RESEARCH PAPER

Distance decay of similarity among European urban floras: the impact of anthropogenic activities on β diversity

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ABSTRACT

Aim We examine how two categories of non-native species (archaeophyte and neophyte, introduced before and after AD 1500, respectively) have had different impacts on β diversity across European urban floras. Our goal is to use the unique biological perspective provided by urban areas, and the contrasting historical and geographical perspectives provided by archaeophytes and neophytes, to infer how non-native species will impact upon β diversity in the future.

Location Twenty-two urban areas located in seven European countries.

Methods We used the β-sim dissimilarity index to estimate the level of β diversity for 231 unique pair-wise combinations of 22 urban floras. We examined bivariate plots of dissimilarity by geographical separation of city centres to evaluate distance decay of similarity for native species, archaeophytes and neophytes.

Results Based on average percentages, 52.8% (SD = 8.2%) of species in the urban floras were identified as non-native with 28.3% (SD = 6.9%) classified as neophytes and 24.5% (SD = 4.9%) as archaeophytes. Relative to native species, across urban floras, archaeophytes were associated with higher compositional similarity and weaker distance decay patterns, whereas neophytes were associated with lower compositional similarity and stronger distance decay patterns.

Main conclusions Across European urban floras, archaeophytes and neophytes occurred in similar numbers but archaeophytes were consistently associated with lower β diversity and neophytes with higher β diversity. Thus, the impact of non-native species on β diversity can be determined, at least in part, through their historical and geographical associations with anthropogenic activities. If archaeophytes represent the long-term biogeographical outcome for human commensal species, neophytes could develop similar patterns. The consequences, however, are likely to be more substantial ecologically and geographically due to the increasing numbers of neophytes and their global anthropogenic associations. Nevertheless, at present, our findings suggest that, based on occurrence information, neophytes have not achieved this state with European urban floras retaining regionally distinct assemblages of neophytes.

Keywords
Anthropogenic activities, archaeophyte, beta diversity, biotic homogenization, compositional similarity, distance decay, Europe, neophyte, non-native species, urban floras.

INTRODUCTION

Anthropogenic activities are increasingly disrupting biogeographical barriers to dispersal, resulting in the spread and establishment of species beyond their historical ranges, thereby having consequences for the composition, structure and function of ecological communities (Vitousek *et al.*, 1997; Mack *et al.*, 2000; Lockwood, 2004; Hobbs & Mooney, 2005; McNeely, 2005). Two outcomes of this process that are commonly investigated include changes in biological diversity within (species richness or

α diversity) and among (species turnover or β diversity; Whittaker, 1972) species assemblages. Within assemblages at local and regional extents there is evidence that species richness has increased for many taxonomic groups through the addition of new species (Sax & Gaines, 2003; Sax *et al.*, 2005). This includes the addition of native and non-native species that, in many cases, have benefited directly or indirectly from anthropogenic activities (e.g. La Sorte & Boecklen, 2005). Among assemblages, the outcome for β diversity is more complex and is dependent on a combination of factors, including the anthropogenic, biological and geographical characteristics of the region under consideration. This includes, for non-native species found within a region, their time of introduction and place of origin (McKinney, 2005; La Sorte & McKinney, 2006; La Sorte *et al.*, 2007). An outcome of particular interest is the broad-scale decline in β diversity associated with the loss of species with narrow distributions in conjunction with the acquisition of widely distributed species (biotic or taxonomic homogenization; McKinney & Lockwood, 1999).

For vascular plants in European floras, there is evidence that non-native species have had a different impact on β diversity based on their time of introduction and place of origin. Specifically, across European floras, non-native species that were introduced before AD 1500 (archaeophytes) have lower β diversity, and assemblages of non-native species that were introduced after AD 1500 (neophytes; see Pyšek *et al.*, 2004a for definitions) have higher β diversity (Kühn *et al.*, 2003; Kühn & Klotz, 2006; La Sorte *et al.*, 2007). The year AD 1500 signifies the initiation of European exploration of North and South America and the transition from regional (Mediterranean Basin and south-eastern European steppes) to global (primarily North America and Asia) origins of non-native species in Europe. Therefore, contrasting patterns of β diversity for archaeophytes and neophytes reflect, at least in part, differences in their historical and geographical associations with anthropogenic activities. That is, archaeophytes have an ancient association functioning, at least initially, at a regional extent, and neophytes have a modern association functioning at a global extent. These contrasting perspectives provide a unique opportunity to study the long-term and broad-scale impact of non-native species on β diversity.

