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Phyloecology of urban alien floras

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Summary

1. Understanding the mechanisms that affect invasion success of alien species is a major issue in current ecological research. Although many studies have searched for either functional or habitat attributes that drive invasion mechanisms, few researchers have addressed the role of phylogenetic diversity of alien species.

2. Here, using data from 21 urban floras located in Europe and eight in the USA, we show that the phylogenetic diversity of alien species is significantly lower than that of native species, both at the continental scale and at the scale of single cities.

3. Second, we show that if archaeophytes and neophytes (non-native species introduced into Europe before and after AD 1500, respectively) are analysed separately, archaeophytes show lower phylogenetic diversity than neophytes, while the phylogenetic structure of neophytes is indistinguishable from a random sample of species from the entire species pool.

4. Our results suggest that urban aliens are subject to environmental filters that constrain their phylogenetic diversity, although these filters act more strongly upon archaeophytes than neophytes.

5. *Synthesis*. Despite the huge taxonomic diversity of plants imported into European and American cities, the strong environmental filters imposed by cities constrain the functional diversity of urban floras, which is reflected in their generally low phylogenetic diversity. Urban alien floras are mainly composed of phylogenetically related species that are well adapted to anthropogenic habitats, although these filters are stronger for species groups with longer residence times.

Key-words: alien plants, archaeophyte, exotic, invasion, mean phylogenetic distance, neophyte, phylogenetic diversity, randomisation test

Introduction

Through the influence of human-related activities, the Earth's biota have experienced the persistent weakening of biogeographical barriers to dispersal. This has resulted in the establishment and spread at increasingly broader scales of an increasing number of alien species (Vitousek *et al.* 1997; Lockwood 2004; McNeely 2005; Lambdon *et al.* 2008). For vascular plants, there have been substantial increases in species richness at local and regional scales as a consequence of elevated levels of biotic interchange (Sax & Gaines 2003; Sax *et al.* 2005). Therefore, it could be argued that vascular plants have become one of the primary beneficiaries of human-influenced biotic interchange. In addition, urban areas contain the greatest proportion of alien plants and act as hubs for onward dispersal of these species (Sukopp & Werner 1983; Kowarik 1990; Pyšek 1998; Roy, Hill & Rothery 1999; Wittig 2004; Chytrý *et al.* 2005, Chytrý et al. 2008; Tait, Daniels & Hill 2005; Celesti-Grapow *et al.* 2006). Thus, when documenting ecological consequences of biological invasions, urban vascular floras are an informative focal group (La Sorte, McKinney & Pyšek 2007).

A number of studies have shown that human settlements provide distinctive 'niche opportunities' (*sensu* Shea & Chesson 2002) that have allowed many alien species to become established. For instance, alien species with higher temperature requirements and tolerance for arid environments tend to occur in city centres where the 'urban heat island effect' is more pronounced (Godefroid 2001; McKinney 2006).

From an evolutionary perspective, functionally related species that coexist in the same habitat often share a common origin and phylogenetic history, such that what is now called

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phylogenetic diversity and functional diversity are usually interrelated (Darwin 1859). When traits that render a species capable of colonizing a given habitat are phylogenetically conserved, phenotypic attraction (habitat filtering) promotes a taxonomically clumped flora in which co-occurring species that are adapted to similar niches are more related than expected by chance. Conversely, when distantly related taxa are phenotypically attracted and have converged on similar niche use, phenotypic attraction generates phylogenetically overdispersed communities (Cavender-Bares & Wilczek 2003; Kraft *et al.* 2007). Since, in both cases, the environment affects the functional and phylogenetic organization of a species assemblage (Knapp *et al.* 2008), we expect that urbanization will affect the phylogenetic structure of alien species assemblages.

