N. E.), pp. 103–115. Oxford University Press, New York.
Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–258.
Emerson, B. C. & Gillespie, R. G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, **23**, 619–630.
Essl, F., Bacher, S., Blackburn, T. M., Booy, O., Brundu, G., Brunel, S., Cardoso, A.-C., Eschen, R., Gallardo, B., Galil, B., García-Berthou, E., Genovesi, P., Groom, Q., Harrower, C., Hulme, P. E., Katsanevakis, S., Kenis, M., Kühn, I., Kumschick, S., Martinou, A. F., Nentwig, W., O`Flynn, C., Pagad, S., Pergl, J., Pyšek, P., Rabitsch, W., Richardson, D. M., Roques, A., Roy, H. E., Scalera, R., Schindler, S., Seebens, H., Vanderhoeven, S., Vilà, M., Wilson, J. R. U., Zenetos, A. & Jeschke, J. M. (2015) Crossing frontiers in tackling pathways of biological invasions. *BioScience*, **65**, 769–782.
Gassó, N., Pyšek, P., Vilà, M. & Williamson, M. (2010) Spreading to a limit: the time required for a neophyte to reach its maximum range. *Diversity and Distributions*, **16**, 310–311.
Gaston, K. J., Davies, Z. G., & Edmondson, J. L. (2010) Urban environments and ecosystem functions. In K. J. Gaston (Ed.), *Urban Ecology* (pp. 35–52). Cambridge, Cambridge University Press.
Gerhold, P., Cahill, J. F. Jr., Winter, M., Bartish, I. V. & Prinzing, A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, **29**, 600–614.
Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H. J., Fergus, A. J. F., Ozinga, W. A. & Prinzing, A. (2011) Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist*, **177**, 668–680.
Grime, J. P. (1979) *Plant strategies and vegetation processes*. Wiley, Chichester, UK.
Grime, J. P. (2006) Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.
Hanspach, J., Kühn, I., Pyšek, P., Boos, E. & Klotz, S. (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 241–250.
Harvey, P. H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
Hedges, S. B. & Kumar, S. (2009) *The Timetree of Life*. Oxford University Press, New York.
Hedges, S. B., Dudley, J. & Kumar, S. (2006) TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics*, **22**, 2971–2972.
Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W. & Vilà, M. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403–414.
Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P. & Webb, C. O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P, Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., (...) & Peco, B. 2008. The LEDA Traitbase: A database of life-history traits of Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.
Klotz, S. (1990). Species/area and species/inhabitants relations in European cities. *Urban Ecology* (ed. by Sukopp, H., Hejný, S. & Kowarik, I.), pp. 99–104. Den Haag, SPB Academic Publishing.
Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde*, **38**, 1–334.
Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S. E., Jakobsdottir, I., Kattge, J., King, J. Y., Klotz, S., McFadden, J. & Cavender-Bares, J. (2012) Phylogenetic and functional characteristic of household yard floras and their changes along an urbanization gradient. *Ecology*, **93** (*Supplement*), S83–S98.

Knapp, S., Kühn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga, W. A., Poschlod, P., Thompson, K., Thuiller, W. & Römermann, C. (2009) How species traits and affinity to urban land use control large-scale frequency. *Diversity and Distributions*, **14**, 533–546.

Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008) Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters*, **11**, 1054–1064.

Kowarik, I. (1995) On the role of alien species in urban flora and vegetation. *Plant invasions: general aspects and special problems.* (ed. by Pyšek, P., Prach, K., Rejmánek, M. & Wade M.), pp. 85–103. Amsterdam, SPB Academic Publishing.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S. & Levine, J. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, **29**, 592–599.

Kraft, N. J. B., Cornwell, W. K., Webb, C. O. & Ackerly, D. D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist*, **170**, 271–283.

Křivánek, M., Pyšek, P. & Jarošík, V. (2005) Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a Temperate Region. *Conservation Biology*, **20**(5), 1487–1498.

Kühn, I., & Klotz, S. (2006) Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.

Kühn, I., Brandl, R., & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.

Landsberg, H. (1981) *The urban climate*. New York, Academic Press.

Letcher, S. G. (2010) Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B*, **277**, 97–104.

Letcher, S. G., Chazdon, R. L., Andrade, A. C. S., Bongers, F., van Breugel, M., Finegan, B., Laurance, S. G., Mesquita, R. C. G., Martínez-Ramoz, M. & Williamson, G. B. (2012) Phylogenetic community structure during succession: evidence from three Neotropical forest sites. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 79–87.

Levine, J. M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852–854.

Lockwood, J. L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

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

Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Láníková, D., Otýpková, Z. & Řehořek, V. (2012b) Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation*, **145**, 179–184.

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 biota: effects of human-made habitat types on plants and land snails. *Journal of Biogeography*, **38**, 1152–1163.

Luck, G. W., & Smallbone, L. T. (2011) The impact of urbanization on taxonomic and functional similarity among bird communities. *Journal of Biogeography*, **38**, 894–906.

Mason, N. W. H., de Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, **24**, 794–806.

Mayfield, M. M. & Levine, J. M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.

McKinney, M. L. (2002) Urbanization, Biodiversity, and Conservation. *BioScience*, **52**, 883–890.

McKinney, M. L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Mulvaney, M. (2001) The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. *Weed risk assessment* (ed. by Groves, R. H., Panetta, F. D., Virtue, J. G.), pp 186–193, CSIRO Publishing, Collingwood, Victoria, Australia.

Narwani, A., Alexandrou, M. A., Oakley, T. H., Carroll, I. T. & Cardinale, B. J. (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, **16**, 1373–1381.

Niemelä, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D., & de Oca, E.M. (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, **17**, 387–401.

Oke, T. R. (1982) The energetic basis of the urban heat-island. *Quarterly Journal of the Royal Meteorological Society*, **108**, 1–24.
Parker, J. D., Torchin, M. E., Hufbauer, R. A., Lemoine, N. P., Alba, C., Blumenthal, D. M., Bossdorf, O., Byers, J. E., Dunn, A. M., Heckmann, R. W., Hejda, M., Jarošík, V., Kanarek, A. R., Martin, L. B., Perkins, S. E., Pyšek, P., Schierenbeck, K., Schlöder, C., van Klinken, R., Vaughn, K. J., Williams, W. & Wolfe, L. M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985–994.
Pavoine, S. & Bonsall, M. B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, **86**, 792–812.
Pavoine, S., Gasc, A., Bonsall, M. B. & Mason, N. W. H. (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science*, **24**, 781–793.
Perronne, R., Mauchamp, L., Mouly, A. & Gillet, F. (2014) Contrasted taxonomic, phylogenetic and functional diversity patterns in semi-natural permanent grasslands along an altitudinal gradient. *Plant Ecology and Evolution*, **147**, 165–175.
Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B*, **268**, 2383–2389.
Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M. & Prentice, H. C. (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, **101**, 857–866.
Pyšek, P. & Jarošík, V. (2005) Residence time determines the distribution of alien plants. *Invasive Plants: Ecological and Agricultural Aspects* (ed. by Inderjit), pp 77–96, Birkhäuser Verlag, Switzerland.
Pyšek, P. (1993) Factors affecting the diversity of flora and vegetation in Central-European settlements. *Vegetatio*, **106**, 89–100.
Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
Pyšek, P., Danihelka, J., Sádlo, J., Chrtek, J. Jr., Chytrý, M., Jarošík, V., Kaplan, Z., Krahulec, F., Moravcová, L., Pergl, J., Štajerová, K. & Tichý, L. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia*, **84**, 155–255.
Pyšek, P., Jarošík, V., Pergl, J., Moravcová, L., Chytrý, M. & Kühn, I. (2014) Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits. *Biological Invasions*, **16**, 577–589.
Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L. & Kühn, I. (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. *Ecology*, **96**(3), 762–774.
Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
R Core team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
Ricotta, C., Di Nepi, M., Guglietta, D. & Celesti-Grapow, L. (2008) Exploring taxonomic filtering in urban environments. *Journal of Vegetation Science*, **19**, 229–238.
Ricotta, C., Godefroid, S. & Rocchini, D. (2010) Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. *Biological Invasions*, **12**, 233–240.
Ricotta, C., Heathfield, D., Godefroid, S. & Mazzoleni, S. (2012) The effects of habitat filtering on the phylogenetic structure of the urban flora of Brussels (Belgium). *Community Ecology*, **13**, 97–101.
Ricotta, C., La Sorte, F. A., Pyšek, P., Rapson, G. L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.
Schmidt, K. J., Poppendieck, H.-H., & Jensen, K. (2014) Effects of urban structure on plant species richness in a large European city. *Urban Ecosystems*, **17**, 427–444.
Silvertown, J., McConway, K. J., Gowing, D. J., Dodd, M. E., Fay, M. F., Joseph, J. A. & Dolphin, K. (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B*, **273**, 39–44.
Simberloff, D., Souza, L., Nuñez, M. A., Barrios-Garcia, M. N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.
Stadler, J., Trefflich, A., Klotz, S., & Brandl, R. (2000) Exotic plant species invade diversity hot spots: the alien flora of north western Kenya. *Ecography*, **23**, 169–176.
Swenson, N. G. & Enquist, B. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, 2161–2170.

Swenson, N. G., Enquist, B. J., Thompson, J. & Zimmerman, J. K. (2007) The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.

Wania, A., Kühn, I., & Klotz, S. (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, **75**, 97–110.

Warwick, R. M. & Clarke, K. R. (1998) Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology*, **35**, 532–543.

Webb, C. O. & Donoghue, M. J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes,* **5**, 181–183.

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution and Systematics*, **33**, 475–505.

Wikström, N., Savolainen, V. & Chase, M. W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B*, **268**, 2211–2220.

Williamson, M. (1996) *Biological invasions*. Chapman and Hall, London.

Williamson, M. (1999) Invasions. *Ecography*, **22**, 5–12.

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delípetrou, P., Didžiulis, V., Hejda, M., Hulme, P. E., Lambdon, P. W., Pergl, J., Pyšek, P., Roy, D. B. & Kühn, I. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the USA*, **106**, 21721–21725.

Wittig, R. (2002) *Siedlungsvegetation*. Stuttgart, Ulmer.

Wittig, R., & Durwen, K.-J. (1982) Ecological indicator-value spectra of spontaneous urban floras. *Urban Ecology* (ed. by Bornkamm, R.,Lee, J. A. & Seaward, M. R. D.), pp. 23–31, Oxford, Blackwell Science Publishing.

Zerbe, S., Maurer, U., Schmitz, S., & Sukopp, H. (2003) Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, **62**, 139–148.

Paper I

Čeplová, N., Lososová, Z. & Kalusová, V. (submitted) Urban ornamental trees: a source of recent invaders; A case study from a European city.

Urban ornamental trees: a source of recent invaders. A case study from European city

Natálie Čeplová[1,2*], Zdeňka Lososová[1], Veronika Kalusová[1]

[1]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic*
[2]*Department of Biology, Faculty of Education, Masaryk University, Poříčí 7, CZ-603 00 Brno, Czech Republic*

ABSTRACT

Man-made habitats are considered to be important hotspots of biodiversity of native as well as alien plant species. Due to high propagule pressure caused by human activities they serve as a source of introduction of alien plant species. We used the database of planted ornamental trees and shrubs for Brno, Czech Republic, to determine the significance of introduction effort as a factor in woody plant naturalization. Of all planted woody taxa, 15 % were recognized as spontaneously growing in the urban area and there was a significant relationship between the number of planted individuals and the ability of a species to spontaneously occur in the urban area. Temperate European native species, followed by neophytes originated from North America and Central-eastern Asia, were observed to escape the most often from cultivations. Although only a minor portion of planted woody species is able to escape from cultivation, this still could represent a potential risk for the native vegetation.

Keywords: Archaeophytes, Europe, invasive biology, native species, neophytes, propagule pressure

INTRODUCTION

Escape from cultivation is an important pathway of introduction of alien plant species (Dehnen-Schmutz 2007a, Hulme et al. 2008, Essl et al. 2015). In the Czech Republic, the vast majority of alien vascular plants was introduced as ornamental plants and crops which subsequently escaped from cultivation (Pyšek et al. 2002). Focusing on woody species, the proportion of alien species introduced as a traded commodity is high in comparison with other pathways (Křivánek & Pyšek 2006, Pyšek et al. 2011). The probability that planted alien species escape from cultivation depends on the propagule pressure, which means that with high frequency of planted individuals the risk of escape and establishment becomes even higher (Williamson 1996, 1999, Lockwood et al. 2005, Dehnen-Schmutz et al. 2007a, b, Hanspach et al. 2008). For example Mulvaney (2001) showed that more frequently planted woody ornamental alien species in Australian cities were more likely to escape from cultivation than the less frequently planted species. Once introduced, alien species may spread across the region through natural dispersal. Over time, it is quite likely that species successfully introduced to a single location will spread over a large area (Hulme et al. 2008) and impact biodiversity of adjacent habitats (Gaertner et al. 2009, Taylor et al. 2016).

Urban areas with tree avenues and parks and gardens full of planted plants are hotspots of introduced alien species (Moro & Castro 2015). Planting of alien species helps overcome dispersal barriers that species with poor dispersal abilities would hardly pass through. Once have been introduced, we know a lot about their invasion success, but there is a gap in our knowledge about the first stages of introduction, e.g. escape, establishment success and possible failures that are not recorded later and thus are not usually detected.

Woody species are planted in urbanized areas, these include native species, alien species and species known only from cultivations, usually of hybrid origin. We assume that the tendency to spread from cultivation differs between these groups of species. Native species which are well established in their native range should easily spread from cultivation, however it is unlikely that these species will negatively impact biodiversity of particular habitats (Simberloff et al. 2012). Alien species often grow larger and more densely in their introduced range (Parker et al. 2013), and once successfully established, might have negative impact on plant biodiversity through competition. Finally, hybrids and other species known only from cultivation are less likely to spread and consequently impact adjacent habitats. The probability of establishment and spontaneous spread of plant species also increases with their residence time. Species with longer residence time usually have a larger area of occurrence (Křivánek et al. 2005, Pyšek et al. 2014, 2015).

In our study we tested the role of planted ornamental trees and shrubs for invasion success in Brno city. We used the frequency of planting of woody plants in public urban areas as a proxy for propagule pressure. We determined the influence of propagule pressure, origin of species, their residence time and frequencies of spontaneous occurrences on the risk that planted woody species would escape from cultivations.

MATERIAL AND METHODS

A list of planted trees and high shrubs with a mean height of over 1 m was compiled based on information about planted individuals in public areas (streets and urban parks), the botanical garden of Masaryk University and Arboretum of Mendel University. The list does not include shrubby species of genera *Amorpha*, *Berberis*, *Budleja*, *Chaenomeles*, *Colutea*, *Cotoneaster*, *Forsythia*, *Ilex*, *Kerria*, *Lonicera*, *Philadelphus*, *Physocarpus*, *Pyracantha*, *Rosa*, *Rubus*, *Sambucus*, *Spiraea*, and *Symphoricarpos*. Even that these taxa were found spontaneously growing in the urban area, these species were excluded from analyses as they were missing in data about planting. There is also missing information concerning recent planting of *Ailanthus altissima*, *Populus* × *canadensis* and *P*. × *canescens*. These species are no more planted for a few decades, but are still spontaneously occurring due to older individuals planted in the past. The number of planted individuals in public area, i.e. the frequency of planted species, was used as a proxy for propagule pressure of planted species. It is a rough proxy, as information about planted woody species in urban private gardens is not available for the analysis. However, it is likely that the same species will be also planted there.

Information about escaping woody species was obtained from the floristic database of flora of Brno (http://www.sci.muni.cz/botany/vraticka/www/). The database includes information about the presence of species in 113 grid cells of the size 1.1 × 1.5 km covering the whole urban area. The number of grid cells occupied by each woody species, i.e. the frequency of escaping species, was used to characterize the capacity of species to escape from cultivation.

The species were divided into groups according to their origin, residence time and invasive status following Pyšek et al. (2012). Based on the origin and residence time native species, archaeophytes (introduced before the discovery of America, ~ 1500 AD) and neophytes (after 1500 AD) were distinguished. In origin-based analysis species originated from more than one region were excluded (12 species in total), as well as species recognized as anecophytes (species with unknown region of origin, 5 species; Pyšek et al. 2012). Based on invasive status, archaeophytes and neophytes were further divided: casual species (species that do not form self-sustaining populations, their persistence depending on repeated introductions of propagules), naturalized species (form self-sustaining populations, their persistence independent of introduction of propagules), and invasive species (subset of naturalized species that produce large numbers of offspring and have the potential to spread over long distances; for details see Pyšek et al. 2012). Species which were absent in the database of alien flora of the Czech Republic, but were planted in public areas of Brno were categorised as “known from cultivation”. Nomenclature follows Danihelka et al. (2012); names of species not present in this checklist were unified according to The Plant List (http://www.theplantlist.org/). All taxa are hereafter referred to as species.

Linear regressions were used to examine relationship betweenthe frequencies with which a species is planted and is spontaneously-occurring. The analysis was performed in R program, version 2.14 (R Core Team 2014).

All above mentioned categorical variables (origin, residence time, invasive status) and one continuous variable (number of planted individuals) were used to assess which characteristics generally promote species escaping from cultivation in the city. Frequency of escaping species was related as dependent variable to the species characteristics as explanatory variables using a regression tree (Breiman et al. 1984, De'ath & Fabricius 2000). Regression tree was used due it`s ability to predict interactions among continuous dependent variable and more than one explanatory variable, both continuous and categorical (De'ath & Fabricius 2000). The dependent variable, frequency of escaping species, was hierarchically dichotomously splitted into more homogeneous groups based on explanatory variables (species` characteristics) and their interactions. Optimal tree size was selected using 10-fold cross-validation with SE = 1 rule to minimize the risk of tree overfitting. For each node of the tree possible surrogate variables were calculated as additional variables which are able to split the groups similarly to the main predictor. No surrogates with an associated value > 0.2 were found.

The explained variation in the dependent variable (number of planted individuals) was calculated from resubstitution relative errors corresponding to residual sums of squares. Each of the explanatory variables used in the model contributes to the explained variation on the relative importance scale from 0 to 100. The best explanatory variable has value of 100. The influence of categorical variables with high relative importance value, but not shown as predictors in the tree, were tested by t-tests. The analyses were performed in Statistica 12 (http://www.statsoft.com).

RESULTS

The dataset contains 823 taxa of ornamental trees or high shrubs planted in public areas of the Brno city. The most commonly planted taxa are *Prunus serrulata*, *Acer plantanoides*, *Tilia cordata*, *Acer campestre*, and *Robinia pseudacacia* (Table 1), whereas the most commonly escaping taxa are *Sambucus nigra*, *Robinia pseudoacacia*, *Acer platanoides*, *Cornus sanguinea*, and *Ligustrum vulgare* (Table 1). The relative frequency of spontaneously escaping woody species is significantly positively related with the frequency of planted individuals (R^2=0.252, $p < 0.001$, n=823, Fig. 1a) in the urban area. The same pattern was found also for native and alien species separately (Fig. 1b, c). In the Arboretum, there is a large collection of exotic individuals of the *Salix* genus, containing more than 100 taxa, and this artificially inflates the number of taxa which can "escape". When omitting this genus from the analysis, the relationship between the frequency of escaping and planted individuals is slightly stronger (R^2=0.269, $p < 0.001$, n=698, not shown).

Table 1. A list of the most commonly planted and escaping ornamental trees and high shrubs. The most commonly planted ornamental species which are also frequently escaping are in bold.

Planted trees and shrubs		Escaping trees and shrubs	
Taxon	number of planted individuals	Taxon	frequency in grid cells
Prunus serrulata	1314	*Sambucus nigra*	82
Acer platanoides	1102	***Robinia pseudoacacia***	80
Tilia cordata	905	***Acer platanoides***	76
Acer campestre	826	*Cornus sanguinea*	76
Robinia pseudoacacia	549	*Ligustrum vulgare*	73
Quercus robur	514	***Fraxinus excelsior***	72
Acer pseudoplatanus	483	***Acer pseudoplatanus***	70
Carpinus betulus	433	*Corylus avellana*	69
Salix hybrids	432	*Juglans regia*	69
Hibiscus syriacus	375	***Acer campestre***	68
Prunus hilieri	364	*Prunus avium*	68
Tilia platyphyllos	359	*Prunus domestica*	67
Fraxinus excelsior	343	*Euonymus europaeus*	64
Platanus x hispanica	314	***Carpinus betulus***	63
Fagus sylvatica	302	*Quercus petraea*	62
Tilia tomentosa	283	***Tilia cordata***	60
Sorbus x thuringiaca	278	*Betula pendula*	60
Pyrus calleryana	273	*Salix caprea*	59
Prunus fruticosa	259	*Pinus sylvestris*	58
Prunus x gondounii	247	*Acer negundo*	58

The tendency to escape from cultivations differs between species with different residence time (Table 2) and origin (Table 3). The most commonly escaping species are native European species followed by North American species and those originating from Central and Eastern Asia. Species from these regions are also the most commonly planted woody species in the city.

The optimal regression tree for the frequency of escaping species (Fig. 2) explained 58.33 % of variance. The most important characteristics for species escaping from cultivation was being a native species. For species that are not native the most important characteristics was the frequency of planting (> 16.5 planted individuals). If the importance of all used variables across all nodes was compared (Table 4), additional variables appear to influence the frequency of escaping species: species known from cultivation ($t = 18.29$, $p < 0.001$) generally form the homogeneous group of species, which are not escaping from the cultivation.

Table 2. Numbers and proportions of species planted and escaping from the cultivation. The invasive status followed Pyšek et al. (2012).

	number of planted species	proportion of all planted species	number of escaping species	proportion of all escaping species	proportion of escaping species within given alien status
natives	93	11.3%	59	49.2%	63.4%
archaeophytes	12	1.4%	10	8.3%	83.3%
casual	5	0.6%	4	3.3%	80.0%
naturalized	6	0.7%	5	4.2%	83.3%
invasive	1	0.1%	1	0.8%	100%
neophytes	60	7.3%	36	30.0%	60.0%
casual	43	5.2%	22	18.3%	51.1%
naturalized	11	1.3%	9	7.5%	81.8%
invasive	6	0.7%	5	4.2%	83.3%
known from cultivation	658	80.0%	15	12.5%	1.8%
Total	823		120		

Table 3. Numbers and proportions of species planted and escaping from the cultivation. Species are divided into groups according to their origin. Species originated from more than one region and anecophytes were excluded.

	number of planted species	proportion of all planted species	number of escaping species	proportion of all escaping species
Temperate and Boreal Europe	152	18.9%	63	57.3%
Mediterranean	51	6.3%	7	6.4%
North America	200	24.8%	22	20.0%
South America	7	0.9%	0	
Eastern and Central Asia	326	40.4%	15	13.6%
Western Asia	32	4.0%	0	
Australia and New Zealand	2	0.2%	0	
hybrid	36	4.5%	3	2.7%
Total	806		110	

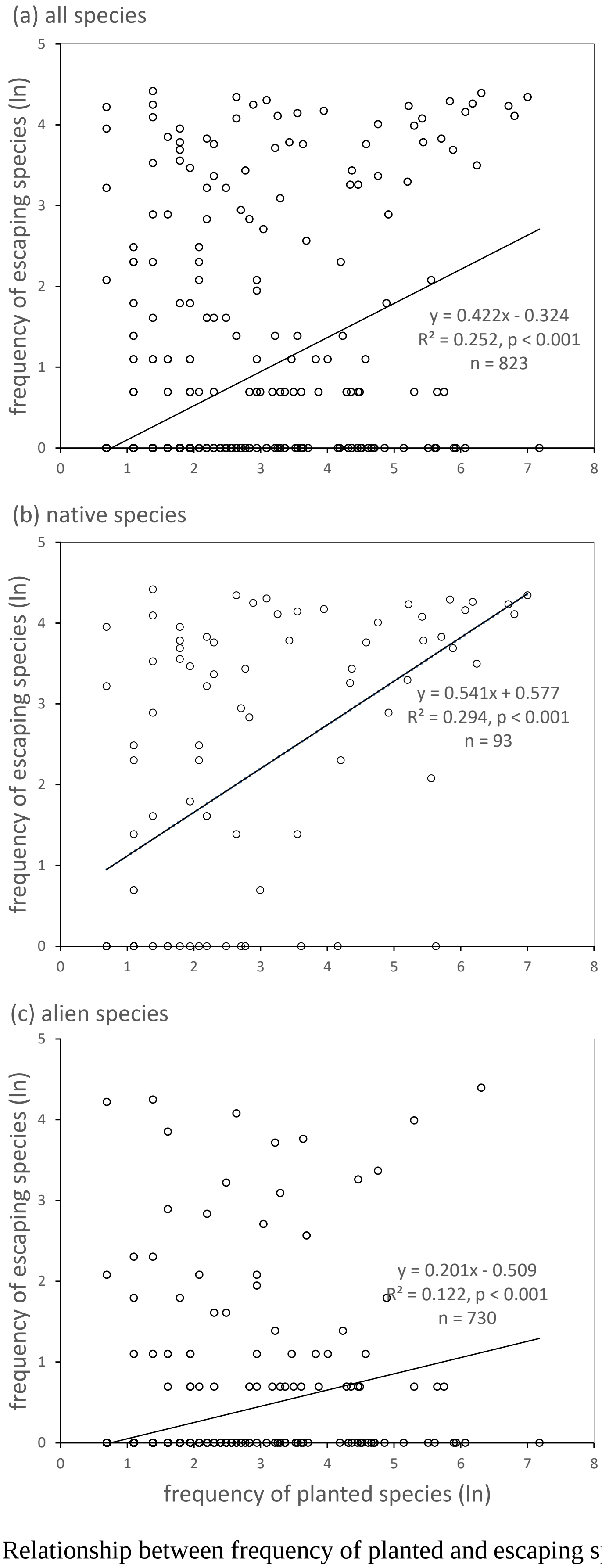


Fig. 1. Relationship between frequency of planted and escaping species.

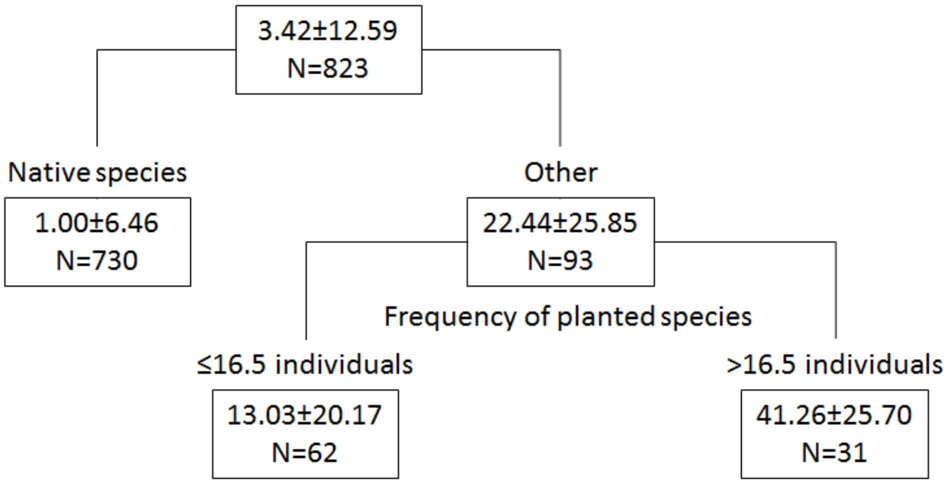


Fig. 2. Regression tree explaining frequency of escaping species. Each node is characterized by mean±SD of total frequency of escaping species and the number of cases (N) assigned to the particular node. Total variation explained R^2 = 58.33 %.

Table 4. Values of relative variable importance of the explanatory variables based on the regression tree. Explanatory variables are ranked according to the decreasing value of the contribution to variance explanation in frequency of escaping species.

Variable	
Frequency of planted species	100
Natives	94
Known from cultivation	94
Temperate and boreal Europe	61
Eastern and central Asia	14
Archaeophytes	12
Hybrid	5
North America	3
Western Asia	3
Mediterranean	3
Australia and New Zealand	3
South America	3
Neophytes	2

DISCUSSION

The presented results provide quantitative evidence for the role of planted ornamental woody species as an important source for plant invasion of woody species. It is shown that not only deliberate planting (Pyšek et al. 2011) but also spontaneous escape from cultivation could be an effective pathway for woody species. It is likely that the importance of this source in time could even increase, as showed when considering the effect of the horticultural industry on the invasive process in Britain (Dehnen-Schmutz et al. 2007a, b). The probability of escape of planted woody species increased with propagule pressure, which is a strongly significant explanatory factor for native species and less important but still significant for alien species. Such results are in accordance with data coming from East Australian cities (Mulvaney 2001).

Despite of the fact that alien species in Brno are planted more often than native species, the relationship between the frequency of planting and escaping is weaker for aliens than for natives. Our results suggest that native species are better adapted to local environmental conditions and so their probability of escaping from cultivations is higher. Their spontaneous occurrence in the city area could be also caused by diaspores originating from surrounding landscape, not only from cultivations. Alien species` success is closely related to their residence time (Pyšek & Jarošík 2005, Pyšek et al. 2015). Among planted woody species, archaeophytes which had a longer time to establish in a new region (Pyšek et al. 2015) are more likely to escape than neophytes (83% vs 60% of woody species).

Most of the commonly planted alien species in Brno originated from North America and Central-eastern Asia; thus human preferences show a bias towards species from climatically similar regions. Such species probably better withstand cultivation because they are adapted to similar environmental conditions (Dehnen-Schmutz 2007b) and therefore they can have higher probability of escaping to surroundings. Their establishment can be facilitated by additional properties preferred by horticulture such as easy propagation or resistance to pests (Dehnen-Schmutz 2007b).

Our findings show that the vast majority of planted ornamental woody species fail to escape from cultivation. These species are rarely used in horticultural market, but they are planted in specialized collections of botanical gardens of universities. These species are not able to transit the first step of the invasion process. Well-established native species, which are in their native range, easily escaped from cultivations, but it is less likely that these species will negatively impact biodiversity of adjacent habitats (Simberloff et al. 2012). In contrary, escaping alien species could potentially have negative impact on adjacent habitats (Parker et al. 2013). Of the 120 woody species detected as escaping from cultivation in the city, 14 (11.7%) are naturalized and 6 (5.0%) have invasive status. These values are slightly lower than reported for the whole alien Czech woody flora by Křivánek and Pyšek (2006).

We consider it important to mention, that three frequent spontaneously occurring invasive tree species were not included to our analyses. These are *Ailathus altissima* (neophyte, escaping in 45 grid cells), *Populus* × *canadensis* (hybrid, 46 grid cells) and *Populus* × *canescens* (hybrid, 11 grid cells). Although we have data on their escaping, they are no more planted for a few decades, after they were considered to be highly invasive. However these species spontaneously occur in the city area, as seed sources serve either old solitary trees growing in house yards or younger spontaneous (not planted) populations.

Most alien species are usually noticed after successful establishment, spread and possible impact in habitats. In present paper we tried to fill the gap in our knowledge about the first step in invasion process – escape and initial establishment of woody species. Many alien tree species are planted in the city parks and gardens and although most of them never escape, they may pose a potential risk for the native vegetation.

ACKNOWLEDGEMENTS

We thank Jozef Kasala, director of Public Green Agency of Brno, Magdaléna Chytrá, director of Botanical Garden of the Faculty of Science, Masaryk University, for providing data and Petra Štěpánková for and digitization of data. This work was supported by the Czech Science Foundation, project 14-10723S.

REFERENCES

Breiman, L., Friedman, J. H., Olshen, R. A. & Stone, C. G. (1984) *Classification and regression trees*. Wadsworth International Group, Belmont.

Danihelka, J., Chrtek, J. Jr. & Kaplan, Z. (2012) Checklist of vascular plants of the Czech Republic. *Preslia,* **84,** 647–811.

De'ath, G. & Fabricius, K. E. (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology,* **81,** 3178–3192.

Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M. (2007a) A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, **13**, 527–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C. & Williamson, M. (2007b) The horticultural trade and ornamental plant invasion in Britain. *Conservation Biology*, **21**, 224–231

Essl, F., Bacher, S., Blackburn, T. M., Booy, O., Brundu, G., Brunel, S., Cardoso, A.-C., Eschen, R., Gallardo, B., Galil, B., García-Berthou, E., Genovesi, P., Groom, Q., Harrower, C., Hulme, P. E., Katsanevakis, S., Kenis, M., Kühn, I., Kumschick, S., Martinou, A. F., Nentwig, W., O`Flynn, C., Pagad, S., Pergl, J., Pyšek, P., Rabitsch, W., Richardson, D. M., Roques, A., Roy, H. E., Scalera, R., Schindler, S., Seebens, H., Vanderhoeven, S., Vilà, M., Wilson, J. R. U., Zenetos, A. & Jeschke, J. M. (2015) Crossing frontiers in tackling pathways of biological invasions. *BioScience*, **65**, 769–782.

Gaertner, M., Den Breyen, A., Hui, C. & Richardson, D. M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319–338.

Hanspach, J., Kühn, I., Pyšek, P., Boos, E. & Klotz, S. (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 241–250.

