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Phylogenetic beta diversity of native and alien species in European urban floras

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ABSTRACT

Aim Human activities have weakened biogeographical barriers to dispersal, increasing the rate of introduction of alien plants. However, their impact on beta diversity and floristic homogenization is poorly understood. Our goal is to compare the phylogenetic beta diversity of native species with that of two groups of alien species, archaeophytes and neophytes (introduced before and after AD 1500, respectively), across European urban floras to explore how biological invasions affect phylogenetic turnover at a continental scale.

Location Twenty European cities located in six countries between 49 and 53° N latitude in continental Europe and the British Isles.

Methods To compare the phylogenetic beta diversity of native and alien species we use the average phylogenetic dissimilarity of individual floras from their group centroid in multivariate space. Differences in phylogenetic beta diversity among different species groups are then assessed using a randomization test for homogeneity of multivariate dispersions.

Results Across European urban floras, and when contrasted with natives, archaeophytes are usually associated with lower levels of phylogenetic beta diversity while neophytes tend to increase phylogenetic differentiation.

Main conclusions While archaeophytes tend to promote limited homogenization in phylogenetic beta diversity, because of their diverse geographical origin together with short residence times in the invaded regions, neophytes are not promoting biotic homogenization of urban floras across Europe. Therefore, in spite of the increasing rate of alien invasion, an intense phylogenetic homogenization of urban cities is not to be expected soon.

Keywords

Alien plants, archaeophyte, biotic homogenization, cities, Europe, invasion, neophyte, phylogenetic dissimilarity.

INTRODUCTION

Anthropogenic activities have weakened biogeographical barriers to dispersal, resulting in the global spread and establishment of an increasing number of alien species, the impact of which on the structure and composition of biological communities at coarse geographical scales remains poorly understood (Lambdon *et al.*, 2008; Vilà *et al.*, 2010). Alien plant species occur in a wide range of habitats, with urban and industrial areas harbouring the highest numbers of species (Chytrý *et al.*,

2008a; Pyšek *et al.*, 2010). In addition, given the high availability of long-distance anthropogenic vectors of dispersal, urban areas act as the focal point for the broad-scale introduction of alien plants (Pyšek, 1998; Chytrý *et al.*, 2005). Therefore, urban vascular plants are, in terms of alien species richness, an appropriate pool of species for documenting the ecological consequences of biological invasions, including changes in biological diversity within (alpha diversity) and among (beta diversity) species assemblages (Ricotta *et al.*, 2009). Also, while urban floras represent a special case of species assemblages as compared with

more natural vegetation, nonetheless cities represent the largest alien species pool for the colonization of the surrounding less disturbed sites.

Urban floras are generally rich in species, harbouring more species than the surrounding landscapes (Wittig & Durwen, 1981; Kowarik, 1985). On average, in central European cities 40% of plant species are alien species, with archaeophytes and neophytes contributing 25% and 15% of the total city flora (Pyšek, 1998). The fact that a large proportion of urban species are of alien origin makes cities a suitable subject for studying the impact of alien species on diversity at and among urban localities (alpha and beta diversity, respectively). Nevertheless, while the number of species that can be accommodated in a city of a certain size remains relatively stable (Pyšek, 1993), the composition of the flora may vary dramatically between cities. Within assemblages there is evidence that in central European cities total plant species richness over the last one to two centuries has remained at comparable levels while approximately 20–40% of the original urban floras has been replaced by alien species (Chochołoušková & Pyšek, 2003; Knapp *et al.*, 2010).

Between assemblages, there is evidence that alien species have had different impacts based primarily on their time of introduction; this criterion is used to distinguish two groups of alien species in European regions (for definitions see Pyšek *et al.*, 2004). Archaeophytes are alien species introduced before AD 1500, primarily from the Mediterranean Basin and south-eastern European steppes, and are typically weeds of arable land. Neophytes were introduced into Europe after that date, which signifies the discovery of the New World and the initiation of relatively rapid and substantial changes in human movement, demography, agriculture, commerce and industry. Archaeophytes represent an ecologically distinct group that differs from neophytes in habitat affinities and invasion dynamics that reflect millennia of invasion history (Pyšek & Jarošík, 2005; Pyšek *et al.*, 2005). For European cities, archaeophytes usually show lower rates of species turnover among urban floras than neophytes (Kühn *et al.*, 2004; Kühn & Klotz, 2006; La Sorte *et al.*, 2007, 2008). Therefore, distinct patterns of beta diversity for archaeophytes and neophytes reflect in large part the transition from regional to global origins of alien species in Europe. European archaeophytes that were introduced into North America show similar spatial patterns to those found in Europe, with broad distributions and low spatial turnover reflecting the consequences of their early introduction with European settlers and their long residence time as aliens in Europe (La Sorte & Pyšek, 2009).