While the influence of urbanization on plant functional traits has been confirmed by several authors (e.g. Kleyer 2002; Chocholoušková & Pyšek 2003; Williams *et al.* 2005; Lososová *et al.* 2006), little is known about the effects of urbanization on the phylogenetic diversity of alien species. It has been suggested that phenotypic and phylogenetic relatedness between native and alien species reduces the success of invasion (Darwin's naturalization hypothesis; see e.g. Daehler 2001; Duncan & Williams 2002). The implication is that, because of limiting similarity due to overlap in resource use, native species can hinder the invasion of close relatives (see Procheş *et al.* 2008). In support of the proposed pattern, Strauss, Webb & Salamin (2006) found that highly invasive grass species are, on average, significantly less related to native grasses than expected from a random sampling of the phylogenetic supertree of all grass species of California. This confirmed previous work of Rejmánek (1996), who found that European grasses from alien genera were over-represented in California's naturalized flora.

An alternative perspective to Darwin's naturalization hypothesis suggests that, as native species possess functional traits that render them compatible with local environmental conditions, alien species with high phylogenetic relatedness to natives are more likely to share those well-suited traits, which enable them to succeed (Procheş *et al.* 2008). The idea that phylogenetic similarity between native and alien species may favour invasion processes is supported by work showing that taxonomic clustering is a major driver of community assembly (Webb *et al.* 2002; Cavender-Bares *et al.* 2004). This effect is particularly important at coarse spatial scales where plant-to-plant competitive interactions become irrelevant. Ricotta *et al.* (2008) tested the importance of taxonomic similarity in regulating species' co-occurrence using data from 15 local species assemblages from portions of the urban flora of Rome, Italy. Their results indicate that in most cases the local species assemblages have a higher degree of taxonomic similarity than species assemblages randomly put together from the entire flora of Rome. Knapp *et al.* (2008) compared the phylogenetic diversity of urbanized areas in Germany with those of rural areas. They found that phylogenetic diversity of urban areas does not reflect the high species richness found there. Hence, high urban species richness is mainly due to closely related species that are functionally similar and adapted to disturbances associated with urbanization.

In principle, due to their very diverse origin, the phylogenetic structure of urban aliens could be expected to be significantly overdispersed when contrasted with the entire urban species pool. In this study we (i) test this assumption by analysing the phylogenetic diversity of alien species assemblages from a number of urban floras located on two continents, Europe and North America, and (ii) explore whether there is a difference in patterns shown by two groups of European alien species, archaeophytes and neophytes. The two groups differ in their residence times, with archaeophytes present in European landscapes for several millenia and neophytes present for several centuries (Pyšek, Richardson & Williamson 2004; Pyšek & Jarošík 2005). Another principle difference is the region of origin, which is more diverse for neophytes (Lambdon *et al.* 2008). Further, the majority of archaeophytes is confined to arable land and urban wasteland, while neophytes occur in a wider range of habitats (Pyšek, Richardson & Williamson 2004; Pyšek *et al.* 2005).

Materials and methods

DATA

We analysed urban floras for eight cities of the USA and 21 European cities located in seven countries (Table 1). All US cities are within the same biome (temperate deciduous forest). Twenty of the European cities were located between 49° and 53°N, while Rome (Italy) was an outlier occurring at 41°N. The lists for individual cities included only spontaneous species, excluding all those occurrences that were obviously planted.

For each flora, all varieties and subspecies were combined into single species. The taxonomic nomenclature was then standardized using TaxonScrubber, version 1.2 (Boyle 2004). This resulted in a total of 4152 unique species in US floras and 4108 species in European floras. Each species in the US floras was designated as native (indigenous) or alien (non-native, non-indigenous, exotic) based on original sources compiled by Clemants & Moore (2003).

The alien group of each European flora was further divided into archaeophytes and neophytes. Archaeophytes are alien species introduced into Europe before AD 1500, primarily from the Mediterranean basin, and are typically weeds of arable land. Neophytes were introduced into Europe after that date, signifying the discovery of the New World and the initiation of relatively rapid and substantial changes in human movement, demography, agriculture, commerce and industry. This classification system corresponds to one widely used in Central-European phytogeographical studies (e.g. Holub & Jirásek 1967; Schroeder 1969). For comparison with other classification systems see Pyšek (1995) and Pyšek, Sádlo & Mandák (2002).

The internal classification of the European floras into neophytes and archaeophytes is not geographically or temporally consistent, reflecting differences in the time of introduction and place of origin for alien species across Europe (Pyšek & Jarošík 2005). For example, species that were identified as native in the southern or eastern parts of Europe could be classified as archaeophytes or neophytes in the northern or western parts, depending on their time of arrival.

