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 typu stanoviště

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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 habitats 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 in the null model. 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 histories and origins (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 occur 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, therefore they 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 present 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 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). Due to 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 analysed for particular habitats.

Here we test the following hypotheses: (i) 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. (ii) As urban plant communities contain a large proportion of alien species, which have a relatively low phylogenetic diversity, the expectation is that the introduction of alien species decreases their phylogenetic diversity. (iii) 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 plant species 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 streets 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 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 nine 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, 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 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:

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

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 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 phylogenetic community 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).

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

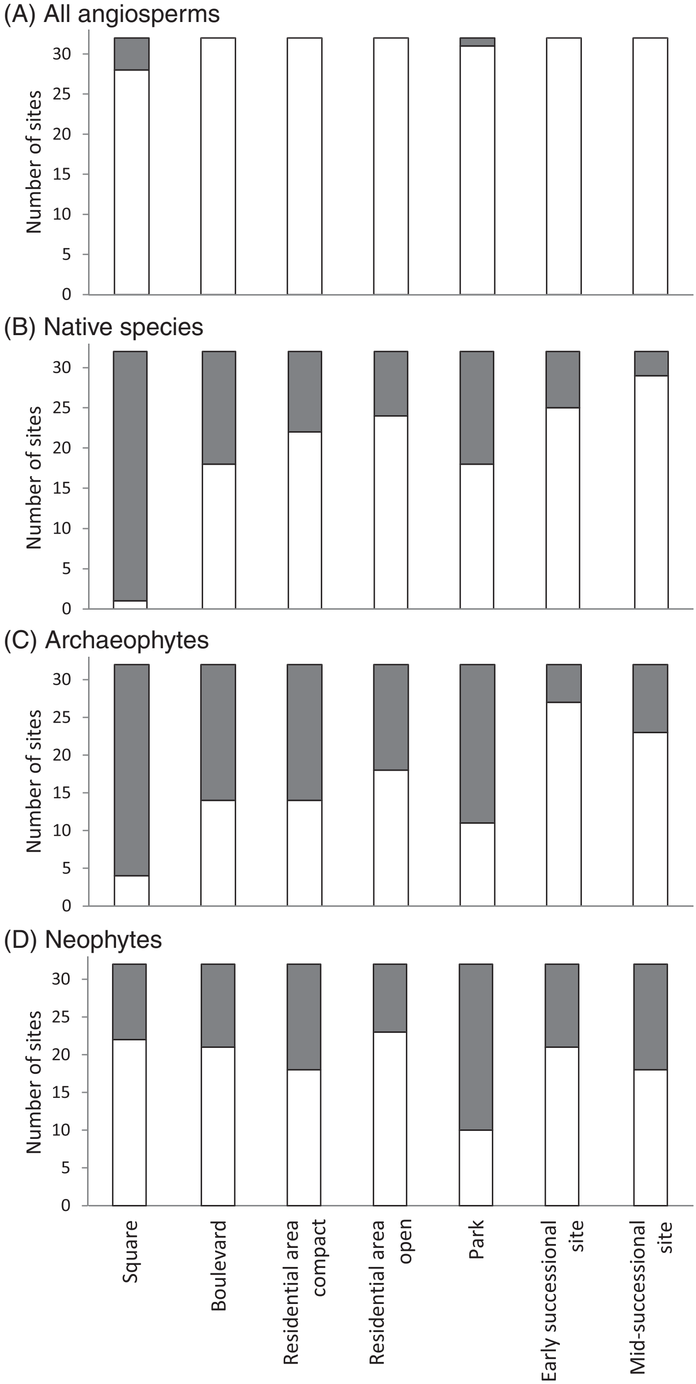

Fig. 1. – Numbers of sites (1-ha plots) with a ☐ clustered and ■ random community structure, calculated for seven urban habitats using the first null model, which does not include species frequency. No site had an overdispersed structure. Total number of sites studied per habitat was 32.