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W. & Vilà, M. (2008) Grasping at the routes of

biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403–414.
Křivánek, M., Pyšek, P. & Jarošík, V. (2005) Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a Temperate Region. *Conservation Biology*, **20**(5), 1487–1498.
Křivánek, M. & Pyšek, P. (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). *Diversity and Distribuitons*, **12**, 319–327.
Lockwood, J. L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
Moro, M.F. & Castro, A. S. F. (2015) A check list of plant species in the urban forestry of Fortaleza, Brazil: where are the native species in the country of megadiversity? *Urban Ecosystems*, **18**, 47–71.
Mulvaney, M. (2001) The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. *Weed risk assessment* (ed. by Groves, R. H., Panetta, F. D., Virtue, J. G.), pp 186–193, CSIRO Publishing, Collingwood, Victoria, Australia.
Parker, J. D., Torchin, M. E., Hufbauer, R. A., Lemoine, N. P., Alba, C., Blumenthal, D. M., Bossdorf, O., Byers, J. E., Dunn, A. M., Heckmann, R. W., Hejda, M., Jarošík, V., Kanarek, A. R., Martin, L. B., Perkins, S. E., Pyšek, P., Schierenbeck, K., Schlöder, C., van Klinken, R., Vaughn, K. J., Williams, W. & Wolfe, L. M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985–994.
Pyšek, P. & Jarošík, V. (2005) Residence time determines the distribution of alien plants. *Invasive Plants: Ecological and Agricultural Aspects* (ed. by Inderjit), pp 77–96, Birkhäuser Verlag, Switzerland.
Pyšek, P., Danihelka, J., Sádlo, J., Chrtek, J. Jr., Chytrý, M., Jarošík, V., Kaplan, Z., Krahulec, F., Moravcová, L., Pergl, J., Štajerová, K. & Tichý, L. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. *Preslia*, **84**, 155–255.
Pyšek, P., Jarošík, V. & Pergl, J. (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. *PLoS ONE*, **6**(9), e24890.
Pyšek, P., Jarošík, V., Pergl, J., Moravcová, L., Chytrý, M. & Kühn, I. (2014) Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits. *Biological Invasions*, **16**, 577–589.
Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L. & Kühn, I. (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. *Ecology*, **96**(3), 762–774.
Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
R Core team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
Simberloff, D., Souza, L., Nuñez, M. A., Barrios-Garcia, M. N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.
Taylor, K. T., Maxwell, B. D., Pauchard, A., Nuñez, M. A., Rew, L. J. (2016) Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Diversity and Distributions*, **22**, 578–588.
Williamson, M. (1996) *Biological invasions*. Chapman and Hall, London.
Williamson, M. (1999) Invasions. *Ecography*, **22**, 5–12.

Paper II

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

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

Natálie Čeplová[1,2], Veronika Kalusová[1], Zdeňka Lososová[1]

[1]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic,*
[2]*Department of Biology, Faculty of Education, Masaryk University, Poříčí 7, CZ-603 00 Brno, Czech Republic*

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.

Keywords: Alpha diversity, archaeophytes, Central Europe, native species, neophytes, urban habitats

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 et al. 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 et al. 2003, Klotz 1990, Kühn et al. 2004, Stadler et al. 2000).

From the perspective of island biogeography (McArthur & Wilson 1967), cities can be considered as a type of ecological island isolated from the other city islands by the surrounding landscape (Begon et al. 2006, Clergeau et al.2004, Davis & Glick 1978, McGregor-Fors et al. 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 et al. 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 & 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 et al. 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 et al. 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 et al. 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 et al. (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.

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 hours.

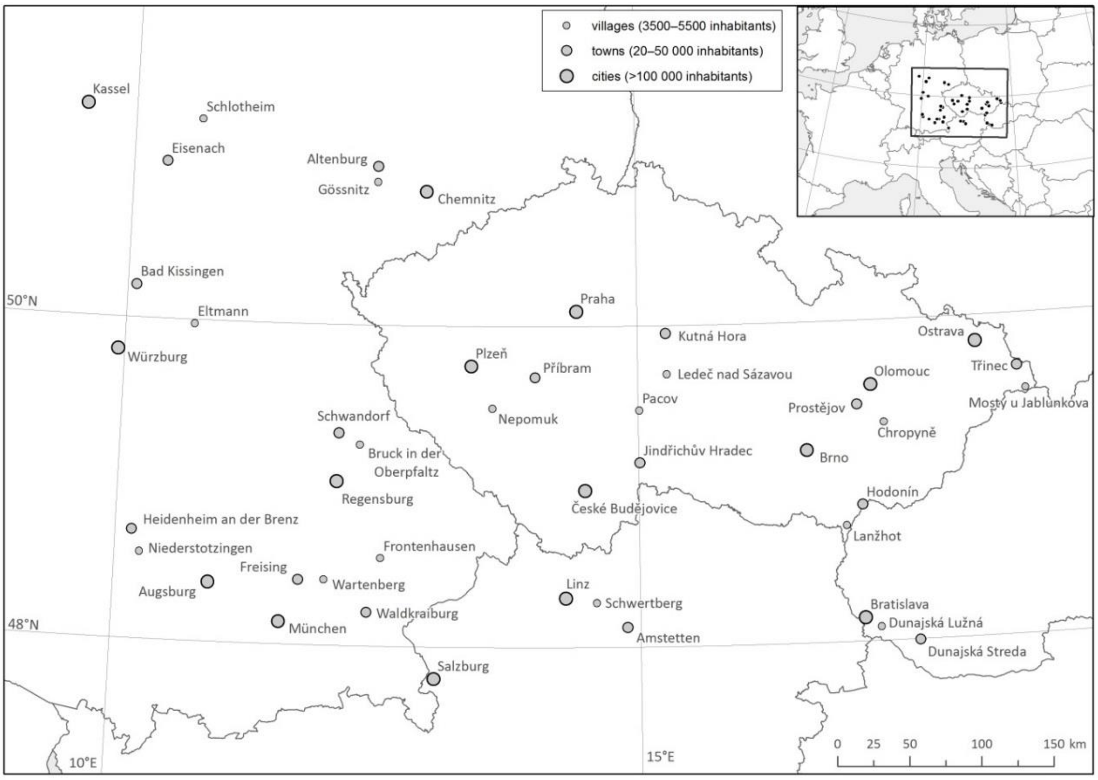


Fig. 1. Map of studied settlements.

The taxonomy and nomenclature of the recorded taxa mainly followed Jäger and Werner (2005) and Jäger et al. (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).

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 et al. (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 & 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 et al. 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 et al. 1992). 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).

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).

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

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 successional 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.

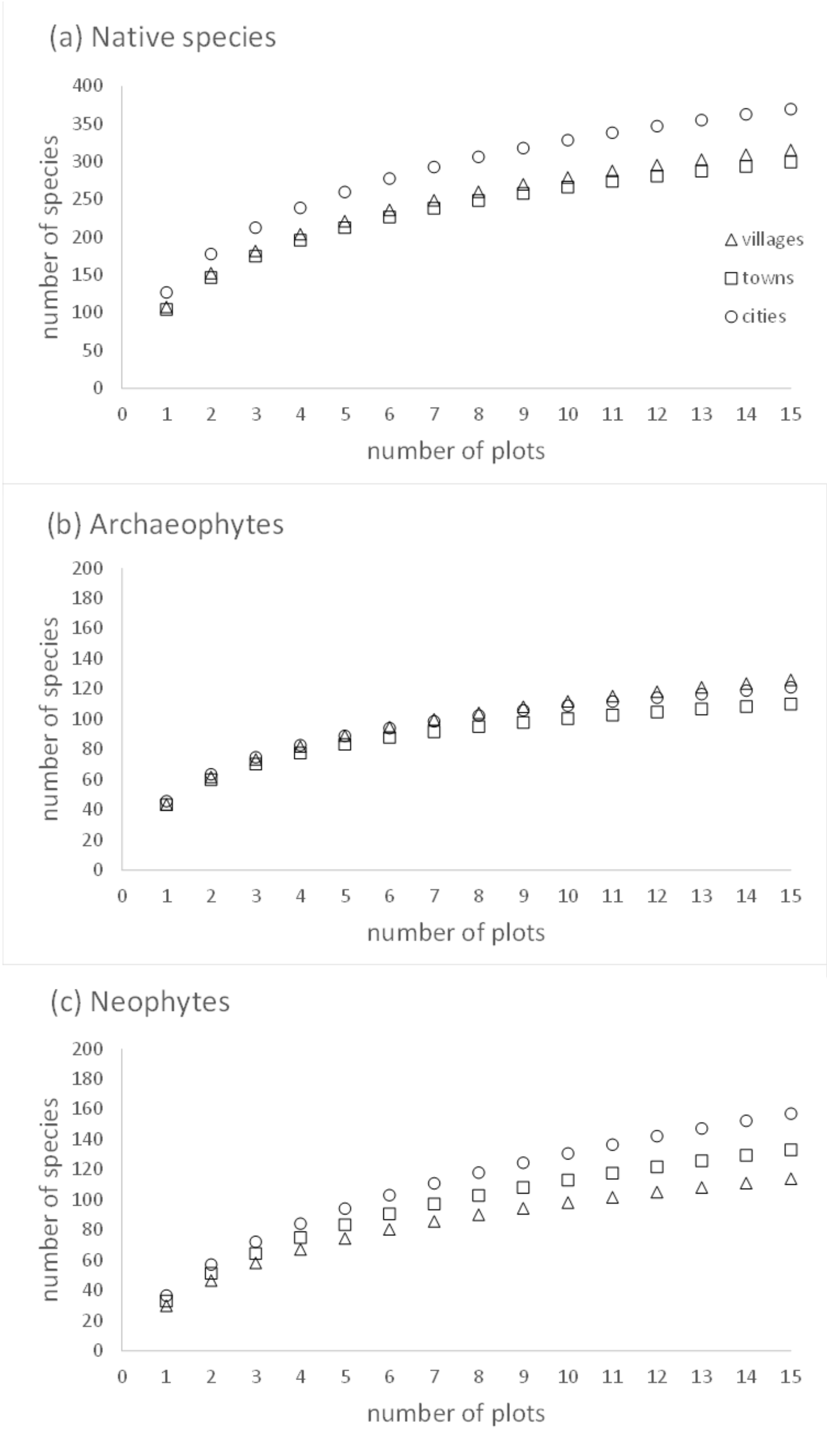


Fig. 2. Sample-based rarefaction curves showing accumulation of species across plots in settlements of different sizes calculated for groups of species with different origin and residence time (native species, archaeophytes and neophytes).

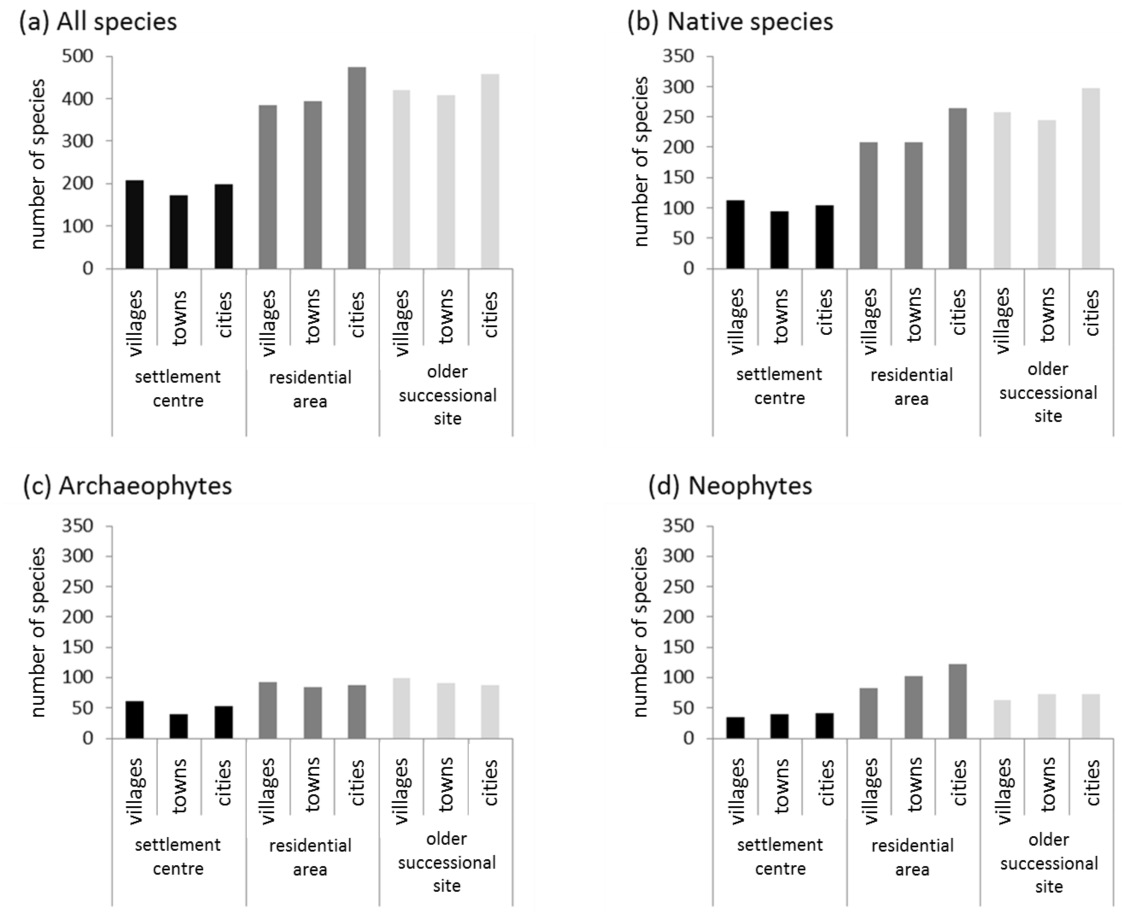


Fig. 3. Total number of species recorded in three settlement sizes studied (villages, towns, cities) and three habitat types (settlement centre, residential area, older successional site).

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).

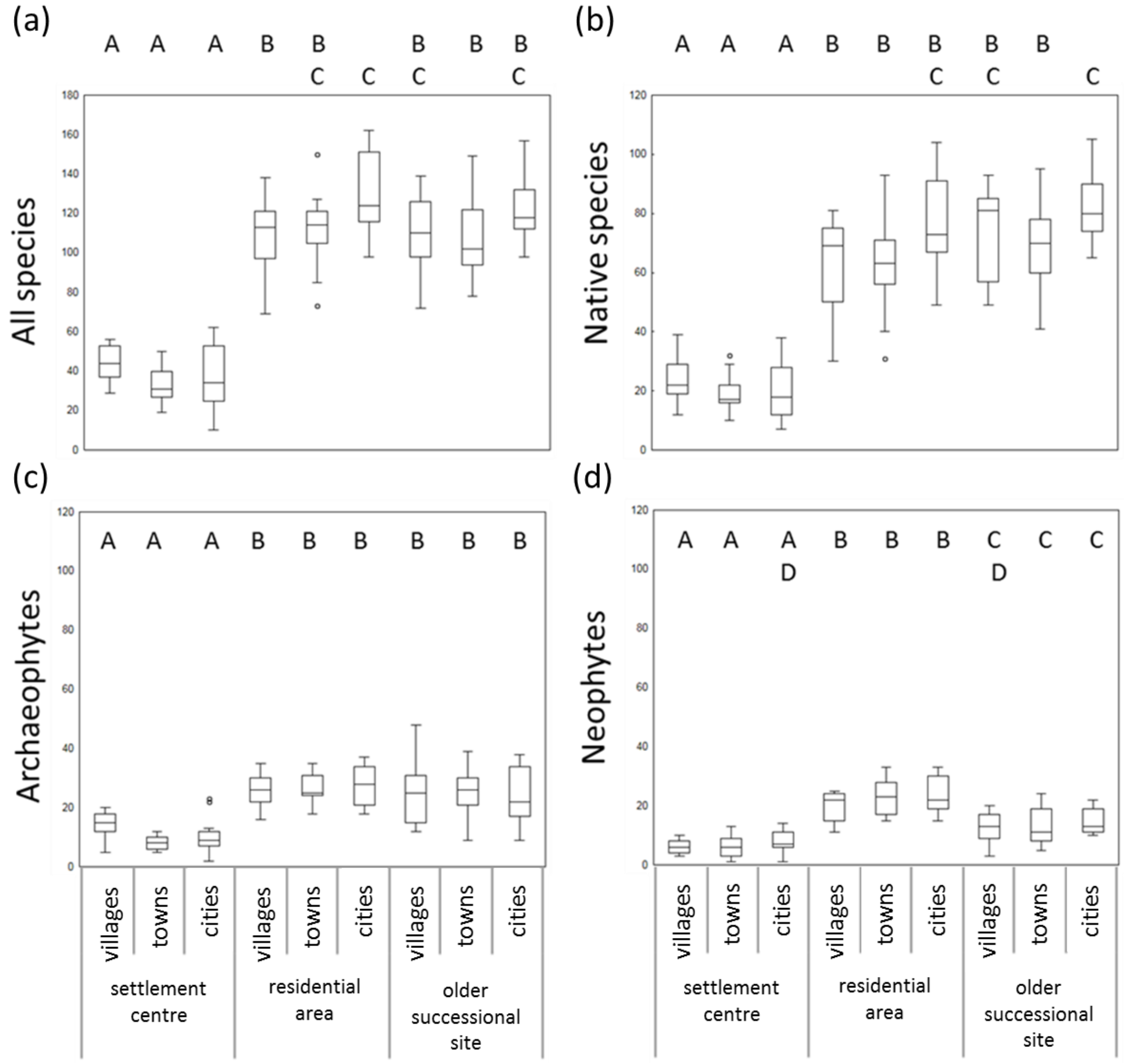


Fig. 4. Species richness recorded in three settlement sizes studied (villages, towns, cities) and three habitat types (settlement centre, residential area, older successional site). Boxes and whiskers indicate medians, 25–75% quantiles, non-outlier range, and outliers. Same letters indicate homogeneous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

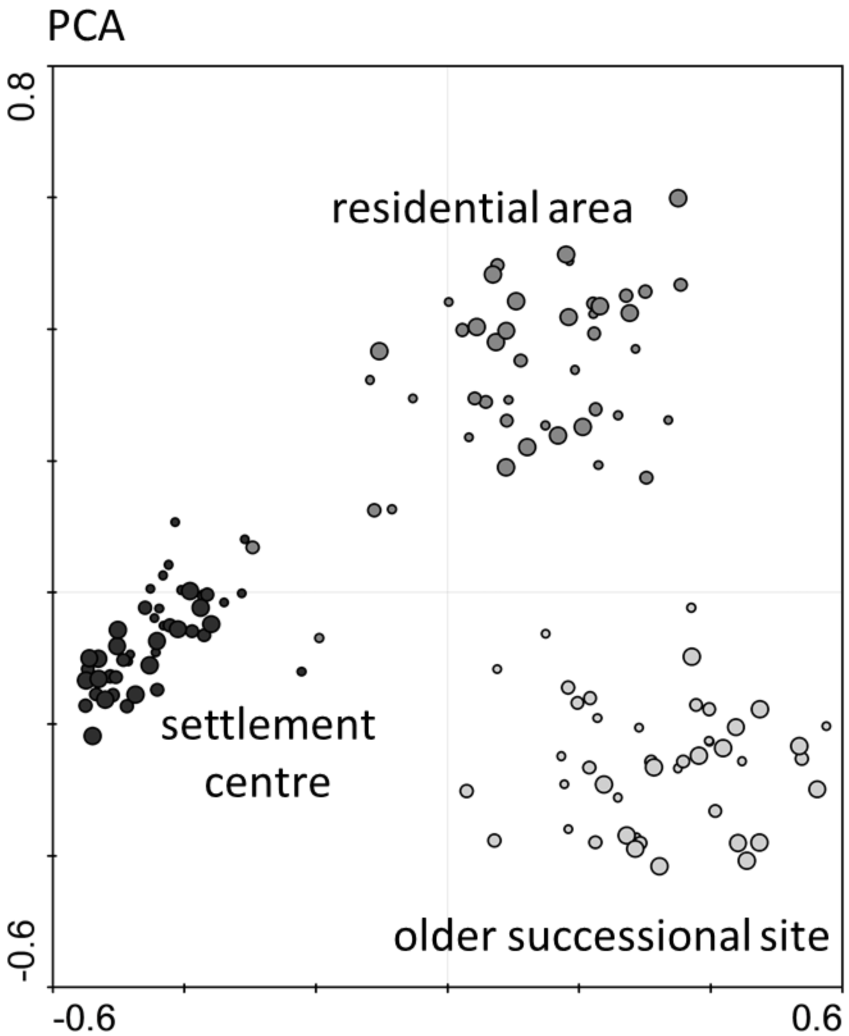


Fig. 5. PCA ordination plot of all studied sites shows clustering of habitat types across different settlement sizes. The size of the settlement corresponds to the size of the symbol.

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*

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 of island biogeography (McArthur & 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).

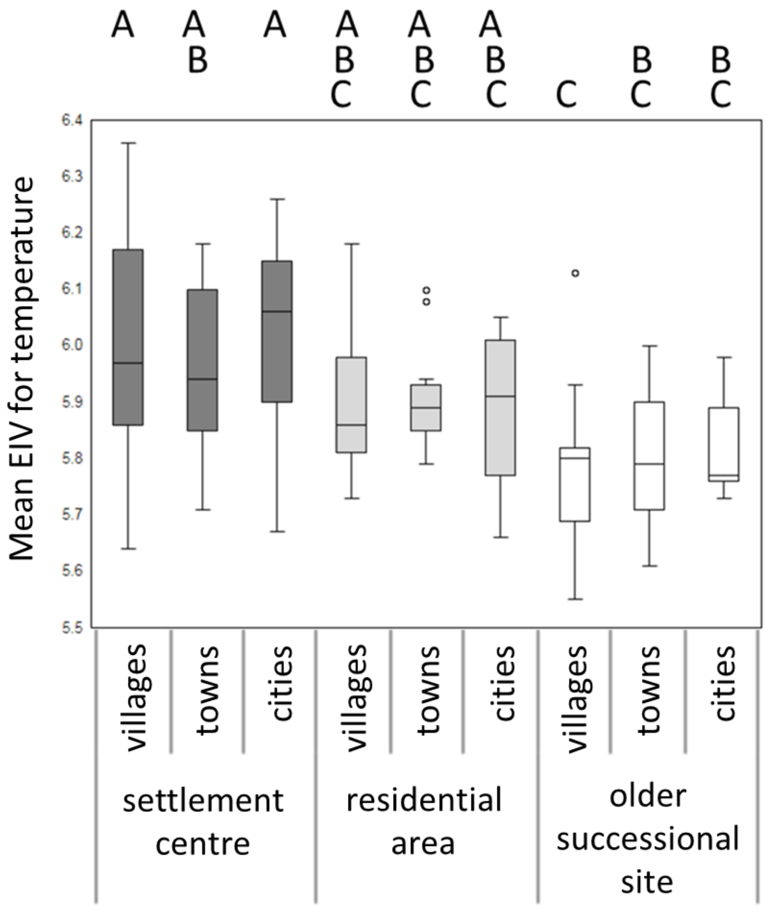


Fig. 6. Mean Ellenberg indicator values (EIV) for temperature for each plot. Boxes and whiskers indicate medians, 25–75% quantiles, non-outlier range, and outliers. Same letters indicate homogeneous groups of habitat types according to ANOVA followed by Tukey post-hoc tests at $p < 0.05$.

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 et al. 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 et al. 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 et al. 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 et al. 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.

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).

REFERENCES

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**, 683–693.

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., 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. *Proceedings of the Royal Society B*, **281**, 20133330.

Begon, M., Townsend, C. R., & Harper, J. L. (2006) *Ecology: from individuals to ecosystems*. Oxford, Blackwell.

Blair, R.B., & Launer, A.E. (1997) Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological Conservation*, **80**, 113–125.

Boecklen, W. J. (1986) Effects of habitat heterogeneity on the species-area relationships of forest birds. *Journal of Biogeography*, **13**, 59–68.

Cain, S. A. (1938) The species-area curve. *American Midland Naturalist*, **19**, 573–581.

Celesti-Grapow, L., Pyšek, P., & Jarošík, V., (2006) Determinants of native and alien species richness in the urban flora of Rome. *Diversity and Distributions*, **12**, 490–501.

Clarke, K. R., & Gorley, R. N. (2006) *PRIMER v.6: user manual/tutorial*. Plymouth, PRIMER-E.

Clergeau, P., Croci, S., & Jokimäki, J. (2004) How useful are urban island ecosystems for defining invader patterns? *Environmental Conservation*, **31**, 181–184.

Colwell, R. K., Mao, C. X., & Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.

Conell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1340.

Connor, E. F., & McCoy, E. D. (1979) The statistics and biology of the species-area relationship. *American Naturalist*, **113**, 791–833.

DAISIE (Eds.) (2009) *Handbook of alien species in Europe*. Berlin, Springer.

Davis, A. M., & Glick, T. F. (1978) Urban ecosystems and island biogeography. *Environmental Conservation*, **5**, 299–304.

Davis, M. A., Grime, J. P., & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007) A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, **13**, 527–534.

Deutschewitz, K., Lausch, A., Kühn, I., & Klotz, S. (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12**, 299–311.

Duhme, F., & Pauleit, S. (1998) Some examples of different landscape systems and their biodiversity potential. *Landscape and Urban Planning*, **41**, 249–261.

Dunn, C. P., & Heneghan, L. (2011) Composition and diversity of urban vegetation. *Urban Ecology: Patterns, Processes, and Applications* (ed. by Niemelä, J., Breuste, J. H., Elmqvist, T., Guntenspregen, G., James, P. & McIntyre, N. E.), pp. 103–115. Oxford University Press, New York.

Dupré, C., & Ehrlén, J. (2002) Habitat configuration, species traits and plant distributions. *Journal of Ecology*, **90**, 796–805.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–258.

Ernst, D., Felinks, B., Henle, K., Klotz, S., Sandermann, H., & Wiencke, C. (2000) Von der numerischen zur funktionellen Biodiversität: Neue Forschungsansätze (From numerical to functional diversity:

New research projects). *GAIA – Mitt Hermann Von Helmholtz-Gemeinschaft Deutscher Forschszentren*, **9**, 140–145.

Garaffa, P. I., Filloy, J., & Bellocq, M. I. (2009) Bird community responses along urban-rural gradients: does the size of the urbanized area matter? *Landscape and Urban Planning*, **90**, 33–41.

Gaston, K. J., Davies, Z. G., & Edmondson, J. L. (2010) Urban environments and ecosystem functions. In K. J. Gaston (Ed.), *Urban Ecology* (pp. 35–52). Cambridge, Cambridge University Press.

Gotelli, N. J., & Colwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Hobbs, R. J., & Huenneke, L. F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6** (3), 324–337.

Jackson, S. T., & Sax, D. F. (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*, **25**, 153–160.

Jäger, E. J., & Werner, K. (Eds.) (2005) *Exkursionsflora von Deutschland. Band 4. Gefäßpflanzen: Kritischer Band*. (10th ed.). München, Spektrum Akademischen Verlag, Elsevier.

Jäger, E. J., Ebel, F., Hanelt, P., & Müller, G. K. (Eds.) (2008) *Exkursionsflora von Deutschland. Band 5. Krautige Zier- und Nutpflanzen*. Berlin and Heidelberg, Spektrum Akademischen Verlag, Springer-Verlag.

Jokimäki, J., & Kaisanlahti-Jokimäki, M. L. (2003) Spatial similarity of urban bird communities: a multiscale approach. *Journal of Biogeography*, **30**, 1183–1193.

Klotz, S. (1990). Species/area and species/inhabitants relations in European cities. *Urban Ecology* (ed. by Sukopp, H., Hejný, S. & Kowarik, I.), pp. 99–104. Den Haag, SPB Academic Publishing.

Knapp, S., Kühn, I., Bakker, J. P., Kleyer, M., Klotz, S., Ozinga, W. A., Poschlod, P., Thompson, K., Thuiller, W., & Römermann C. (2009) How species traits and affinity to urban land use control large-scale species frequency. *Diversity and Distributions*, **15**, 533–546.

Kowarik, I. (1995) On the role of alien species in urban flora and vegetation. *Plant invasions: general aspects and special problems*. (ed. by Pyšek, P., Prach, K., Rejmánek, M. & Wade M.), pp. 85–103. Amsterdam, SPB Academic Publishing.

Kühn, I., & Klotz, S. (2006) Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.

Kühn, I., Brandl, R., & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.

Landsberg, H. (1981) *The urban climate*. New York, Academic Press.

Levine, J. M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852–854.

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

Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Láníková, D., Otýpková, Z., & Řehořek, V. (2012b) Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation*, **145**, 179–184.

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. *Journal of Biogeography*, **38**, 1152–1163.

Luck, G. W., & Smallbone, L. T. (2011) The impact of urbanization on taxonomic and functional similarity among bird communities. *Journal of Biogeography*, **38**, 894–906.

MacArthur, R. H., & Wilson, E. O. (1967) *The Theory of Island Biogeography*. Princeton, Princeton University Press.

Marzluff, J. M., Bradley, G., Shulenberger, E., Ryan, C., Endlicher, W., Simon, U., Alberti, M., & Zum Brunnen, C. (2008) *Urban Ecology. An International Perspective on the Interaction Between Humans and Nature*. Berlin, Springer.

McGregor-Fors, I., Morales-Pérez, L., & Schondube, J. E. (2011) Does size really matter? Species–area relationships in human settlements. *Diversity and Distributions*, **17**, 112–121.

McIntyre, N. E. (1995) Effect of forest patch size on avian diversity. *Landscape Ecology*, **10**, 85–99.

McKinney, M. L. (2002) Urbanization, Biodiversity, and Conservation. *BioScience*, **52**, 883–890.

McKinney, M. L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Niemelä, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D., & de Oca, E.M. (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, **17**, 387–401.

Oke, T. R. (1982) The energetic basis of the urban heat-island. *Quarterly Journal of the Royal Meteorological Society*, **108**, 1–24.

Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215.

Pyšek, P. (1993) Factors affecting the diversity of flora and vegetation in Central-European settlements. *Vegetatio*, **106**, 89–100.

Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.

Pyšek, P., Danihelka, J., Sádlo, J., Chrtek, J. Jr., Chytrý, M., Jarošík, V., Kaplan, Z., Krahulec, F., Moravcová, L., Pergl, J., Štajerová, K., & Tichý, L. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): Checklist update, taxonomic diversity and invasion patterns. *Preslia*, **84**, 155–255.

Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge, Cambridge University Press.

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

Stadler, J., Trefflich, A., Klotz, S., & Brandl, R. (2000) Exotic plant species invade diversity hot spots: the alien flora of north western Kenya. *Ecography*, **23**, 169–176.

ter Braak, C. J. F, & Šmilauer, P. (2002) *CANOCO reference manual and CanoDraw for Windows user`s guide: software for Canonical community Ordination, version 4.5*. New York, Microcomputer Power, Ithaca.

Tichý, L. (2002) JUICE, software for vegetation classification. Journal of Vegetation Science, **13**, 451–453.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Wania, A., Kühn, I., & Klotz, S. (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, **75**, 97–110.

Williams, C. B. (1964) *Patterns in the Balance of Nature and Related Problems in quantitative Ecology*. London and New York, Academic Press.

Winter, M., Johnson, D. H., Shaffer, J. A., Donovan, T. M., & Svedarsky, W. D. (2006) Patch size and landscape effects on density and nesting success of grassland birds. *The Journal of Wildlife Management*, **70**, 158–172.

Wittig, R. (2002) *Siedlungsvegetation*. Stuttgart, Ulmer.

Wittig, R., & Durwen, K.-J. (1982) Ecological indicator-value spectra of spontaneous urban floras. *Urban Ecology* (ed. by Bornkamm, R.,Lee, J. A. & Seaward, M. R. D.), pp. 23–31, Oxford, Blackwell Science Publishing.

Zerbe, S., Maurer, U., Schmitz, S., & Sukopp, H. (2003) Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, **62**, 139–148.

Paper III

Čeplová, N., Lososová, Z., Zelený, D., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z. Řehořek, V. & Tichý, L. (2015) Phylogenetic diversity of central European urban plant communities: effects of alien species and habitat types. *Preslia*, **87**, 1–16.

Phylogenetic diversity of central European urban plant communities: effects of alien species and habitat types

Fylogenetická diverzita rostlinných společenstev středoevropských měst: vliv nepůvodních druhů a typů stanovišť

Natálie Čeplová[1,2], Zdeňka Lososová[1], David Zelený[1], Milan Chytrý[1], Jiří Danihelka[1,3], Karel Fajmon[1], Deana Láníková[1,3], Zdenka Preislerová[1], Vladimír Řehořek[1] & Lubomír Tichý[1]

[1]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.* [2]*Department of Biology, Faculty of Education, Masaryk University, Poříčí 7, CZ-603 00 Brno, Czech Republic*
[3]*Department of Vegetation Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25/27, CZ-657 20 Brno, Czech Republic*

ABSTRACT

Urban habitats differ in their disturbance regimes, which act as an environmental filter determining plant community species composition. This is why plant communities in different urban habitats provide a suitable model for studying the effects of disturbance on phylogenetic diversity. We explore how phylogenetic diversity varies across urban plant communities and whether the introduction of alien species changes the phylogenetic diversity of resident communities of native species. In 32 cities in central Europe and Benelux countries we studied seven types of habitat subject to different disturbance regimes. Plots of 1 ha were sampled in each habitat by recording all spontaneously occurring species of vascular plants. A phylogenetic tree was constructed for all recorded species and phylogenetic diversity based on phylogenetic distances was calculated for each plot. A null model corresponding to random distribution of species on the phylogenetic tree was used to test whether phylogenetic diversity is non-random. Phylogenetic diversity was compared between the subsets of native and alien species, further divided into archaeophytes and neophytes. Phylogenetic diversity of plant communities in all the urban habitats studied was lower than random. It varied with the disturbance regime in all the species subsets (native species, archaeophytes and neophytes). Introduction of alien species reduced phylogenetic diversity of the urban plant communities studied. Archaeophytes (widespread and common species that had enough time to spread to all suitable habitats), tended to decrease phylogenetic diversity more strongly than neophytes (often rare species which are still spreading and depend on dispersal vectors). Low phylogenetic diversity of disturbed plant communities in urban habitats probably results from strong environmental filtering, which selects species from a limited number of lineages that have traits that enable them to survive in disturbed habitats.