Table 1. Summary of the data used in this study with the geographical location and human population size for 8 US cities and 21 European cities. Alien species in the European floras are classified into two categories: archaeophytes and neophytes

City	Latitude/longitude	Inhabitants (million)	Number of species: Total	Native	Alien	Archaeophyte	Neophyte	Source
United States of America								
Boston	42°22′ N/71°20′ W	0.589	2246	1488	758	–	–	Clemants & Moore (2003) and references therein
Chicago	41°59′ N/87°54′ W	2.896	1728	1289	439	–	–	
Detroit	42°25′ N/83°10′ W	0.951	1616	1225	391	–	–	
Minneapolis	44°53′ N/93°13′ W	0.383	1356	1109	247	–	–	
New York	40°47′ N/73°58′ W	8.008	2442	1705	737	–	–	
Philadelphia	39°53′ N/75°15′ W	1.518	2471	1677	794	–	–	
Saint Louis	38°45′ N/90°23′ W	0.348	1711	1332	379	–	–	
Washington DC	38°51′ N/77°20′ W	0.572	2331	1640	691	–	–	
Europe								
Berlin, West (Germany)	52°31′ N/13°24′ E	1.930	955	512	443	101	342	Kunick (1974)
Birmingham (UK)	51°29′ N/01°54′ W	0.977	565	400	165	71	94	Cadbury, Hawkes & Readett (1971)
Brighton (UK)	50°49′ N/00°08′ W	0.248	529	347	182	85	97	Hall (1980)
Brno (Czech Republic)	49°12′ N/16°37′ E	0.388	765	311	454	176	278	Grüll (1979)
Brussels (Belgium)	50°50′ N/04°21′ E	0.970	696	479	217	58	159	IBGE (1999)
Chemnitz (Germany)	50°50′ N/12°55′ E	0.246	837	409	428	207	221	Grundmann (1992)
Dublin (Ireland)	53°20′ N/06°15′ W	0.506	306	198	108	41	67	Jackson & Skeffington (1984)
Exeter (UK)	50°43′ N/03°31′ W	0.118	473	331	142	66	76	Ivimey-Cook (1984)
Halle an der Saale (Germany)	51°28′ N/11°58′ E	0.238	896	406	490	237	253	Klotz (1984)
Hannover (Germany)	52°22′ N/09°44′ E	0.516	782	549	233	94	139	Haeupler (1976)
Kingston upon Hull (UK)	53°43′ N/00°20′ W	0.244	696	423	273	91	182	Middleton (1998)
Leeds (UK)	53°47′ N/01°32′ W	0.715	410	295	115	46	69	Lavin & Wilmore (1994)
Leicester (UK)	52°38′ N/01°08′ W	0.280	563	373	190	74	116	Primavesi & Evans (1988)
Leipzig (Germany)	51°20′ N/12°23′ E	0.539	1732	721	1011	139	872	Gutte (1989)
London (UK)	51°30′ N/07°39′ W	7.172	1147	615	532	113	419	Burton (1983)
Plymouth (UK)	50°22′ N/04°08′ W	0.246	730	476	254	94	160	Stevens (1990)
Plzeň (Czech Republic)	49°43′ N/13°29′ E	0.165	1014	681	333	159	174	Pyšek & Pyšek (1988) Nesvadbová & Sofron (1997) Chocholoušková & Pyšek (2003)
Prague (Czech Republic)	50°05′ N/14°26′ E	1.212	1856	1157	699	265	434	Špryňar & Münzbergová (1998)
Rome (Italy)	41°54′ N/12°30′ E	2.554	1251	1027	224	66	158	Celesti-Grapow (1995)
Sheffield (UK)	53°23′ N/01°28′ W	0.513	1418	820	598	128	470	Shaw (1988), Hodgson (unpublished data)
Warsaw (Poland)	52°15′ N/21°00′ E	1.650	1379	918	461	124	337	Sudnik-Wójcikowska (1987)

For two of the 21 European floras (Halle and Chemnitz, Germany) the classification of alien species was not accessible to us. To provide a classification for these floras, we used the approach described by La Sorte, McKinney, & Pyšek (2007). Specifically, a species was classified as an archaeophyte if it was designated as an archaeophyte in at least one European flora, and as a neophyte if it was not designated as an archaeophyte in any flora and was designated as a neophyte in at least one flora. In doing so, the alien status was ranked higher than the native status because, if a species was identified as alien anywhere within the European floras, it had the ability to become established outside of its historical range. Likewise, 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, McKinney & Pyšek 2007 for details).