From an evolutionary perspective, the phylogenetic alpha diversity of alien urban plants has been recently investigated by Ricotta *et al.* (2009). Using data from 21 urban floras located in Europe and eight in the USA, Ricotta *et al.* (2009) showed that in spite of the very diverse origin of plant species introduced into European and American cities, the strong environmental filters imposed by urbanization constrain the functional diversity of urban floras, which is expressed in their generally low phylogenetic diversity (see also Knapp *et al.*,

2008). Accordingly, urban alien floras are mainly composed of phylogenetically related species that are well adapted to anthropogenic habitats.

By contrast, little is known about the effects of urbanization on the phylogenetic beta diversity of alien species. In this study we complete the picture by comparing the phylogenetic beta diversity of archaeophytes and neophytes with the phylogenetic beta diversity of the corresponding native species from 20 European urban floras. The goal of this study is to use the contrasting historical and geographical perspectives provided by archaeophytes and neophytes (see, e.g., Pyšek *et al.*, 2005; La Sorte *et al.*, 2008; Chytrý *et al.*, 2008b) to explore how alien species affect phylogenetic turnover at a continental scale under increasingly weaker biogeographical barriers to dispersal.

MATERIALS AND METHODS

Data

For the purposes of this study, we used the database of European urban floras described by Ricotta *et al.* (2009). The database consists of floras for 20 European cities located in six countries between 49 and 53° N latitude (Table 1). All urban areas contained more than 0.1 million inhabitants and climatically and environmentally similar regions were sampled within the temperate deciduous forest biome. A major geographical feature distinguished the 20 urban areas with 10 cities located on continental Europe and 10 in the British Isles (Table 1). The floras for individual cities included only spontaneous species, excluding all those occurrences that were obviously planted, resulting in a total of 3584 species.

Each species was designated as native, archaeophyte or neophyte according to the approach described by La Sorte *et al.* (2007). For instance, internal classification of the European floras into neophytes and archaeophytes is sometimes not consistent, reflecting differences in the time of introduction and place of origin for alien species across Europe (Pyšek & Jarošík, 2005). To provide a consistent classification scheme where each species was identified by only one category, a species was classified as an archaeophyte if it was designated as an archaeophyte in at least one flora. In doing so, archaeophytes were ranked higher than neophytes because a species with both labels should have been identified as an archaeophyte in one region before being identified as a neophyte in another (see La Sorte *et al.*, 2007, for details).

Supertree construction

We constructed an aged phylogenetic tree for all species in the 20 urban floras using the online software PHYLOMATIC (<http://www.phylodiversity.net/phyloomatic>; Webb & Donoghue, 2005). PHYLOMATIC uses the base tree of the Angiosperm Phylogeny Group (APG, 2003) as the backbone in combination with numerous published molecular phylogenies to create a tree containing the 3584 species belonging to 117 families and 977

Table 1 Floristic data used in this study with the geographical location, the human population size, the total number of species, the number of species designated as native and alien and the number of alien species designated as archaeophyte and neophyte in 20 European urban floras.