Keywords: Archaeophytes, biological invasions, central Europe, city, neophytes, non-native, phylogenetic community structure, urban ecology, vascular plants

INTRODUCTION

Phylogenetic diversity is an important component of plant community diversity (Webb et al. 2002). Theoretically, species composition of a community can be phylogenetically clustered, random or overdispersed. Phylogenetically clustered communities are characterized by low phylogenetic diversity, because their species tend to be closely related. It is assumed that in this case environmental filters control community structure (Webb 2000, Ricotta et al. 2012b). Such a pattern is documented for vegetation strongly affected by disturbance such as coastal dune grasslands (Brunbjerg et al. 2012) or fire-maintained coastal woody vegetation (Verdú & Pausas 2007). In randomly structured communities, species composition does not significantly differ from a random subset of the regional flora. This pattern probably results from a complex interplay of factors including environmental filtering, competitive exclusion of closely related species with similar traits or presence of species from distant lineages sharing phylogenetically convergent traits (Webb et al. 2002). Random phylogenetic structure is reported for some types of meadows (Silvertown et al. 2006). In phylogenetically overdispersed communities, species are phylogenetically more distant than expected in a random sample of the regional flora. Different factors cause ovedispersion. It is suggested that phylogenetically related species or lineages share similar traits and are dependent on the same resources therefore, overdispersed community structure is a result of competitive exclusion (Webb et al. 2002 but see Mayfield & Levine 2010). However, there are several other mechanisms and factors that may affect the phylogenetic diversity of communities, including differences in regional species pools or the spatial scales studied (Brunbjerg et al. 2012, Jucker et al. 2013).

Over a short time scale, disturbance is the key factor shaping the phylogenetic diversity of plant communities (Brunbjerg et al. 2012). Strongly disturbed or early successional habitats tend to host phylogenetically clustered communities, which change to overdispersed during the course of succession (Letcher 2010, Brunbjerg et al. 2012, Letcher et al. 2012). However, disturbed habitats contain many alien species (Lososová et al. 2012a) and it is unclear how they influence phylogenetic diversity. It is hypothesized that the phylogenetic structures of native and alien species differ because of their different origin and residence time (Ricotta et al. 2009).

Urban plant communities are a suitable model system for exploring the effects of alien species and different habitats on phylogenetic diversity. Many of these communities are in recently created habitats affected by strong and frequent disturbance such as trampling or application of herbicides (Knapp et al. 2012). Urban communities are rich in native species of plants, but also contain large proportions of aliens (Pyšek 1993, Lososová et al. 2012a) often with different residence times. Residence time is the period of time that a non native species has been present in a new region (Pyšek & Jarošík 2005). Where residence time is long, various studies indicate that alien species will tend to occupy most of the suitable habitats across larger areas, and thus contribute to biotic homogenization. In contrast, recently introduced species have had less time to colonize all of their potential distribution range and all of the suitable habitats within this range and, therefore temporarily contribute to biotic differences between regions (Olden & Poff 2003, La Sorte & McKinney 2006, Williamson et al. 2009).

The occurrence of alien species can affect the phylogenetic diversity of communities in different ways. Theoretically, it may cause either clustering, for instance, if a specific (e.g. strongly disturbed) habitat is invaded by preadapted alien species that belong to the same lineages and share the same traits as extant native species (Knapp et al. 2012), or overdispersion, if native species are unable to occupy all possible niches while unrelated aliens with other traits are successful in using free resources and colonizing habitats unsuitable for native species. The latter mechanism was proposed by Darwin (1859) and is usually referred to as Darwin's naturalization hypothesis (Daehler 2001).

We suggest that most urban plant communities have a lower than random phylogenetic diversity, because of strong habitat filtering. This is supported by previous studies (Knapp et al. 2008, Ricotta et al. 2009), which show that floras of entire European and American cities are comprised of a limited number of lineages. However, cities host mosaics of different habitats, each harbouring a specific group of species and each with a different proportion of aliens (Ricotta et al. 2010, Lososová et al. 2012a). Because of their affinities to different habitats, some species in the same city never meet and never compete. Therefore the patterns of phylogenetic diversity of urban floras can be fully understood only if phylogenetic diversity is analyzed for particular habitats.

Here we test the following hypotheses: (1) As urban plant communities are subject to strong environmental filtering caused especially by disturbance, the expectation is that disturbance intensity decreases the phylogenetic diversity of these communities. (2) As urban plant communities contain a large proportion of alien species and their phylogenetic diversity is relatively low, the expectation is that the introduction of alien species decreases their phylogenetic diversity. (3) As the origin and biogeographical history of plant species in the urban environments are diverse, the expectation is that native species and groups of alien species with different residence times have different phylogenetic diversities.

MATERIALS AND METHODS

Data sampling

Data on the occurrence of vascular species of plants were collected in 32 cities, each with more than 100 000 inhabitants, in central and north-western Europe (Table 1), between 2007 and 2009 from mid June to late August. Seven habitats subject to different regimes of disturbance were sampled in each city: (i) historical city square, usually with pre-19th century houses, and with total paved or sealed areas > 90%; (ii) boulevard with 19th-century houses, lines of trees, small lawns and paved or sealed areas > 70%; (iii) residential area with compact building pattern, consisting of family houses at least 50 years old and private gardens; (iv) residential area with open building pattern, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs; (v) city park with old deciduous trees (tree cover 10–50%) and frequently mown lawns; (vi) early successional site, strongly disturbed 1–3 years ago, with prevailing bare ground and sparse vegetation cover, usually within or around construction sites; (vii) mid-successional site, abandoned for 5–15 years, dominated by perennial grassland, with scattered shrubs and young trees.

Table 1. A list of the 32 cities in central and north-western Europe studied.

City (country)	Latitude	Longitude
Amsterdam (The Netherlands)	52°21´N	4°52´E
Antwerpen (Belgium)	51°12´N	4°25´E
Augsburg (Germany)	48°22´N	10°53´E
Bern (Switzerland)	46°57´N	7°27´E
Bratislava (Slovakia)	48°08´N	17°07´E
Brno (Czech Republic)	49°12´N	16°35´E
Budapest (Hungary)	47°30´N	19°03´E
Debrecen (Hungary)	47°31´N	21°37´E
Freiburg (Germany)	48°01´N	7°51´E
Genève (Switzerland)	46°12´N	6°07´E
Groningen (The Netherlands)	53°13´N	6°34´E
Halle (Germany)	51°29´N	11°57´E
Hamburg (Germany)	53°33´N	9°57´´E
Chemnitz (Germany)	50°50´N	12°55´E
Innsbruck (Austria)	47°16´N	11°23´E
Kassel (Germany)	51°18´N	9°29´E
Köln (Germany)	50°55´N	6°56´E
Košice (Slovakia)	48°43´N	21°15´E
Kraków (Poland)	50°04´N	19°55´E
Linz (Austria)	48°17´N	14°17´E
Ljubljana (Slovenia)	46°02´N	14°30´E
Maribor (Slovenia)	46°33´N	15°39´E
München (Germany)	48°08´N	11°33´E
Oldenburg (Germany)	53°08´N	8°12´E
Ostrava (Czech Republic)	49°50´N	18°16´E
Praha (Czech Republic)	50°05´N	14°23´E
Regensburg (Germany)	49°00´N	12°06´E
Salzburg (Austria)	47°48´N	13°02´E
Stuttgart (Germany)	48°46´N	9°10´E
Szczecin (Poland)	53°25´N	14°33´E
Utrecht (The Netherlands)	52°05´N	5°07´E
Würzburg (Germany)	49°46´N	9°55´E

One plot of 1-ha size was sampled in each type of habitat in each city by recording all spontaneously occurring species of vascular plants, including garden escapes and spontaneously regenerating trees and shrubs. Planted species were not recorded. Because of restricted access to private gardens and yards, 500 m of street instead of a 1-ha plot were sampled in residential areas with a compact building pattern. For details see Lososová et al. (2011).

All species of plants recorded were classified into groups according to their origin, as native or alien (non-native) in central Europe. Alien species were further divided according to their residence time into archaeophytes (introduced before the discovery of America, ~1500 AD) and neophytes (after 1500 AD, Pyšek et al. 2002). The national lists of alien species and specialized databases were used for this classification (Klotz et al. 2002, Pyšek et al. 2002, DAISIE 2009, http://www.europe-aliens.org). For phylogenetic analyses subspecies were aggregated to the species level. Besides angiosperms the data set contained 12 species of pteridophytes and 9 of gymnosperms. These non-angiosperms were excluded from the data set, because their outlying position on the phylogenetic tree might considerably affect the values of phylogenetic diversity. The data set used in the analyses contained 1087 species, of which 544 were native, 187 archaeophytes and 356 neophytes.

Phylogenetic tree

The phylogenetic tree was constructed for the cumulative list of species spontaneously occurring in the plots sampled in the 32 cities. The tree was constructed using the online tool *Phylomatic* (Webb & Donoghue 2005; http://phylodiversity.net/phylomatic/) based on the phylogenetic information provided by Davies et al. (2004) and Bremer et al. (2009). Node ages were assigned according to *Time Tree* (Hedges et al. 2006, Hedges & Kumar 2009; http://www.timetree.org/) and Wikström et al. (2001). When there were differences between *Time Tree* and Wikström et al. (2001), priority was given to information from the more recent *Time Tree*. Branch lengths were calculated using Phylocom algorithm *bladj*.

There are several methods for constructing phylogenetic trees. We acknowledge that our tree is not resolved and also node age information is hypothetical, nevertheless for such a large set of species complete resolved phylogenetic trees are still not available and the phylogenetic information used by *Phylomatic* (Webb & Donoghue 2005) is also accepted as a pragmatic approximation of the true seed-plant phylogeny. Moreover it has been shown that there is little difference between a fully resolved molecular phylogenetic tree with age information based on sequence divergence and a tree dated using Wikström’s node ages (Wikström et al. 2001), in particular when considering community assembly patterns (Cadotte et al. 2009, Anacker & Harrison 2012, Ricotta et al. 2012a).

Statistical analysis

Average phylogenetic distinctiveness (*avpd*) was used to describe the phylogenetic diversity of communities. This originally taxonomical index (Warwick & Clarke 1998) can also be used for analysing phylogenetic data (Gerhold et al. 2008, Knapp et al. 2008, 2012). We used the following version:

$$avpd = \sum_{i>j} Br_{ij} \Big/ \frac{S(S-1)}{2}$$

where Br_{ij} is the summed length of branches connecting species i and j ($i \neq j$), and S is the total number of species ($i, j = 1, 2, \ldots, S$). *Avpd* indicates mean phylogenetic distance separating two species in a community. Lower values of *avpd* indicate that species in the community tend to be more closely related (they are located on nearby branches of the phylogenetic tree).

The null models, which correspond to a random distribution of species on the phylogenetic tree, were calculated to test if phylogenetic diversity recorded for each plot significantly differs from the phylogenetic diversity of a plot with random species composition. Values significantly lower than random indicate a phylogenetically clustered community structure, while those significantly greater than random indicate an overdispersed structure.

We used two different null models. The first null model was obtained using a random permutation of species between terminal branches across the phylogenetic tree, and subsequent calculation of *avpd* based on the random structure of each plot. For the second null model the null distribution of phylogenies was created by setting the probability of selecting a given species from the available species pool proportional to its number of occurrences in the plots sampled. In this model common species had higher probabilities of being included in the random community than rarer species (Hardy 2008).

The null distribution of $avpd_{random}$ was generated using 999 permutations for both null models, and significance was determined using a two-tailed test by comparing a reference value of *avpd* (calculated from real data) with the generated null distribution.

These analyses were calculated for each plot sampled. Further calculations were performed separately for native species, archaeophytes and neophytes occurring in each plot to determine the effect of urban habitats (and associated disturbance regimes) on groups of species with different residence times. *Avpd* values and null models were calculated using the R program, version 2.14 (R Core Team 2014), using the package *picante* (Kembel et al. 2010). The relationship between the phylogenetic diversity of communities and the proportion of alien species was tested using linear regressions.

RESULTS

Using the first null model (disregarding species frequencies) the phylogenetic structures of plant communities in particular urban habitats were clustered in most cases. Only phylogenetically clustered communities were recorded in five of the seven habitats: boulevard, residential area with compact building pattern, residential area with open building pattern, early successional site and mid-successional site. Clustered phylogenetic structures were also recorded at all but one park site and 28 (88%) city squares, while the communities at the other sites had a random structure (Fig. 1a).

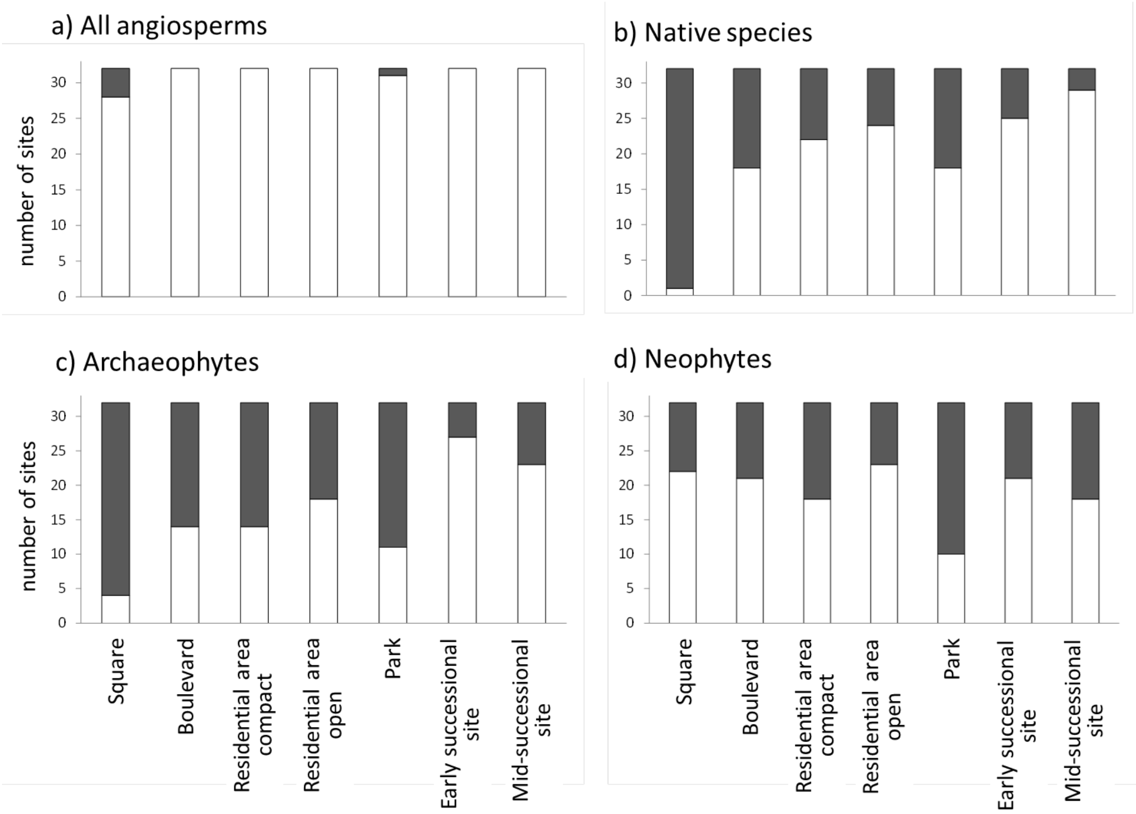


Fig. 1. Numbers of sites (1-ha plots) with a ☐ clustered and ▩ random community structure, calculated for seven urban habitats using the first null model, which does not include species frequency. No site had an overdispersed structure. Total number of sites studied per habitat was 32.

When results for native species were analysed separately, phylogenetic community structure was mostly clustered, especially at mid-successional sites, early successional sites and in residential areas with open building pattern. The lowest number of cases with a clustered pattern were recorded in squares (1; 3%), where random phylogenetic structure prevailed (Fig. 1b). Phylogenetic community structures calculated only for archaeophytes were clustered especially at both successional sites; in contrast, few sites with clustered phylogenetic structure were recorded in squares (Fig.

1c). Neophytes were phylogenetically clustered especially in residential areas with an open building pattern, in squares, boulevards and early successional sites (Fig. 1d).

Using the second null model (considering species frequencies) phylogenetic structure of plant communities in all the urban habitats was mostly random (Fig. 2a). For the native species that were analysed separately, phylogenetic community structure was also mostly random. Only random communities were recorded in squares. Several sites with clustered structure were recorded in both types of residential areas and parks, and several sites with overdispersed structures were sampled in residential areas with an open building pattern and at mid-successional sites (Fig. 2b). Phylogenetic community structure of archaeophytes was mostly random in all habitats. The largest number of cases with a clustered phylogenetic structure was recorded at successional sites, most cases with an overdispersed phylogenetic structure were in residential areas with a compact building pattern (Fig. 2c). For neophytes, all three types of phylogenetic structure were recorded in residential areas with an open building pattern and parks. Phylogenetic structure recorded for the other habitats was random and clustered, with a random structure prevailing. The largest number of communities with a clustered phylogenetic structure was recorded in squares (Fig. 2d). For detailed results see Appendix S1.

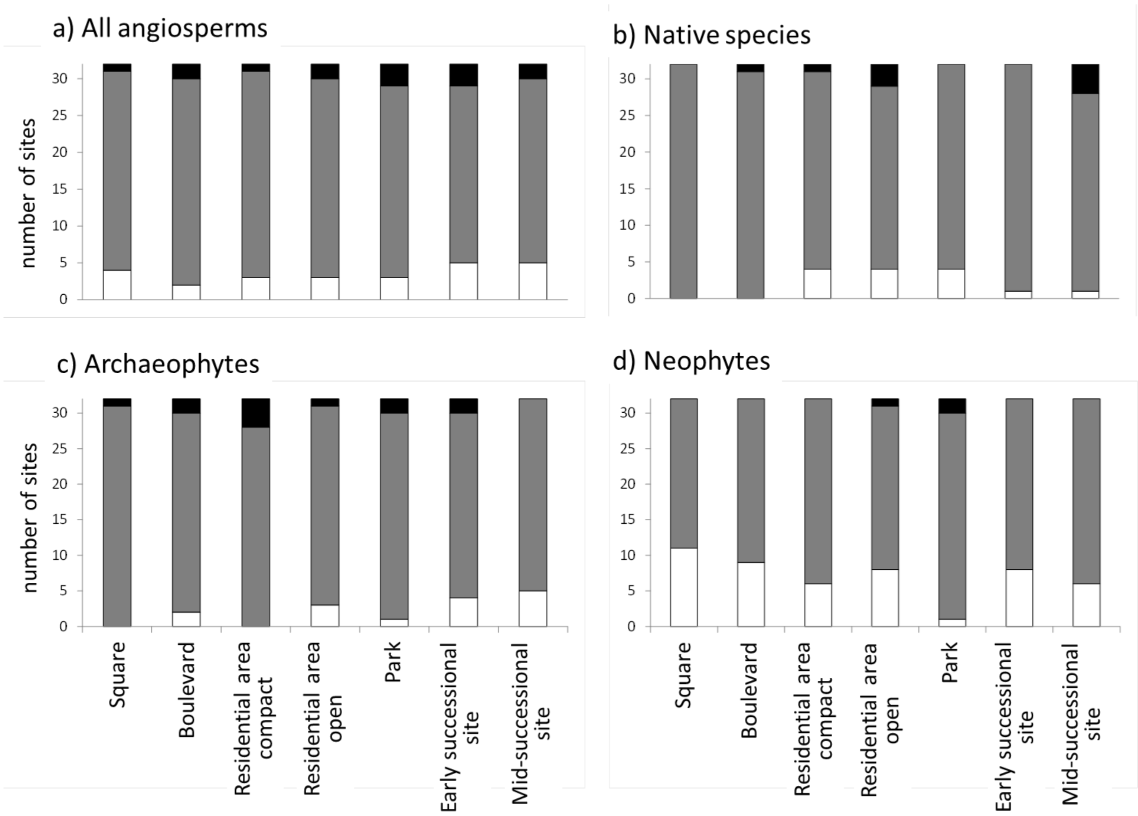


Fig. 2. Numbers of sites (1-ha plots) with a □ clustered, ■ random, or ■ overdispersed community structure, calculated for seven urban habitats using the second (frequency-based) null model. Total number of sites studied per habitat was 32.

Phylogenetic diversity of all the communities, measured in terms of their *avpd* values, increased with increasing proportion of native species. The opposite trend was found for archaeophytes and neophytes: there was a decrease in the phylogenetic diversity of the communities with an increase in the proportion of these species and the community became phylogenetically more clustered (Fig. 3). This decrease was also recorded in the data for the different habitats (Appendices S2–4), although most linear regressions were non-significant due to the small number of data points.

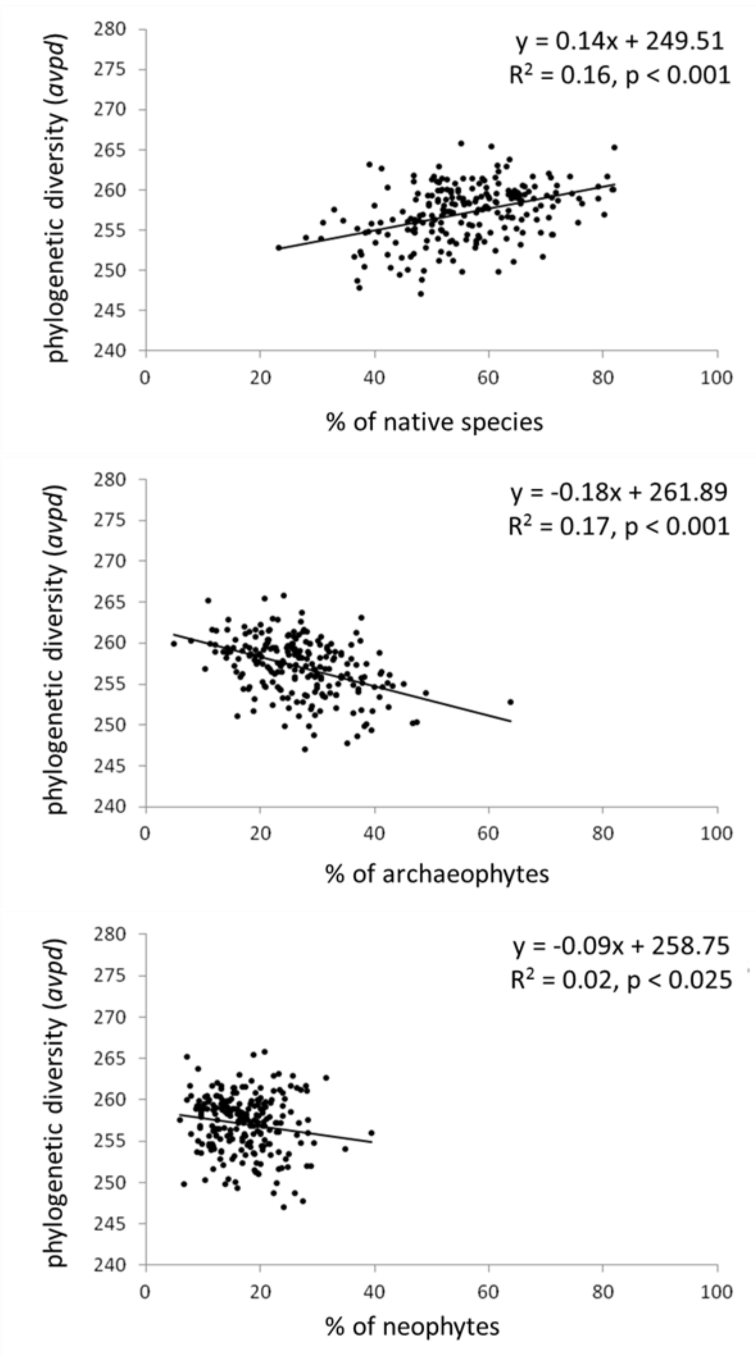


Fig. 3. Relationship between phylogenetic diversity (*avpd*) and percentages of native species, archaeophytes and neophytes in each community. Data points correspond to 1-ha plots surveyed in seven urban habitats in 32 cities (n = 224).

DISCUSSION

Hypothesis 1: Disturbance intensity decreases the phylogenetic diversity of urban plant communities through habitat filtering

Consistent with our first hypothesis, phylogenetic diversity of central European urban plant communities tended to be smaller than random. Our analyses of cumulative lists of species recorded in 7 habitats in 32 cities confirmed the results of previous studies that showed that the floras of Rome and Brussels were phylogenetically clustered (Ricotta et al. 2008, 2012b). We demonstrated that phylogenetic clustering also occurs within individual habitats. Nevertheless, we did not find any clear evidence that disturbance regime affects the phylogenetic diversity of urban plant communities. Communities were phylogenetically clustered across different habitats with different frequency or intensity of disturbance. Less disturbed habitats, such as mid-successional stages or park grasslands were clustered to a similar degree as the heavily disturbed sites in city centres. We found no clear trend related to the level of disturbance, which is similar to the findings for household yard flora in the Minneapolis-Saint Paul metropolitan area in Minnesota (Knapp et al. 2012), where phylogenies of particular urban habitats were clustered and differences among fine-scale sites had no significant effect on phylogenetic diversity. In contrast, Brunbjerg et al. (2012) suggest that clustering increases with increase in the effect of human disturbance. This pattern may hold for the natural and semi-natural plant communities included in their study, but if the level of disturbance exceeds a certain threshold, such as in most urban habitats, an increase in the frequency, magnitude or form of disturbance may no longer cause a significant change in the phylogenetic structure of these communities.

We suggest that the main reason for the low phylogenetic diversity recorded for urban plant communities is environmental filtering (e.g. Knapp et al. 2008, Ricotta et al. 2008, 2009). In cities, abiotic conditions such as climate, together with constraints on dispersal and competition, are supplemented by human-induced factors such as disturbance, soil degradation or application of chemicals (Hobbs et al. 2006, Knapp et al. 2012). These factors favour sets of ecologically similar species, which are often phylogenetically related.

We suggest that the difference between the high number of phylogenetically clustered plots predicted by the first null model (which implies a balanced phylogenetic tree in terms of species frequencies) and the low number of clustered plots predicted by the second (frequency-based) null model (which also accommodates potentially unbalanced trees) indicates that the whole urban species pool had previously been subject to some kind of severe filtering. Compared to the total urban species pool, few of the plots sampled showed an additional filtering effect, which was probably because the main filtering effect was related to the entire pool of urban species.

However, it is possible that our results are partly biased by differences in species numbers. Cumulative species lists for the whole cities are clustered, species-rich urban communities (e.g. those recorded at mid-successional sites) also tend to be clustered, but species-poor communities dominated by common species (e.g. those on city squares; Lososová et al. 2011) tend to have a random phylogenetic diversity.

Hypothesis 2: Introduction of alien species decreases the phylogenetic diversity of urban plant communities

We found that introduction of alien species decreases phylogenetic diversity of urban plant communities. The relationship between the proportion of alien species and phylogenetic diversity has only previously been studied for broadly defined types of vegetation (Winter et al. 2009, Gerhold et al. 2011) or small areas (Cadotte et al. 2010). These studies indicate that introduction of alien species is associated with a decrease in phylogenetic diversity, i.e. communities with a high proportion of aliens are significantly more clustered. Moreover, Ricotta et al. (2010) show that the more alien species there are in a community the lower its phylogenetic diversity. This is not surprising as alien species in central and north-western European cities are usually those that thrive in warmer and drier conditions, which are typical of the most disturbed urban environments.

We studied communities in habitats with a large proportion of alien species and subject to strong human impact, and our results show the same pattern. Carboni et al. (2013) assume that the influence of environmental filters can only be recognized in studies of phylogenetic diversity on a coarser scale than the one at which direct biotic interactions occur. The area of 1 ha used in this study is relatively large for interspecific interactions to be important. Moreover, in habitats with sparse herbaceous cover (squares, boulevards) biotic interactions hardly occur even at a fine scale, because species are not in direct contact. Therefore we also assume that environmental filters have a major effect.

Although increasing phylogenetic clustering is caused by both groups of alien species, it is stronger in the case of archaeophytes than neophytes. Most archaeophytes are associated with human activities and (pre)adapted to habitats affected by anthropogenic disturbance, particularly in agricultural areas (Pyšek et al. 2002). Many widespread and common archaeophytes tend to have an affinity for frequently disturbed habitats in urban areas and usually increase the phylogenetic similarity of plant communities at such sites (Ricotta et al. 2009, 2012b, Knapp et al. 2012). In contrast, neophytes are still being introduced and come from a broad spectrum of geographic regions (Pyšek et al. 2002). Many of these species are rather scarce and their occurrences are often casual, as they have not had enough time to colonize the whole range of possible habitats (Gassó et al. 2010). This may be the reason why neophytes do not affect the phylogenetic diversity of communities so much. Their occurrences are more dependent on their propagule pressure and less on environmental filtering than those of archaeophytes (Chytrý et al. 2008).

Another reason why archaeophytes decrease the phylogenetic diversity of communities could be their relationships with native species. They come from families whose representatives are also present among native species such as *Amaranthaceae* (incl. *Chenopodiaceae*) or *Apiaceae* (Pyšek et al. 2002). Neophytes reduce phylogenetic diversity less strongly because they include not only species from the same families as native species (e.g. *Fabaceae* and *Solanaceae*), but also species that belong to families that are rarely represented among native species (e.g. *Balsaminaceae*).

Hypothesis 3: Native species and groups of alien species with different residence time have different phylogenetic diversities

Our results comply with the third hypothesis stating that groups of species with different residence times have different phylogenetic diversities. Although all the groups of species studied (archaeophytes, neophytes and native species) usually have clustered phylogenetic structures according to the first null model, levels of phylogenetic clustering differ between habitats. Also the results of the frequency-based null model indicate different patterns for the groups of species and habitats studied.

The first null model, which does not include species frequency, indicates that although the native plant communities in cities are already clustered, their colonization by alien species leads to further clustering, because aliens tend to be related to native species. Ricotta et al. (2009) conclude that phylogenetic diversity of native species is higher than that of alien species, because the effects of environmental filters on native species are much weaker than on aliens. In our data, this is valid only for city squares, while in the other habitats phylogenetic diversity of native species is often lower than random and in some habitats native species are even more frequently clustered than aliens. Phylogenetic structure of native species was most frequently clustered in mid-successional stages, mostly represented by open grassland with low levels of disturbances. Number of species is higher in these habitats than in the others (see Lososová et al. 2012a), but most species belong to a few families including *Apiaceae*, *Asteraceae* and *Poaceae*.

City squares were the only habitat in which phylogenetic diversity of native species was random in nearly all cases (or in all cases predicted by frequency-based null model). Even though this habitat is subject to the strongest human impact and spontaneous plant occurrences are restricted to isolated microhabitats in pavement crevices, walls and flower pots, species from different lineages with different life strategies are able to survive there. Most species occurring in city squares are fast-growing annuals (e.g. *Herniaria glabra* and *Stellaria media*) or seedlings of native wind-dispersed trees such as *Salix* or *Populus* (Lososová et al. 2011). They belong to different families with distant positions in the phylogenetic tree. This is likely the reason for the random phylogenetic diversity of native species.

Archaeophytes are mostly represented by annual weeds belonging to the families *Brassicaceae*, *Amaranthaceae* and *Lamiaceae* (Pyšek et al. 2002). This species group occurs in cities especially at frequently disturbed, early successional sites where vegetation cover is removed and often the soil is disturbed or transferred. Only some species from the whole spectrum of central European archaeophytes are able to survive in such habitats. Other urban habitats, including city squares, boulevards or parks, are affected by different types of disturbance such as trampling, application of herbicides or cutting. Still, archaeophytes contribute to phylogenetic homogenization even in these habitats. Lososová et al. (2012b) reveal that archaeophytes contribute to homogenization of species composition of urban vegetation. Our analyses of the same data set show the same trend for phylogenetic diversity. Both findings are probably related to the characteristics of archaeophytes as a functionally and phylogenetically homogeneous group composed of species sharing a similar geographical origin, which have had enough time to colonize most of the suitable habitats in their invaded range.

In contrast, neophytes are a large group of taxa originating from a large number of families (Pyšek et al. 2002). It is therefore expected that their phylogenetic structure will be random or overdispersed. However, predictions of both null models indicate that although neophytes belong to a phylogenetically wide group of taxa, their phylogenetic structure in urban habitats is still clustered.

We showed that although the phylogenetic diversity of urban plant communities is probably controlled mainly by environmental filtering, these filters affect different species groups in different ways. While most urban archaeophytes (widespread and common species that have had enough time to colonize many suitable habitats) tend to decrease the phylogenetic diversity of urban plant communities considerably, neophytes may have not yet colonized all the suitable habitats. Together with their heterogeneous geographical and taxonomical origin they have less effect on phylogenetic diversity, but still decrease it. Our results suggest that continuing introduction of neophytes and their spread to all possible sites in future will decrease not only taxonomic and functional but also the phylogenetic diversity of urban plant communities.

ACKNOWLEDGEMENTS

We thank Carlo Ricotta and an anonymous referee for their valuable suggestions that helped improve the manuscript, and Tony Dixon for improving our English. This work was supported by the Czech Science Foundation (project 14-10723S). M. C. and J. D. were supported by Centre of Excellence PLADIAS, 14-36079G.