SUPERTREE CONSTRUCTION

To characterize the phylogenetic uniqueness of urban invaders, we created a phylogenetic tree for each urban flora using the highly resolved reference tree of seed plants supplied with the online software *Phylomatic* (http://www.phylodiversity.net/phylomatic; Webb & Donoghue 2005) with nodes aged according to Wikstrom, Savolainen & Chase (2001). *Phylomatic* takes as input a list of species, matches the species to the most resolved position possible in a reference tree, and returns the phylogeny of the input species list in one of a number of alternative formats.

Phylomatic uses the base tree of the Angiosperm Phylogeny Group (APG) at APweb (http://www.mobot.org/MOBOT/research/APweb; Stevens 2001) as the backbone in combination with recently published family phylogenies to form its reference tree. All monophyletic families in APG II (APG 2003) are included in the reference tree. The reference tree is not a true supertree (e.g. Sanderson, Purvis & Henze 1998), in that it has been assembled by hand, rather than by an automated supertree algorithm, with conflicting branching patterns being resolved subjectively. It is, however, intended to represent a pragmatic approximation of the true phylogeny of seed plants (Webb & Donoghue 2005). Full details of the decisions involved in phylogenetic tree construction are given at the *Phylomatic* website. Branch lengths were assigned to the phylogenetic tree based on the minimum age of nodes estimated for genera, families, and higher orders from the fossil data (Wikstrom, Savolainen & Chase 2001), while spacing of undated nodes was done evenly between dated nodes in the tree.

ANALYSIS

We quantified the phylogenetic diversity of a given species assemblage in terms of the mean phylogenetic distance (MPD; measured in millions of years) separating two species in a rooted phylogeny averaged over all pairwise comparisons of species. MPD is equivalent to the 'mean nodal distance' of Webb (2000) for a dated phylogeny, and reflects the taxonomic aggregation of species over the entire species pool's phylogeny after controlling for species richness. At the continental scale, differences in the MPD of alien and native species were tested using paired *t*-tests separately for USA cities and European cities. At the local scale, to determine whether the phylogenetic structure of each alien or native species assemblage was significantly clustered or overdispersed, as compared to the phylogenetic structure of the entire species pool composed of all alien and native species in the urban flora, we constructed the following null model. For each alien or native species assemblage in the 29 urban floras, the observed MPD was compared to a distribution of MPD values derived from 999 species lists of the same size obtained by resampling species without replacement from the urban species pool of each single city. The null hypothesis is that from a phylogenetic perspective, both species groups are a random sample of the entire urban species' pool. *P*-values (two-tailed test) were computed as the proportion of randomized values of MPD that were as small or smaller than the actual MPD. In order to highlight possible differences between neophytes and archaeophytes in their phylogenetic relationship with urban natives for the 21 European floras, the same procedure was run on neophytes and archaeophytes separately.

While MPD summarizes the phylogenetic aggregation of taxa over the whole pool of species, we also quantified the phylogenetic structure of each species assemblage for the extent to which species are locally aggregated within particular terminal clades, regardless of the phylogenetic relationship among those clades. To compare the extent to which neophytes and archaeophytes are locally aggregated, we used a second metric, the mean phylogenetic distance of each species to its nearest relative in the rooted phylogeny (NMPD; Webb 2000; Strauss, Webb & Salamin 2006). At the European scale, differences in the MPD and NMPD of archaeophytes and neophytes were analyzed using paired *t*-tests. All diversity analyses were run with *Phylocom* (Webb, Ackerly & Kembel 2008), freely available at: http://www.phylodiversity.net/phylocom.