The structure and composition of natural communities within urban areas represent the consequences of intensive anthropogenic activities. Specifically, urban areas act as the focal point for the local extinction of native species and the broad-scale introduction (both intentional and unintentional) of new species, especially vascular plants (Sukopp & Werner, 1983; Kowarik, 1990; Wittig, 2004; McKinney, 2002, 2006; Wania *et al.*, 2006). Urban areas also contain more species of vascular plants than surrounding areas due to the presence of non-native species and also the presence of additional native species (Kühn *et al.*, 2004; Wania *et al.*, 2006). The higher richness of native species is thought to be due to a combination of 'natural' and 'artificial' factors, including greater environmental heterogeneity, the location of cities in diversity hotspots, intermediate levels of disturbance and the presence of abundant dispersal vectors (Klotz, 1990; Deutschewitz *et al.*, 2003; Kühn *et al.*, 2004; McKinney, 2006; Wania *et al.*, 2006). Lastly, although habitat structure plays an important role

in determining local patterns in urban floras (Celesti-Grapow *et al.*, 2006), habitat structure across cities tends to share many commonalities that are distinct from the surrounding landscape. This island-like characteristic of urban areas makes them suitable for evaluating the broad-scale impact of the intentional and unintentional translocation of species by humans. Therefore, by focusing on urban areas – particularly in Europe which contains some of the oldest and best studied examples of these environments (Sukopp, 2002; Antrop, 2004) – we can assess some of the long-term consequences of the globalization of the Earth's biota (Vitousek *et al.*, 1997) and the transformation of landscapes into urban environments (Berry, 1990; Douglas, 1994).

In this study, we examine β diversity for native species, archaeophytes and neophytes across 22 major urban areas located in seven European countries. We use distance decay of similarity (Nekola & White, 1999; McKinney, 2004; Soininen *et al.*, 2007) to represent these patterns and we compare the outcome with an analysis conducted on urban floras in the north-eastern United States (La Sorte & McKinney, 2006). The goal of this study is to use the unique biological perspective provided by European urban areas and the contrasting historical and geographical perspectives provided by archaeophytes and neophytes in Europe to infer how non-native species, in association with expanding anthropogenic activities, will impact upon β diversity or spatial patterns of diversity in the future.

MATERIALS AND METHODS

We assembled urban floras for 22 European cities located in seven countries (Fig. 1 & Table 1). Twenty-one of the cities were located between latitude 49° and 55° N. Rome, Italy was an outlier occurring at latitude 41° N (Fig. 1). The exclusion of Rome from the analysis did not alter our conclusions, thus our analysis considered all 22 cities. For each flora, we combined all varieties and subspecies into single species. We then standardized the taxonomic nomenclature using the Missouri Botanical Garden's TROPICOS data base and the program TaxonScrubber, version 1.2 (Boyle, 2004) resulting in a data base of 4108 species. We then designated each species as native (indigenous, autochthonous) or non-native (non-indigenous, alien, exotic, allochthonous) within each flora (Pyšek *et al.*, 2004a) using three categories: (1) evolved in Europe or arrived before the beginning of the Neolithic period or arrived after that period independent of human activity (native; Webb, 1985); (2) introduced into Europe before AD 1500 (archaeophyte); (3) introduced into Europe after AD 1500 (neophyte). Two of the 22 floras lacked any such classification and the remaining 20 floras presented classifications that were not geographically consistent. These inconsistencies reflect differences in the time of introduction and place of origin for non-native species across the study region (Fig. 1). For example, species that were identified as native in the south or east could be classified as archaeophyte or neophyte in the north or west depending on their time of arrival. Therefore, to provide a classification scheme that was biogeographically consistent (i.e. where each species was identified by only one category) we used the approach described by La Sorte *et al.*
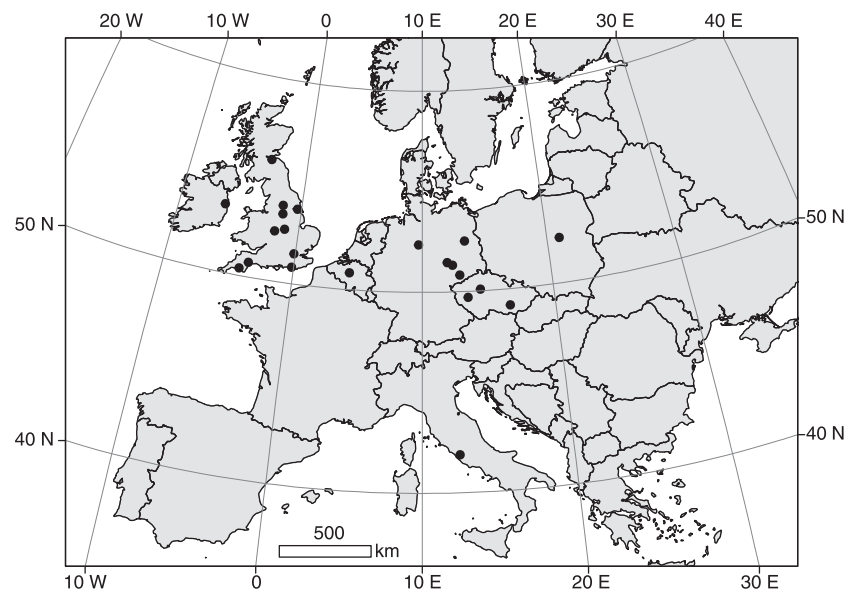
Figure 1 Location of 22 European cities (circles) whose urban floras were used in the analysis. The map is overlaid with a 10° interval grid of latitude and longitude.