SOUHRN

Městské biotopy jsou vhodným modelem pro studium vlivu disturbancí a šíření nepůvodních druhů na diverzitu rostlinných společenstev. V této studii jsme se zaměřili na fylogenetickou diverzitu společenstev různých městských biotopů. Studovali jsme stanoviště ve 32 velkých městech střední a severozápadní Evropy. V každém městě bylo vytipováno sedm biotopů s různým režimem disturbancí. Na plochách o rozloze 1 ha jsme zaznamenali všechny druhy spontánně se vyskytujících cévnatých rostlin. Pro veškeré nalezené druhy byl vytvořen fylogenetický strom a pro každou studovanou plochu byla vypočtena průměrná fylogenetická vzdálenost mezi zaznamenanými druhy, tzv. fylogenetická diverzita společenstva. Pomocí dvou různých nulových modelů jsme testovali, zda je fylogenetická diverzita jednotlivých biotopů nenáhodná (odlišná od fylogenetické diverzity podmnožiny druhů náhodně vybraných z celé flóry). Dále jsme stanovili a porovnali fylogenetickou diverzitu podmnožin původních a nepůvodních druhů. Zjistili jsme, že fylogenetická diverzita rostlinných společenstev ve všech zkoumaných typech městských biotopů je menší než náhodná. Fylogenetická diverzita původních i nepůvodních druhů (jak archeofytů, tak neofytů) se mění s režimem disturbancí. Introdukce nepůvodních druhů dále snižuje fylogenetickou diverzitu městských společenstev. Tento vliv se výrazněji projevuje u archeofytů (běžné druhy, které měly v minulosti dostatek času k rozšíření na většinu vhodných stanovišť) než u neofytů (často vzácnější druhy, které se stále šíří na nová stanoviště). Menší než náhodná fylogenetická diverzita silně narušovaných městských společenstev vzniká pravděpodobně jako důsledek působení environmentálních filtrů, jako jsou například disturbance. Tyto filtry umožňují přežití pouze omezeného spektra druhů se specifickými vlastnostmi, které zpravidla pocházejí z omezeného počtu vývojových linií.

REFERENCES

Anacker, B. L. & Harrison, S. P. (2012) Historical and ecological controls on phylogenetic diversity in Californian plant communities. *American Naturalist*, **180**, 257–269.

Bremer, B., Bremer, K., Chase, M. V., Fay, M. F., Reveal, J. L., Soltis, D. E., Soltis, P. S., Stevens, P. F., Anderberg, A. A., Moore, M. J., Olmstead, R. G., Rudall, P. J., Sytsmar, J., Tank, D. C., Wurdack, K., Xiang, J. Q. Y., Zmarzty, S. & Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Brunbjerg, A. K., Borchsenius, F., Eiserhardt, W. L., Ejrnæs, R. & Svenning, J.-C. (2012) Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science*, **23**, 1082–1094.

Cadotte, M. W., Borer, E. T., Seabloom, E. W., Cavender-Bares, J., Harpole, W. S., Cleland, E. & Davies, K. F. (2010) Phylogenetic patterns differ for native and exotic plant communities across a richness gradient in Northern California. *Diversity and Distributions*, **16**, 892–901.

Cadotte, M. W., Cavender-Bares, J., Tilman, D. & Oakley, T. H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLos ONE* **4**, e5695.

Carboni, M., Münkemüller, T., Gallien, L., Lavergne, S., Acosta, A. & Thuiller, W. (2013) Darwin's naturalization hypothesis: scale matters in coastal plant communities. *Ecography*, **36**, 560–568.

Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. & Danihelka, J. (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, **89**, 1541–1553.

Daehler, C. C. (2001) Darwin's naturalization hypothesis revisited. *American Naturalist*, **158**, 324–330.

DAISIE (Eds.) (2009) *Handbook of alien species in Europe*. Berlin, Springer.

Darwin, C. (1859) *The origin of species by means of natural selection*. J. Murray, London.

Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the USA*, 101, 1904–1909.

Gassó, N., Pyšek, P., Vilà, M. & Williamson, M. (2010) Spreading to a limit: the time required for a neophyte to reach its maximum range. *Diversity and Distributions*, **16**, 310–311.
Gerhold, P., Pärtel, M., Liira, J., Zobel, K. & Prinzing, A. (2008) Phylogenetic structure of local communities predicts the size of the regional species pool. *Journal of Ecology,* **96**, 709–712.
Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H. J., Fergus, A. J. F., Ozinga, W. A. & Prinzing, A. (2011) Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist*, **177**, 668–680.
Hardy, O. J. (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology*, **96**, 914–926.
Hedges, S. B., Dudley, J. & Kumar, S. (2006) TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics*, **22**, 2971–2972.
Hedges, S. B. & Kumar, S. (2009) *The Timetree of Life*. Oxford University Press, New York.
Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
Jucker, T., Carboni, M. & Acosta, A. T. R. (2013) Going beyond taxonomic diversity: deconstructing biodiversity patterns reveals the true cost of iceplant invasion. *Diversity and Distributions*, **19**, 1566–1577.
Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P. & Webb, C. O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde*, **38**, 1–334.
Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S. E., Jakobsdottir, I., Kattge, J., King, J. Y., Klotz, S., McFadden, J. & Cavender-Bares, J. (2012) Phylogenetic and functional characteristic of household yard floras and their changes along an urbanization gradient. *Ecology*, **93** (*Supplement*), S83–S98.
Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008) Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters*, **11**, 1054–1064.
La Sorte, F. A. & McKinney, M. L. (2006) Compositional similarity and the distribution of geographical range size for assemblages of native and non-native species in urban floras. *Diversity and Distributions*, **12**, 679–686.
Letcher, S. G. (2010) Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B*, **277**, 97–104.
Letcher, S. G., Chazdon, R. L., Andrade, A. C. S., Bongers, F., van Breugel, M., Finegan, B., Laurance, S. G., Mesquita, R. C. G., Martínez-Ramoz, M. & Williamson, G. B. (2012) Phylogenetic community structure during succession: evidence from three Neotropical forest sites. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 79–87.
Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Kühn, I., Láníková, D., Otýpková, Z. & Řehořek, V. (2012a) Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. *Global Ecology and Biogeography*, **21**, 545–555.
Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Láníková, D., Otýpková, Z. & Řehořek, V. (2012b) Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation*, **145**, 179–184.
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 biota: effects of human-made habitat types on plants and land snails. *Journal of Biogeography*, **38**, 1152–1163.
Mayfield, M. M. & Levine, J. M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
Olden, J. D. & Poff, N. L. (2003) Towards a mechanistic understanding and prediction of biotic homogenization. *American Naturalist*, **162**, 442–460.
Pyšek, P. (1993) Factors affecting the diversity of flora and vegetation in central European settlements. *Vegetatio*, **106**, 89–100.
Pyšek, P. & Jarošík, V. (2005) Residence time determines the distribution of alien plants. *Invasive plants: ecological and agricultural aspects* (ed. by Inderjit), pp. 77–96, Birkhäuser Verlag, Basel.
Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.

R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
Ricotta, C., Bacaro, G., Marignani, M., Godefroid, S. & Mazzoleni, S. (2012a) Computing diversity from dated phylogenies and taxonomic hierarchies: does it make a difference to the conclusions? *Oecologia*, **170**, 501–506.
Ricotta, C., DiNepi, M., Guglietta, D. & Celesti-Grapow, L. (2008) Exploring taxonomic filtering in urban environments. *Journal of Vegetation Science*, **19**, 229–238.
Ricotta, C., Godefroid, S. & Rocchini, D. (2010) Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. *Biological Invasions*, **12**, 233–240.
Ricotta, C., Heathfield, D., Godefroid, S. & Mazzoleni, S. (2012b) The effects of habitat filtering on the phylogenetic structure of the urban flora of Brussels (Belgium). *Community Ecology*, **13**, 97–101.
Ricotta, C., La Sorte, F. A., Pyšek, P., Rapson, G. L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.
Silvertown, J., McConway, K. J., Gowing, D. J., Dodd, M. E., Fay, M. F., Joseph, J. A. & Dolphin, K. (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B*, **273**, 39–44.
Verdú, M. & Pausas, J. (2007) Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, **95**, 1316–1323.
Warwick, R. M. & Clarke, K. R. (1998) Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology*, **35**, 532–543.
Webb, C. O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145–155.
Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution and Systematics*, **33**, 475–505.
Webb, C. O. & Donoghue, M. J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.
Wikström, N., Savolainen, V. & Chase, M. W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society B*, **268**, 2211–2220.
Williamsonm, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., Stout, J. & Pyšek, P. (2009) The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*, **15**, 158–166.
Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delípetrou, P., Didžiulis, V., Hejda, M., Hulme, P. E., Lambdon, P. W., Pergl, J., Pyšek, P., Roy, D. B. & Kühn, I. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the USA*, **106**, 21721–21725.

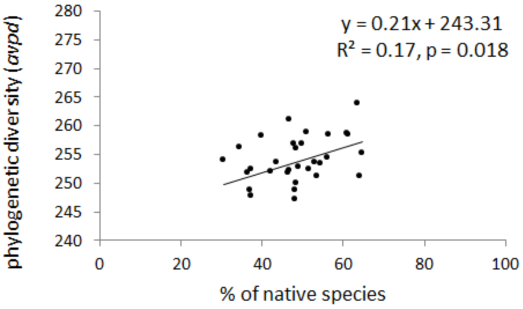
Supplementary materials, Paper III

Appendix S1. Numbers of sites (1-ha plots) with clustered, random and overdispersed community structure, calculated for seven types of urban habitats, using both types of null models. Total number of study sites per habitat was 32.

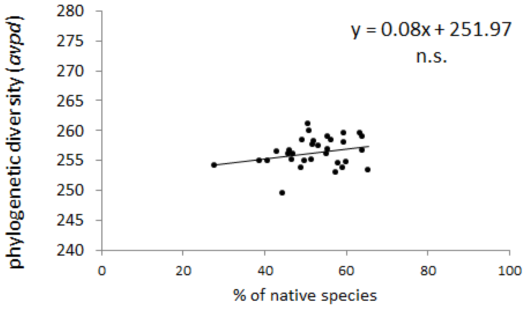
		First null model (disregarding species frequencies)						Second (frequency-based) null model					
		clustered		random		overdispersed		clustered		random		overdispersed	
		number of plots	%	number of plots	%	number of plots	%	number of plots	%	number of plots	%	number of plots	%
All species	square	28	88	4	12	0	0	4	12	27	84	1	3
	boulevard	32	100	0	0	0	0	2	6	28	88	2	6
	residential area compact	32	100	0	0	0	0	3	9	28	88	1	3
	residential area open	32	100	0	0	0	0	3	9	27	84	2	6
	park	31	97	1	3	0	0	3	9	26	81	3	9
	early successional site	32	100	0	0	0	0	5	16	24	75	3	9
	mid-successional site	32	100	0	0	0	0	5	16	25	78	2	6
Native species	square	1	3	31	97	0	0	0	0	32	100	0	0
	boulevard	18	56	14	44	0	0	0	0	31	97	1	3
	residential area compact	22	69	10	31	0	0	4	13	27	84	1	3
	residential area open	24	75	8	25	0	0	4	13	25	78	3	9
	park	18	56	14	44	0	0	4	13	28	88	0	0
	early successional site	25	78	7	22	0	0	1	3	31	97	0	0
	mid-successional site	29	91	3	9	0	0	1	3	27	84	4	13
Archaeophytes	square	4	12	28	88	0	0	0	0	31	97	1	3
	boulevard	14	44	18	56	0	0	2	6	28	88	2	6
	residential area compact	14	44	18	56	0	0	0	0	28	88	4	13
	residential area open	18	56	14	44	0	0	3	9	28	88	1	3
	park	11	34	21	66	0	0	1	3	29	91	2	6
	early successional site	27	84	5	16	0	0	4	13	26	81	2	6
	mid-successional site	23	72	9	28	0	0	5	16	27	84	0	0
Neophytes	square	22	69	10	31	0	0	11	34	21	66	0	0
	boulevard	21	66	11	34	0	0	9	28	23	72	0	0
	residential area compact	18	56	14	44	0	0	6	19	26	81	0	0
	residential area open	23	72	9	28	0	0	8	25	23	72	1	3
	park	10	31	22	69	0	0	1	3	29	91	2	6
	early successional site	21	66	11	34	0	0	8	25	24	75	0	0
	mid-successional site	18	56	14	44	0	0	6	19	26	81	0	0

Appendix S2. Relationships between phylogenetic diversity (*avpd*) and percentage number of native species (relative to the total count of all species) for individual urban habitats. Data points correspond to 1-ha plots (n = 32).
n.s. = non significant ($p \geq 0.05$)

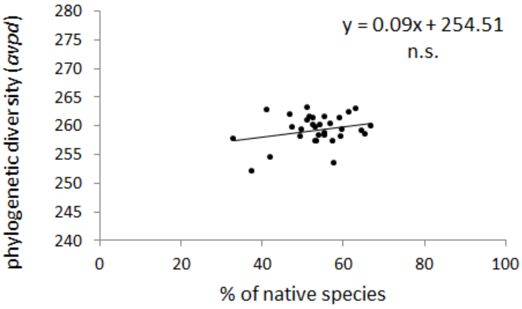
a) Square



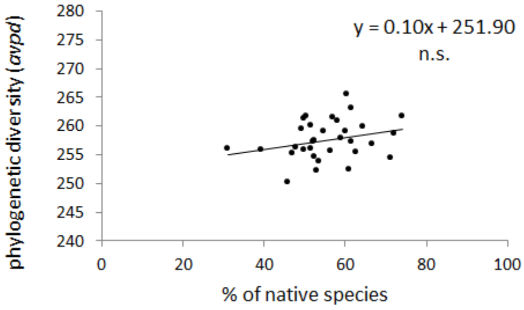
b) Boulevard



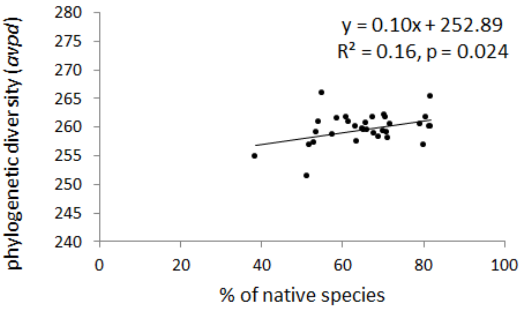
c) Residential area compact



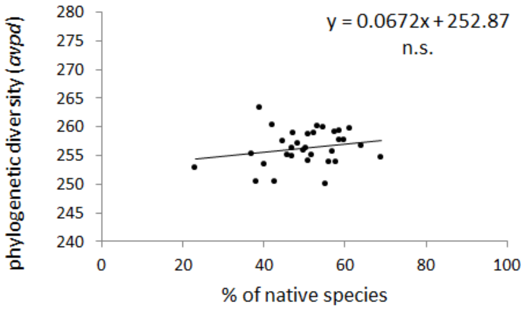
d) Residential area open



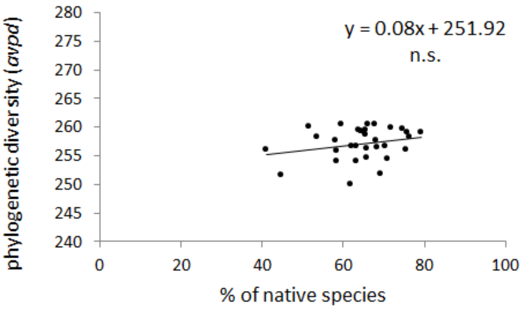
e) Park



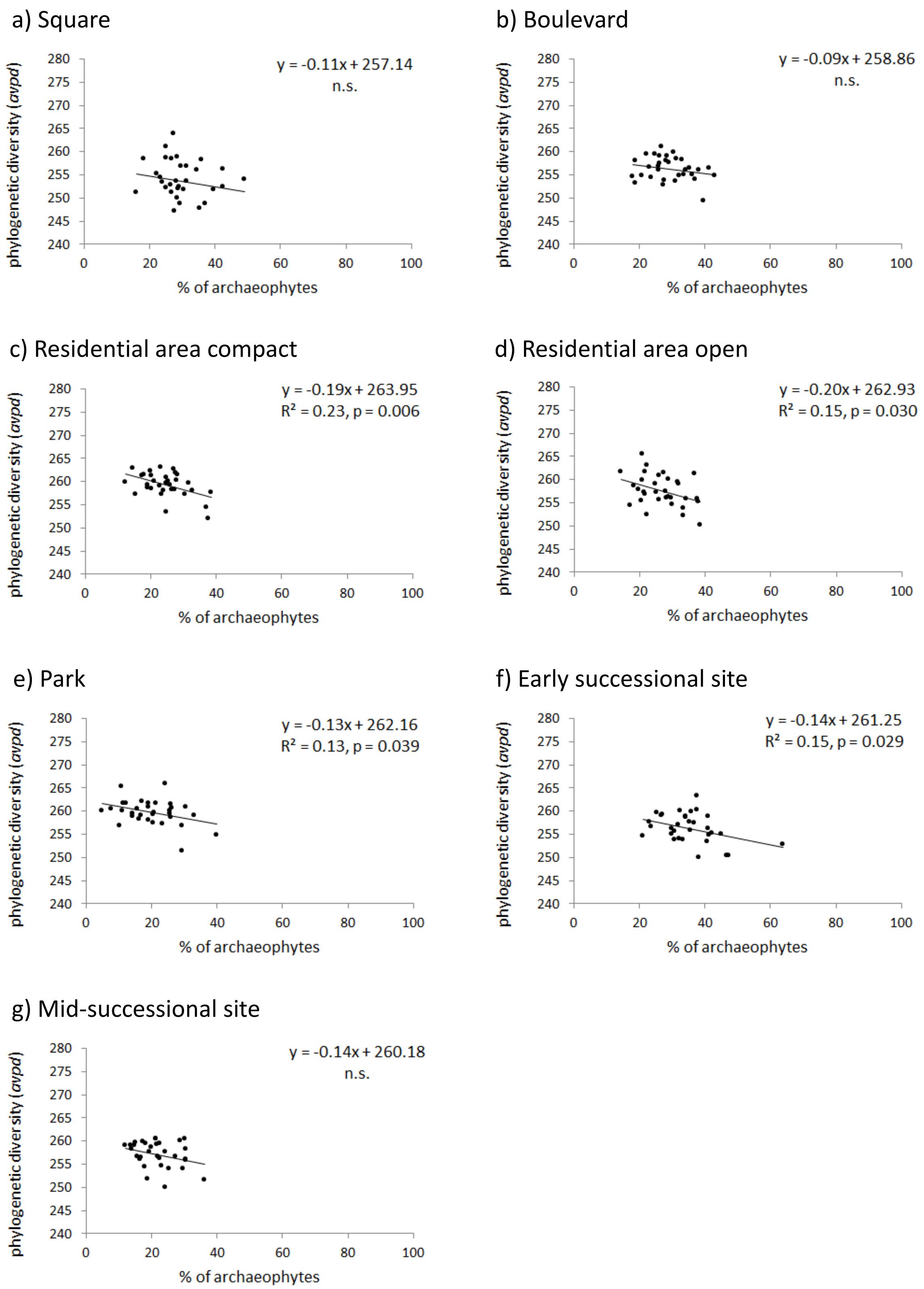
f) Early successional site



g) Mid-successional site

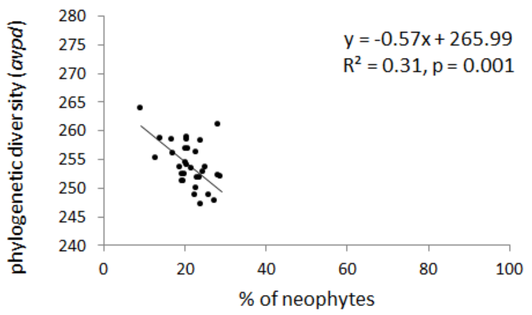


Appendix S3. Relationships between phylogenetic diversity (*avpd*) and percentage number of archaeophytes (relative to the total count of all species) for individual urban habitats. Data points correspond to 1-ha plots (n = 32).
n.s. = non significant ($p \geq 0.05$)

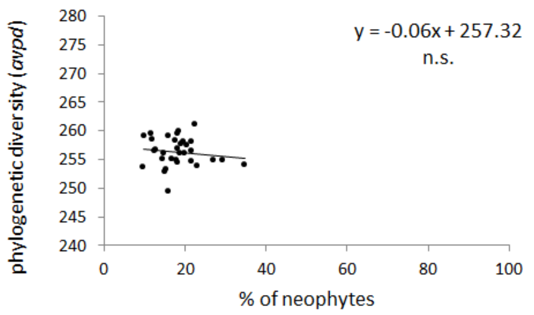


Appendix S4. Relationships between phylogenetic diversity (*avpd*) and percentage number of neophytes (relative to the total count of all species) for individual urban habitats. Data points correspond to 1-ha plots (n = 32).
n.s. = non significant ($p \geq 0.05$)

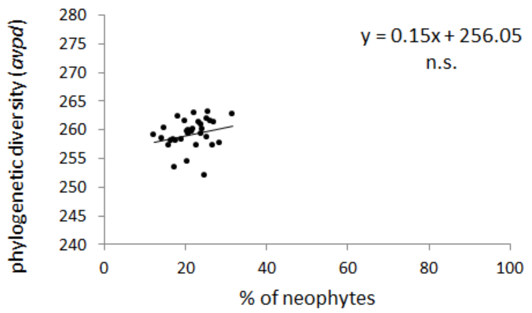
a) Square



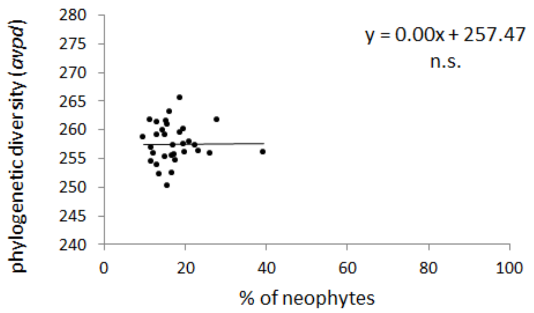
b) Boulevard



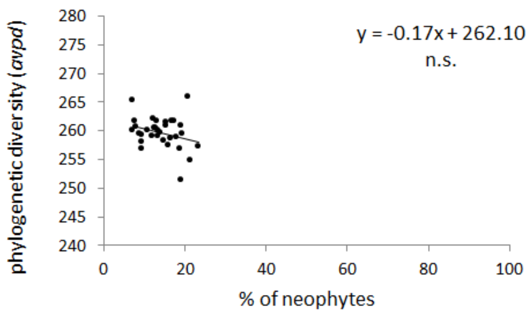
c) Residential area compact



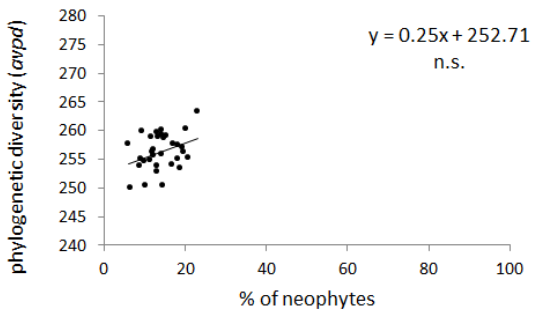
d) Residential area open



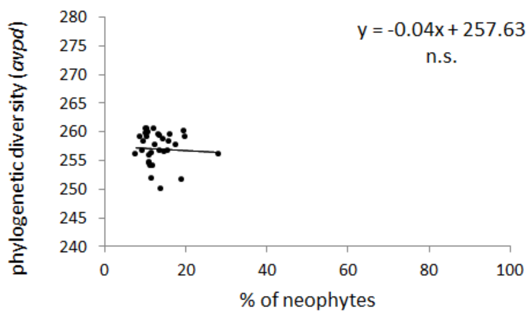
e) Park



f) Early successional site



g) Mid-successional site




PELUQUERIA SEÑORAS

Paper IV

Lososová Z., Čeplová, N., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Láníková, D., Presilerová, Z. & Řehořek, V. (2016) Is phylogenetic diversity a good proxy for functional diversity of plant communities? A case study from urban habitats. *Journal of Vegetation Science*, **27**, 1036–1046.

Is phylogenetic diversity a good proxy for functional diversity of plant communities? A case study from urban habitats

Zdeňka Lososová[1], Natálie Čeplová[,2] , Milan Chytrý[1], Lubomír Tichý[1], Jiří Danihelka[1,3], Karel Fajmon[1], Deana Láníková[1,3], Zdenka Preislerová[1] & Vladimír Řehořek[1]

[1] *Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.*
[2] *Department of Biology, Masaryk University, Poříčí 7, CZ-603 00 Brno, Czech Republic.*
[3] *Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-657 20 Brno, Czech Republic.*

ABSTRACT

Question: It is often assumed but poorly tested that patterns of phylogenetic diversity reflect functional diversity in plant communities. Here we test whether phylogeny can be used as a proxy for functional diversity in general and specifically for diversity in plant niche preferences, dispersal strategies and competitiveness-related traits.

Location: Central Europe, Belgium and the Netherlands.

Methods: We used a species composition dataset from seven urban habitats, each sampled in 32 large cities of 10 countries, and combined this with information about species phylogeny and functional traits, the latter divided into categories representing niche preferences, dispersal strategies and competitiveness.

Results: We found positive significant yet very weak relationships between phylogenetic diversity and overall functional diversity, and between phylogenetic diversity and diversity in both species dispersal strategies and competitiveness. The relationship between phylogenetic diversity and diversity in species niche preferences was not significant.

Conclusions: We suggest that the combination of multiple trait states that co-exist in urban plant communities and even within the same lineages weakens the phylogeny-function relationship. Phylogenetic diversity is a weak proxy for functional diversity of urban plant communities. For some facets of functional diversity, the phylogeny-function relationship may not apply at all.

Abbreviations: CWM = community weighted mean; FD = functional diversity; LDMC = leaf dry matter content; MNTD = mean nearest-taxon distance; MPD = mean pairwise distance; PD = phylogenetic diversity; SES = standard effect size; SLA = specific leaf area

Keywords: Central Europe, city, community assembly, competitiveness, dispersal strategy, niche preferences, species traits, urban habitats

INTRODUCTION

Phylogenetic and functional diversity are emergent community properties that help us understand community assembly processes. As information on species functional traits is often incomplete or missing, phylogenetic diversity has been proposed as a proxy for functional diversity (Harvey & Pagel 1991, Prinzing et al. 2001, Webb et al. 2002, Kraft et al. 2007, Cavender-Bares et al. 2009). The use of this proxy is based on the assumption that the phylogenetic distance between species is proportional to the evolutionary time during which distinct traits and environmental preferences could have evolved, but this would be valid only if evolutionary processes were stationary (Diniz-Filho et al. 2010). Actually, values and states of the same traits can change at different rates in different lineages, and parallel evolution of similar traits in phylogenetically distant lineages also occurs, loosening the relationship between phylogeny and function (see Webb et al. 2002, Pausas & Verdú 2010 for reviews). It has been demonstrated that the contribution of phylogeny and function to community assembly are independent to a large extent (Swenson & Enquist 2009, Bernard-Verdier et al. 2013, Cadotte et al. 2013, Pavoine et al. 2013, Purschke et al. 2013, Gerhold et al. 2015), but it has been poorly tested to what extent can phylogenetic diversity be used to estimate functional diversity.

Community assembly is influenced simultaneously by multiple trait-based processes (de Bello et al. 2013), with environmental filtering suggested to increase functional similarity among species in the species pool and competition suggested to reduce functional similarity among species coexisting at the same site (Kembel & Hubbell 2006). Although evidence for environmental filtering has often been found (e.g. Cahill et al. 2008, Götzenberger et al. 2012, Price & Pärtel 2013, Gerhold et al. 2015, Lososová et al. 2015, but see Kraft et al. 2015), studies assessing the effect of competition on functional similarity among species have often failed to find evidence of this process (Brunbjerg et al. 2012, Gerhold et al. 2015). Different filters select for different subsets of traits that can be important at different stages of the assembly process. Some traits are important for dispersal to a new site, others are important for establishment at the site and yet others are necessary for persistence of the established species in the community.

Plant communities in urban habitats are exposed to disturbance types and intensities that are different from those occurring in more natural areas. Disturbances tend to promote plant communities with a broad interspecific variation in dispersal traits such as seed mass, dispersal vectors and soil seed bank type (Grime 2006). Thus, divergence in dispersal traits may reflect recent post-disturbance re-establishment of a community. In contrast, convergence in dispersal traits may indicate a longer established community. Because the probability of species establishment is related to the number of propagules arriving in the target area (propagule pressure), human preferences in gardening or in use of different crops may act as an important filter favouring some species over others, especially in residential areas and city centres. As species planted by humans often establish spontaneous populations in urban environments, human-imposed filters are likely to influence the relationship between the phylogenetic diversity and diversity of dispersal traits in urban plant communities.

Plant height, life span, specific leaf area (SLA) and leaf dry matter content (LDMC) characterize species competitiveness. Such traits tend to be less important for colonizing new habitats but more important for persistence within an established community. The importance of competitiveness-related traits changes along environmental gradients (Spasojevic & Suding 2012, Gerhold et al. 2013, Mason et al. 2013). In undisturbed habitats, competition is expected to be strongest among species that are dissimilar in competitiveness traits: competition will be asymmetric and stronger species will win, resulting in convergence in competitiveness traits. By contrast, in disturbed habitats, competition is expected to be more symmetric with fewer winners and losers, leading to divergence in competitiveness traits (Grime 2006, Gerhold et al. 2015). Under this assumption, we can expect that strongly disturbed urban habitats will harbour communities of species with similar niche preferences but relatively high variation in competitiveness traits. In contrast, less-disturbed habitats will support functionally and phylogenetically convergent communities with over-represented values of competitiveness traits due to the exclusion of phylogenetically related weaker competitors (Swenson et al. 2007, Narwani et al. 2013, Purschke et al. 2013).

Under the assumption that species traits are phylogenetically conserved, diversity in the subsets of traits representing niche preferences, dispersal strategy and competitiveness should be related to phylogenetic diversity (Prinzing et al. 2001, Cavender-Bares et al. 2009). However, this expectation has not been sufficiently tested with real data. Some studies have been performed on the relationships between phylogenetic and functional diversity for different subsets of traits (Silvertown et al. 2006, Cahill et al. 2008, Carboni et al. 2013, Perronne et al. 2014), but there are still many uknowns. Here we use a data set on urban plant communities from ten countries of Central and Northwestern Europe to test whether community phylogenetic diversity can be used as a proxy for functional diversity. This data set contains standardized information from 32 large cities on species composition of main types of urban habitats differing in frequency and intensity of disturbances. The urban environment is a suitable model for such a test as it imposes a set of distinct filters on community structure and composition. In cities, abiotic environmental filters act simultaneously with human-imposed filters such as disturbances and human preferences for certain (often non-native) plant species. Both environmental and human-imposed filters create a strong selective pressure on the functional types of plant species establishing in urban habitats (Knapp et al. 2008, Williams et al. 2009, Kendal et al. 2012). However, human activities such as cultivation of ornamental plants and various uses of different crops that eventually establish wild populations may change fundamental biological trade-offs in urban habitats. Therefore, we hypothesize that phylogenetic diversity could be only a weak predictor of diversity of dispersal strategies and competitiveness traits among species in urban plant communities. In contrast, we hypothesize that human preferences have much weaker effect on the relationship between species niche preferences and phylogeny, therefore phylogeny can be a good proxy for niche preferences.

METHODS

Data sampling

We studied vascular plant species in 32 cities with more than 100 000 inhabitants in Belgium, the Netherlands, Germany, Poland, the Czech Republic, Slovakia, Hungary, Slovenia, Austria and Switzerland. In each city, we sampled the following seven types of urban habitats:

Square – a square in the historical city centre, usually with pre-19th century houses and with more than 90% of its area paved or sealed.

Boulevard – a broad street with 19th century houses, lines of trees, small lawns, and more than 70% of its area paved or sealed.

Residential area compact – residential area with a compact building pattern, consisting of family houses at least 50 years old and private gardens.

Residential area open – residential area with an open building pattern, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs.

Park – urban park with old deciduous trees covering 20–50% of the area and frequently mown lawns.

Early successional site – recently disturbed site with prevailing bare ground and vegetation cover less than 20%, usually in or around construction sites.

Mid-successional site – site abandoned for 5–15 years, dominated by perennial grassland with scattered shrubs and young trees.

We collected the data in 2007–2009. In each habitat, we recorded occurrences of vascular plant species in 1-ha plots of square or rectangular shape, the latter in habitat patches narrower than 100 m. Due to the restricted access to private gardens in residential areas with compact building pattern, we recorded species occurring in the accessible public area and those growing in private gardens visible from the street. In total, we sampled 224 plots (32 cities × 7 habitats). At each site, we recorded all spontaneously occurring vascular plant species, including garden escapes and seedlings of spontaneously regenerating planted trees, but we excluded species that were only represented by planted individuals (see Lososová et al. 2011 for further details). Before analyses, we deleted all the records of taxa identified only to the genus level and aggregated subspecies to the species level. The data set used for the analyses included 1065 species (Appendix S1).

Plant functional traits

For each species, we compiled information about its niche preferences and life-history traits that are relevant to plant functional ecology in the urban environment, in particular, species dispersal strategy and competitiveness (Table 1). All these characteristics are further referred to as “traits”. We used Ellenberg indicator values (Ellenberg et al. 1992), which reflect realized ecological niches, to characterize the species niche preferences with respect to light, temperature, continentality, moisture, soil reaction and nutrients. We characterized the levels of disturbance and stress the species are adapted to using Grime’s (1979) life-history strategy categories (competitive, stress-tolerant and ruderal). Species with intermediate life strategy were included in two (or three) categories with 0.5 (or 0.33) weight for each. We further classified species into three categories according to their immigration pathways to the urban habitats: ornamental plants escaping from cultivation, crops escaping from cultivation and non-cultivated species. The life-history traits comprised mean plant height at maturity (m), specific leaf area (SLA; $mm^2 \cdot mg^{-1}$), leaf dry matter content (LDMC; $mg \cdot g^{-1}$), life form, dispersal type, seed mass (mg) and seed bank type. Dispersal type, seed mass and seed bank type reflect the species ability to colonize new habitats or to regenerate from a persistent seed bank after disturbance. Plant height, SLA, LDMC and life form reflect species competitiveness (Williams et al. 2015). The trait information was obtained from the LEDA database (Kleyer et al. 2008).