Results

At the continental scale, the MPD of alien species was significantly lower than that of native species ($t = 11.768$; $P < 0.001$ for US cities and $t = 6.035$; $P < 0.001$ for European cities). At the local scale, for all US floras and for 17 out of 21 European floras, the actual MPD of urban aliens was significantly lower than the corresponding null values ($P < 0.05$; two-tailed test; Table 2). That is, on average, the phylogenetic structure of alien species assemblages was more clumped than that of assemblages randomly compiled from the entire urban species pool, rejecting the null hypothesis that urban aliens are just a random sample of the urban species pool. Also, for six US floras and for 11 European floras, the actual MPD of native species assemblages was significantly higher than the null expectation, meaning that native species are phylogenetically less clumped than expected from the null model.

When archaeophytes and neophytes of the European floras are analysed separately, the results become more complex. For MPD, the null hypothesis that the phylogenetic structure of alien species is indistinguishable from the structure of the entire urban species pool is rejected 19 times out of 21 for archaeophytes (Table 3). For 18 urban floras, the phylogenetic structure of the archaeophytes is more clumped than in random assemblages. But for the flora of Rome the archaeophytes show a phylogenetic structure that is significantly overdispersed (with a larger MPD for the archaeophytes than the entire flora) as compared to the corresponding null values. On the other hand, for MPD, the null hypothesis is accepted 14 times out of 21 for neophyte assemblages (Table 3). This means that in most cases, the phylogenetic structure of the neophytes is indistinguishable from a random sample of species from the entire species pool. For the remaining seven cities, the phylogenetic structure of neophytes was more clumped than in random assemblages.

For NMPD the phylogenetic structure of the archaeophytes was significantly clumped within particular clades for 18 out of 21 urban floras (Table 4), whereas for neophytes the general tendency was towards actual NMPD values that were slightly, though non-significantly, higher than the corresponding null values.

At the European scale, these local discrepancies between the phylogenetic structure of archaeophytes and neophytes resulted in a significant difference in the MPD and NMPD values of both species groups ($t = 4.011$, $P < 0.001$ for MPD, and $t = 2.865$, $P = 0.009$ for NMPD; Fig. 1).

Discussion

Phylogenetic diversity summarizes the degree of evolutionary relationships within species assemblages, thus providing valuable information about mechanisms of community organization (Webb *et al.* 2002; Knapp *et al.* 2008). The availability of detailed phylogenies, along with methods for the construction of supertrees, now allows for the integration of phylogenetic information into studies of species assembly (Webb *et al.* 2002). Phylogenies constructed from supertrees usually contain pervasive polytomies below the family and genus level. Due to this lack of resolution, information on the phylogenetic organization of species assemblages is inevitably lost. However, given the robustness of the method used, we can be quite confident that the lack of resolution in the original supertree does not influence the results obtained (see Webb 2000).

Overall, our results suggest that alien species play a significant role in determining plant diversity within urban floras both in Europe and the USA. However, that diversity is not distributed at random within floras. Under the assumption of evolutionary trait conservatism (Donoghue 2008), phylogenetic niche conservatism together with the presence of selective environmental filters is an important mechanism in shaping the phylogenetic structure of urban alien plant assemblages. On the one hand, urbanization is closely associated with increasing opportunities for the introduction of alien species; on the other hand, cities are richly endowed with favourable habitats for the establishment of alien plants (McKinney 2006). Human disturbance creates physical conditions allowing the establishment of alien species outside their natural habitat. A straightforward example is the tendency for urban areas to have higher air temperatures compared to their rural surroundings. This 'urban heat island effect' promotes the establishment of species whose distribution is limited by cooler temperatures (Sukopp & Werner 1983; Godefroid & Koedam 2007). Other examples are the high proportion of surface runoff and of hard surfaces that increase the aridity of some urban habitats, and the high alkalinity of many urban soils (affected by adjacent concrete and other lime-based materials), which promotes the growth of plants that are adapted to soils with higher pH values (Sukopp 2004; Godefroid, Monbaliu & Koedam 2007; Thompson & McCarthy 2008).