Table 1 Summary of the data used in the study with the geographical location of the 22 European cities, the number of human inhabitants in each city, the total number of species identified in each flora, the number of species classified as native and the number of species classified in two non-native categories: archaeophyte and neophyte (introduced into Europe before and after AD 1500, respectively). [Correction added 27 February 2008 after publication: in Table 1, columns Neophyte, Archaeophyte and Native changed, respectively, from: Berlin: 323, 217, 435; Brno: 301, 249, 220; Brussels: 186, 169, 359; Leipzig: 823, 292, 630; Plzeň: 247, 215, 572; Prague: 548, 320, 1022; and Warsaw: 356, 268, 786. Corrected values are presented in the table, as below.]

City (country)	Latitude/longitude	Inhabitants (million)	Total	Neophyte	Archaeophyte	Native	Source
Berlin, West (Germany)	52°31′ N/13°24′ E	1.93	975	321	240	414	Kunick (1974)
Birmingham (UK)	52°29′ N/01°54′ W	0.977	578	115	131	332	Cadbury et al. (1971)
Brighton (UK)	50°49′ N/00°08′ W	0.248	537	129	159	249	Hall (1980)
Brno (Czech Republic)	49°12′ N/16°37′ E	0.388	770	291	269	210	Grüll (1979)
Brussels (Belgium)	50°50′ N/04°21′ E	0.97	714	184	193	337	IBGE (1999)
Chemnitz (Germany)	50°50′ N/12°55′ E	0.246	863	222	207	434	Grundmann (1992)
Dublin (Ireland)	53°20′ N/06°15′ W	0.506	315	75	83	157	Jackson and Skeffington (1984)
Edinburgh (UK)	55°57′ N/03°11′ W	0.449	333	117	122	94	McKean (1989)
Exeter (UK)	50°43′ N/03°31′ W	0.118	488	102	126	260	Ivimey-Cook (1984)
Halle an der Saale (Germany)	51°28′ N/11°58′ E	0.238	906	253	237	416	Klotz (1984)
Hannover (Germany)	52°22′ N/09°44′ E	0.516	803	160	199	444	Haeupler (1976)
Kingston upon Hull (UK)	53°43′ N/00°20′ W	0.244	708	202	189	317	Middleton (1998)
Leeds (UK)	53°47′ N/01°32′ W	0.715	421	85	95	241	Lavin and Wilmore (1994)
Leicester (UK)	52°38′ N/01°08′ W	0.28	574	131	148	295	Primavesi and Evans (1988)
Leipzig (Germany)	51°20′ N/12°23′ E	0.539	1745	816	327	602	Gutte (1989)
London (UK)	51°30′ N/07°39′ W	7.172	1171	444	229	498	Burton (1983)
Plymouth (UK)	50°22′ N/04°08′ W	0.246	752	204	177	371	Stevens (1990)
Plzeň (Czech Republic)	49°43′ N/13°29′ E	0.165	1034	260	235	539	Pyšek and Pyšek (1988), Nesvadbová and Sofron (1997), Chocholoušková and Pyšek (2003)
Prague (Czech Republic)	50°05′ N/14°26′ E	1.212	1890	558	347	985	Špryňar and Münzbergová (1998)
Rome (Italy)	41°54′ N/12°30′ E	2.554	1272	390	244	638	Celesti-Grapow (1995)
Sheffield (UK)	53°23′ N/01°28′ W	0.513	1458	517	259	682	Shaw (1988), J. Hodgson (pers. comm.)
Warsaw (Poland)	52°15′ N/21°00′ E	1.65	1410	361	294	755	Sudnik-Wójcikowska (1987)