Phylogeny

We constructed a dated phylogenetic tree including all 1065 plant species using the software Phylomatic and Phylocom (Webb & Donoghue 2005, Webb et al. 2008). As a backbone we used the angiosperm consensus tree of Davies et al. (2004) and more recent systematical information from the Angiosperm Phylogeny Group (http://www.mobot.org/mobot/research/

apweb/). We assigned node ages according to Time Tree (www.timetree.org), which is a public information database allowing exploration of divergence times among organisms. We computed branch lengths with a branch length algorithm (bladj) in Phylocom software. Although such a phylogenetic tree is not resolved in detail and node-age information is hypothesized, we used it because completely resolved phylogenetic trees are not yet available for such a large set of species. The phylogenetic information used by Phylomatic represents a pragmatic approximation of the real seed plant phylogeny (Webb & Donoghue 2005). Furthermore, phylogenetic structure or diversity metrics are more sensitive to basal phylogenetic uncertainties than to terminal ones (Swenson 2009).

Analyses

We calculated the K statistic of the phylogenetic signal (Blomberg et al. 2003) for each trait based on the variance of phylogenetically independent contrasts. To determine if phylogenetic signal is statistically significant, we compared the variance of contrasts for the real data with the values obtained after the trait data were randomly permuted 999 times across the tips of the phylogenetic tree.

Table 1. Functional traits and their characteristics. Blomberg's *K* together with respective *p* values represent the phylogenetic signal (values higher than random are in bold).

Trait	Type	Number and proportion of species with available information	Mean value	Blomberg's K	p value
Niche preferences					
Ellenberg indicator value for light	categorial	788 (74.0%)	6.9	**0.10**	**0.001**
Ellenberg indicator value for temperature	categorial	639 (60.0%)	6	**0.07**	**0.001**
Ellenberg indicator value for continentality	categorial	694 (65.1%)	4	**0.06**	**0.037**
Ellenberg indicator value for moisture	categorial	735 (69.0%)	5	**0.07**	**0.001**
Ellenberg indicator value for soil reaction	categorial	603 (56,6%)	6.6	**0.07**	**0.025**
Ellenberg indicator value for nutrients	categorial	724 (68.0%)	5.1	**0.11**	**0.001**
Competitive life strategy	categorial	918 (86.2%)	0.55	**0.09**	**0.001**
Stress-tolerant life strategy	categorial	918 (86.2%)	0.17	**0.08**	**0.001**
Ruderal life strategy	categorial	918 (86.2%)	0.28	**0.09**	**0.001**
Dispersal strategy					
Non-planted species	nominal	1065 (100%)	0.67	**0.09**	**0.001**
Planted as ornamental plant	nominal	1065 (100%)	0.28	**0.11**	**0.001**
Planted as crop	nominal	1065 (100%)	0.05	0.07	0.075
Anemochory	nominal	890 (83.6%)	0.15	**0.14**	**0.001**
Zoochory	nominal	890 (83.6%)	0.48	**0.15**	**0.001**
Hemerochory	nominal	890 (83.6%)	0.24	**0.13**	**0.001**
Autochory	nominal	890 (83.6%)	0.13	**0.13**	**0.001**
Seed mass	continuous	868 (81.5%)	64.3	**0.15**	**0.004**
Transient seed bank	nominal	698 (65.5%)	0.6	**0.07**	**0.001**
Short-term-persistent seed bank	nominal	698 (65.5%)	0.15	0.06	0.119
Long-term-persistent seed bank	nominal	698 (65.5%)	0.1	0.06	0.195
Competitiveness					
Plant height	continuous	977 (91.7%)	2.03	**0.85**	**0.001**
Phanerophyte	nominal	1033 (97.0%)	0.16	**0.53**	**0.001**
Chamaephyte	nominal	1033 (97.0%)	0.06	**0.09**	**0.001**
Geophyte	nominal	1033 (97.0%)	0.05	**0.20**	**0.001**
Hemicryptophyte	nominal	1033 (97.0%)	0.46	**0.11**	**0.001**
Therophyte	nominal	1033 (97.0%)	0.25	**0.11**	**0.001**
Liana	nominal	1033 (97.0%)	0.02	**0.18**	**0.001**
Specific leaf area (SLA; $mm^2 \cdot mg^{-1}$)	continuous	798 (74.9%)	24.7	**0.13**	**0.001**
Leaf dry mass content (LDMC; $mg \cdot g^{-1}$)	continuous	743 (69.8%)	208.3	**0.09**	**0.001**

We measured functional diversity (FD) and phylogenetic diversity (PD) of each plot using the **m**ean **p**airwise **d**istance of all possible species pairs (*mpd*; Pavoine & Bonsall 2011). For FD, we calculated the functional distance matrix from Gower (1971) distances as described by Podani (1999). This measure uses principal coordinate analysis (PCoA) to calculate PCoA axes which are then used to compute FD. This enabled information from different trait types (continuous, ordinal or binary) to be summarized.

In addition to *mpd*, we also measured phylogenetic diversity using the **m**ean **n**earest **t**axon **d**istance (*mntd*; Webb et al. 2002), with both *mpd* and *mntd* obtained from a distance matrix of a pruned phylogenetic tree. *Mpd* calculates mean phylogenetic distance between all species pairs for each community, whereas *mntd* measures the mean phylogenetic distance between each species and its phylogenetically nearest neighbour in the community. These two indices determine phylogenetic diversity on two scales: *mpd* measures overall relatedness of species, whereas *mntd* especially reflects the relatedness closer to the tips of the phylogenetic tree. Thus, the latter is more sensitive to the effects of biotic interactions between closely related species.

We used the standardized effect size (*ses*), which is independent of species richness (Pavoine & Bonsall 2011) to quantify the difference between the observed diversity measure and the distribution of the diversity measure for 999 random-permutation-based communities with constant species richness. *Ses* was calculated as (observed diversity – mean of randomized diversity)/standard deviation of randomized diversity. Negative or positive values of *ses* indicate lower or higher diversity than random, respectively. For all randomization tests all species recorded across all cities were used. For each plot, we further computed the community-level weighted means of trait values (CWM) to identify functional composition of individual communities. For continuous traits (e.g. plant height, Table 1), CWM was calculated as the mean of trait values of all species present in the community. For ordinal and binary traits (e.g. ornamental plant), the numbers of occurrences of each class were used. The species with missing trait values were excluded from these analyses.

Linear regressions were used to quantify the relationship between functional and phylogenetic diversity. The differences in taxonomic, functional and phylogenetic diversities were compared among urban habitat types. The goal was to detect variability in FD and PD among habitats with different regimes and intensities of human land use. The differences in FD among plots belonging to the same habitat type were tested using ANOVA with Tukey post-hoc tests.

Spearman correlation coefficients were used to characterize the importances of individual community-level weighted means of trait values (CWM) for functional diversity of the target community (FD).

All the analyses were run using the R program, version 3.1.3 (R Core Team 2015). Blomberg's K, both functional indices and phylogenetic indices were computed using the R package *picante* (Kembel et al. 2010).

RESULTS

Phylogenetic diversity as a proxy for functional diversity

Both phylogenetic diversity indices (*ses mpd* and *ses mntd*) were positively significantly yet weakly related to the functional diversity index *ses* FD ($R^2 = 0.074$, $p < 0.001$ for *ses mpd* and $R^2 = 0.083$, $p < 0.001$ for *ses mntd*; Fig. 1). Significance was slightly weaker or disappeared when individual trait groups were considered separately. Both phylogenetic indices predicted the variation in traits indicating dispersal strategy and competitiveness of plant species in urban habitats very poorly, and neither could predict the variation in species niche preferences or traits that indicate these preferences (Fig. 1). The variation explained by phylogeny was very low for dispersal strategy and for competitiveness ($R^2 = 0.030$, $p < 0.05$ for *ses mpd*(dispersal) and $R^2 = 0.078$, $p < 0.001$ for *ses mpd*(competitiveness); $R^2 = 0.076$, $p < 0.001$ *mntd*(dispersal) and $R^2 = 0.157$, $p < 0.001$ *mntd*(competitiveness); Fig. 1). We found almost no relationships between functional and phylogenetic diversity indices in the analyses within individual urban habitats (Appendix S2).

Differences among urban habitats

In all urban habitats, functional diversity was lower than random (*ses FD* < 0), which means that all the studied plant communities were functionally more or less convergent (Fig. 2). The highest degree of convergence was at successional sites. Convergence also appeared in all habitats for the trait subsets representing niche preferences and disperal strategies, while both convergence and divergence were found for the subset of traits related to species competitiveness (Fig. 2). The highest values of functional diversity in competitiveness-related traits were found in both types of residential areas and in urban parks.

Importance of individual traits for functional diversity

Traits used in the analyses varied widely in their degree of associated phylogenetic signal (Table 1). The strongest phylogenetic signals were found for the phanerophyte (tree or shrub) life form and for plant height, i.e. traits responsible for species competitiveness. Very weak phylogenetic signals were found for niche preferences and dispersal strategies. Species planting as crops and presence of persistent soil seed banks (i.e., either short- or long-term persistent as opposed to transient) were not related to phylogeny. Functionally diverse urban plant communities were characterized by spontaneously occurring (i.e., not directly planted by humans) ornamental plants with high temperature requirements (Table 2). Species in these communities tended to be relatively tall, and often phanerophytes, chamaephytes, or therophytes with ruderal life-history strategy. The prevailing dispersal type was by humans and the seed bank was short-term persistent or long-term persistent. In contrast, functionally homogeneous communities were composed mainly of spontaneously occurring hemicryptophytes or geophytes, which prefer humid conditions with abundant light. They were mainly competitors with high LDMC values, dispersed through zoochory and with transient soil seed banks (Table 2).

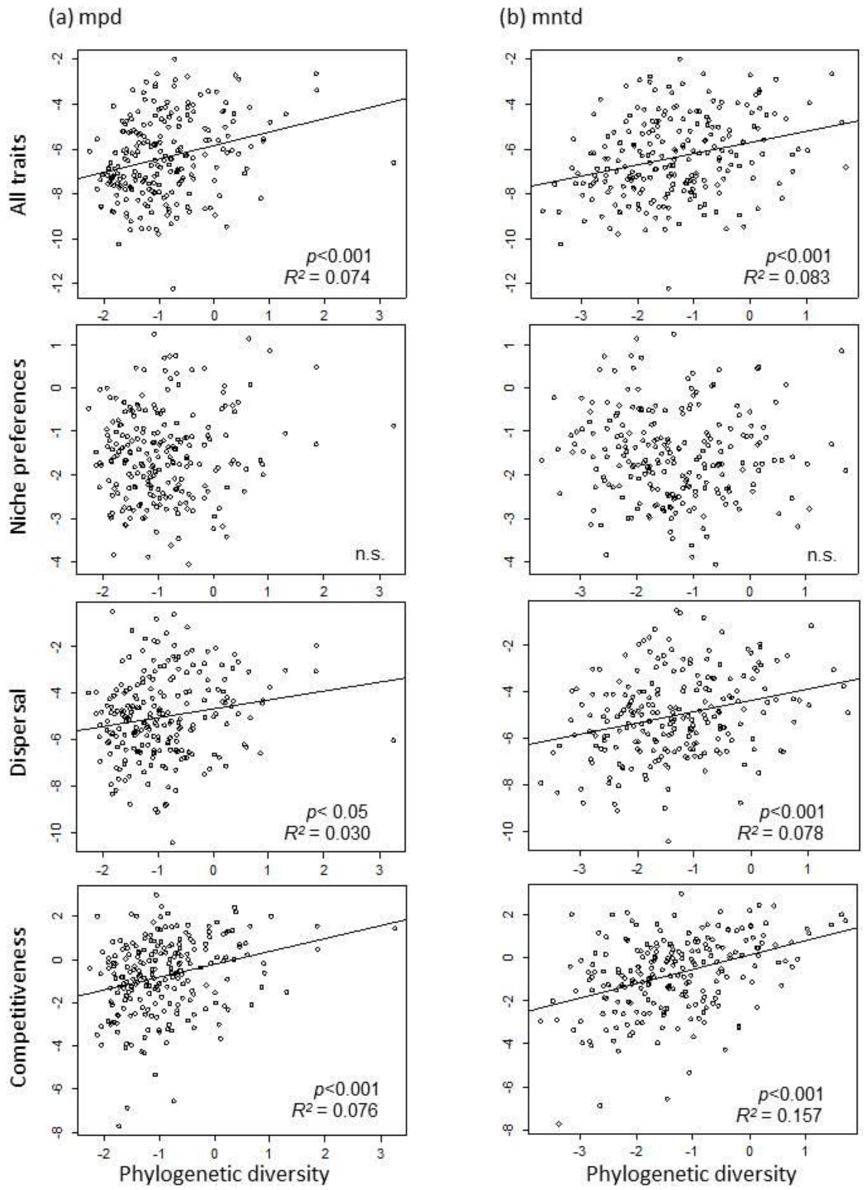


Fig. 1. Relationships between functional diversity (*ses FD* of all traits, species niche preferences, dispersal strategies and competitiveness traits) and phylogenetic diversity calculated as (a) *ses* of mean pairwise distance (*mpd*) and (b) *ses* of mean nearest taxonomic distance (*mntd*).

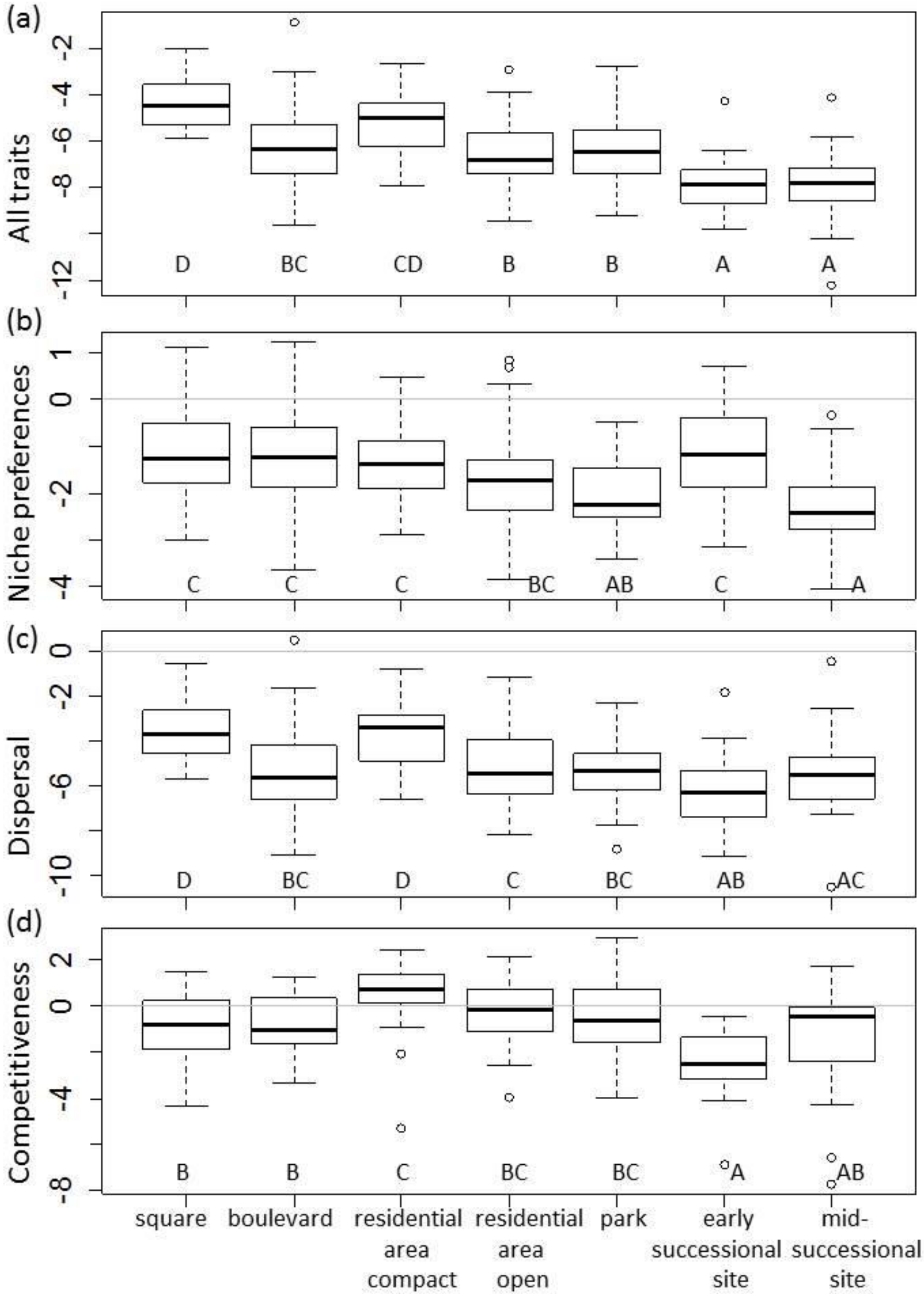


Fig. 2. Functional diversity of plant communities in individual urban habitats. Standard effect sizes (*ses*) are shown for the dataset of all plant functional traits and for subsets of traits that characterize species niche preferences, dispersal strategies and competitiveness. Boxes and whiskers indicate medians, 25–75% quantiles, non-outlier range, and outliers. Each letter indicates a homogeneous groups of habitat types according to ANOVA followed by Tukey post-hoc tests at $p < 0.05$.

Table 2. Correlations between community-weighted means of particular trait values (CWM) and community functional diversity expressed as FD index. Significance levels: *** = p<0.001; ** = p< 0.01; * = p< 0.05; n.s. = non-significant.

Trait	Spearman's correlation coefficient	Significance
Planted as ornamental plant	0.57	***
Ellenberg indicator value for temperature	0.39	***
Plant height	0.36	***
Phanerophyte	0.31	***
Hemerochory	0.31	***
Short-term-persistent seed bank	0.28	***
Therophyte	0.19	**
Ruderal life strategy	0.18	**
Chamaephyte	0.18	**
Long-term-persistent seed bank	0.14	*
Autochory	0.13	n.s.
Ellenberg indicator value for nutrients	0.12	n.s.
Seed mass	0.11	n.s.
Liana	0.10	n.s.
Specific leaf area (SLA)	0.10	n.s.
Anemochory	0.07	n.s.
Stress-tolerant life strategy	-0.04	n.s.
Planted as crop	-0.07	n.s.
Ellenberg indicator value for soil reaction	-0.11	n.s.
Ellenberg indicator value for continentality	-0.12	n.s.
Ellenberg indicator value for light	-0.15	*
Leaf dry mass content (LDMC)	-0.15	*
Geophyte	-0.18	**
Competitive life strategy	-0.18	**
Transient seed bank	-0.19	**
Ellenberg indicator value for moisture	-0.22	***
Zoochory	-0.28	***
Hemicryptophyte	-0.52	***
Non-planted species	-0.52	***

DISCUSSION

Phylogenetic diversity as a proxy for functional diversity

In this study we asked whether phylogenetic diversity of plant communities can be used as a proxy for functional diversity. The results suggest that the relationship between these two diversity measures is very weak for European urban plant communities. It becomes even weaker when assessed for subsets of traits. Such results are in accordance with some previous studies (Kraft et al. 2007, Bernard-Verdier et al. 2013, Carboni et al. 2013, Pavoine et al. 2013).

Our analyses only slightly support the general expectation of ecological similarity among closely related species (Harvey & Pagel 1991, Prinzing et al. 2001, Webb et al. 2002, Kraft et al. 2007). Strong phylogenetic signal in traits is necessary to predict functional diversity from phylogenetic diversity (Swenson & Enquist 2009). In our study, traits varied widely in the degree to which they showed phylogenetic signal, with traits responsible for species competitiveness (e.g. plant height and life form) possessing strong phylogenetic signal and traits indicating niche preferences and dispersal strategies showing much weaker signal. Consistently with this, we found no relationship between phylogenetic diversity and traits related to niche preferences or dispersal traits, and only a very weak relationship between phylogenetic diversity and traits determining competitiveness. Traits related to niche preferences are expected to show different evolutionary patterns than traits detemining competitiveness, because coexisting species must evolve similarities in the former and differences in the latter (Silvertown et al. 2006, Cavender-Bares et al. 2009, but see Mayfield & Levine 2010, Kraft et al. 2015). In accordance with this expectation, we obtained different evolutionary patterns for niche preferences and competitiveness traits. However, we detected an opposite pattern in which closely related species do not share similar niche preferences, whereas they do have similar traits connected with competitiveness.

We observed low functional diversity within all the studied urban communities and very low variation in functional diversity among communities. This contrasts with the high variation in species richness among urban habitats (Lososová et al. 2011) and could imply that the whole urban floras are under strong human-induced and environmental filters (Knapp et al. 2008, Ricotta et al. 2008, 2009, 2012, Čeplová et al. 2015). However, there are also other potential explanations of low functional diversity (Kraft et al. 2015). Kunstler et al. (2012) showed that low functinal diversity could not be infered from environmental filtering but it could be due to competition-based sorting of species with different competitive abilities.

Our findings indicate that strong human-induced and environmental filtering in urban habitats causes very low variation (strong convergence) in species niche preferences. The detected variation in this part of functional diversity is unrelated to phylogeny. Our results obtained for niche preferences thus support the idea that phylogenetic diversity cannot be used as a proxy for functional diversity (Emerson & Gillespie 2008, Bernard-Verdier et al. 2013, Carboni et al. 2013, Mason et al. 2013) and contradict the expectation from the literature that niche preferences may be better predicted from phylogeny than competitiveness traits (Silvertown et al. 2006, Kraft et al. 2007, Emerson & Gillespie 2008).

We hypothesized that human activities such as cultivation of ornamental plants in urban areas may change fundamental biological trade-offs such as dispersal strategy versus establishment success (Williams et al. 2015) and consequently reduce the strength of the relationship between phylogeny and dispersal traits in urban plant communities. This was supported by our results. The phylogenetic signal for dispersal traits appears to be weakened by human activities, for example by repeated sowing of species from different lineages but with similar seed characteristics and good germination ability. Such functional types are overrepresented in cities independently of the lineages to which they belong. Moreover, the more uncommon a genus is for a given area, the more attractive it may be for the garden market. In spite of these effects, the relationship between phylogenetic diversity and dispersal trait diversity was stronger than that between phylogenetic diversity and niche preference diversity and comparable with that between phylogenetic diversity and competitiveness trait diversity.

Finally, we expected no relationship between phylogenetic and functional diversity in competitiveness traits. Our results based on both phylogenetic indices do not support this expectation and differ from the results of a previous study of semi-natural grasslands (Cahill et al. 2008) or a study with simulated data (Kraft et al. 2007). In our case, traits responsible for niche preference were found to be less phylogenetically conserved than traits related to competitiveness. For this reason, phylogenetic diversity reflects the variability in competitiveness better than the variability in species niche preferences or dispersal strategies.

Individual urban habitat types differ in the phylogenetic and functional diversity of their plant communities, but the diversity values are very low, suggesting the importance of environmental and human-induced filtering at the scale of the whole urban flora (e.g. Knapp et al. 2008, 2012, Ricotta et al. 2008, 2009, Čeplová et al. 2015).

Limitations of the data used

We used only limited set of traits while other traits not included in this study (e.g. pollination mode or leaf morphology, Knapp et al. 2008, 2009, Kendal et al. 2012) may also shape urban plant community assembly and change the relationships between phylogenetic and functional diversity. However, the traits used here are clearly among the most important ones for species niche preferences, dispersal strategies and competitiveness (Grime 2006, Williams et al. 2015). Therefore we believe that inclusion of other traits would change the results only slightly.

We are also aware of the fact that our results might be limited by the lack of species abundance data and the low phylogenetic resolution. Results for K statistics tend to be overestimated due to the lack of phylogenetic resolution (Davies et al. 2012). Thus, were the phylogenetic resolution higher, K values would tend to decrease even more, and the correlation between phylogenetic and functional diversity could be lower if the phylogenetic data were improved. Therefore we don’t expect better phylogenetic data would change our conclusions.

CONCLUSIONS

We conclude that in urban plant communities, phylogenetic diversity is a very weak predictor of functional diversity. To a small extent, phylogenetic diversity reflects the diversity in dispersal strategies of species and in competitiveness-related traits, but it does not reflect the diversity in species niche preferences. Therefore we do not recommend using phylogenetic diversity as a proxy for functional diversity in human-made habitats.

ACKNOWLEDGEMENTS

We thank Tomáš Čejka, Michal Horsák, Tomáš Juřička, Lucie Juřičková and Stanislav Němejc for their help in the field, Ondřej Hájek for map preparation, David Zelený for statistical advice, and Jonathan Rosenthal for English proofreading. This work was supported by the Czech Science Foundation (project 14-10723S).

REFERENCES

Bernard-Verdier, M., Flores, O., Navas, M. L. & Garnier E. (2013) Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. *Journal of Vegetation Science*, **24**, 877–889.

Blomberg, S.P., Garland, T. Jr. & Ives, A. R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.

Brunbjerg, A. K., Borchsenius, F., Eiserhardt, W. L., Ejrnæs, R. & Svenning, J.-C. (2012) Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science*, **23**, 1082–1094.

Cadotte, M., Albert, C.H. & Walker, S. C. (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters*, **16**, 1234–1244.

Cahill, J. F., Kembel, S. W., Lamb, E. G & Keddy, P. A. (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology Evolution and Systematics*, **10**, 41–50.

Carboni, M., Acosta, A. T. R. & Ricotta, C. (2013) Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? *Journal of Vegetation Sciences*, **24**, 932–941.

Cavender-Bares, J., Kozak, J. K. H., Fine, P. V. A. & Kembel, S. W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Čeplová, N., Lososová, Z., Zelený, D., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z., Řehořek, V. & Tichý, L. (2015) Phylogenetic diversity of Central European urban plant communities: effects of alien species and habitat types. *Preslia*, **87**, 1–16.

Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. (2004) Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the USA*, **10**, 1904–1909.

Davies, T. J., Kraft, N. J. B., Salamin, N. & Wolkovich, E. M. (2012) Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology*, **93**, 242–247.

de Bello, F., Vandewalle, M., Reitalu, T., Lepš, J., Prentice, H. C., Lavorel, S. & Sykes, M. T. (2013) Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology*, **101**, 1237–1244.

Diniz-Filho, J. A. F., Terribile, L. C., Cruz, M. J. R. d. & Vieira, L. C. G. (2010) Hidden patterns of phylogenetic non-stationarity overwhelm comparative analyses of niche conservatism and divergence. *Global Ecology and Biogeography*, **19**, 916–926.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–258.

Emerson, B. C. & Gillespie, R. G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, **23**, 619–630.

Gerhold, P., Price, J. N., Püssa, K., Kalamees, R., Aher, K., Kaasik, A. & Pärtel, M. (2013) Functional and phylogenetic community assembly linked to changes in species diversity in a long-term resource manipulation experiment. *Journal of Vegetation Science*, **24**, 843–852.

Gerhold, P., Cahill, J. F. Jr., Winter, M., Bartish, I. V. & Prinzing, A. (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, **29**, 600–614.

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K. & Zobel, M. (2012) Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews*, **87**, 111–127.

Gower, J. C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, **27**, 857–871.

Grime, J. P. (1979) *Plant strategies and vegetation processes*. Wiley, Chichester, UK.

Grime, J. P. (2006) Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.

Harvey, P. H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.

Kembel, S. W. & Hubbell, S. P. (2006) The phylogenetic structure of a Neotropical forest tree community. *Ecology*, **87**, S86–S99.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P. & Webb, C. O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.

Kendal, D., Williams, K. J. H. & Williams, N. S. G. (2012) Plant traits link people's plant preferences to the composition of their gardens. *Landscape and Urban Planning*, **105**, 34–42.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P, Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., (...) & Peco, B. 2008. The LEDA Traitbase: A database of life-history traits of Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S. E., Jakobsdottir, I., Kattge, J., King, J. Y., Klotz, S., McFadden, J. & Cavender-Bares, J. (2012) Phylogenetic and functional characteristic of household yard floras and their changes along an urbanization gradient. *Ecology*, **93** (*Supplement*), S83–S98.

Knapp, S., Kühn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga, W. A., Poschlod, P., Thompson, K., Thuiller, W. & Römermann, C. (2009) How species traits and affinity to urban land use control large-scale frequency. *Diversity and Distributions*, **14**, 533–546.

Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008) Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters*, **11**, 1054–1064.

Kraft, N. J. B., Cornwell, W. K., Webb, C. O. & Ackerly, D. D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist*, **170**, 271–283.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S. & Levine, J. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, **29**, 592–599.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J. & Coomes, D. A. (2012) Competitive interactions between forest trees are driven by species´ trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, **15**, 831–840.

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 biota: effects of human-made habitat types on plants and land snails. *Journal of Biogeography*, **38**, 1152–1163.

Lososová, Z., Šmarda, P., Chytrý, M., Purschke, O., Pyšek, P., Sádlo, J., Tichý, L. & Winter, M. (2015) Phylogenetic structure of plant species pools reflects habitat age on the geological time scale. *Journal of Vegetation Science,* **26**, 1080–1089.

Mason, N. W. H., de Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, **24**, 794–806.

Mayfield, M. M. & Levine, J. M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.

Narwani, A., Alexandrou, M. A., Oakley, T. H., Carroll, I. T. & Cardinale, B. J. (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecology Letters*, **16**, 1373–1381.

Pausas, J. G. & Verdú, M. (2010) The jungle of methods for evaluation phenotypic and phylogenetic structure of communities. *BioScience*, **60**, 614–625.

Pavoine, S. & Bonsall, M. B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, **86**, 792–812.

Pavoine, S., Gasc, A., Bonsall, M. B. & Mason, N. W. H. (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science*, **24**, 781–793.

Perronne, R., Mauchamp, L., Mouly, A. & Gillet, F. (2014) Contrasted taxonomic, phylogenetic and functional diversity patterns in semi-natural permanent grasslands along an altitudinal gradient. *Plant Ecology and Evolution*, **147**, 165–175.

Podani, J. (1999) Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, **48**, 331–340.

Price, J. N. & Pärtel, M. (2013) Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos*, **122**, 646–656.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B*, **268**, 2383–2389.

Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., Kühn, I., Winter, M. & Prentice, H. C. (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, **101**, 857–866.

Ricotta, C., Di Nepi, M., Guglietta, D. & Celesti-Grapow, L. (2008) Exploring taxonomic filtering in urban environments. *Journal of Vegetation Science*, **19**, 229–238.

Ricotta, C., Heathfield, D., Godefroid, S. & Mazzoleni, S. (2012) The effects of habitat filtering on the phylogenetic structure of the urban flora of Brussels (Belgium). *Community Ecology*, **13**, 97–101.

Ricotta, C., La Sorte, F. A., Pyšek, P., Rapson, G. L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.

Silvertown, J., McConway, K. J., Gowing, D. J., Dodd, M., Fay, M. F., Joseph, J. A. & Dolphin, K. (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B*, **273**, 39–44.

Spasojevic, M. J. & Suding, K. N. (2012) Inferring community assembly mechanisms from functional diversity patterns. the importance of multiple assembly processes. *Journal of Ecology*, **100**, 652–661.

Swenson, N. G. (2009) Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. *PLoS ONE*, **4**, e4390.

Swenson, N. G. & Enquist, B. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, 2161–2170.

Swenson, N. G., Enquist, B. J., Thompson, J. & Zimmerman, J. K. (2007) The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.

Webb, C. O. & Donoghue, M. J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.

Webb, C. O., Ackerly, D. D. & Kembel, S. W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics*, **33**, 475–505.

Williams, N. S. G., Hahs, A. K. & Vesk, P. A. (2015) Urbanisation, plant traits and the composition of urban floras. *Perspectives in Plant Ecology Evolution and Systematics*, **17**, 78–86.

Williams, N. S. G., Schwartz, M. W., Vesk, P. A., McCarthy, M. A., Hahs, A. K., Clemants, S. E. Corlett, R. T., Duncan, R. P., Norton, B. A., Thompson, K. & McDonnell, M. J. (2009) A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, **97**, 4–9.

Supplementary materials, Paper IV

Appendix S1. – Cumulative lists of species recorded in seven urban habitats of 32 European cities.