City	Latitude/longitude	Inhabitants (million)	Number of species				
			Total	Native	Alien	Archaeophyte	Neophyte
Continental Europe							
Berlin, West (Germany)	52°31' N/13°24' E	1.930	955	512	443	101	342
Brno (Czech Republic)	49°12' N/16°37' E	0.388	765	311	454	176	278
Brussels (Belgium)	50°50' N/04°21' E	0.970	696	479	217	58	159
Chemnitz (Germany)	50°50' N/12°55' E	0.246	837	409	428	207	221
Halle an der Saale (Germany)	51°28' N/11°58' E	0.238	896	406	490	237	253
Hannover (Germany)	52°22' N/09°44' E	0.516	782	549	233	94	139
Leipzig (Germany)	51°20' N/12°23' E	0.539	1732	721	1011	139	872
Plzeň (Czech Republic)	49°43' N/13°29' E	0.165	1014	681	333	159	174
Prague (Czech Republic)	50°05' N/14°26' E	1.212	1856	1157	699	265	434
Warsaw (Poland)	52°15' N/21°00' E	1.650	1379	918	461	124	337
British Isles							
Birmingham (UK)	51°29' N/01°54' W	0.977	565	400	165	71	94
Brighton (UK)	50°49' N/00°08' W	0.248	529	347	182	85	97
Dublin (Ireland)	53°20' N/06°15' W	0.506	306	198	108	41	67
Exeter (UK)	50°43' N/03°31' W	0.118	473	331	142	66	76
Kingston upon Hull (UK)	53°43' N/00°20' W	0.244	696	423	273	91	182
Leeds (UK)	53°47' N/01°32' W	0.715	410	295	115	46	69
Leicester (UK)	52°38' N/01°08' W	0.280	563	373	190	74	116
London (UK)	51°30' N/07°39' W	7.172	1147	615	532	113	419
Plymouth (UK)	50°22' N/04°08' W	0.246	730	476	254	94	160
Sheffield (UK)	53°23' N/01°28' W	0.513	1418	820	598	128	470

The source literature used for each urban area can be found in Ricotta *et al.* (2009).

genera in our database. Branch lengths are assigned to the phylogenetic tree based on aged nodes reported mainly by Wikström *et al.* (2001) from fossil data. Nodes in the phylogenetic tree for which age estimates were available were fixed, while all remaining nodes were spaced evenly between dated nodes to minimize variance in branch lengths (Kembel & Hubbel, 2006). The resulting phylogenetic tree was used for all subsequent analyses of phylogenetic beta diversity.

Phylogenies constructed from PHYLOMATIC usually contain pervasive polytomies at the family and genus level. Due to this lack of resolution, information on the phylogenetic organization of species assemblages is inevitably lost. Nonetheless, PHYLOMATIC is virtually the sole operational tool that enables community ecologists to reconstruct a meaningful aged community phylogeny for thousands of species without detailed phylogenetic information below the family level. To overcome this problem, one solution consists of imposing a crude topological structure on the tree without taking into account estimated branch lengths (i.e. assuming that all branch lengths are equal to 1). However, as emphasized by Crozier (1997, p. 243): '[Phylogenetic] measures using branch-lengths are better than procedures relying solely on topology'. In this framework, unpublished data of one of the authors (C.R.) clearly show that diversity analyses of aged and un-aged phylogenetic trees provide very different results even for the simplest diversity

measures. Therefore, assuming that all branch lengths are equal to 1 is not a good approximation of an aged tree.

On the other hand, to the best of our knowledge none of the more sophisticated alternatives to the PHYLOMATIC approach are really able to reconstruct an aged phylogeny for such high numbers of species belonging to different taxa; rather, they have usually been applied to selected taxonomic groups (e.g. Buerki *et al.*, 2011) or for selected growth forms like trees. A recent example is Kress *et al.* (2010). The use of more sophisticated methods for constructing very large aged community phylogenies may be made only at the cost of excluding species without phylogenetic information from the analysis. This would exclude much of our database in a non-random fashion and result in potentially biased interpretations. Therefore, although PHYLOMATIC is only a 'suboptimal' tool for reconstructing aged phylogenies, because in this paper all analyses are based on the same phylogenetic tree, they are cross-interpretable and are internally unbiased. As a potential improvement for future studies, the amount of uncertainty associated with the use of suboptimal trees with many unresolved nodes may be accessed through simulations (e.g. Spinks *et al.*, 2009), although these analyses usually require high computational power, even for relatively small data sets (see Kress *et al.*, 2010). Overall, the accuracy of our analyses will increase as more resolved plant phylogenies are produced.

Phylogenetic beta diversity

To determine whether the phylogenetic beta diversity of archaeophytes and neophytes was significantly different from the phylogenetic beta diversity of natives we used the PHYLOCOM software package (<http://www.phylodiversity.net/phylocom>; Webb *et al.*, 2008) to calculate two different measures of pairwise phylogenetic dissimilarity between cities for each of the three species groups.