(2007). Species were classified as archaeophyte if they were designated as an archaeophyte in at least one flora, and species were classified as neophytes if they were not designated as archaeophyte and were designated as neophyte in at least one flora.

Therefore, across the 22 urban floras, any species that was not designated exclusively as native was placed into one of the two non-native categories with archaeophyte taking precedence over neophyte. We ranked non-native status higher than native status

because, if a species was identified as non-native anywhere within the study region, it had the ability to become established outside of its historical range. We ranked archaeophytes 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.

We used ANOVA to examine differences in the average number of species among the three categories and *t*-tests to examine differences for pairs of categories. To control the family-wise Type I error rate for the *t*-tests, we used adjusted *P*-values based on the Holm (1979) step-down method. Species numbers were log-transformed to comply with statistical assumptions and we report two-sided *P*-values for the *t*-tests.

We examined β diversity based on the level of compositional similarity for pairs of floras as a function of distance between city centres. It is typical for β diversity or compositional similarity to decrease or decay as geographical separation increases (Nekola & White, 1999; McKinney, 2004; Soininen *et al.*, 2007). Unique city pairs numbered 231 for the 22 European cities. We estimated the distance between city pairs using the great-circle distance between city centres. We estimated the level of compositional similarity between pairs of floras using the β-sim dissimilarity index which has a range from 0 to 1, high similarity to low similarity, respectively (Lennon *et al.*, 2001; Koleff *et al.*, 2003). We chose the β-sim dissimilarity index because it has better properties, relative to other common indices such as the Jaccard, when strong species richness differences exist between paired assemblages.

We applied ordinary least-squares (OLS) regression to bivariate plots of the β-sim dissimilarity index by distance between city pairs to examine the nature of distance decay patterns for the three categories of species. We used the permutation procedure described by La Sorte and McKinney (2006) to test whether the estimated linear regression coefficients, intercept and slope, differed between the three categories of species. Test values for the permutation procedure were differences in regression coefficients between pairs of categories. The pairs included: neophyte vs. native, native vs. archaeophyte and neophyte vs. archaeophyte. This approach allowed us to estimate error probabilities without relying on parametric models that contained inflated degrees of freedom due to the pseudoreplication of cities. The permutation procedure involved shuffling or resampling without replacement the three categories across the 4108 species. The resampled species/category associations were then applied to the species found in each of the 22 cities. The β-sim index was then recalculated for each category across the pair-wise combinations of cities and the same OLS regression models were applied. This procedure was conducted independently for each of two intercept locations based on the minimum (32 km) and maximum (1930 km) distance between city centres. We estimated the probability of the observed differences in regression coefficients occurring by chance alone based on where the differences occurred within the distribution of differences based on 9999 permutations of the three categories. All analyses were conducted using the statistical software R, version 2.4.1 (R Development Core Team, 2007).

RESULTS

The 22 European cities contained an average population of 0.994 million human inhabitants (SD = 1.518; Table 1) and were separated by an average of 782 km (SD = 479). The 22 European urban floras contained, on average, 896 species (SD = 437) with 421 classified as native (SD = 213), 270 as neophyte (SD = 185) and 205 as archaeophyte (SD = 72; Table 1). Based on average percentages, 52.8% (SD = 8.2%) of species were identified as non-native with 28.3% (SD = 6.9%) classified as neophyte and 24.5% (SD = 4.9%) as archaeophyte. The number of species in the three categories differed on average within the urban floras ($F_{2,63}$ = 9.188, $P < 0.001$). Differences were limited to comparisons between the native category and the two non-native categories ($P \leq 0.004$); the number of neophyte and archaeophyte species in urban floras did not differ on average (t_{63} = –0.855, $P = 0.396$).