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Acer campestre	Abies cephalonica	Acer campestre	Abutilon theophrasti	Abies cephalonica	Abutilon theophrasti	Acer campestre
Acer negundo	Acer campestre	Acer cappadocicum	Acer campestre	Acer campestre	Acer campestre	Acer ginnala
Acer platanoides	Acer negundo	Acer negundo	Acer ginnala	Acer negundo	Acer negundo	Acer negundo
Acer pseudoplatanus	Acer platanoides	Acer platanoides	Acer negundo	Acer platanoides	Acer platanoides	Acer platanoides
Acer saccharinum	Acer pseudoplatanus	Acer pseudoplatanus	Acer platanoides	Acer pseudoplatanus	Acer pseudoplatanus	Acer pseudoplatanus
Aegopodium podagraria	Acer saccharinum	Acer saccharinum	Acer pseudoplatanus	Acer saccharinum	Aegopodium podagraria	Acer saccharinum
Aethusa cynapium+cynapioides	Aegopodium podagraria	Aegopodium podagraria	Acer saccharinum	Aegopodium podagraria	Aethusa cynapium+cynapioides	Acinos arvensis
Agrostis capillaris	Aesculus hippocastanum	Aesculus hippocastanum	Aegopodium podagraria	Aesculus hippocastanum	Agrimonia eupatoria	Aegopodium podagraria
Agrostis gigantea+stolonifera	Aethusa cynapium+cynapioides	Aethusa cynapium+cynapioides	Aesculus hippocastanum	Aethusa cynapium+cynapioides	Agrostis capillaris	Aesculus hippocastanum
Achillea millefolium agg.	Ageratum houstonianum	Agrimonia eupatoria	Aethusa cynapium+cynapioides	Agrimonia eupatoria	Agrostis gigantea+stolonifera	Aethusa cynapium+cynapioides
Ailanthus altissima	Agrostis capillaris	Agrostis capillaris	Agrimonia eupatoria	Agrostis capillaris	Achillea millefolium agg.	Agrimonia eupatoria
Alcea rosea	Agrostis gigantea+stolonifera	Agrostis gigantea+stolonifera	Agrostis capillaris	Agrostis gigantea+stolonifera	Achillea nobilis	Agrostis capillaris
Amaranthus albus	Achillea millefolium agg.	Achillea millefolium agg.	Agrostis gigantea+stolonifera	Achillea millefolium agg.	Ailanthus altissima	Agrostis gigantea+stolonifera
Amaranthus blitoides	Achillea ptarmica	Ailanthus altissima	Achillea millefolium agg.	Ailanthus altissima	Ajuga chamaepitys	Agrostis vinealis
Amaranthus blitum	Ailanthus altissima	Ajuga reptans	Ailanthus altissima	Ajuga reptans	Ajuga reptans	Achillea millefolium agg.
Amaranthus deflexus	Aira praecox	Alcea rosea	Ajuga reptans	Alliaria petiolata	Alcea rosea	Achillea ptarmica
Amaranthus powellii	Ajuga reptans	Alliaria petiolata	Alcea ficifolia	Allium oleraceum	Alisma plantago-aquatica	Ailanthus altissima
Amaranthus retroflexus	Alcea rosea	Allium schoenoprasum	Alcea rosea	Allium ursinum	Alliaria petiolata	Ajuga genevensis
Ambrosia artemisiifolia	Alliaria petiolata	Amaranthus blitum	Alliaria petiolata	Allium vineale	Allium sativum	Ajuga reptans
Anagallis arvensis	Allium schoenoprasum	Amaranthus deflexus	Allium schoenoprasum	Amaranthus albus	Allium schoenoprasum	Alcea rosea
Anethum graveolens	Alopecurus pratensis	Amaranthus powellii	Allium ursinum	Amaranthus blitum	Allium vineale	Alliaria petiolata
Antirrhinum majus	Amaranthus blitum	Amaranthus retroflexus	Alnus incana	Amaranthus powellii	Alnus glutinosa	Allium oleraceum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Aquilegia vulgaris agg.	Amaranthus deflexus	Ambrosia artemisiifolia	Alopecurus geniculatus	Amaranthus retroflexus	Alopecurus aequalis	Allium sativum
Arctium lappa/tomentosa	Amaranthus powellii	Ampelopsis brevipedunculata	Alopecurus myosuroides	Ambrosia artemisiifolia	Alopecurus geniculatus	Allium scorodoprasum
Arenaria serpyllifolia agg.	Amaranthus retroflexus	Anagallis arvensis	Alopecurus pratensis	Amorpha fruticosa	Alopecurus myosuroides	Allium schoenoprasum
Arrhenatherum elatius	Ambrosia artemisiifolia	Anemone nemorosa	Althaea officinalis	Anagallis arvensis	Alopecurus pratensis	Allium vineale
Artemisia absinthium	Anagallis arvensis	Anethum graveolens	Amaranthus blitum	Anemone nemorosa	Amaranthus albus	Alnus cordata
Artemisia vulgaris	Anemone nemorosa	Anthemis arvensis	Amaranthus caudatus	Anthriscus cerefolium	Amaranthus blitoides	Alnus glutinosa
Asclepias curassavica	Anethum graveolens	Anthemis tinctoria	Amaranthus cruentus	Anthriscus sylvestris	Amaranthus blitum	Alopecurus aequalis
Asplenium ruta-muraria	Anthriscus sylvestris	Anthriscus caucalis	Amaranthus deflexus	Aquilegia vulgaris agg.	Amaranthus cruentus	Alopecurus myosuroides
Atriplex patula	Antirrhinum majus	Anthriscus sylvestris	Amaranthus powellii	Arabidopsis thaliana	Amaranthus deflexus	Alopecurus pratensis
Ballota nigra	Aquilegia vulgaris agg.	Antirrhinum majus	Amaranthus retroflexus	Arabis hirsuta agg.	Amaranthus powellii	Althaea hirsuta
Bellis perennis	Arabidopsis thaliana	Apera spica-venti	Ambrosia artemisiifolia	Arctium lappa/tomentosa	Amaranthus retroflexus	Althaea officinalis
Betula pendula	Aralia elata	Aphanes arvensis	Ambrosia psilostachya	Arctium minus	Ambrosia artemisiifolia	Alyssum alyssoides
Brassica napus	Arctium lappa/tomentosa	Aquilegia vulgaris agg.	Anagallis arvensis	Arenaria serpyllifolia agg.	Anacyclus valentinus	Amaranthus blitoides
Bromus carinatus	Arctium minus	Arabidopsis thaliana	Anethum graveolens	Armoracia rusticana	Anagallis arvensis	Amaranthus powellii
Bromus hordeaceus	Arenaria serpyllifolia agg.	Arctium lappa/tomentosa	Anthemis arvensis	Arrhenatherum elatius	Anagallis foemina	Amaranthus retroflexus
Bromus sterilis	Arrhenatherum elatius	Arctium minus	Anthemis tinctoria	Artemisia vulgaris	Anagallis monelli	Ambrosia artemisiifolia
Buddleja davidii	Artemisia vulgaris	Arenaria serpyllifolia agg.	Anthoxanthum odoratum	Arum cylindraceum	Anethum graveolens	Anacamptis pyramidalis
Calamagrostis epigejos	Asarum europaeum	Armoracia rusticana	Anthoxanthum puelii	Arum maculatum	Angelica sylvestris	Anagallis arvensis
Calystegia sepium	Asplenium ruta-muraria	Arrhenatherum elatius	Anthriscus sylvestris	Asarum europaeum	Anchusa officinalis	Anemone hupehensis
Camelina microcarpa	Astrantia major	Artemisia annua	Antirrhinum majus	Asplenium ruta-muraria	Anthemis arvensis	Anemone nemorosa
Campanula rapunculoides	Atriplex oblongifolia	Artemisia vulgaris	Apera spica-venti	Aster tripolium	Anthemis tinctoria	Anethum graveolens
Cannabis ruderalis+sativa	Atriplex patula	Aruncus vulgaris	Aphanes australis	Astragalus glycyphyllos	Anthriscus sylvestris	Angelica sylvestris
Capsella bursa-pastoris	Atriplex tatarica	Asarum europaeum	Aquilegia vulgaris agg.	Athyrium filix-femina	Antirrhinum majus	Anchusa officinalis
Cardamine hirsuta	Avena sativa	Asplenium ruta-muraria	Arabidopsis thaliana	Atriplex patula	Apera spica-venti	Anthemis ruthenica
Cardamine impatiens	Ballota nigra	Asplenium trichomanes	Arctium lappa/tomentosa	Atriplex prostrata subsp. latifolia	Aphanes arvensis	Anthemis tinctoria
Cardaminopsis arenosa	Bellis perennis	Aster novae-angliae	Arctium minus	Atriplex sagittata	Arabidopsis thaliana	Anthoxanthum odoratum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Cardaria draba	Berberis julianae	Aster novi-belgii s.l.	Arenaria serpyllifolia agg.	Ballota nigra	Arabis glabra	Anthriscus sylvestris
Carduus acanthoides	Berberis thunbergii	Athyrium filix-femina	Armoracia rusticana	Bellis perennis	Arctium lappa/tomentosa	Anthyllis vulneraria
Carex brizoides	Berteroa incana	Atriplex hortensis	Arrhenatherum elatius	Berberis thunbergii	Arctium minus	Antirrhinum majus
Carex hirta	Betula pendula	Atriplex oblongifolia	Artemisia vulgaris	Betonica officinalis	Arenaria serpyllifolia agg.	Apera spica-venti
Carex muricata agg.	Bidens frondosa	Atriplex patula	Asplenium ruta-muraria	Betula pendula	Armoracia rusticana	Aquilegia vulgaris agg.
Carex pseudocyperus	Brachypodium sylvaticum	Atriplex prostrata subsp. latifolia	Asplenium trichomanes	Bidens frondosa	Arrhenatherum elatius	Arctium lappa/tomentosa
Carex sylvatica	Brassica napus	Atriplex tatarica	Aster novi-belgii s.l.	Brachypodium pinnatum	Artemisia absinthium	Arctium minus
Carpinus betulus	Brassica oleracea	Aubrieta deltoides	Athyrium filix-femina	Brachypodium sylvaticum	Artemisia annua	Arenaria serpyllifolia agg.
Cerastium holosteoides subsp. triviale	Bromus erectus	Aurinia saxatilis subsp. arduini	Atriplex oblongifolia	Bromus benekenii	Artemisia vulgaris	Armoracia rusticana
Cerastium pumilum s.l.	Bromus hordeaceus	Avena fatua	Atriplex patula	Bromus erectus	Aster novi-belgii s.l.	Aronia x prunifolia
Cirsium arvense	Bromus inermis	Avena sativa	Atriplex prostrata subsp. latifolia	Bromus hordeaceus	Astragalus cicer	Arrhenatherum elatius
Cirsium vulgare	Bromus sterilis	Avenula pubescens	Atriplex sagittata	Bromus japonicus	Astragalus glycyphyllos	Artemisia absinthium
Citrullus lanatus	Bromus tectorum	Ballota nigra	Aurinia saxatilis subsp. arduini	Bromus sterilis	Atriplex littoralis	Artemisia vulgaris
Clematis vitalba	Bryonia alba	Bellis perennis	Avena fatua	Bromus tectorum	Atriplex oblongifolia	Asclepias syriaca
Convolvulus arvensis	Bryonia dioica	Berberis thunbergii	Avena sativa	Bryonia alba	Atriplex patula	Asparagus officinalis
Conyza canadensis	Buddleja davidii	Berteroa incana	Ballota nigra	Bryonia dioica	Atriplex prostrata subsp. latifolia	Asperula cynanchica
Coreopsis tinctoria	Calamagrostis epigejos	Betula pendula	Bellis perennis	Buddleja davidii	Atriplex sagittata	Aster laevis
Cornus alba s.l.	Calendula officinalis	Bidens frondosa	Berberis thunbergii	Buxus sempervirens	Atriplex tatarica	Aster novi-belgii s.l.
Coronopus didymus	Calystegia sepium	Borago officinalis	Bergenia crassifolia	Calamagrostis epigejos	Avena fatua	Astragalus glycyphyllos
Corylus colurna	Campanula patula	Brachypodium pinnatum	Berteroa incana	Calystegia sepium	Avena sativa	Atriplex oblongifolia
Crepis biennis	Campanula persicifolia	Brachypodium sylvaticum	Betula pendula	Campanula patula	Ballota nigra	Atriplex patula
Crepis capillaris	Campanula rapunculoides	Brassica napus	Bidens frondosa	Campanula rapunculoides	Barbarea vulgaris	Atriplex prostrata subsp. latifolia
Cruciata glabra	Campanula trachelium	Brassica nigra	Bidens tripartita	Campanula rotundifolia agg.	Bellis perennis	Atriplex sagittata
Cymbalaria muralis	Capsella bursa-pastoris	Brassica oleracea	Brachypodium pinnatum	Campanula trachelium	Berteroa incana	Atriplex tatarica
Cynodon dactylon	Cardamine hirsuta	Bromus hordeaceus	Brachypodium sylvaticum	Capsella bursa-pastoris	Betula pendula	Avenula pubescens

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Dactylis glomerata+polygama	Cardamine pratensis agg.	Bromus inermis	Brassica napus	Cardamine hirsuta	Bidens frondosa	Ballota nigra
Datura stramonium	Cardaria draba	Bromus secalinus subsp. secalinus	Brassica oleracea	Cardamine impatiens	Bolboschoenus maritimus	Barbarea vulgaris
Daucus carota	Carduus acanthoides	Bromus sterilis	Bromus commutatus	Cardamine pratensis agg.	Borago officinalis	Bellis perennis
Deschampsia cespitosa	Carduus crispus	Bromus tectorum	Bromus erectus	Cardaminopsis arenosa	Brachypodium sylvaticum	Berberis thunbergii
Digitalis purpurea	Carex hirta	Brunnera macrophylla	Bromus hordeaceus	Cardaria draba	Brassica napus	Berteroa incana
Digitaria ischaemum	Carex muricata agg.	Bryonia alba	Bromus japonicus	Carduus acanthoides	Brassica nigra	Beta vulgaris
Digitaria sanguinalis	Carex praecox	Bryonia dioica	Bromus sterilis	Carduus crispus	Brassica oleracea	Betonica officinalis
Diplotaxis muralis	Carex sylvatica	Buddleja davidii	Bromus tectorum	Carex digitata var. digitata	Bromus erectus	Betula pendula
Diplotaxis tenuifolia	Carpinus betulus	Calamagrostis epigejos	Brunnera macrophylla	Carex hirta	Bromus hordeaceus	Bidens frondosa
Dipsacus fullonum	Celtis australis	Calamagrostis varia	Bryonia alba	Carex muricata agg.	Bromus inermis	Brachypodium pinnatum
Dryopteris carthusiana	Celtis occidentalis	Calamintha menthifolia	Bryonia dioica	Carex panicea	Bromus japonicus	Brachypodium sylvaticum
Dryopteris dilatata	Centaurea cyanus	Calendula officinalis	Buddleja davidii	Carex pendula	Bromus marginatus	Brassica napus
Dryopteris filix-mas s.l.	Centaurea jacea	Calystegia pulchra	Bupleurum falcatum	Carex remota	Bromus sterilis	Brassica oleracea
Duchesnea indica	Centaurea scabiosa	Calystegia sepium	Buxus sempervirens	Carex sylvatica	Bromus tectorum	Briza media
Echinochloa crus-galli	Cerastium arvense	Campanula patula	Calamagrostis epigejos	Carpinus betulus	Broussonetia papyrifera	Bromus carinatus
Elytrigia repens	Cerastium glomeratum	Campanula persicifolia	Calendula officinalis	Carum carvi	Bryonia alba	Bromus commutatus
Epilobium angustifolium	Cerastium holosteoides subsp. triviale	Campanula poscharskyana	Calystegia sepium	Celtis australis	Bryonia dioica	Bromus erectus
Epilobium ciliatum	Cerastium pumilum s.l.	Campanula rapunculoides	Campanula glomerata	Celtis occidentalis	Buddleja davidii	Bromus hordeaceus
Epilobium hirsutum	Cichorium intybus	Campanula rotundifolia agg.	Campanula patula	Centaurea jacea	Calamagrostis epigejos	Bromus inermis
Epilobium lamyi+tetragonum	Circaea lutetiana	Campanula trachelium	Campanula persicifolia	Centranthus ruber	Calendula officinalis	Bromus japonicus
Epilobium montanum	Cirsium arvense	Campsis radicans	Campanula poscharskyana	Cephalanthera rubra	Callistephus chinensis	Bromus sterilis
Epilobium obscurum	Cirsium vulgare	Capsella bursa-pastoris	Campanula rapunculoides	Cerastium glomeratum	Calystegia sepium	Bromus tectorum
Epilobium parviflorum	Clematis vitalba	Cardamine hirsuta	Campanula rotundifolia agg.	Cerastium holosteoides subsp. triviale	Camelina microcarpa	Buddleja davidii
Epilobium roseum	Commelina communis	Cardamine impatiens	Campanula trachelium	Cerastium tomentosum agg.	Campanula glomerata	Bunias orientalis
Epipactis helleborine	Consolida ajacis	Cardaminopsis arenosa	Campsis radicans	Cichorium intybus	Campanula patula	Calamagrostis arundinacea
Equisetum arvense	Convallaria majalis	Cardaria draba	Cannabis ruderalis+sativa	Circaea lutetiana	Campanula rapunculoides	Calamagrostis epigejos

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Eragrostis albensis	Convolvulus arvensis	Carduus acanthoides	Capsella bursa-pastoris	Cirsium arvense	Cannabis ruderalis+sativa	Calluna vulgaris
Eragrostis minor	Conyza bonariensis	Carduus crispus	Caragana arborescens	Cirsium oleraceum	Capsella bursa-pastoris	Calystegia pulchra
Eragrostis multicaulis	Conyza canadensis	Carex digitata var. digitata	Cardamine hirsuta	Cirsium vulgare	Cardamine hirsuta	Calystegia sepium
Eragrostis pilosa	Corispermum nitidum	Carex hirta	Cardamine impatiens	Clematis vitalba	Cardamine impatiens	Campanula patula
Erigeron annuus+strigosus	Cornus alba s.l.	Carex muricata agg.	Cardamine pratensis agg.	Clerodendrum trichotomum	Cardamine pratensis agg.	Campanula rapunculoides
Erodium cicutarium	Cornus sanguinea	Carex pendula	Cardaria draba	Clinopodium vulgare	Cardaminopsis arenosa	Campanula rapunculus
Euphorbia humifusa	Coronopus didymus	Carex sylvatica	Carduus acanthoides	Commelina communis	Cardaria draba	Campanula trachelium
Euphorbia maculata	Coronopus squamatus	Carpinus betulus	Carduus crispus	Convallaria majalis	Carduus acanthoides	Cannabis ruderalis+sativa
Euphorbia peplus	Corydalis lutea	Caryopteris x clandonensis	Carex hirta	Convolvulus arvensis	Carduus crispus	Capsella bursa-pastoris
Euphorbia prostrata	Corylus avellana	Castanea sativa	Carex muricata agg.	Conyza bonariensis	Carex hirta	Cardamine hirsuta
Fallopia baldschuanica	Cotoneaster divaricatus	Catalpa bignonioides	Carex remota	Conyza canadensis	Carex muricata agg.	Cardaminopsis arenosa
Fallopia convolvulus	Cotoneaster suecicus	Celtis australis	Carex sylvatica	Cornus alba s.l.	Carex otrubae	Cardaria draba
Fallopia dumetorum	Crataegus monogyna	Celtis occidentalis	Carpinus betulus	Cornus mas	Carlina biebersteinii+vulgaris	Carduus acanthoides
Festuca brevipila	Crepis biennis	Centaurea montana	Carum carvi	Cornus sanguinea	Carpinus betulus	Carduus crispus
Festuca pratensis subsp. pratensis	Crepis capillaris	Centranthus ruber	Celtis australis	Coronopus didymus	Celtis australis	Carduus nutans
Festuca rubra agg.	Cucumis sativus	Cephalanthera damasonium	Centaurea dealbata	Corydalis lutea	Centaurea cyanus	Carex flacca
Ficus carica	Cymbalaria muralis	Cerastium arvense	Centaurea jacea	Corylus avellana	Centaurea jacea	Carex hirta
Fragaria vesca	Cynodon dactylon	Cerastium glomeratum	Centaurea montana	Corylus colurna	Centaurea scabiosa	Carex muricata agg.
Fragaria x magna	Cynosurus cristatus	Cerastium holosteoides subsp. triviale	Centaurea scabiosa	Cotoneaster divaricatus	Centaurea stoebe	Carex otrubae
Fraxinus excelsior	Cystopteris fragilis	Cerastium pumilum s.l.	Centranthus ruber	Cotoneaster przewalskii	Centaurium pulchellum	Carex ovalis
Galeopsis tetrahit s.l.	Dactylis glomerata+polygama	Cerastium tomentosum agg.	Cerastium arvense	Crataegus monogyna	Cerastium glomeratum	Carex pallescens
Galinsoga parviflora	Datura stramonium	Cichorium intybus	Cerastium glomeratum	Crepis biennis	Cerastium holosteoides subsp. triviale	Carex pilulifera
Galinsoga quadriradiata	Daucus carota	Circaea lutetiana	Cerastium holosteoides subsp. triviale	Crepis capillaris	Cerastium lucorum	Carex praecox
Galium aparine+spurium	Descurainia sophia	Cirsium arvense	Cerastium tomentosum agg.	Crepis foetida subsp. rhoeadifolia	Cerastium pumilum s.l.	Carex sylvatica
Galium mollugo agg.	Deschampsia cespitosa	Cirsium vulgare	Cichorium intybus	Cymbalaria muralis	Cerastium tomentosum agg.	Carlina biebersteinii+vulgaris

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Galium rotundifolium	Dianthus barbatus	Clematis vitalba	Circaea lutetiana	Cynodon dactylon	Cichorium intybus	Carpinus betulus
Geranium pusillum	Dianthus carthusianorum agg.	Commelina communis	Cirsium arvense	Cynosurus cristatus	Circaea lutetiana	Castanea sativa
Geum urbanum	Digitaria ischaemum	Consolida ajacis	Cirsium oleraceum	Dactylis glomerata+polygama	Cirsium arvense	Celtis australis
Gleditsia triacanthos	Digitaria sanguinalis	Convallaria majalis	Cirsium palustre	Daucus carota	Cirsium palustre	Centaurea jacea
Glechoma hederacea	Diplotaxis muralis	Convolvulus arvensis	Cirsium vulgare	Deschampsia cespitosa	Cirsium vulgare	Centaurea scabiosa
Gnaphalium uliginosum	Diplotaxis tenuifolia	Conyza canadensis	Clematis vitalba	Deutzia scabra	Clematis vitalba	Centaurea stoebe
Hedera helix	Dryopteris filix-mas s.l.	Coreopsis verticillata	Clinopodium vulgare	Digitalis purpurea	Clinopodium vulgare	Centaurium erythraea
Helianthus annuus	Duchesnea indica	Cornus mas	Colutea arborescens	Digitaria sanguinalis	Conium maculatum	Cephalaria transsylvanica
Heracleum sphondylium	Echinochloa crus-galli	Cornus sanguinea	Commelina communis	Dipsacus fullonum	Consolida ajacis	Cerastium arvense
Herniaria glabra	Echium vulgare	Coronopus didymus	Consolida ajacis	Dryopteris carthusiana	Consolida regalis	Cerastium glomeratum
Herniaria hirsuta	Elsholtzia ciliata	Corydalis lutea	Convallaria majalis	Dryopteris filix-mas s.l.	Convolvulus arvensis	Cerastium holosteoides subsp. triviale
Heuchera sanguinea	Elymus caninus	Corylus avellana	Convolvulus arvensis	Duchesnea indica	Conyza canadensis	Cerastium pumilum s.l.
Hieracium aurantiacum	Elytrigia repens	Corylus colurna	Conyza canadensis	Echinochloa crus-galli	Coreopsis tinctoria	Cichorium intybus
Hieracium pilosella	Epilobium angustifolium	Cosmos bipinnatus	Cornus alba s.l.	Echium vulgare	Corispermum leptopterum	Circaea lutetiana
Hieracium sabaudum	Epilobium ciliatum	Cotoneaster adpressus	Cornus mas	Elymus caninus	Cornus sanguinea	Cirsium arvense
Hieracium subgen. Pilosella	Epilobium dodonaei	Cotoneaster dielsianus	Cornus sanguinea	Elytrigia repens	Coronopus didymus	Cirsium furiens
Holcus lanatus	Epilobium hirsutum	Cotoneaster horizontalis	Coronopus didymus	Epilobium angustifolium	Corylus avellana	Cirsium oleraceum
Hordeum murinum	Epilobium lamyi+tetragonum	Crataegus monogyna	Corydalis lutea	Epilobium ciliatum	Cosmos bipinnatus	Cirsium palustre
Humulus lupulus	Epilobium montanum	Crepis biennis	Corylus avellana	Epilobium hirsutum	Cotoneaster divaricatus	Cirsium vulgare
Hypericum perforatum	Epilobium obscurum	Crepis capillaris	Corylus maxima	Epilobium lamyi+tetragonum	Crepis biennis	Clematis vitalba
Hypochaeris radicata	Epilobium parviflorum	Crepis setosa	Cosmos bipinnatus	Epilobium montanum	Crepis capillaris	Clinopodium vulgare
Chelidonium majus	Epilobium roseum	Crocosmia x crocosmiiflora	Cotinus coggygria	Epilobium parviflorum	Crepis foetida subsp. foetida	Colutea arborescens
Chenopodium album agg.	Epipactis helleborine	Cupressus sempervirens	Cotoneaster divaricatus	Epilobium roseum	Crepis foetida subsp. rhoeadifolia	Conium maculatum
Chenopodium ficifolium	Equisetum arvense	Cymbalaria muralis	Cotoneaster integerrimus	Epipactis helleborine	Crepis pulchra	Consolida ajacis
Chenopodium glaucum	Equisetum palustre	Cynodon dactylon	Cotoneaster przewalskii	Equisetum arvense	Crepis setosa	Consolida regalis

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Chenopodium hybridum	Eragrostis minor	Cynosurus cristatus	Cotoneaster salicifolius	Eragrostis minor	Crepis tectorum	Convallaria majalis
Chenopodium murale	Eragrostis pilosa	Dactylis glomerata+polygama	Crataegus monogyna	Erigeron annuus+strigosus	Cymbalaria muralis	Convolvulus arvensis
Chenopodium polyspermum	Erigeron acris s.l.	Daucus carota	Crepis biennis	Erodium cicutarium	Cynodon dactylon	Conyza canadensis
Chenopodium pumilio	Erigeron annuus+strigosus	Deschampsia cespitosa	Crepis capillaris	Euonymus europaea	Cyperus fuscus	Coreopsis tinctoria
Chenopodium vulvaria	Erodium cicutarium	Deutzia scabra	Crepis foetida subsp. rhoeadifolia	Euonymus fortunei	Cytisus scoparius	Corispermum leptopterum
Impatiens balsamina	Erysimum cheiranthoides	Dianthus armeria	Crepis setosa	Eupatorium cannabinum	Dactylis glomerata+polygama	Cornus alba s.l.
Inula britannica	Eupatorium cannabinum	Dianthus deltoides	Crepis tectorum	Euphorbia myrsinites	Datura stramonium	Cornus sanguinea
Ipomoea purpurea	Euphorbia helioscopia	Digitalis purpurea	Cucurbita pepo	Euphorbia peplus	Daucus carota	Corylus avellana
Iva xanthiifolia	Euphorbia maculata	Digitaria ischaemum	Cynodon dactylon	Fagus sylvatica	Descurainia sophia	Cotinus coggygria
Juncus bufonius	Euphorbia peplus	Digitaria sanguinalis	Dactylis glomerata+polygama	Fallopia convolvulus	Deschampsia cespitosa	Cotoneaster divaricatus
Juncus compressus	Euphorbia prostrata	Diplotaxis muralis	Daucus carota	Fallopia dumetorum	Deutzia scabra	Cotoneaster lacteus
Juncus tenuis	Falcaria vulgaris	Diplotaxis tenuifolia	Deschampsia cespitosa	Festuca altissima	Dianthus armeria	Crataegus fallacina
Lactuca serriola	Fallopia convolvulus	Dipsacus fullonum	Deutzia scabra	Festuca arundinacea	Dianthus deltoides	Crataegus monogyna
Lamium album	Fallopia dumetorum	Dryopteris carthusiana	Dianthus armeria	Festuca brevipila	Digitaria ischaemum	Crepis biennis
Lamium amplexicaule	Festuca arundinacea	Dryopteris filix-mas s.l.	Digitalis purpurea	Festuca gigantea	Digitaria sanguinalis	Crepis capillaris
Lamium purpureum	Festuca brevipila	Duchesnea indica	Digitaria ischaemum	Festuca pratensis subsp. pratensis	Diplotaxis muralis	Crepis foetida subsp. rhoeadifolia
Lapsana communis	Festuca gigantea	Echinochloa crus-galli	Digitaria sanguinalis	Festuca rubra agg.	Diplotaxis tenuifolia	Crepis tectorum
Leontodon autumnalis	Festuca heterophylla	Echium vulgare	Diplotaxis muralis	Ficus carica	Dipsacus fullonum	Cruciata glabra
Lepidium densiflorum	Festuca pallens	Elytrigia repens	Diplotaxis tenuifolia	Filipendula ulmaria	Dipsacus laciniatus	Cynodon dactylon
Lepidium ruderale	Festuca pratensis subsp. pratensis	Epilobium angustifolium	Dipsacus fullonum	Fragaria vesca	Dittrichia graveolens	Cynoglossum officinale
Leucanthemum vulgare agg.	Festuca rubra agg.	Epilobium ciliatum	Dipsacus laciniatus	Fragaria viridis	Duchesnea indica	Cynosurus cristatus
Lobelia erinus	Festuca rupicola	Epilobium hirsutum	Dryopteris filix-mas s.l.	Fragaria x magna	Echinochloa crus-galli	Cytisus scoparius
Lobularia maritima	Fragaria vesca	Epilobium lamyi+tetragonum	Duchesnea indica	Fraxinus excelsior	Echinops sphaerocephalus	Dactylis glomerata+polygama
Lolium perenne	Fraxinus excelsior	Epilobium montanum	Echinochloa crus-galli	Galeobdolon argentatum	Echium vulgare	Danthonia decumbens
Lonicera standishii	Galeopsis pubescens	Epilobium obscurum	Echium vulgare	Galeobdolon montanum	Elaeagnus umbellata	Daucus carota