Given two cities, A and B, the first measure we used calculates the average minimum phylogenetic dissimilarity (NNPD) between A and B (Izsák & Price, 2001). Specifically, for each species in A it finds the nearest phylogenetic neighbour in B (and vice versa), records these phylogenetic distances and calculates their mean

$$\text{NNPD} = \frac{\sum_i \min d_{iB} + \sum_j \min d_{jA}}{S_A + S_B} \quad (1)$$

where d_{iB} is the minimum phylogenetic distance between species i in A and all species in B, and d_{jA} is the minimum phylogenetic distance between species j in B and all species in A. S_A and S_B are the number of species in A and B, respectively. The phylogenetic distance between two species is the total branch length separating those species in the rooted phylogeny. For an aged ultrametric tree this will be twice the time since divergence from the most recent common ancestor (branch length from species 1 to the most recent common ancestor plus branch length from the most recent common ancestor to species 2).

NNPD is thus a measure of the average phylogenetic turnover between each species in A and its 'phylogenetic nearest neighbour' in B and vice versa. High values of NNPD denote high phylogenetic turnover between cities, while low values of NNPD imply high phylogenetic overlap between the species in A and their nearest neighbours in B regardless of the phylogenetic relationships among the species in A and in B.

To compare the extent to which the whole pool of species in A and B are phylogenetically (dis)similar, PHYLOCOM calculates the mean phylogenetic distance (MPD_{AB}) of all possible species pairs in A to the species in B. For presence and absence data, this is equivalent to the expected phylogenetic distance between any two species selected at random from two cities, A and B

$$\text{MPD}_{AB} = \frac{\sum_{ij} d_{ij}}{S_A \times S_B} \quad (2)$$

However, it is easily shown that unlike NNPD, MPD_{AB} is not a statistically valid coefficient of dissimilarity, as for any two identical species assemblages it is possible to have any value of $\text{MPD}_{AB} > 0$, depending on the number of species within the assemblages and on their phylogenetic relationships, while $\text{MPD}_{AB} = 0$ would be valid in those circumstances. Nonetheless, using the Jensen difference we obtain a genuine coefficient of dissimilarity, MPD that is defined as

$$\text{MPD} = \text{MPD}_{AB} - \frac{1}{2}(\text{MPD}_{AA} + \text{MPD}_{BB}) \quad (3)$$

where MPD_{AA} and MPD_{BB} are the mean phylogenetic distances of all possible species pairs in A and B, respectively (Champely & Chessel, 2002).

Having compiled a dissimilarity matrix for each species group containing all pairwise phylogenetic dissimilarities (NNPD and MPD) between European cities, we can then test for differences in phylogenetic beta diversity among different species groups using a test for homogeneity of multivariate dispersions. For this test, Anderson (2006) proposed that beta diversity be measured as the average dissimilarity of individual cities from their group centroid in multivariate space. Differences in beta diversity among different species groups can then be tested comparing the average dissimilarity of observation units from their group centroid; a P -value may be obtained by permuting least-squares residuals among the set of plots. In principle, the test can be based on any dissimilarity index. For Euclidean distances, the centroid can be simply computed as the arithmetic mean for each variable in the multi-species space. However, for dissimilarity measures that are not Euclidean embeddable, the computation of the centroid is much more difficult, and principal coordinate ordination is needed to place the observations into a Euclidean space that preserves the original dissimilarities among them. For instance, the Euclidean distance between two observations in the principal coordinate space is equal to the original dissimilarity value between both observations using the chosen dissimilarity index on the original variables (see Anderson, 2006).

Using the phylogenetic dissimilarity matrices, differences in phylogenetic beta diversity between archaeophytes and natives and between neophytes and natives were tested using deviations from centroids and 999 permutations of least-squares residuals, with the program PERMDISP2 (<http://www.stat.auckland.ac.nz/~mja/Programs.htm>; Anderson, 2004). This software calculates principal coordinates from the input dissimilarity matrix chosen, and then it calculates appropriate centroids and deviations from these. Prior to analysis, both dissimilarity coefficients NNPD and MPD were scaled in the range 0–1. In order to highlight possible differences between cities of continental Europe and cities of the British Isles in their phylogenetic beta diversity of native versus alien species, the same procedure was run separately on both groups of cities. Finally, to evaluate the effects of alien species on the phylogenetic beta diversity of all the urban floras, we also compared the phylogenetic beta diversity of urban floras with and without neophytes.