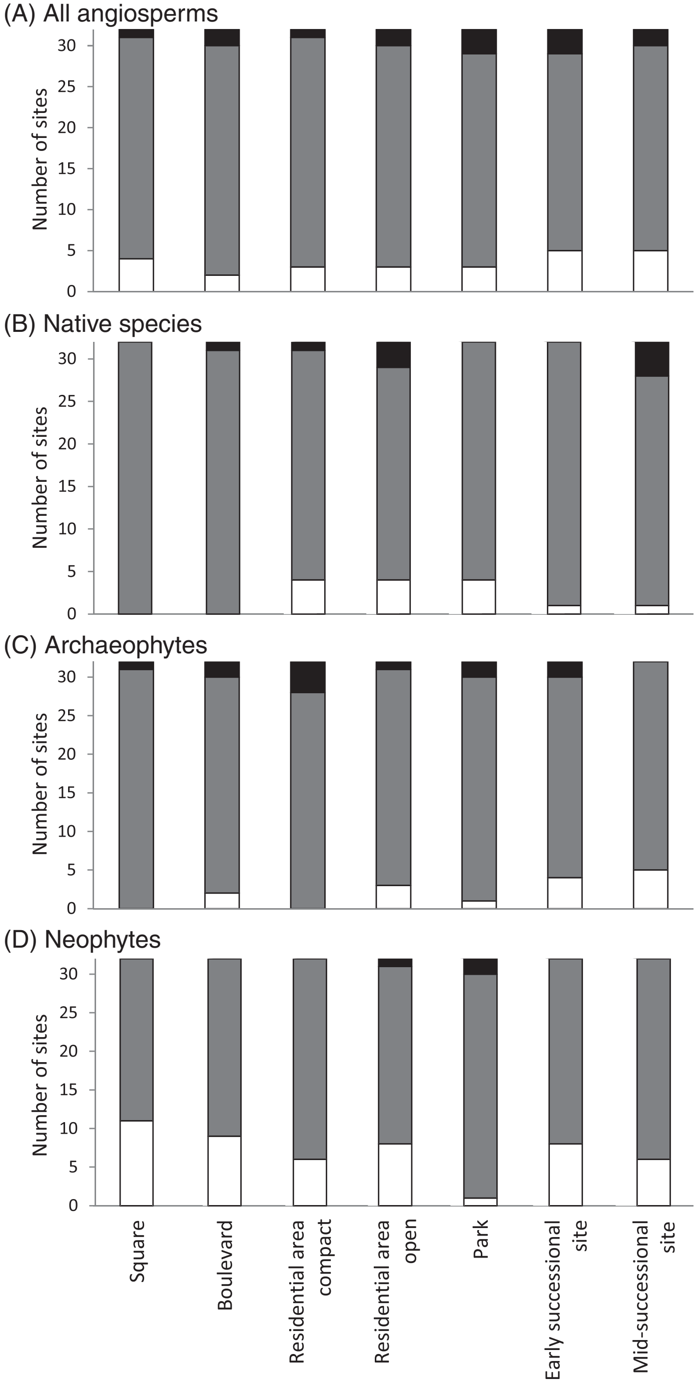

Fig. 2. – Numbers of sites (1-ha plots) with a □ clustered, ▨ random, or ■ overdispersed community structure, calculated for seven urban habitats using the second (frequency-based) null model. Total number of sites studied per habitat was 32.