Accordingly, we found that for all US and for most European floras, alien species have a higher phylogenetic aggregation than a random sample of the entire species pool. Using the general approach proposed by Cadotte & Lovett-Doust (2001), we found that alien species in the USA are significantly overrepresented by six families: Boraginaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Fabaceae and Solanaceae, while alien species in Central Europe are mainly overrepresented by the families Asteraceae, Brassicaceae, Chenopodiaceae, Poaceae and Solanaceae (see Pyšek, Sádlo & Mandák 2002).

Nonetheless, looking separately at archaeophytes and neophytes in European floras, substantial differences in MPD and NMPD across these two classes of residence time were found.

Table 2. Mean phylogenetic distances (MPD) of alien and native species in 8 US and 21 European cities and the average (mean of 999 randomisations) MPD values of an equal-sized random sample of the entire urban species pool

	Alien species		Native species	
City	Actual MPD	Average random MPD	Actual MPD	Average random MPD
United States of America				
Boston	250.566**	267.303	271.855**	267.314
Chicago	250.334**	264.283	266.605**	264.238
Detroit	245.503**	265.490	268.724**	265.417
Minneapolis	257.431**	271.010	272.258	271.156
New York	260.782**	271.532	273.294	271.552
Philadelphia	252.841**	265.441	267.892**	265.442
Saint Louis	252.708**	262.909	264.695**	262.939
Washington DC	249.734**	262.991	266.113**	262.967
Europe				
Berlin, West (Germany)	258.514	260.276	261.003	260.155
Birmingham (UK)	246.908**	261.771	264.991	261.944
Brighton (UK)	238.520**	251.863	256.872**	251.804
Brno (Czech Republic)	247.051	249.070	250.806	249.183
Brussels (Belgium)	250.626*	256.614	258.735*	256.383
Chemnitz (Germany)	251.654**	260.622	264.711	260.679
Dublin (Ireland)	246.044**	256.857	260.922*	256.861
Exeter (UK)	244.370**	258.996	263.012	258.896
Halle an der Saale (Germany)	252.182**	259.100	263.289	258.943
Hannover (Germany)	247.907**	260.531	263.612**	260.569
Kingston upon Hull (UK)	243.642**	257.453	264.097**	257.568
Leeds (UK)	243.812**	261.106	265.256**	261.176
Leicester (UK)	247.157**	259.952	264.666*	259.941
Leipzig (Germany)	248.921**	254.912	260.481**	254.842
London (UK)	252.210**	259.651	264.151**	259.603
Plymouth (UK)	250.281**	259.143	262.464*	259.067
Plzeň (Czech Republic)	250.631*	259.751	262.794	259.806
Prague (Czech Republic)	254.070**	259.933	261.565	259.975
Rome (Italy)	267.930	260.352	258.386	260.182
Sheffield (UK)	259.193	261.877	262.807	261.954
Warsaw (Poland)	244.514**	260.688	266.274**	260.619

The significance levels are: ** = $P < 0.01$; * = $P < 0.05$.

Table 3. Mean phylogenetic distances (MPD) of archaeophyte and neophyte alien species in 21 European cities with the average MPD values of an equal-sized random sample of the entire urban species pool (mean of 999 randomisations)

	Archaeophytes		Neophytes	
City	Actual MPD	Average random MPD	Actual MPD	Average random MPD
Berlin, West (Germany)	251.397	260.332	259.507	260.163
Birmingham (UK)	233.070**	261.990	256.761	262.136
Brighton (UK)	236.443**	252.411	238.823**	251.860
Brno (Czech Republic)	243.496*	249.080	248.059	249.135
Brussels (Belgium)	245.941	256.431	252.416	256.606
Chemnitz (Germany)	243.158**	260.709	258.716	260.477
Dublin (Ireland)	234.123**	256.773	245.170*	256.759
Exeter (UK)	234.075**	259.019	253.876	258.614
Halle an der Saale (Germany)	242.165**	259.058	261.001	259.027
Hannover (Germany)	236.639**	260.744	253.918	260.491
Kingston upon Hull (UK)	238.823**	257.269	244.516**	257.565
Leeds (UK)	241.344**	260.649	242.854**	261.140
Leicester (UK)	237.640**	259.844	252.539	260.286
Leipzig (Germany)	245.645**	254.902	248.880**	254.942
London (UK)	237.033**	259.851	254.139*	259.767
Plymouth (UK)	236.862**	259.107	254.304	259.099
Plzeň (Czech Republic)	242.557**	259.889	257.118	259.879
Prague (Czech Republic)	240.930**	260.202	261.179	259.966
Rome (Italy)	287.306*	260.085	257.857	260.045
Sheffield (UK)	239.904**	261.869	262.310	262.042
Warsaw (Poland)	243.691**	260.574	244.229**	260.640

The significance levels are: ** = $P < 0.01$; * = $P < 0.05$.