RESULTS

Irrespective of the dissimilarity coefficient used for analysis (i.e. NNPD or MPD), archaeophytes tend to be associated with lower values of phylogenetic dissimilarity from their group centroid, and neophytes with higher values (Figs 1–2). When the phylogenetic dissimilarity between cities is calculated with the NNPD coefficient, results show that at a continental scale the phylogenetic beta diversity of archaeophytes is indistinguishable from that of native species ($F = 0.341$, $P = 0.659$), while the

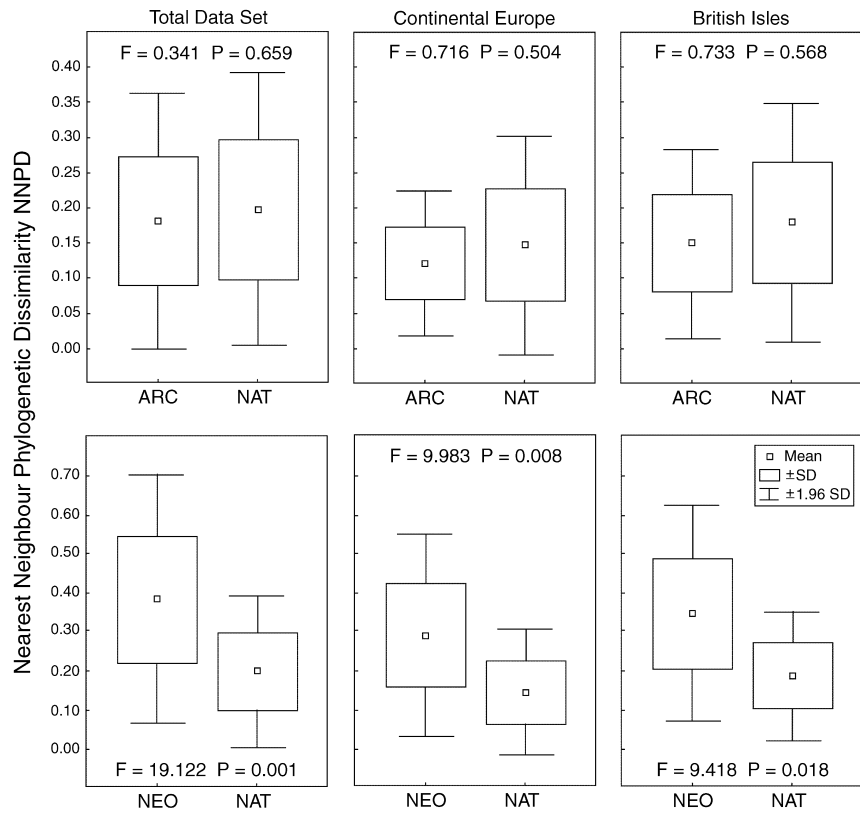


Figure 1 Box plots of the nearest neighbour phylogenetic dissimilarity (NNPD) of individual cities from their group centroid in multivariate space (NAT = native species, ARC = archaeophytes, NEO = neophytes). The *F* tests are from an ANOVA comparing the average dissimilarities among species groups (archaeophytes and neophytes versus natives; see Anderson, 2006). *P*-values are obtained using 999 permutations of least squares residuals.