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Lotus corniculatus	Galeopsis tetrahit s.l.	Epilobium parviflorum	Elytrigia repens	Galeopsis pubescens	Elymus caninus	Descurainia sophia
Lunaria annua	Galinsoga parviflora	Epilobium roseum	Epilobium angustifolium	Galeopsis speciosa	Elytrigia repens	Deschampsia cespitosa
Lycopus europaeus	Galinsoga quadriradiata	Epipactis helleborine	Epilobium ciliatum	Galeopsis tetrahit s.l.	Epilobium angustifolium	Deutzia scabra
Mahonia aquifolium	Galium aparine+spurium	Equisetum arvense	Epilobium hirsutum	Galinsoga parviflora	Epilobium ciliatum	Dianthus armeria
Malus sylvestris agg.	Galium mollugo agg.	Eragrostis minor	Epilobium lamyi+tetragonum	Galinsoga quadriradiata	Epilobium collinum	Dianthus barbatus
Malva neglecta	Galium verum	Eragrostis pilosa	Epilobium montanum	Galium aparine+spurium	Epilobium dodonaei	Dianthus carthusianorum agg.
Matricaria discoidea	Geranium macrorrhizum	Erechtites hieraciifolia	Epilobium obscurum	Galium boreale	Epilobium hirsutum	Digitaria sanguinalis
Matricaria recutita	Geranium molle	Erigeron annuus+strigosus	Epilobium parviflorum	Galium mollugo agg.	Epilobium lamyi+tetragonum	Diplotaxis muralis
Meconopsis cambrica	Geranium pratense	Erigeron karvinskianus	Epilobium roseum	Galium palustre	Epilobium montanum	Diplotaxis tenuifolia
Medicago lupulina	Geranium pusillum	Erodium cicutarium	Epipactis helleborine	Galium rotundifolium	Epilobium parviflorum	Dipsacus fullonum
Melissa officinalis	Geranium pyrenaicum	Erysimum cheiranthoides	Equisetum arvense	Galium verum	Equisetum arvense	Dipsacus laciniatus
Microrrhinum minus	Geranium robertianum	Erysimum cheiri	Equisetum palustre	Geranium dissectum	Equisetum palustre	Dryopteris filix-mas s.l.
Morus alba	Geum urbanum	Eschscholzia californica	Eragrostis minor	Geranium macrorrhizum	Equisetum ramosissimum	Duchesnea indica
Mycelis muralis	Glechoma hederacea	Euonymus europaea	Eragrostis pilosa	Geranium molle	Eragrostis minor	Echinochloa crus-galli
Myosotis arvensis	Gnaphalium uliginosum	Eupatorium cannabinum	Erigeron annuus+strigosus	Geranium phaeum	Eragrostis pilosa	Echium vulgare
Myosoton aquaticum	Gypsophila muralis	Euphorbia cyparissias	Erodium cicutarium	Geranium pratense	Erigeron acris s.l.	Elaeagnus angustifolia
Odontites vernus	Hedera helix	Euphorbia helioscopia	Eryngium campestre	Geranium pusillum	Erigeron annuus+strigosus	Elytrigia repens
Oenothera biennis s.l.	Heracleum mantegazzianum	Euphorbia humifusa	Erysimum durum+hieracifolium	Geranium pyrenaicum	Erodium cicutarium	Epilobium angustifolium
Oxalis corniculata	Heracleum sphondylium	Euphorbia lathyris	Erysimum cheiranthoides	Geranium robertianum	Erucastrum gallicum	Epilobium ciliatum
Oxalis debilis	Herniaria glabra	Euphorbia maculata	Erysimum cheiri	Geranium sibiricum	Eryngium campestre	Epilobium dodonaei
Oxalis dillenii	Heuchera sanguinea	Euphorbia peplus	Euonymus europaea	Geum urbanum	Erysimum durum+hieracifolium	Epilobium hirsutum
Oxalis fontana	Hibiscus syriacus	Fagus sylvatica	Eupatorium cannabinum	Gleditsia triacanthos	Erysimum cheiranthoides	Epilobium lamyi+tetragonum
Oxalis tetraphylla	Hieracium aurantiacum	Falcaria vulgaris	Euphorbia esula	Glechoma hederacea	Eupatorium cannabinum	Epilobium montanum
Panicum miliaceum	Hieracium bauhini	Fallopia baldschuanica	Euphorbia helioscopia	Gymnocladus dioica	Euphorbia cyparissias	Epilobium parviflorum
Parietaria officinalis	Hieracium lachenalii	Fallopia convolvulus	Euphorbia humifusa	Gypsophila muralis	Euphorbia exigua	Epilobium roseum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Pastinaca sativa	Hieracium murorum	Fallopia dumetorum	Euphorbia lathyris	Hedera helix	Euphorbia helioscopia	Equisetum arvense
Paulownia tomentosa	Hieracium pilosella	Festuca arundinacea	Euphorbia peplus	Helianthus annuus	Euphorbia lathyris	Equisetum palustre
Persicaria amphibia	Hieracium sabaudum	Festuca brevipila	Falcaria vulgaris	Helianthus tuberosus	Euphorbia marginata	Equisetum ramosissimum
Persicaria lapathifolia	Hieracium subgen. Pilosella	Festuca gigantea	Fallopia convolvulus	Helleborus dumetorum	Euphorbia peplus	Eragrostis minor
Persicaria maculosa	Holcus lanatus	Festuca ovina subsp. ovina	Fallopia dumetorum	Helleborus niger	Euphorbia platyphyllos	Erigeron acris s.l.
Petroselinum crispum	Holcus mollis	Festuca pratensis subsp. pratensis	Festuca arundinacea	Heracleum mantegazzianum	Fagopyrum esculentum	Erigeron annuus+strigosus
Petunia x atkinsiana	Hordeum murinum	Festuca rubra agg.	Festuca brevipila	Heracleum sphondylium	Falcaria vulgaris	Erodium cicutarium
Phacelia tanacetifolia	Humulus lupulus	Festuca rupicola	Festuca gigantea	Hieracium aurantiacum	Fallopia convolvulus	Eryngium campestre
Phalaris canariensis	Hydrangea arborescens	Fragaria moschata	Festuca pratensis subsp. pratensis	Hieracium lachenalii	Fallopia dumetorum	Erysimum durum+hieracifolium
Phleum bertolonii+pratense	Hypericum androsaemum	Fragaria vesca	Festuca rubra agg.	Hieracium murorum	Festuca arundinacea	Erysimum cheiranthoides
Physalis alkekengi	Hypericum perforatum	Fragaria viridis	Festuca rupicola	Hieracium pilosella	Festuca brevipila	Euonymus europaea
Physalis peruviana	Hypochaeris radicata	Fragaria x magna	Filipendula ulmaria	Holcus lanatus	Festuca filiformis	Eupatorium cannabinum
Picris hieracioides	Chaenomeles japonica	Fraxinus excelsior	Fragaria moschata	Holcus mollis	Festuca gigantea	Euphorbia cyparissias
Pinus sylvestris	Chaerophyllum hirsutum	Fumaria officinalis	Fragaria vesca	Hordelymus europaeus	Festuca ovina subsp. ovina	Euphorbia esula
Plantago lanceolata	Chaerophyllum temulum	Gaillardia aristata	Fragaria viridis	Hordeum murinum	Festuca pratensis subsp. pratensis	Euphorbia helioscopia
Plantago major+uliginosa	Chelidonium majus	Galeobdolon argentatum	Fraxinus excelsior	Humulus lupulus	Festuca rubra agg.	Euphorbia lathyris
Platanus occidentalis	Chenopodium album agg.	Galeobdolon montanum	Fumaria capreolata	Hypericum humifusum	Filago minima	Euphorbia peplus
Platanus x hispanica	Chenopodium ficifolium	Galeopsis pubescens	Galeobdolon argentatum	Hypericum maculatum	Filipendula ulmaria	Euphorbia platyphyllos
Poa annua	Chenopodium glaucum	Galeopsis tetrahit s.l.	Galeopsis pubescens	Hypericum perforatum	Fragaria x magna	Euphorbia salicifolia
Poa compressa	Chenopodium hybridum	Galinsoga parviflora	Galeopsis speciosa	Hypericum tetrapterum	Fraxinus excelsior	Euphorbia stricta
Poa pratensis s.l.	Chenopodium murale	Galinsoga quadriradiata	Galeopsis tetrahit s.l.	Hypochaeris radicata	Fumaria officinalis	Euphorbia waldsteinii
Poa trivialis	Chenopodium polyspermum	Galium aparine+spurium	Galinsoga parviflora	Chaerophyllum aromaticum	Fumaria schleicheri	Euphrasia stricta
Polycarpon tetraphyllum	Chenopodium vulvaria	Galium mollugo agg.	Galinsoga quadriradiata	Chaerophyllum bulbosum	Fumaria vaillantii subsp. vaillantii	Fagus sylvatica
Polygonum aviculare agg.	Ilex aquifolium	Galium odoratum	Galium aparine+spurium	Chaerophyllum temulum	Gaillardia aristata	Falcaria vulgaris
Polypodium vulgare	Impatiens parviflora	Galium verum	Galium mollugo agg.	Chelidonium majus	Galega officinalis	Fallopia convolvulus
Populus alba	Juglans regia	Geranium dalmaticum	Galium odoratum	Chenopodium album agg.	Galeopsis angustifolia	Fallopia dumetorum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Populus nigra agg.	Juncus bufonius	Geranium dissectum	Galium palustre	Chenopodium ficifolium	Galeopsis pubescens	Festuca altissima
Populus tremula	Juncus compressus	Geranium endressii	Galium verum	Chenopodium glaucum	Galeopsis segetum	Festuca arundinacea
Portulaca oleracea	Juncus tenuis	Geranium macrorrhizum	Geranium dissectum	Chenopodium hybridum	Galeopsis speciosa	Festuca brevipila
Potentilla anserina	Kerria japonica	Geranium palustre	Geranium molle	Chenopodium murale	Galeopsis tetrahit s.l.	Festuca ovina subsp. ovina
Potentilla argentea	Knautia arvensis	Geranium phaeum	Geranium phaeum	Chenopodium polyspermum	Galinsoga parviflora	Festuca pratensis subsp. pratensis
Potentilla fruticosa	Kochia scoparia	Geranium pratense	Geranium pratense	Chenopodium rubrum	Galinsoga quadriradiata	Festuca rubra agg.
Potentilla recta	Laburnum anagyroides agg.	Geranium pusillum	Geranium pusillum	Ilex aquifolium	Galium aparine+spurium	Festuca rupicola
Potentilla reptans	Lactuca serriola	Geranium pyrenaicum	Geranium pyrenaicum	Impatiens glandulifera	Galium mollugo agg.	Filipendula ulmaria
Potentilla supina	Lamium album	Geranium robertianum	Geranium robertianum	Impatiens parviflora	Galium verum	Foeniculum vulgare
Prunella vulgaris	Lamium amplexicaule	Geranium sanguineum	Geum urbanum	Iris pseudacorus	Geranium dissectum	Fragaria vesca
Prunus avium	Lamium maculatum	Geranium sibiricum	Gleditsia triacanthos	Juglans nigra	Geranium molle	Fragaria viridis
Prunus cerasifera	Lamium purpureum	Geranium x oxonianum	Glechoma hederacea	Juglans regia	Geranium pratense	Fragaria x magna
Prunus domestica s.l.	Lapsana communis	Geum urbanum	Glyceria fluitans	Juncus articulatus	Geranium purpureum	Frangula alnus
Prunus persica	Lathyrus tuberosus	Glaucium flavum	Gnaphalium uliginosum	Juncus bufonius	Geranium pusillum	Fraxinus excelsior
Pseudognaphalium luteoalbum	Leontodon autumnalis	Glechoma hederacea	Hedera helix	Juncus effusus	Geranium pyrenaicum	Fumaria vaillantii subsp. vaillantii
Puccinellia distans	Leontodon hispidus	Gnaphalium uliginosum	Helianthus annuus	Juncus tenuis	Geranium robertianum	Gaillardia x grandiflora
Pyracantha coccinea	Lepidium densiflorum	Hedera helix	Helianthus tuberosus	Kerria japonica	Geranium sylvaticum	Galega officinalis
Pyrethrum parthenium	Lepidium ruderale	Helianthus annuus	Heliopsis helianthoides	Knautia arvensis	Geum urbanum	Galeobdolon argentatum
Pyrus communis	Leucanthemum vulgare agg.	Helianthus tuberosus	Helminthotheca echioides	Koelreuteria paniculata	Glechoma hederacea	Galeopsis angustifolia
Quercus robur	Ligustrum vulgare	Helianthus x laetiflorus	Hemerocallis fulva	Laburnum anagyroides agg.	Glyceria fluitans	Galeopsis pubescens
Ranunculus repens	Linaria purpurea	Hemerocallis fulva	Heracleum sphondylium	Lactuca serriola	Gnaphalium uliginosum	Galeopsis tetrahit s.l.
Raphanus raphanistrum	Linaria vulgaris	Hepatica nobilis	Herniaria glabra	Lamium album	Gypsophila muralis	Galinsoga parviflora
Ribes alpinum	Linum usitatissimum	Heracleum mantegazzianum	Hesperis matronalis+sylvestris	Lamium maculatum	Helianthus annuus	Galinsoga quadriradiata
Robinia pseudacacia	Lobularia maritima	Heracleum sphondylium	Hibiscus syriacus	Lamium purpureum	Helianthus tuberosus	Galium aparine+spurium
Rorippa palustris	Lolium multiflorum	Herniaria glabra	Hieracium aurantiacum	Lapsana communis	Hemerocallis fulva	Galium mollugo agg.
Rorippa sylvestris	Lolium perenne	Hesperis matronalis+sylvestris	Hieracium bauhini	Lathyrus latifolius	Heracleum sphondylium	Galium rivale

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Rosa canina agg.	Lonicera pileata	Heuchera sanguinea	Hieracium lachenalii	Lathyrus pratensis	Herniaria glabra	Galium uliginosum
Rubus caesius	Lotus corniculatus	Hibiscus syriacus	Hieracium murorum	Leontodon autumnalis	Hibiscus trionum	Galium verum
Rubus fruticosus agg.	Lycopus europaeus	Hieracium aurantiacum	Hieracium pilosella	Leontodon hispidus	Hieracium pilosella	Geranium columbinum
Rubus idaeus	Lysimachia nummularia	Hieracium bauhini	Hieracium sabaudum	Leonurus cardiaca s.l.	Hieracium piloselloides	Geranium dissectum
Rumex acetosa	Lythrum salicaria	Hieracium lachenalii	Hieracium subgen. Pilosella	Lepidium ruderale	Hieracium sabaudum	Geranium divaricatum
Rumex obtusifolius	Mahonia aquifolium	Hieracium maculatum	Holcus lanatus	Leucanthemum vulgare agg.	Hieracium subgen. Pilosella	Geranium molle
Rumex thyrsiflorus	Malus prunifolia	Hieracium murorum	Holcus mollis	Ligustrum vulgare	Hippophae rhamnoides	Geranium palustre
Sagina apetala	Malus sylvestris agg.	Hieracium pilosella	Hordeum murinum	Linaria vulgaris	Holcus lanatus	Geranium pratense
Sagina procumbens	Malva moschata	Hieracium sabaudum	Hordeum vulgare	Lolium multiflorum	Holcus mollis	Geranium pusillum
Salix alba	Malva neglecta	Hieracium subgen. Pilosella	Humulus lupulus	Lolium perenne	Hordeum jubatum	Geranium pyrenaicum
Salix caprea	Malva sylvestris	Holcus lanatus	Hydrangea macrophylla	Lonicera pileata	Hordeum murinum	Geranium robertianum
Salix fragilis	Matricaria discoidea	Holcus mollis	Hydrocotyle vulgaris	Lonicera xylosteum	Humulus lupulus	Geum urbanum
Sambucus ebulus	Matricaria recutita	Hordeum murinum	Hyoscyamus niger	Lotus corniculatus	Hylotelephium spectabile	Gleditsia triacanthos
Sambucus nigra	Meconopsis cambrica	Hordeum vulgare	Hypericum humifusum	Lotus tenuis	Hyoscyamus niger	Glechoma hederacea
Satureja hortensis	Medicago falcata	Hosta plantaginea	Hypericum maculatum	Lunaria annua	Hypericum perforatum	Glyceria fluitans
Scirpus sylvaticus	Medicago lupulina	Humulus lupulus	Hypericum perforatum	Lycopus europaeus	Hypochaeris radicata	Glyceria maxima
Sedum acre	Medicago sativa s.l.	Hypericum maculatum	Hypochaeris radicata	Lychnis coronaria	Chaerophyllum aromaticum	Gnaphalium uliginosum
Sedum album	Melilotus albus	Hypericum patulum	Chaerophyllum aromaticum	Lychnis flos-cuculi	Chaerophyllum bulbosum	Gypsophila paniculata
Senecio inaequidens	Melilotus officinalis	Hypericum perforatum	Chaerophyllum temulum	Lysimachia nummularia	Chaerophyllum hirsutum	Hedera helix
Senecio jacobaea	Melissa officinalis	Hypochaeris glabra	Chelidonium majus	Lysimachia punctata	Chaerophyllum temulum	Helianthus annuus
Senecio viscosus	Mentha arvensis	Hypochaeris radicata	Chenopodium album agg.	Lysimachia vulgaris	Chelidonium majus	Helianthus tuberosus
Senecio vulgaris	Mercurialis annua	Chaenomeles japonica	Chenopodium ficifolium	Lythrum salicaria	Chelone obliqua	Helminthotheca echioides
Setaria verticillata	Microrrhinum minus	Chaerophyllum aureum	Chenopodium glaucum	Macleaya microcarpa	Chenopodium album agg.	Hemerocallis fulva
Setaria viridis	Morus alba	Chaerophyllum temulum	Chenopodium hybridum	Mahonia aquifolium	Chenopodium botrys	Heracleum mantegazzianum
Sinapis arvensis	Mycelis muralis	Chelidonium majus	Chenopodium murale	Malus sylvestris agg.	Chenopodium ficifolium	Heracleum sphondylium
Sisymbrium loeselii	Myosotis arvensis	Chenopodium album agg.	Chenopodium opulifolium	Malva neglecta	Chenopodium glaucum	Hieracium aurantiacum
Sisymbrium officinale	Nepeta racemosa	Chenopodium ficifolium	Chenopodium polyspermum	Malva sylvestris	Chenopodium hybridum	Hieracium murorum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Solanum decipiens+nigrum	Odontites vernus	Chenopodium hybridum	Chenopodium rubrum	Matricaria discoidea	Chenopodium murale	Hieracium pilosella
Solanum dulcamara	Oenothera biennis s.l.	Chenopodium opulifolium	Ilex aquifolium	Matricaria recutita	Chenopodium opulifolium	Hieracium piloselloides
Solanum lycopersicum	Origanum vulgare	Chenopodium polyspermum	Impatiens balfourii	Medicago falcata	Chenopodium polyspermum	Hieracium rothianum
Solidago canadensis	Oxalis articulata	Chenopodium pumilio	Impatiens glandulifera	Medicago lupulina	Chenopodium rubrum	Hieracium sabaudum
Solidago gigantea	Oxalis corniculata	Iberis umbellata	Impatiens parviflora	Medicago sativa s.l.	Chondrilla juncea	Hieracium subgen. Pilosella
Sonchus arvensis	Oxalis dillenii	Ilex aquifolium	Inula britannica	Melilotus albus	Impatiens glandulifera	Hieracium umbellatum
Sonchus asper	Oxalis fontana	Impatiens glandulifera	Ipomoea purpurea	Melilotus officinalis	Impatiens parviflora	Hippophae rhamnoides
Sonchus oleraceus	Panicum capillare	Impatiens parviflora	Iva xanthiifolia	Melissa officinalis	Inula britannica	Holcus lanatus
Sorbus aucuparia	Panicum miliaceum	Inula britannica	Juglans nigra	Mentha arvensis	Ipomoea purpurea	Holcus mollis
Spergularia rubra	Papaver rhoeas	Ipomoea purpurea	Juglans regia	Mercurialis annua	Iris germanica agg.	Hordeum murinum
Stellaria media agg.	Papaver somniferum	Juglans nigra	Juncus articulatus	Microrrhinum minus	Iva xanthiifolia	Humulus lupulus
Tanacetum vulgare	Parietaria officinalis	Juglans regia	Juncus bufonius	Milium effusum	Juglans regia	Hylotelephium spectabile
Taraxacum sect. Ruderalia	Parthenocissus inserta+quinquefolia	Juncus bufonius	Juncus effusus	Moehringia trinervia	Juncus articulatus	Hypericum hirsutum
Taxus baccata	Parthenocissus tricuspidata	Juncus compressus	Juncus inflexus	Morus alba	Juncus bufonius	Hypericum maculatum
Thlaspi arvense	Paspalum paspalodes	Juncus effusus	Juncus tenuis	Mycelis muralis	Juncus compressus	Hypericum perforatum
Tilia cordata	Pastinaca sativa	Juncus inflexus	Kerria japonica	Myosotis arvensis	Juncus effusus	Hypochaeris radicata
Tilia platyphyllos	Persicaria amphibia	Juncus tenuis	Kickxia elatine	Myosoton aquaticum	Juncus inflexus	Chaenomeles japonica
Torilis japonica	Persicaria lapathifolia	Kerria japonica	Kickxia spuria	Nepeta x faasenii	Juncus tenuis	Chaerophyllum aureum
Tragopogon pratensis agg.	Persicaria maculosa	Kickxia spuria	Knautia arvensis	Oenothera biennis s.l.	Kickxia spuria	Chaerophyllum temulum
Trifolium dubium	Petrorhagia saxifraga	Koelreuteria paniculata	Koelreuteria paniculata	Origanum vulgare	Knautia arvensis	Chelidonium majus
Trifolium pratense	Petroselinum crispum	Kochia scoparia	Kochia scoparia	Oxalis acetosella	Kochia scoparia	Chenopodium album agg.
Trifolium repens	Phleum bertolonii+pratense	Laburnum anagyroides agg.	Laburnum anagyroides agg.	Oxalis corniculata	Lactuca saligna	Chenopodium ficifolium
Tripleurospermum inodorum	Phragmites australis	Lactuca serriola	Lactuca serriola	Oxalis dillenii	Lactuca serriola	Chenopodium glaucum
Triticum aestivum	Phytolacca esculenta	Lamium album	Lamium album	Oxalis fontana	Lamium album	Chenopodium polyspermum
Tussilago farfara	Picris hieracioides	Lamium maculatum	Lamium amplexicaule	Panicum miliaceum	Lamium amplexicaule	Chenopodium rubrum
Ulmus glabra	Pimpinella saxifraga	Lamium purpureum	Lamium maculatum	Papaver rhoeas	Lamium maculatum	Chondrilla juncea
Ulmus laevis	Pinus strobus	Lapsana communis	Lamium purpureum	Parietaria officinalis	Lamium purpureum	Impatiens glandulifera

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
Urtica dioica	Plantago coronopus	Larix decidua	Lapsana communis	Parthenocissus inserta+quinquefolia	Lapsana communis	Impatiens parviflora
Urtica urens	Plantago lanceolata	Lathyrus latifolius	Lathyrus latifolius	Parthenocissus tricuspidata	Lathyrus odoratus	Inula britannica
Verbascum phlomoides	Plantago major+uliginosa	Lathyrus odoratus	Lathyrus pratensis	Pastinaca sativa	Lathyrus pratensis	Inula conyzae
Verbascum thapsus	Plantago media	Lathyrus pratensis	Lathyrus tuberosus	Persicaria amphibia	Lathyrus sylvestris	Inula germanica
Verbena officinalis	Platanus occidentalis	Lathyrus sylvestris	Lavandula angustifolia	Persicaria lapathifolia	Lathyrus tuberosus	Inula helenium
Veronica agrestis	Platanus orientalis	Lavandula angustifolia	Leontodon autumnalis	Persicaria maculosa	Lavatera thuringiaca	Inula salicina
Veronica arvensis	Platanus x hispanica	Lavatera thuringiaca	Leontodon hispidus	Persicaria minor	Legousia speculum-veneris	Iris germanica agg.
Veronica hederifolia agg.	Poa annua	Leontodon autumnalis	Lepidium densiflorum	Persicaria mitis	Leontodon autumnalis	Juglans regia
Veronica peregrina	Poa compressa	Leontodon hispidus	Lepidium ruderale	Petasites hybridus	Leontodon hispidus	Juncus articulatus
Veronica persica	Poa nemoralis	Leontodon saxatilis	Leucanthemum vulgare agg.	Petrorhagia saxifraga	Lepidium campestre	Juncus bufonius
Veronica polita	Poa palustris	Lepidium densiflorum	Ligustrum vulgare	Phalaris arundinacea	Lepidium densiflorum	Juncus compressus
Veronica serpyllifolia	Poa pratensis s.l.	Lepidium ruderale	Linaria arvensis	Phleum bertolonii+pratense	Lepidium graminifolium	Juncus conglomeratus
Vicia sativa agg.	Poa trivialis	Leucanthemum vulgare agg.	Linaria purpurea	Phyteuma spicatum	Lepidium ruderale	Juncus effusus
Viola arvensis	Polycarpon tetraphyllum	Ligustrum vulgare	Linaria vulgaris	Phytolacca esculenta	Lepidium virginicum	Juncus inflexus
Viola odorata	Polygonum aviculare agg.	Linaria arvensis	Linum usitatissimum	Picris hieracioides	Leucanthemum vulgare agg.	Juncus tenuis
Viola papilionacea	Populus alba	Linaria repens	Lithospermum purpurocaeruleum	Pimpinella major	Ligustrum vulgare	Kerria japonica
Viola x wittrockiana	Populus nigra agg.	Linaria vulgaris	Lobularia maritima	Pimpinella saxifraga	Linaria genistifolia	Kickxia spuria
Vitis sp.	Populus tremula	Lithospermum purpurocaeruleum	Lolium multiflorum	Plantago lanceolata	Linaria repens	Knautia arvensis
Vulpia myuros	Portulaca grandiflora	Lobularia maritima	Lolium perenne	Plantago major+uliginosa	Linaria vulgaris	Laburnum anagyroides agg.
	Portulaca oleracea	Lolium multiflorum	Lonicera pileata	Plantago media	Linum perenne	Lactuca perennis
	Potentilla anserina	Lolium perenne	Lonicera xylosteum	Platanus x hispanica	Lobelia erinus	Lactuca serriola
	Potentilla argentea	Lonicera pileata	Lotus corniculatus	Poa annua	Lolium multiflorum	Lamium album
	Potentilla recta	Lonicera tatarica	Lotus uliginosus	Poa compressa	Lolium perenne	Lamium maculatum
	Potentilla reptans	Lotus corniculatus	Lunaria annua	Poa nemoralis	Lolium remotum	Lamium purpureum
	Potentilla sterilis	Lotus uliginosus	Lupinus polyphyllus	Poa palustris	Lotus corniculatus	Lappula squarrosa
	Potentilla supina	Lunaria annua	Luzula campestris	Poa pratensis s.l.	Lotus tenuis	Lapsana communis

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Primula veris	Lupinus polyphyllus	Lycium barbarum	Poa trivialis	Lupinus polyphyllus	Lathyrus pratensis
	Prunella vulgaris	Luzula sylvatica	Lycopsis arvensis subsp. arvensis	Polygonatum latifolium	Lycopsis arvensis subsp. arvensis	Lathyrus sylvestris
	Prunus armeniaca	Lycium barbarum	Lychnis coronaria	Polygonatum multiflorum	Lycopus europaeus	Lathyrus tuberosus
	Prunus avium	Lycopus europaeus	Lysimachia nummularia	Polygonum aviculare agg.	Lysimachia nummularia	Lavatera thuringiaca
	Prunus cerasifera	Lychnis coronaria	Lysimachia punctata	Polypodium vulgare	Lysimachia punctata	Lavatera trimestris
	Prunus laurocerasus	Lysimachia nummularia	Mahonia aquifolium	Populus alba	Lysimachia vulgaris	Leontodon autumnalis
	Prunus persica	Lysimachia punctata	Malus sargentii	Populus nigra agg.	Lythrum salicaria	Leontodon hispidus
	Prunus serotina	Lysimachia vulgaris	Malus sylvestris agg.	Populus tremula	Malus sylvestris agg.	Leontodon saxatilis
	Puccinellia distans	Mahonia aquifolium	Malva neglecta	Portulaca oleracea	Malva moschata	Leonurus cardiaca s.l.
	Pulicaria dysenterica	Malus sylvestris agg.	Malva pusilla	Potentilla anserina	Malva neglecta	Lepidium campestre
	Pyracantha coccinea	Malva neglecta	Malva sylvestris	Potentilla reptans	Malva sylvestris	Lepidium densiflorum
	Pyrethrum parthenium	Malva sylvestris	Matricaria discoidea	Potentilla sterilis	Matricaria discoidea	Lepidium ruderale
	Quercus petraea	Matricaria discoidea	Matricaria recutita	Potentilla supina	Matricaria recutita	Leucanthemum vulgare agg.
	Quercus robur	Matricaria recutita	Meconopsis cambrica	Potentilla verna agg.	Matteuccia struthiopteris	Ligustrum vulgare
	Ranunculus acris	Meconopsis cambrica	Medicago falcata	Primula veris	Medicago falcata	Linaria genistifolia
	Ranunculus bulbosus	Medicago lupulina	Medicago lupulina	Primula vulgaris	Medicago lupulina	Linaria purpurea
	Ranunculus repens	Medicago sativa s.l.	Medicago sativa s.l.	Prunella grandiflora	Medicago sativa s.l.	Linaria vulgaris
	Reseda lutea	Melica uniflora	Melica ciliata	Prunella vulgaris	Melilotus albus	Linum catharticum
	Reynoutria japonica	Melilotus albus	Melica uniflora	Prunus avium	Melilotus officinalis	Lolium multiflorum
	Rhus hirta	Melissa officinalis	Melilotus albus	Prunus cerasifera	Mentha arvensis	Lolium perenne
	Ribes alpinum	Mentha arvensis	Melilotus officinalis	Prunus mahaleb	Mentha longifolia	Lonicera tatarica
	Ribes uva-crispa	Mentha longifolia	Melissa officinalis	Prunus padus	Mentha spicata	Lonicera xylosteum
	Robinia pseudacacia	Mentha spicata	Mentha arvensis	Prunus serotina	Mentha suaveolens	Lotus corniculatus
	Rorippa palustris	Mentha x dumetorum+piperita	Mentha longifolia	Pseudognaphalium luteoalbum	Mercurialis annua	Lotus tenuis
	Rorippa sylvestris	Mercurialis annua	Mentha spicata	Pterocarya fraxinifolia	Microrrhinum minus	Lotus uliginosus
	Rosa canina agg.	Microrrhinum minus	Mentha x dumetorum+piperita	Pulmonaria obscura+officinalis	Minuartia hybrida	Lupinus polyphyllus

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Rubus caesius	Morus alba	Mercurialis annua	Pyracantha coccinea	Misopates orontium	Luzula campestris
	Rubus fruticosus agg.	Muscari armeniacum	Microrrhinum minus	Pyrus pyraster	Myosotis arvensis	Luzula multiflora
	Rumex acetosa	Mycelis muralis	Mirabilis jalapa	Quercus cerris	Myosoton aquaticum	Lycopus europaeus
	Rumex acetosella	Myosotis arvensis	Mycelis muralis	Quercus petraea	Nicandra physalodes	Lychnis coronaria
	Rumex crispus	Myosotis stricta	Myosotis arvensis	Quercus robur	Nigella damascena	Lychnis flos-cuculi
	Rumex obtusifolius	Nepeta cataria	Myosotis sylvatica	Quercus rubra	Odontites vernus	Lysimachia nummularia
	Rumex palustris	Nepeta x faasenii	Myosoton aquaticum	Ranunculus acris	Oenothera biennis s.l.	Lysimachia punctata
	Rumex thyrsiflorus	Nigella damascena	Nepeta racemosa	Ranunculus bulbosus	Onobrychis viciifolia	Lysimachia vulgaris
	Sagina apetala	Oenothera biennis s.l.	Nicandra physalodes	Ranunculus repens	Onopordum acanthium	Lythrum salicaria
	Sagina procumbens	Omphalodes verna	Oenothera biennis s.l.	Reseda lutea	Origanum vulgare	Mahonia aquifolium
	Salix caprea	Ononis spinosa	Onopordum acanthium	Reynoutria japonica	Oxalis corniculata	Malus prunifolia
	Salix fragilis	Onopordum acanthium	Origanum vulgare	Rhamnus cathartica	Oxalis dillenii	Malus sylvestris agg.
	Salvia pratensis	Origanum vulgare	Ornithopus perpusillus	Rhinanthus alectorolophus	Oxalis fontana	Malva moschata
	Sambucus nigra	Ornithopus perpusillus	Oxalis acetosella	Ribes alpinum	Panicum capillare	Malva neglecta
	Sanguisorba minor	Oxalis acetosella	Oxalis corniculata	Ribes uva-crispa	Panicum miliaceum	Malva sylvestris
	Saponaria officinalis	Oxalis corniculata	Oxalis debilis	Robinia pseudacacia	Papaver argemone	Matricaria discoidea
	Scrophularia scopolii	Oxalis debilis	Oxalis dillenii	Rorippa austriaca	Papaver dubium agg.	Matricaria recutita
	Scutellaria galericulata	Oxalis dillenii	Oxalis fontana	Rorippa palustris	Papaver rhoeas	Medicago falcata
	Securigera varia	Oxalis fontana	Panicum miliaceum	Rorippa sylvestris	Papaver somniferum	Medicago lupulina
	Sedum acre	Oxybaphus nyctagineus	Papaver rhoeas	Rosa canina agg.	Parthenocissus inserta+quinquefolia	Medicago sativa s.l.
	Sedum album	Pachysandra terminalis	Papaver somniferum	Rubus caesius	Pastinaca sativa	Melica ciliata
	Sedum sexangulare	Panicum capillare	Parietaria judaica	Rubus fruticosus agg.	Persicaria amphibia	Melica transsilvanica
	Sedum spurium	Panicum miliaceum	Parthenocissus inserta+quinquefolia	Rubus laciniatus	Persicaria hydropiper	Melilotus albus
	Senecio inaequidens	Papaver dubium agg.	Parthenocissus tricuspidata	Rumex acetosa	Persicaria lapathifolia	Melilotus officinalis
	Senecio jacobaea	Papaver rhoeas	Paspalum paspalodes	Rumex acetosella	Persicaria maculosa	Melissa officinalis
	Senecio viscosus	Papaver somniferum	Pastinaca sativa	Rumex conglomeratus	Persicaria minor	Mentha aquatica

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Senecio vulgaris	Parietaria officinalis	Persicaria amphibia	Rumex crispus	Persicaria mitis	Mentha arvensis
	Setaria pumila	Parthenocissus inserta+quinquefolia	Persicaria hydropiper	Rumex obtusifolius	Persicaria orientalis	Mentha longifolia
	Setaria verticillata	Parthenocissus tricuspidata	Persicaria lapathifolia	Rumex sanguineus	Petrorhagia prolifera	Mentha spicata
	Setaria viridis	Pastinaca sativa	Persicaria maculosa	Rumex thyrsiflorus	Petrorhagia saxifraga	Mentha x dumetorum+piperita
	Sherardia arvensis	Persicaria lapathifolia	Petrorhagia saxifraga	Sagina apetala	Petroselinum crispum	Mentha x gracilis
	Sida hermaphrodita	Persicaria maculosa	Petroselinum crispum	Sagina procumbens	Petunia x atkinsiana	Mentha x rotundifolia
	Silene latifolia subsp. alba	Petrorhagia saxifraga	Petunia x atkinsiana	Salix alba	Phacelia tanacetifolia	Mercurialis annua
	Silene vulgaris	Phalaris arundinacea	Phacelia tanacetifolia	Salix caprea	Phalaris arundinacea	Microrrhinum minus
	Sinapis arvensis	Phalaris canariensis	Phalaris arundinacea	Salvia pratensis	Phalaris paradoxa	Miscanthus sacchariflorus
	Sisymbrium altissimum	Phleum bertolonii+pratense	Phalaris canariensis	Sambucus ebulus	Phleum bertolonii+pratense	Molinia arundinacea
	Sisymbrium loeselii	Physalis alkekengi	Phleum bertolonii+pratense	Sambucus nigra	Phlox paniculata	Mycelis muralis
	Sisymbrium officinale	Physalis peruviana	Phlox subulata	Sanguisorba minor	Phragmites australis	Myosotis arvensis
	Solanum decipiens+nigrum	Phytolacca esculenta	Phragmites australis	Sanguisorba officinalis	Phytolacca esculenta	Myosoton aquaticum
	Solanum dulcamara	Picea abies	Physalis alkekengi	Saponaria officinalis	Picea abies	Nardus stricta
	Solanum lycopersicum	Picris hieracioides	Physalis peruviana	Scrophularia nodosa	Picris hieracioides	Odontites vernus
	Solanum tuberosum	Pimpinella saxifraga	Physocarpus opulifolius	Scutellaria altissima	Pinus nigra	Oenothera biennis s.l.
	Solidago canadensis	Pinus strobus	Phytolacca esculenta	Securigera varia	Pinus sylvestris	Onobrychis viciifolia
	Solidago gigantea	Plantago coronopus	Picea abies	Sedum kamtschaticum	Plantago coronopus	Ononis repens
	Sonchus arvensis	Plantago lanceolata	Picris hieracioides	Sedum sexangulare	Plantago lanceolata	Ononis spinosa
	Sonchus asper	Plantago major+uliginosa	Pimpinella major	Senecio inaequidens	Plantago major+uliginosa	Onopordum acanthium
	Sonchus oleraceus	Plantago media	Pimpinella saxifraga	Senecio jacobaea	Poa annua	Origanum vulgare
	Sorbus aucuparia	Poa annua	Plantago coronopus	Senecio vulgaris	Poa compressa	Ornithopus perpusillus
	Spergularia rubra	Poa compressa	Plantago lanceolata	Setaria pumila	Poa nemoralis	Oxalis corniculata
	Stachys palustris	Poa nemoralis	Plantago major+uliginosa	Setaria verticillata	Poa palustris	Oxalis dillenii
	Stellaria media agg.	Poa palustris	Plantago media	Setaria viridis	Poa pratensis s.l.	Oxalis fontana
	Stellaria nemorum	Poa pratensis s.l.	Poa annua	Silene dioica	Poa trivialis	Paeonia officinalis