Distance decay patterns for the 231 unique pair-wise combinations of 22 urban floras presented strongly divergent patterns for the three categories of species (Fig. 2). All permutation tests of paired regression coefficients indicated the presence of differences that were unlikely to have occurred by chance alone (Table 2). Relative to native species, archaeophytes presented the weakest distance decay patterns and the highest compositional similarity; neophytes, in contrast, presented the strongest distance decay patterns and lowest compositional similarity. Thus, native species presented intermediate patterns with archaeophytes having consistently lower, and neophytes consistently higher, β diversity.
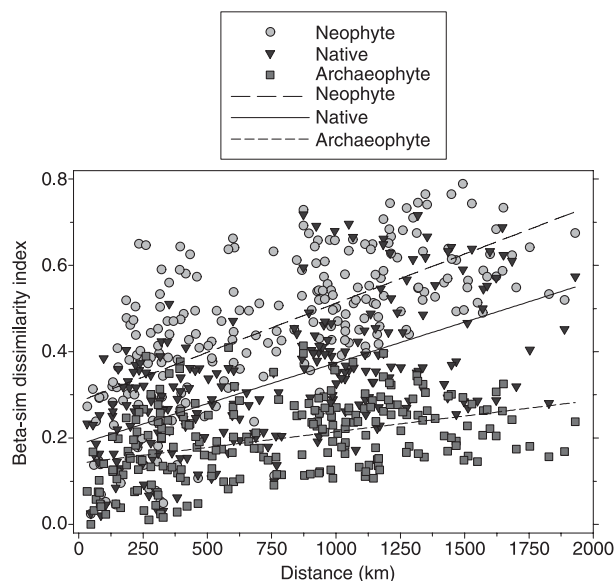
Figure 2 Bivariate plot of the β-sim dissimilarity index by distance between 231 unique pairs of 22 European cities. Ordinary least-squares regression lines are presented for native species and two categories of non-native species: archaeophyte and neophyte (introduced into Europe before and after AD 1500, respectively).

Table 2 Results from ordinary least-squares regression of the β-sim dissimilarity index by distance between 231 unique pairs of 22 European cities. Regression models were applied separately for native species and two categories of non-native species: archaeophyte and neophyte (introduced into Europe before and after AD 1500, respectively). Intercept and slope coefficients are presented for the original regression models and *P*-values are given based on permutation tests that examined differences in coefficients for pairs of categories. Differences in intercept are examined at the minimum (32 km) and maximum (1930 km) distance between city pairs.

	Minimum distance		Maximum distance			
	Intercept	*P*-value	Intercept	*P*-value	Slope	*P*-value
Permutation tests						
Neophyte – Native	0.101	≤0.001	0.175	≤0.001	3.90×10^{-5}	0.009
Native – Archaeophyte	0.047	0.015	0.267	≤0.001	1.16×10^{-4}	≤0.001
Neophyte – Archaeophyte	0.148	≤0.001	0.442	≤0.001	1.55×10^{-4}	≤0.001
Regression models	Intercept	Slope				
Neophyte	0.284	2.28×10^{-4}				
Native	0.185	1.89×10^{-4}				
Archaeophyte	0.142	7.29×10^{-5}				

DISCUSSION

Our results indicate that non-native species have had a substantial role in shaping vascular plant diversity within and among European urban floras. Approximately half of the species in urban floras were non-native, and half of these were identified as archaeophytes with the remaining half identified as neophytes. We also found substantial differences in the form and structure of distance decay patterns, differences that confirm and enhance the findings of previous investigations (Kühn *et al.*, 2003; Kühn & Klotz, 2006; La Sorte *et al.*, 2007). Relative to neophytes and native species, archaeophytes had weaker distance decay patterns, indicating low turnover among floras or low β diversity. In contrast, neophytes had stronger distance decay patterns, indicating high turnover among floras or high β diversity. Thus, archaeophytes in urban floras had the highest proportion of shared species which remained consistent across space; neophytes, in contrast, had the lowest proportion of shared species which decreased with increasing geographical separation. These findings also suggest the presence of differences in range-size distributions, with archaeophytes having a greater, and neophytes a lower, proportion of species with widespread geographical distributions (Pyšek *et al.*, 2004b; La Sorte & McKinney, 2006).