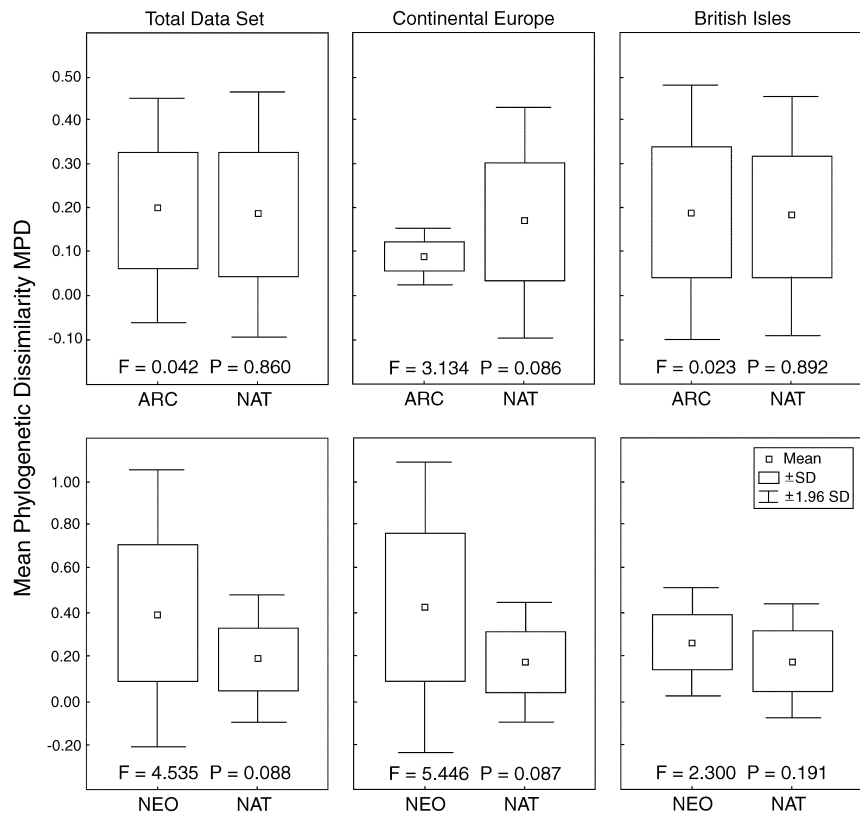


Figure 2 Box plots of the mean phylogenetic dissimilarity (MPD) of individual cities from their group centroid in multivariate space (NAT = native species, ARC = archaeophytes, NEO = neophytes). The *F* tests are from an ANOVA comparing the average dissimilarities among species groups (archaeophytes and neophytes versus natives; see Anderson, 2006). *P*-values are obtained using 999 permutations of least squares residuals.

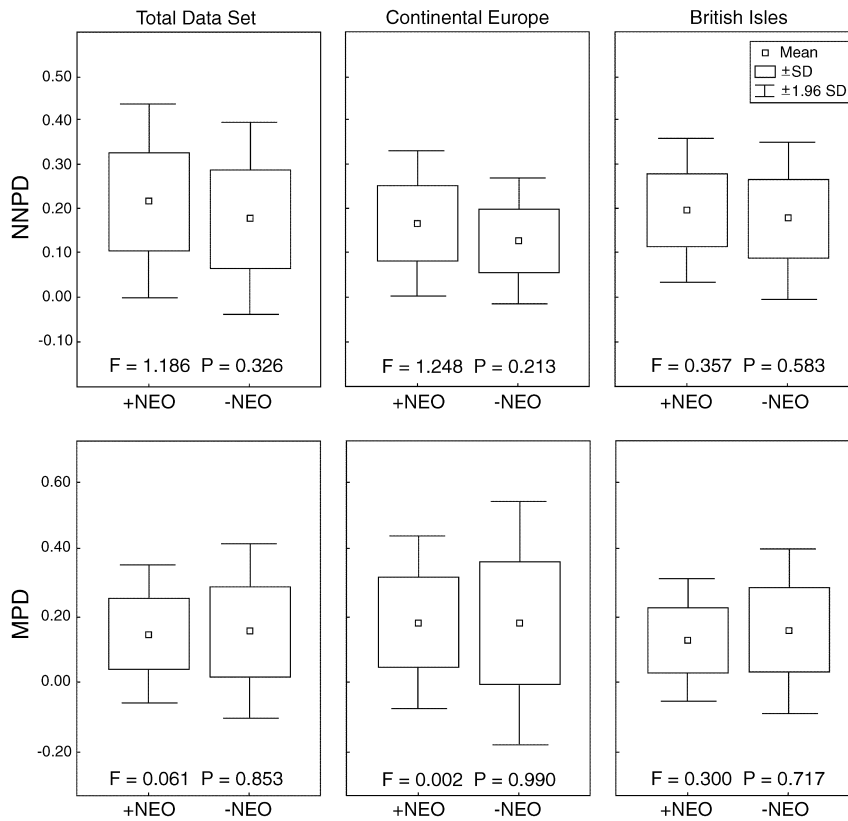


Figure 3 Box plots of the phylogenetic dissimilarities of urban floras with (+NEO) and without (–NEO) neophytes from their group centroid in multivariate space (NNPD = nearest neighbour phylogenetic dissimilarity; MPD = mean phylogenetic dissimilarity). The *F* tests are from an ANOVA comparing the average dissimilarities among species groups (see Anderson, 2006). *P*-values are obtained using 999 permutations of least squares residuals.

phylogenetic beta diversity of neophytes is significantly higher than that of native species ($F = 19.122$, $P = 0.001$). That is, for neophytes, the average phylogenetic dissimilarity of individual cities from their group centroid in multivariate space (here assumed as a measure of phylogenetic beta diversity) is significantly higher than that of native species. The same result holds when the cities of continental Europe and those of the British Isles are analysed separately (for continental Europe $F = 0.716$, $P = 0.504$ for archaeophytes versus natives, and $F = 9.983$, $P = 0.008$ for neophytes versus natives; for the British Isles $F = 0.733$, $P = 0.568$ for archaeophytes versus natives, and $F = 9.418$, $P = 0.018$ for neophytes versus natives).