Table 4. Mean phylogenetic distances to the nearest relative (NMPD) of archaeophyte and neophyte alien species in 21 European cities with the average NMPD values of an equal-sized random sample of the entire urban species pool (mean of 999 randomisations)

	Archaeophytes		Neophytes	
City	Actual NMPD	Average random NMPD	Actual NMPD	Average random NMPD
Berlin, West (Germany)	47.807**	68.700	48.813	47.836
Birmingham (UK)	59.404*	76.023	80.427	69.344
Brighton (UK)	50.668**	70.684	61.552	67.490
Brno (Czech Republic)	38.324	43.426	36.814	38.575
Brussels (Belgium)	57.811**	82.469	62.302	58.846
Chemnitz (Germany)	37.812**	53.346	54.380	52.302
Dublin (Ireland)	53.908**	95.704	89.469	78.238
Exeter (UK)	65.538	77.376	81.792	73.915
Halle an der Saale (Germany)	38.514**	52.801	53.314	51.918
Hannover (Germany)	50.723**	69.031	55.907	60.561
Kingston upon Hull (UK)	54.010**	70.817	58.751	56.136
Leeds (UK)	62.961*	86.492	87.312	75.187
Leicester (UK)	55.207**	75.758	73.560	65.267
Leipzig (Germany)	46.579**	57.886	34.455	35.953
London (UK)	49.318**	69.547	47.124	46.063
Plymouth (UK)	54.216*	69.212	56.698	57.008
Plzeň (Czech Republic)	43.112**	60.323	65.833	58.769
Prague (Czech Republic)	38.702**	52.551	47.689	46.208
Rome (Italy)	82.645	83.517	57.499	64.217
Sheffield (UK)	47.642**	68.125	50.442*	46.145
Warsaw (Poland)	42.314**	64.438	48.130	47.814

The significance levels are: ** = $P < 0.01$; * = $P < 0.05$.

That is, archaeophytes displayed the highest and neophytes the lowest level of phylogenetic aggregation. The lower MPD and NMPD of archaeophytes are probably related to the archaeophytes' more restricted origin in comparison to that of neophytes, and to their strong habitat specificity, resulting from their adaptation to anthropogenic habitats having taken place

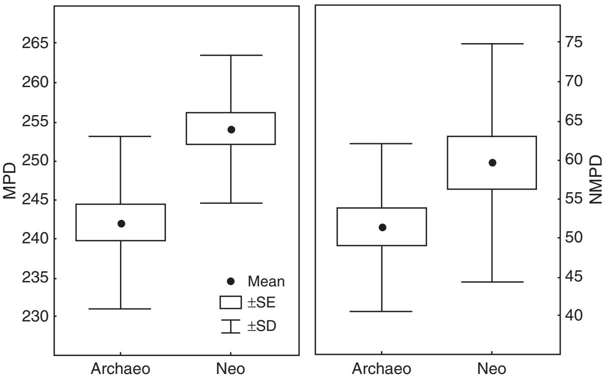

Fig. 1. Box plots of MPD and NMPD values of archaeophyte (Archaeo) and neophyte (Neo) alien species in 21 European cities.

mainly in agricultural areas. Accordingly, Apiaceae, Caryophyllaceae, Chenopodiaceae and Scrophulariaceae are typical archaeophyte families.

Given their habitat specificity, demonstrated by their high local phylogenetic aggregation (high NMPD values), archaeophytes possess a number of ecological, evolutionary and biogeographical characteristics that have promoted their successful colonization of warm and dry urban environments within Europe, including large distributional ranges, long-term associations with anthropogenic environments and human-mediated biotic interchange (Lososová *et al.* 2004; Pyšek *et al.* 2005; Sádlo, Chytrý & Pyšek 2007; La Sorte *et al.* 2008).