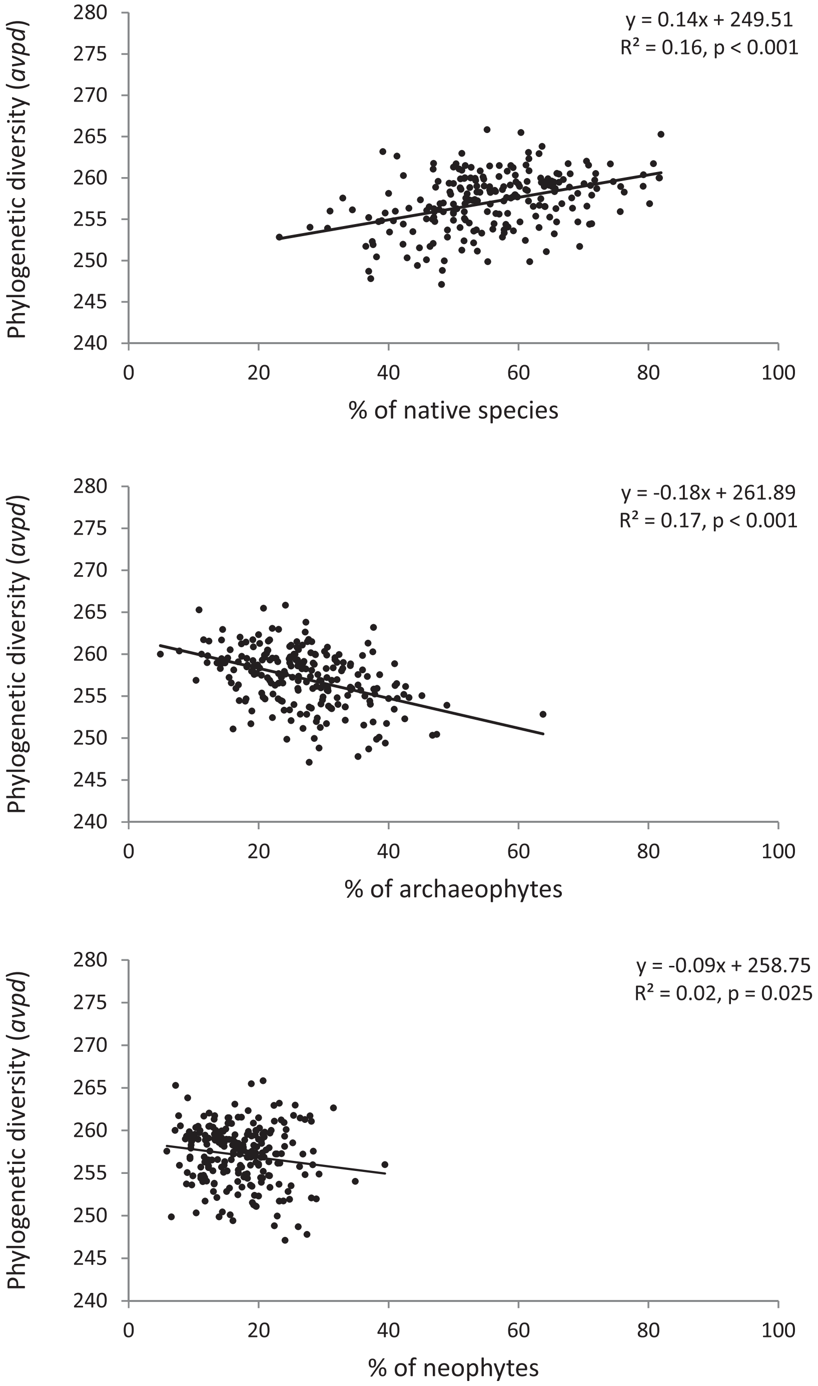

Fig. 3. – Relationship between phylogenetic diversity (*avpd*) and percentages of native species, archaeophytes and neophytes in each community. Data points correspond to 1-ha plots surveyed in seven urban habitats in 32 cities (n = 224).

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 Electronic Appendix 1.

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 consequently the community became phylogenetically more clustered (Fig. 3). This decrease was also recorded in the data for the different habitats (Electronic Appendices 2–4), although most linear regressions were non-significant due to the small number of data points.

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 seven 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.

See www.preslia.cz for Electronic Appendices 1–4

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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 zkoumaných měst). 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, například disturbancí. Tyto filtry umožňují přežití pouze omezeného spektra druhů se specifickými vlastnostmi, které zpravidla pocházejí z omezeného počtu vývojových linií.

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