By contrast, calculating the pairwise phylogenetic dissimilarity across all European cities with the MPD coefficient, the phylogenetic beta diversity of archaeophytes is still indistinguishable from that of native species ($F = 0.042$, $P = 0.860$), while the phylogenetic beta diversity of neophytes is only marginally higher than that of native species ($F = 4.535$, $P = 0.088$). Analysing both groups of cities separately, we observe that, for the British Isles, the phylogenetic beta diversity of neither archaeophytes nor neophytes is statistically distinguishable from that of the native species ($F = 0.023$, $P = 0.892$ for archaeophytes versus natives, and $F = 2.300$, $P = 0.191$ for neophytes versus natives). For the cities of continental Europe, the phylogenetic beta diversity of archaeophytes is marginally lower (Fig. 2) than that of native species ($F = 3.134$, $P = 0.086$), while the phylogenetic beta diversity of neophytes is marginally higher than that of natives ($F = 5.446$, $P = 0.087$).

Finally, as shown in Fig. 3, the phylogenetic beta diversities of urban floras with and without neophytes are not statistically distinguishable from each other. Using the index NNPD we obtain $F = 1.186$, $P = 0.326$ for all European cities, $F = 1.248$, $P = 0.213$ for the cities of continental Europe and $F = 0.357$, $P = 0.583$ for the British Isles, while using the index MPD we have $F = 0.061$, $P = 0.853$ for all European cities, $F = 0.002$, $P = 0.990$ for the cities of continental Europe and $F = 0.300$, $P = 0.717$ for the British Isles. Accordingly, while the index NNPD shows a slight (non-significant) tendency for neophytes to increase phylogenetic differentiation, overall there is no evidence for a role of neophytes in promoting phylogenetic homogenization of urban floras.

DISCUSSION

It was first hypothesized by Elton (1958) that the weakening of biogeographical barriers to dispersal would lead to the homogenization of regional biotas through the introduction and establishment of alien species. However, in spite of the fact that (1) the measures of pairwise phylogenetic dissimilarity used for calculating beta diversity quantify slightly different aspects of phylogenetic differentiation among European cities, and (2) the pervasive polytomies at the genus and family level contained in the phylogenetic tree may influence the phylogenetic diversity metrics used (see Swenson, 2009), our study emphasizes that neophytes are not promoting the phylogenetic homogenization of urban floras in Europe, but a slight differentiation. This is in

agreement with previous findings based on species occurrence in Europe (Kühn & Klotz, 2006; La Sorte *et al.*, 2007, 2008; Wittig & Becker, 2010; but see McKinney, 2006 for North America). Conversely, in contrast to work on European archaeophytes in North America (La Sorte & Pyšek, 2009), this study found little evidence that archaeophytes are promoting intense phylogenetic homogenization. The much broader geographical and taxonomic origin of neophytes when contrasted with archaeophytes and the more recent introductions of neophytes into Europe provide likely explanations for these differences.

Biological patterns within urban areas represent the consequences of intensive anthropogenic activities. On the one hand, urbanization provides favourable environmental conditions for the establishment of alien plants (McKinney, 2006). In central European cities, most alien species tend to occur in warm, well-lit, dry, nitrogen-rich and alkaline locations that reflect the environment in their native ranges. Higher temperatures and aridity can be better met in the city centre where the urban heat-island effect is more pronounced (Sukopp & Werner, 1983), while the pH values of many urban soils are increased by adjacent concrete and other lime-based materials (Thompson & McCarthy, 2008).

On the other hand, these environmental constraints generally limit the phylogenetic alpha diversity of the urban alien flora, although these constraints are stronger for archaeophytes than for neophytes (Ricotta *et al.*, 2009). This difference in the intensity of environmental filters between archaeophytes and neophytes is probably related to the more restricted geographical origin of archaeophytes and to their strong association with agricultural and ruderal habitats (Pyšek *et al.*, 2005). Phylogenetically, archaeophytes are thus preferentially clustered within a few families, like Apiaceae, Caryophyllaceae, Chenopodiaceae and Scrophulariaceae. In contrast, due to their much broader origin, neophytes have maintained a high level of phylogenetic diversity. Therefore, while neophytes tend to be better represented within the families Amaranthaceae, Fabaceae, Onagraceae, Polygonaceae and Solanaceae, their degree of clustering within particular clades of the phylogenetic tree is much weaker than for archaeophytes (Ricotta *et al.*, 2009).