A notable exception is the flora of Rome in which archaeophytes have a phylogenetic structure that is significantly overdispersed. This may be ascribed to the fact that the composition of archaeophytes in Rome is quite different from that in cities in Central or Northern Europe (Celesti-Grapow 1995). Besides a group of species from the steppes of Central Asia (such as cereal weeds), which are common in Central and Northern Europe, archaeophytes in Central Europe also include species of Mediterranean origin (e.g. Pyšek, Sádlo & Mandák 2002; Preston, Pearman & Hall 2004) that persist thanks to the 'heat island effect'. The origin of the archaeophytes in Italy is more diverse (Celesti-Grapow *et al.* 2009). Most Southern European species belong to the local flora, with the majority of Roman archaeophytes having been introduced through trade occurring in the Mediterranean among civilizations that established in ancient times in peninsular Italy and on surrounding islands. First, there were the Phoenicians and the Greeks, whose colonies occurred along the coasts of the Mediterranean Basin. These cultures were followed by the Etruscans and the Romans, whose trade extended to Central Italy, Northern Africa, Southwest Asia and Southern Europe. Furthermore, the city of Rome is much older than the other cities in our analysis such that archaeophytes have had more time to adapt to human land use than species in other parts of Europe. Finally, the generally warmer climate of the Mediterranean compared to Northern and Central Europe also contributes to the high phylodiversity of achaeophytes in Rome: even with the urban heat island effect promoting archaeophytes from warmer climates, their diversity in cities might depend, at least partially, on migration of species from source populations in rural areas. The rural areas can support species from warmer climates in Italy, but they only do so in a restricted way in the cooler areas of Northern and Central Europe.

In contrast, while, by definition, the species pool of archaeophytes is restricted, neophytes are still being introduced and represent a continually expanding species pool with a much broader geographical origin (Pyšek, Jarošík & Kučera 2003; Lambdon *et al.* 2008). Whereas neophytes tend to be better represented within the families Amaranthaceae, Fabaceae, Onagraceae, Polygonaceae and Solanaceae, they have maintained a high level of phylogenetic diversity in European cities, in terms of both MPD and NMPD, that is not distinguishable in most cases from the entire urban species pool. Nonetheless, in spite of their diverse origin, except for Sheffield (where the effect is non-significant), none of the urban neophytic floras shows a significantly overdispersed phylogenetic structure. This means that urban neophytes are still subject to environmental filters that constrain their phylogenetic structure, although these filters are weaker than for archaeophytes.

As already noted by Thompson, Hodgson & Rich (1995), ecological attributes of successful aliens are strongly habitat-dependent, such that relatedness of invaders to the native biota may be one useful criterion for predicting the key ecological characteristics of invasive species and potentially invasible ecosystems. For instance, while in the essentially closed communities of cool, damp climates, clonal growth and competitive ability seem to be important attributes of invasiveness, r-selected characteristics assume greater significance in drier, more open habitats (Thompson, Hodgson & Rich 1995). As ecologically important traits are usually conserved through evolutionary history (Donoghue 2008), it follows that phylogenetic community structure has important consequences for understanding invasiveness.

In light of our results, we can estimate how alien species will impact upon the (phylogenetic) diversity of urban areas based on their time of introduction. Our findings suggest that while the phylogenetic aggregation of urban archaeophytes reflects their long-term and broad-scale association with anthropogenic activities, neophytes, which are more recent invaders, are likely not to be as well-adapted to the environmental, ecological and anthropogenic conditions of urban habitats (Pyšek, Richardson & Williamson 2004). In addition, this temporal approach to urban invasibility automatically considers the ecological, evolutionary and geographical dissimilarity between introduced and native species: the farther back in time the introduction occurred, the shorter the geographical distance to the native flora; and the less dissimilar the environments in the native and introduced regions, the more likely the species will be adapted to biotic and abiotic conditions in the new region. Accordingly, phylogenetic relatedness of invaders to native communities may be one useful parameter for identifying threats to local native species and for prioritizing management efforts regarding alien species.

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