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Symphoricarpos albus	Poa trivialis	Poa bulbosa	Silene latifolia subsp. alba	Polygonum aviculare agg.	Papaver dubium agg.
	Symphoricarpos x chenaultii	Polycarpon tetraphyllum	Poa compressa	Silene vulgaris	Populus alba	Papaver rhoeas
	Symphytum officinale	Polygonatum latifolium	Poa nemoralis	Sinapis arvensis	Populus nigra agg.	Papaver somniferum
	Syringa vulgaris	Polygonatum multiflorum	Poa palustris	Sisymbrium loeselii	Populus tremula	Parthenocissus inserta+quinquefolia
	Tanacetum vulgare	Polygonum aviculare agg.	Poa pratensis s.l.	Sisymbrium officinale	Populus trichocarpa	Parthenocissus tricuspidata
	Taraxacum sect. Ruderalia	Populus nigra agg.	Poa trivialis	Solanum decipiens+nigrum	Portulaca oleracea	Pastinaca sativa
	Taxus baccata	Portulaca grandiflora	Polygonum aviculare agg.	Solanum dulcamara	Potentilla anserina	Persicaria amphibia
	Thlaspi arvense	Portulaca oleracea	Populus alba	Solanum lycopersicum	Potentilla argentea	Persicaria lapathifolia
	Thymus pulegioides	Potentilla anserina	Populus nigra agg.	Solidago canadensis	Potentilla norvegica	Persicaria maculosa
	Tilia cordata	Potentilla argentea	Populus tremula	Solidago gigantea	Potentilla recta	Petasites hybridus
	Tilia platyphyllos	Potentilla fruticosa	Portulaca grandiflora	Sonchus arvensis	Potentilla reptans	Petrorhagia prolifera
	Torilis japonica	Potentilla reptans	Portulaca oleracea	Sonchus asper	Potentilla sterilis	Petrorhagia saxifraga
	Tragopogon dubius	Potentilla supina	Potentilla anserina	Sonchus oleraceus	Potentilla supina	Petroselinum crispum
	Tragopogon pratensis agg.	Potentilla verna agg.	Potentilla argentea	Sophora japonica	Potentilla verna agg.	Phalaris arundinacea
	Trifolium arvense	Primula elatior	Potentilla reptans	Sorbaria sorbifolia	Prunella vulgaris	Phleum bertolonii+pratense
	Trifolium campestre	Primula veris	Potentilla supina	Sorbus aucuparia	Prunus armeniaca	Phragmites australis
	Trifolium dubium	Primula vulgaris	Primula veris	Stachys annua	Prunus avium	Physalis alkekengi
	Trifolium hybridum	Prunella vulgaris	Primula vulgaris	Stachys sylvatica	Prunus cerasifera	Physocarpus opulifolius
	Trifolium pratense	Prunus avium	Prunella vulgaris	Stellaria graminea	Prunus domestica s.l.	Picea abies
	Trifolium repens	Prunus cerasifera	Prunus avium	Stellaria media agg.	Prunus persica	Picris hieracioides
	Tripleurospermum inodorum	Prunus cerasus	Prunus cerasifera	Stellaria nemorum	Prunus serotina	Pimpinella major
	Trisetum flavescens	Prunus domestica s.l.	Prunus cerasus	Symphoricarpos albus	Prunus spinosa agg.	Pimpinella saxifraga
	Triticum aestivum	Prunus laurocerasus	Prunus domestica s.l.	Symphytum officinale	Pseudognaphalium luteoalbum	Pinus nigra
	Tussilago farfara	Prunus mahaleb	Prunus laurocerasus	Syringa vulgaris	Pterocarya fraxinifolia	Pinus sylvestris
	Ulmus glabra	Prunus persica	Prunus mahaleb	Taraxacum sect. Ruderalia	Puccinellia distans	Plantago lanceolata
	Ulmus laevis	Prunus serotina	Prunus padus	Taxus baccata	Pulicaria dysenterica	Plantago major+uliginosa

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Ulmus minor	Pseudosasa japonica	Prunus serotina	Telekia speciosa	Pyrethrum parthenium	Plantago media
	Urtica dioica	Puccinellia distans	Prunus spinosa agg.	Thymus pulegioides	Quercus robur	Poa annua
	Urtica urens	Pulmonaria obscura+officinalis	Pulmonaria obscura+officinalis	Tilia cordata	Quercus rubra	Poa bulbosa
	Verbascum phlomoides	Pyrethrum parthenium	Pyracantha coccinea	Tilia platyphyllos	Ranunculus acris	Poa compressa
	Verbena officinalis	Quercus petraea	Pyrethrum parthenium	Tilia tomentosa	Ranunculus bulbosus	Poa nemoralis
	Veronica arvensis	Quercus robur	Quercus petraea	Torilis arvensis	Ranunculus repens	Poa palustris
	Veronica filiformis	Quercus rubra	Quercus robur	Torilis japonica	Ranunculus sceleratus	Poa pratensis s.l.
	Veronica chamaedrys agg.	Ranunculus acris	Quercus rubra	Tragopogon pratensis agg.	Raphanus raphanistrum	Poa trivialis
	Veronica persica	Ranunculus bulbosus	Ranunculus acris	Tribulus terrestris	Rapistrum rugosum	Polygala multicaulis+vulgaris
	Veronica polita	Ranunculus repens	Ranunculus bulbosus	Trifolium arvense	Reseda lutea	Polygonum aviculare agg.
	Veronica serpyllifolia	Reseda lutea	Ranunculus repens	Trifolium campestre	Reseda luteola	Populus alba
	Viburnum lantana	Reynoutria japonica	Reseda lutea	Trifolium dubium	Reseda odorata	Populus candicans
	Viburnum rhytidophyllum	Reynoutria x bohemica	Reynoutria japonica	Trifolium hybridum	Reynoutria japonica	Populus nigra agg.
	Vicia cracca	Rhamnus cathartica	Rhamnus cathartica	Trifolium pratense	Reynoutria x bohemica	Populus tremula
	Vicia hirsuta	Rhus hirta	Rhus hirta	Trifolium repens	Robinia pseudacacia	Populus trichocarpa
	Vicia sativa agg.	Ribes alpinum	Ribes alpinum	Tripleurospermum inodorum	Rorippa amphibia	Populus x berolinensis
	Vicia sepium	Ribes nigrum	Ribes nigrum	Trisetum flavescens	Rorippa palustris	Populus x canescens
	Vicia tetrasperma	Ribes rubrum agg.	Ribes uva-crispa	Triticum aestivum	Rorippa sylvestris	Portulaca oleracea
	Vinca minor	Robinia pseudacacia	Robinia pseudacacia	Tussilago farfara	Rorippa x armoracioides	Potentilla anserina
	Viola arvensis	Rorippa palustris	Rorippa austriaca	Ulmus glabra	Rosa canina agg.	Potentilla argentea
	Viola hirta	Rorippa sylvestris	Rorippa palustris	Ulmus laevis	Rubus caesius	Potentilla erecta
	Viola odorata	Rosa canina agg.	Rorippa sylvestris	Ulmus minor	Rubus fruticosus agg.	Potentilla inclinata
	Viola papilionacea	Rosa rugosa	Rorippa x armoracioides	Urtica dioica	Rudbeckia hirta	Potentilla recta
	Viola reichenbachiana	Rosa sect. Pimpinellifoliae	Rosa canina agg.	Urtica urens	Rudbeckia laciniata	Potentilla reptans
	Viola tricolor s.l.	Rosmarinus officinalis	Rosa majalis	Verbascum lychnitis	Rumex acetosa	Potentilla sterilis
	Viola x wittrockiana	Rubus caesius	Rosa rubiginosa	Verbascum nigrum	Rumex acetosella	Potentilla verna agg.

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
	Viscum album	Rubus fruticosus agg.	Rosa rugosa	Verbascum thapsus	Rumex conglomeratus	Primula vulgaris
	Vulpia myuros	Rubus idaeus	Rubus caesius	Verbena officinalis	Rumex crispus	Prunella vulgaris
	xTriticosecale rimpaui	Rubus laciniatus	Rubus fruticosus agg.	Veronica arvensis	Rumex maritimus	Prunus avium
		Rumex acetosa	Rubus idaeus	Veronica beccabunga	Rumex obtusifolius	Prunus cerasifera
		Rumex acetosella	Rubus laciniatus	Veronica filiformis	Rumex stenophyllus	Prunus domestica s.l.
		Rumex crispus	Rudbeckia laciniata	Veronica chamaedrys agg.	Rumex thyrsiflorus	Prunus mahaleb
		Rumex obtusifolius	Rumex acetosa	Veronica montana	Sagina apetala	Prunus padus
		Rumex sanguineus	Rumex acetosella	Veronica officinalis	Sagina procumbens	Prunus persica
		Rumex thyrsiflorus	Rumex conglomeratus	Veronica peregrina	Salix alba	Prunus serotina
		Sagina apetala	Rumex crispus	Veronica persica	Salix caprea	Prunus spinosa agg.
		Sagina procumbens	Rumex obtusifolius	Veronica polita	Salix elaeagnos	Pseudolysimachion orchideum
		Salix alba	Rumex sanguineus	Veronica serpyllifolia	Salix fragilis	Puccinellia distans
		Salix caprea	Rumex thyrsiflorus	Viburnum lantana	Salix purpurea	Pulicaria dysenterica
		Salix fragilis	Sagina apetala	Viburnum opulus	Salix triandra	Pyrethrum parthenium
		Salvia officinalis	Sagina procumbens	Vicia hirsuta	Salix viminalis	Pyrus communis
		Salvia pratensis	Salix alba	Vicia sativa agg.	Salsola kali	Pyrus pyraster
		Salvia verticillata	Salix caprea	Vicia sepium	Salvia pratensis	Quercus petraea
		Sambucus nigra	Salix purpurea	Vinca minor	Sambucus nigra	Quercus robur
		Sanguisorba minor	Salvia nemorosa	Viola alba	Sanguisorba minor	Ranunculus acris
		Sanguisorba officinalis	Salvia officinalis	Viola arvensis	Saponaria ocymoides	Ranunculus bulbosus
		Saponaria officinalis	Salvia verticillata	Viola hirta	Saponaria officinalis	Ranunculus polyanthemos
		Satureja hortensis	Sambucus nigra	Viola odorata	Scirpus sylvaticus	Ranunculus repens
		Saxifraga umbrosa agg.	Samolus valerandi	Viola reichenbachiana	Scrophularia nodosa	Ranunculus sceleratus
		Scrophularia nodosa	Sanguisorba minor	Viola riviniana	Scrophularia scopolii	Raphanus raphanistrum
		Scrophularia scopolii	Saponaria officinalis	Viola tricolor s.l.	Securigera varia	Reseda lutea
		Securigera varia	Satureja hortensis	Viola x wittrockiana	Sedum album	Reseda luteola
		Sedum acre	Scabiosa ochroleuca	Vulpia myuros	Sedum montanum s.str.	Reynoutria japonica

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
		Sedum album	Scleranthus annuus		Sedum pallidum	Rhamnus cathartica
		Sedum dasyphyllum	Scrophularia nodosa		Sedum sexangulare	Rhus hirta
		Sedum hispanicum	Scrophularia scopolii		Senecio erucifolius	Ribes nigrum
		Sedum hybridum	Securigera varia		Senecio inaequidens	Ribes rubrum agg.
		Sedum rupestre subsp. erectum	Sedum acre		Senecio jacobaea	Robinia pseudacacia
		Sedum sarmentosum	Sedum album		Senecio vernalis	Rorippa austriaca
		Sedum sexangulare	Sedum hispanicum		Senecio viscosus	Rorippa palustris
		Sedum spurium	Sedum hybridum		Senecio vulgaris	Rorippa sylvestris
		Sempervivum tectorum	Sedum pallidum		Setaria pumila	Rorippa x armoracioides
		Senecio erucifolius	Sedum rupestre subsp. erectum		Setaria verticillata	Rosa canina agg.
		Senecio inaequidens	Sedum sexangulare		Setaria viridis	Rosa elliptica
		Senecio jacobaea	Sedum spurium		Silene dioica	Rosa micrantha
		Senecio viscosus	Senecio erucifolius		Silene latifolia subsp. alba	Rosa multiflora
		Senecio vulgaris	Senecio inaequidens		Silene noctiflora	Rosa rubiginosa
		Setaria pumila	Senecio jacobaea		Silene vulgaris	Rosa rugosa
		Setaria verticillata	Senecio viscosus		Sinapis arvensis	Rubus caesius
		Setaria viridis	Senecio vulgaris		Sisymbrium altissimum	Rubus fruticosus agg.
		Sherardia arvensis	Setaria pumila		Sisymbrium loeselii	Rubus idaeus
		Silene armeria	Setaria verticillata		Sisymbrium officinale	Rumex acetosa
		Silene dioica	Setaria viridis		Sisymbrium orientale subsp. orientale	Rumex acetosella
		Silene latifolia subsp. alba	Sherardia arvensis		Solanum decipiens+nigrum	Rumex conglomeratus
		Silene viscosa	Silene dioica		Solanum dulcamara	Rumex crispus
		Silene vulgaris	Silene latifolia subsp. alba		Solanum lycopersicum	Rumex maritimus
		Sinapis arvensis	Silene vulgaris		Solanum tuberosum	Rumex obtusifolius
		Sisymbrium loeselii	Sinapis arvensis		Solidago canadensis	Rumex palustris
		Sisymbrium officinale	Sisymbrium loeselii		Solidago gigantea	Rumex thyrsiflorus

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
		Solanum decipiens+nigrum	Sisymbrium officinale		Sonchus arvensis	Sagina apetala
		Solanum dulcamara	Solanum decipiens+nigrum		Sonchus asper	Sagina procumbens
		Solanum lycopersicum	Solanum dulcamara		Sonchus oleraceus	Salix alba
		Solidago canadensis	Solanum lycopersicum		Spergula arvensis	Salix aurita
		Solidago gigantea	Solanum tuberosum		Spergularia rubra	Salix caprea
		Sonchus arvensis	Soleirolia soleirolii		Spergularia salina	Salix cinerea
		Sonchus asper	Solidago canadensis		Spiraea chamaedryfolia	Salix fragilis
		Sonchus oleraceus	Solidago gigantea		Stachys annua	Salix purpurea
		Sorbus aria	Sonchus arvensis		Stachys palustris	Salix viminalis
		Sorbus aucuparia	Sonchus asper		Stachys sylvatica	Salix x dasyclados
		Sorbus intermedia	Sonchus oleraceus		Stellaria graminea	Salsola kali
		Spergularia rubra	Sorbus aucuparia		Stellaria media agg.	Salvia nemorosa
		Spiraea x bumalda	Sorbus torminalis		Stellaria nemorum	Salvia pratensis
		Stachys annua	Spergula arvensis		Suaeda maritima	Sambucus ebulus
		Stachys byzantina	Spergularia rubra		Symphoricarpos albus	Sambucus nigra
		Stachys macrantha	Spiraea douglasii		Symphytum officinale	Sanguisorba minor
		Stachys setifera	Stachys annua		Syringa vulgaris	Sanguisorba officinalis
		Stachys sylvatica	Stachys byzantina		Tagetes patula	Saponaria officinalis
		Stellaria graminea	Stachys palustris		Tanacetum vulgare	Satureja hortensis
		Stellaria holostea	Stachys sylvatica		Taraxacum sect. Ruderalia	Scabiosa canescens
		Stellaria media agg.	Stellaria graminea		Thlaspi arvense	Scabiosa ochroleuca
		Symphoricarpos albus	Stellaria media agg.		Thymus pulegioides	Scrophularia canina
		Symphytum grandiflorum	Sutera cordata		Tilia cordata	Scrophularia nodosa
		Symphytum officinale	Symphoricarpos albus		Torilis arvensis	Scrophularia scopolii
		Syringa vulgaris	Symphytum officinale		Torilis japonica	Securigera varia
		Tanacetum vulgare	Syringa vulgaris		Tragopogon dubius	Sedum album
		Taraxacum sect. Ruderalia	Tagetes erecta		Tragopogon pratensis agg.	Sedum rupestre subsp. erectum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
		Taxus baccata	Tanacetum vulgare		Tribulus terrestris	Sedum sexangulare
		Teucrium chamaedrys	Taraxacum sect. Ruderalia		Trifolium alexandrinum	Senecio erucifolius
		Thlaspi arvense	Taxus baccata		Trifolium arvense	Senecio inaequidens
		Thymus pulegioides	Tetragonia tetragonoides		Trifolium aureum	Senecio jacobaea
		Tilia cordata	Thlaspi arvense		Trifolium campestre	Senecio viscosus
		Tilia platyphyllos	Thymus polytrichus		Trifolium dubium	Senecio vulgaris
		Torilis japonica	Thymus pulegioides		Trifolium fragiferum	Setaria viridis
		Trifolium alpestre	Thymus vulgaris		Trifolium hybridum	Schoenoplectus tabernaemontani
		Trifolium arvense	Tilia cordata		Trifolium medium	Silene armeria
		Trifolium campestre	Tilia platyphyllos		Trifolium pratense	Silene dioica
		Trifolium dubium	Tilia tomentosa		Trifolium repens	Silene latifolia subsp. alba
		Trifolium hybridum	Torilis japonica		Tripleurospermum inodorum	Silene vulgaris
		Trifolium pratense	Tragopogon pratensis agg.		Trisetum flavescens	Sinapis arvensis
		Trifolium repens	Trifolium arvense		Triticum aestivum	Sisymbrium loeselii
		Tripleurospermum inodorum	Trifolium campestre		Tussilago farfara	Sisymbrium officinale
		Trisetum flavescens	Trifolium dubium		Typha angustifolia	Solanum decipiens+nigrum
		Triticum aestivum	Trifolium hybridum		Typha latifolia	Solanum dulcamara
		Tropaeolum majus	Trifolium pratense		Ulmus glabra	Solanum lycopersicum
		Tussilago farfara	Trifolium repens		Ulmus minor	Solidago canadensis
		Ulmus glabra	Tripleurospermum inodorum		Urtica dioica	Solidago gigantea
		Ulmus laevis	Trisetum flavescens		Urtica urens	Sonchus arvensis
		Ulmus minor	Triticum aestivum		Valerianella locusta	Sonchus asper
		Urtica dioica	Tropaeolum majus		Verbascum blattaria	Sonchus oleraceus
		Urtica urens	Tussilago farfara		Verbascum densiflorum	Sorbus aria
		Valeriana officinalis agg.	Ulmus glabra		Verbascum chaixii subsp. austriacum	Sorbus aucuparia
		Verbascum densiflorum	Ulmus laevis		Verbascum lychnitis	Sorbus intermedia

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
		Verbascum chaixii subsp. austriacum	Ulmus minor		Verbascum nigrum	Spergularia rubra
		Verbascum nigrum	Urtica dioica		Verbascum phlomoides	Spinacia oleracea
		Verbascum phlomoides	Urtica urens		Verbascum thapsus	Spiraea salicifolia
		Verbascum thapsus	Valeriana officinalis agg.		Verbena bonariensis	Spiraea x vanhouttei
		Verbena officinalis	Verbascum phlomoides		Verbena officinalis	Stachys byzantina
		Veronica arvensis	Verbascum thapsus		Veronica agrestis	Stachys germanica
		Veronica filiformis	Verbena bonariensis		Veronica anagalloides	Stachys palustris
		Veronica chamaedrys agg.	Verbena officinalis		Veronica arvensis	Stachys sylvatica
		Veronica officinalis	Veronica agrestis		Veronica beccabunga	Stellaria graminea
		Veronica peregrina	Veronica arvensis		Veronica filiformis	Stellaria media agg.
		Veronica persica	Veronica beccabunga		Veronica hederifolia agg.	Stellaria nemorum
		Veronica polita	Veronica filiformis		Veronica chamaedrys agg.	Succisa pratensis
		Veronica serpyllifolia	Veronica chamaedrys agg.		Veronica peregrina	Symphoricarpos albus
		Veronica teucrium	Veronica peregrina		Veronica persica	Symphoricarpos orbiculatus
		Viburnum rhytidophyllum	Veronica persica		Veronica polita	Symphytum officinale
		Vicia cracca	Veronica polita		Veronica serpyllifolia	Syringa vulgaris
		Vicia hirsuta	Veronica serpyllifolia		Vicia cracca	Tagetes patula
		Vicia sativa agg.	Viburnum lantana		Vicia hirsuta	Tanacetum vulgare
		Vicia sepium	Viburnum opulus		Vicia lutea	Taraxacum sect. Ruderalia
		Vicia sylvatica	Vicia cracca		Vicia sativa agg.	Tetragonolobus maritimus
		Vicia tenuifolia	Vicia hirsuta		Vicia sepium	Teucrium chamaedrys
		Vicia tetrasperma	Vicia sativa agg.		Vicia tenuifolia	Thlaspi arvense
		Vicia villosa subsp. villosa	Vicia sepium		Vicia tetrasperma	Thymus pulegioides
		Vinca major	Vicia tetrasperma		Vicia villosa subsp. villosa	Thymus vulgaris
		Vinca minor	Vinca minor		Vinca major	Tilia cordata
		Viola alba	Viola arvensis		Viola arvensis	Tilia platyphyllos
		Viola arvensis	Viola hirta		Viola hirta	Torilis arvensis

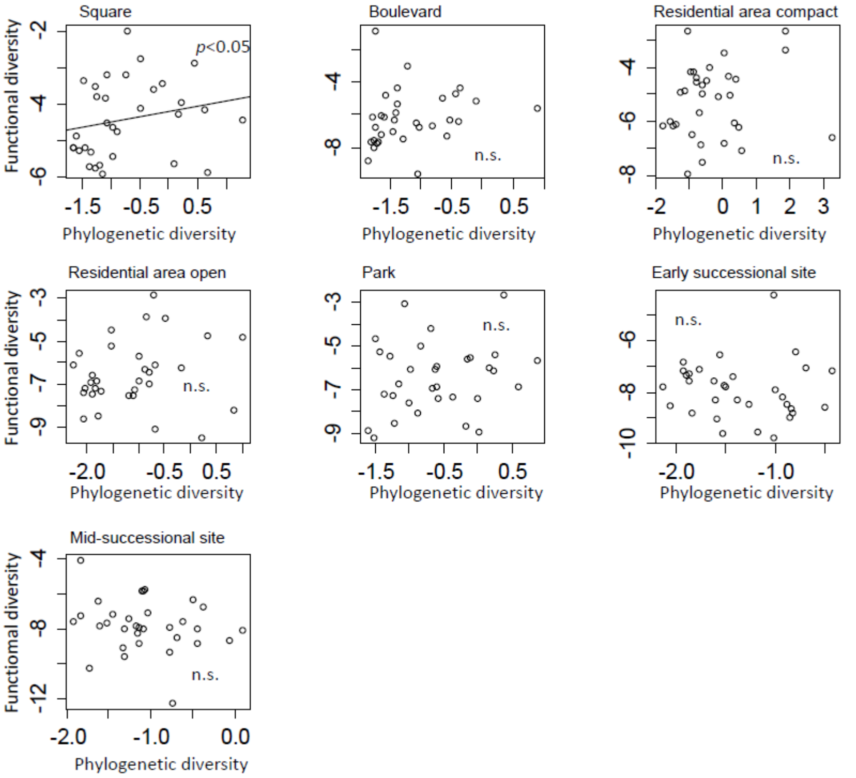
square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
		Viola odorata	Viola odorata		Viola odorata	Torilis japonica
		Viola papilionacea	Viola papilionacea		Viola papilionacea	Tragopogon dubius
		Viola reichenbachiana	Viola reichenbachiana		Viola suavis	Tragopogon pratensis agg.
		Viola riviniana	Viola riviniana		Viola tricolor s.l.	Tribulus terrestris
		Viola suavis	Viola tricolor s.l.		Virga strigosa	Trifolium alpestre
		Viola x wittrockiana	Viola x wittrockiana		Vitis sp.	Trifolium arvense
		Viscum album	Vitis sp.		Vulpia myuros	Trifolium aureum
		Vitis sp.	Vulpia myuros		Weigela florida	Trifolium campestre
		Vulpia myuros	Weigela florida		xTriticosecale rimpaui	Trifolium dubium
		Wisteria sinensis	Zea mays		Zea mays	Trifolium fragiferum
		Zelkova carpinifolia				Trifolium hybridum
						Trifolium medium
						Trifolium pratense
						Trifolium repens
						Tripleurospermum inodorum
						Trisetum flavescens
						Triticum aestivum
						Tussilago farfara
						Typha angustifolia
						Typha latifolia
						Ulmus glabra
						Ulmus laevis
						Ulmus minor
						Urtica dioica
						Vaccinium myrtillus
						Valeriana officinalis agg.
						Veratrum nigrum

square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
						Verbascum blattaria
						Verbascum densiflorum
						Verbascum chaixii subsp. austriacum
						Verbascum lychnitis
						Verbascum nigrum
						Verbascum phlomoides
						Verbascum thapsus
						Verbena officinalis
						Veronica arvensis
						Veronica filiformis
						Veronica chamaedrys agg.
						Veronica persica
						Veronica polita
						Veronica serpyllifolia
						Viburnum lantana
						Viburnum opulus
						Vicia cracca
						Vicia grandiflora
						Vicia hirsuta
						Vicia sativa agg.
						Vicia sepium
						Vicia tenuifolia
						Vicia tetrasperma
						Vicia villosa subsp. villosa
						Vincetoxicum hirundinaria
						Viola alba
						Viola arvensis

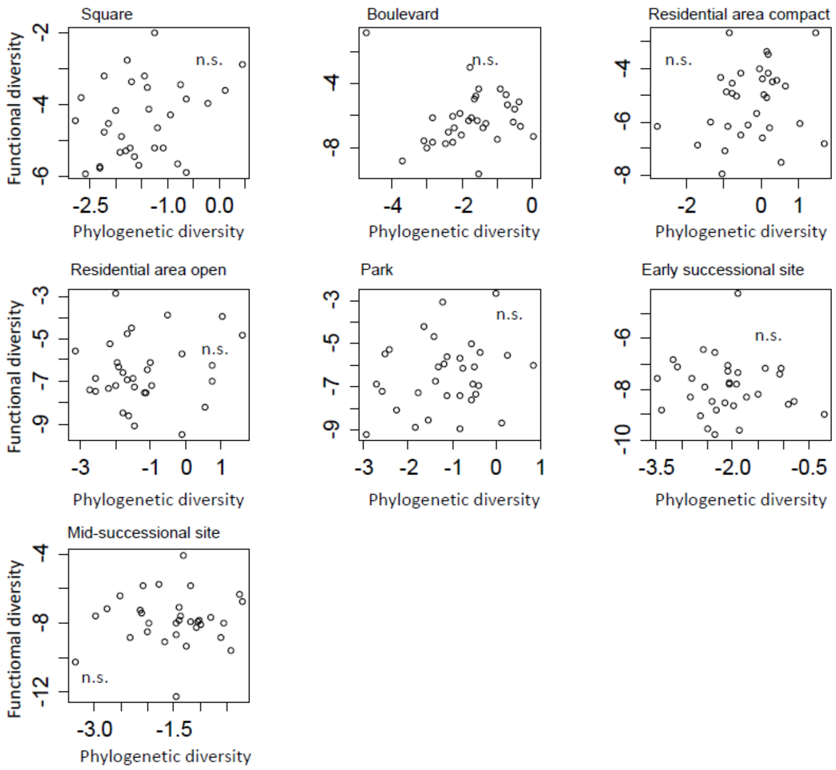
square	boulevard	residential area compact	residential area open	park	early successional site	mid-successional site
						Viola canina
						Viola hirta
						Viola odorata
						Viola riviniana
						Viola suavis
						Virga strigosa
						Vitis sp.
						Vulpia myuros
						Xanthium strumarium
						Zea mays

Appendix S2. – Relationships between functional diversity (*FD* of all traits) and phylogenetic diversity calculated as mean pairwise distance (*mpd*) and mean nearest taxonomic distance (*mntd*).

a) Mean pairwise distance (*mpd*)



b) Mean nearest taxonomic distance (*mntd*)



Curriculum vitae

Personal details

Natálie Čeplová	born on 26th March 1979, Brno, Czech Republic
E-mail	ceplova@ped.muni.cz

Research interest	Urban vegetation (species composition, species richness, factors affecting vegetation in man-made habitats)
Memberships	Česká botanická společnost (Czech Botanical Society), Česká společnost pro ekologii (Czech Ecological Society)

Education and qualification

2011-present	Masaryk University, Faculty of Science, Department of Botany and Zoology Doctoral degree program: Botany Thesis: Diversity of European urban floras Supervisor: doc. RNDr. Zdeňka Lososová, Ph.D.
1997-2002	Masaryk University, Faculty of Science, Department of Botany and zoology Master`s degree programme: Systematic Biology and Ecology Thesis: The expansion of *Arrhenatherum elatius* in dry grasslands Supervisor: prof. RNDr. Milan Chytrý, Ph.D.
Software skills	TURBOVEG, JUICE, PC-ORD, CANOCO, STATISTICA, R, ArcGIS, Microsoft Office
Language skills	English, German

Employment history

2009-present	Assistant at Masaryk University, Faculty of Education, Department of Biology
2011-present	Researcher at Masaryk University, Faculty of Science, Department of Botany and Zoology

Fieldwork experience

1998-2002	Field experiment and vegetation survey of dry grasslands
2010-2013	Field sampling of urban vegetation in small settlements (Czech Republic, Slovakia, Germany, Austria)
2011-present	Field grid mapping of flora of the city of Brno
2013-present	Field sampling of urban vegetation in Mediterranean cities (supported by the Czech Science Foundation, project 14-10723S)
2016	Field sampling of vegetation of parks and chateau gardens

Courses

Species traits: a functional approach to biodiversity, from organisms to ecosystems (6th edition), České Budějovice, Czech Republic. May 29th – June 3rd 2016.

Pedagogické studium učitelů všeobecně vzdělávacích předmětů střední školy (Pedagogical studies for high school teachers), Pedagogická fakulta, Univerzita Palackého v Olomouci, 2007–2010.

Science-popularizing publications

Čeplová, N. & Kalusová, V. (2016) Jak velikost města ovlivňuje druhové složení vegetace? *Fórum ochrany přírody*, **2016/4**, 30–34.

Publications

Čeplová, N., Lososová, Z., Zelený, D., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z., Řehořek, V. & Tichý, L. (2015) Phylogenetic diversity of central-European urban plant communities: effects of alien species and habitat types. *Preslia*, **87**, 1–16.

Lososová, Z., **Čeplová, N.**, Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Láníková, D., Presilerová, Z. & Řehořek V. (2016) Is phylogenetic diversity a good proxy for functional diversity of plant communities? A case study from urban habitats. *Journal of Vegetation Science*, **27**, 1036–1046.

Kalusová, V., **Čeplová, N.** & Lososová, Z. (2016) Which traits influence the frequency of plant species occurrence in urban habitat types? *Urban Ecosystems*, DOI 10.1007/s11252-016-0288-3.

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

Manuscripts submitted to international journals

Čeplová, N., Lososová, Z. & Kalusová, V. (submitted) Urban ornamental trees: a source of recent invaders. A case study from a European city.

Conferences

Čeplová, N. & Chytrý, M. (2001) Expanze *Arrhenatherum elatius* do suchých trávníků v okolí Brna. Konference České botanické společnosti: Botanický výzkum a ochrana přírody. Praha, Czech Republic. Poster.

Čeplová, N. & Lososová, Z. (2011) Diversity of European urban vegetation. Fifth Meeting of Czech, Slovak and Hungarian Ph.D. students in Plant Ecology and Botany. Piesočná, Borská Lowland, Slovakia. Lecture.

Čeplová, N., Lososová, Z., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z. Řehořek, V., Tichý, L. & Zelený, D. (2012) Fylogenetická diverzita vegetace velkých evropských měst. X. sjezd České botanické společnosti. Praha, Czech Republic. Poster.

Čeplová, N., Lososová, Z., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z. Řehořek, V., Tichý, L. & Zelený, D. (2013) Phylogenetic diversity of urban habitats with different levels of disturbance. 56th International Symposium of IAVS. Tartu, Estonia. Poster.

Čeplová, N., Lososová, Z., Chytrý, M., Danihelka, J., Fajmon, K., Láníková, D., Preislerová, Z. Řehořek, V., Tichý, L. & Zelený, D. (2013) Fylogenetická diverzita vegetace velkých evropských měst. Konference České společnosti pro ekologii "Ekologie 2013". Brno, Czech Republic. Poster.

Čeplová, N., Lososová, Z. & Kalusová, V. (2014) Is the proportion of alien species in man-made habitats influenced by city size? 4th International Symposium on Environmental Weeds and Invasive Plants. Montpellier, France. Lecture.

Čeplová, N., Lososová, Z. & Kalusová, V. (2015) Is the proportion of alien species in man-made habitats influenced by city size? 58th Annual Symposium of the International Association for Vegetation Science. Brno, Czech Republic. Poster.

Čeplová, N., Kalusová, V. & Lososová, Z. (2015) Na velikosti záleží? Jak velikost sídla ovlivňuje druhové složení vegetace. The Meeting of the Ph.D. students in ecology and phytosociology. Rožmberk, Czech Republic. Lecture (In Czech).

Čeplová, N., Lososová, Z. & Kalusová, V. (2016) Na velikosti záleží? Jak velikost sídla ovlivňuje druhové složení vegetace. Seminář Přírodě blízká péče o městskou zeleň. České Budějovice, Czech Republic. Lecture (In Czech).

Čeplová, N., Lososová, Z. & Kalusová, V. (2016) Urban ornamental trees: a source of recent invaders? A case study from European city. Neobiota – 9th International Conference on Biological Invasions. Vianden, Luxembourg. Poster.