Our results suggest that the likelihood of alien species reducing phylogenetic beta diversity is related to their time of introduction, place of origin and historical association with human activities. While archaeophytes tend to promote limited homogenization in phylogenetic patterns across European cities, neophytes tend to enhance phylogenetic differentiation. European archaeophytes form a restricted species pool characterized by broad geographical distributions and limited phylogenetic diversity that, through a long history of human-mediated biotic interchange, have developed successful associations with anthropogenic activities, in particular with agricultural areas (Pyšek *et al.*, 2005).

On the contrary, neophytes represent a larger and more phylogenetically diverse species pool of much broader geographical origin, though neophyte species usually have more restricted native geographical range sizes compared with archaeophytes (Lambdon *et al.*, 2008). Due to their shorter residence times,

many neophytes have not had the same historical opportunities as archaeophytes in terms of adaptation to the environmental, ecological and anthropogenic conditions in their introduced ranges (Gassó *et al.*, 2010). Therefore, Chytrý *et al.* (2008a) showed that the distribution of neophytes is relatively more dependent on propagule pressure and less dependent on habitat type than the distribution of archaeophytes.

These two aspects, restricted geographical range of neophytes and their high dependence on propagule pressure, tend to have so far limited their successful colonization and dispersal within Europe. While consistent propagule pressure across spatial scales has been found to be an important aspect for the broad-scale diffusion of alien species (Von Holle & Simberloff, 2005), the level of propagule pressure associated with neophytes is probably not as substantial due to the relatively close proximity of long-established propagule sources and the presence of consistent dispersal vectors for archaeophytes (La Sorte *et al.*, 2007). Likewise, there is evidence that successful invasive plants are usually characterized by large native geographical distributions (Rejmánek, 2000) and limited phylogenetic dissimilarity to native species (Ricotta *et al.*, 2010).

Beta diversity is by definition scale dependent where the choice of spatial extent and grain is integral in determining how beta diversity is estimated. When European floras are examined at coarser resolutions that encompass both urban and non-urban areas, neophytes are similarly associated with lower beta diversity when compared with native assemblages based on occurrence (Winter *et al.*, 2010) and phylogenetic information (Winter *et al.*, 2009). These patterns change when the extent is broadened to include other continents. Between Europe and North America neophytes are associated with more similar species compositions among urban areas (La Sorte *et al.*, 2007) and broader political regions (Winter *et al.*, 2010). Nevertheless, within a region neophytes represent a continually expanding species pool (Lambdon *et al.*, 2008) and the high level of phylogenetic beta diversity in European cities found in this study is likely to be promoted by the continuing introduction of new species (La Sorte *et al.*, 2007). If given enough time, it is conceivable that neophytes could replicate the patterns observed with archaeophytes, especially if neophytes develop similar associations with anthropogenic environments (La Sorte *et al.*, 2008). However, archaeophytes developed these associations over several hundred years. Unless the influence of human-mediated biotic interchange were to diminish, it is likely that introductions of new species will continue to maintain the regional distinctiveness of neophytes in urban floras.

In conclusion, our findings suggest that centuries of human-mediated biotic interchange have resulted in phylogenetic differentiation among urban floras, a trend that is likely to be maintained or to increase as human societies and commerce become increasingly globalized. Although cities are key indicators of the effects of intensive anthropogenic activities on biological diversity, our findings may be important even outside urban areas. Given the present-day climatic conditions of central and northern Europe, urban areas have been the main centres of immigration and establishment of alien species whose

distributions are limited by the cooler temperatures of the surrounding areas (Godefroid & Koedam, 2007). Nonetheless, as the importance of climatic conditions for the colonization of invaded regions by alien species has been demonstrated in a number of studies (Nobis *et al.*, 2009; Walther *et al.*, 2009), under future climate warming scenarios successful urban aliens are likely to possess both the relevant functional characters and the dispersal potential to spread outside urban areas.

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BIOSKETCH

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