When these findings are contrasted with patterns found for urban floras in the north-eastern USA (La Sorte & McKinney, 2006), our results reinforce the conclusion that non-native species in Europe have stronger and more divergent patterns relative to non-native species in the USA (La Sorte *et al.*, 2007). Specifically, non-native species that originated from inside (extra-limital native) and outside (exotic) the USA differed little based on an assessment of overall β diversity (La Sorte *et al.*, 2007). Based on an assessment of distance decay patterns, both US extra-limital natives and exotics were associated with higher β diversity relative to native species, with extra-limital natives presenting distance decay patterns intermediate between exotic and native species (La Sorte & McKinney, 2006). European neophytes and USA

exotics showed higher β diversity relative to native species, but the patterns for European neophytes were considerably stronger. Archaeophytes and extra-limital natives showed patterns that differed both in direction and magnitude. However, both categories showed distance decay patterns that were weaker relative to native species.

Differences in β diversity between USA exotics and European neophytes can be explained based on the presence of European archaeophytes within the USA exotic category. Our findings indicate that archaeophytes were associated with lower β diversity across urban floras in Europe and, based on an intercontinental examination (La Sorte *et al.*, 2007), with weaker gains in β diversity for exotic species in urban floras in the USA. At the coarser resolution of US states, there is contrary evidence suggesting that non-native species are associated with losses in β diversity (Qian & Ricklefs, 2006). However, there is additional evidence that European archaeophytes are responsible for some of these losses (F.A.L., unpublished). Thus, the negative influence of European archaeophytes on β diversity represents a continental and intercontinental phenomenon evident at a variety of geographical resolutions.

The differences between USA extra-limital natives and European archaeophytes can be explained based on differences in the duration and extent of human influence within the USA and Europe. European archaeophytes that exist today represent a limited number of species that, over several millennia within Europe, have developed successful associations with anthropogenic activities, in particular with arable fields, early agricultural activities and ruderal situations characterized by disturbed ground (Preston *et al.*, 2004). For archaeophytes in Europe, habitats associated with these activities can be found consistently both within and outside urban areas (Kühn *et al.*, 2003; Pyšek *et al.*, 2005; Kühn & Klotz, 2006). US extra-limital natives, in contrast, developed associations with anthropogenic activities during the past several centuries and have not had the same historical opportunities as European archaeophytes in terms of adaptation,

dispersal or habitat availability. Thus, USA extra-limital natives retain, at present, associations that are more similar to native species than to archaeophytes.

Our findings suggest that we can estimate how a non-native species will impact upon β diversity based on its time of introduction and place of origin. This perspective represents an extension of the hypothesis that non-native species with regional origins have a greater likelihood of reducing β diversity due to ecological, evolutionary and geographical advantages (McKinney, 2005). In this case, the addition of time allows for a broader spatiotemporal perspective that considers adaptation, dispersal and establishment operating over both space and time. An additional refinement would consider environmental dissimilarity as well. Therefore, the farther back in time the introduction occurred, the shorter the geographical distance to native populations, and the less dissimilar the environments in the native and introduced regions, the more likely the species will be adapted to, or will have adapted to, biotic and abiotic conditions in the new region. In addition, it is more likely the species will have, or will have developed, broad geographical distributions.

If we consider how β diversity for non-native species in European urban floras is likely to develop over time, recent evidence suggests that archaeophytes have diminished as neophytes have become more prevalent in number and extent, and the anthropogenic environments that archaeophytes rely upon (e.g. Old World crops) have declined in quantity and quality (Preston *et al.*, 2004; Pyšek *et al.*, 2005; Baessler & Klotz, 2006). Thus, the role currently played by archaeophytes could be seen as reflecting a 'fleeting' interaction between the ancient and modern world, an interaction with diminishing returns as neophytes and modern anthropogenic activities, including urbanization, become more prevalent. This conclusion is supported by investigations that suggest archaeophytes in European floras are in a post-invasive phase (Pyšek *et al.*, 2002). In addition, archaeophytes have, by definition, a restricted species pool whereas neophytes are still being introduced and represent a continually expanding species pool (Pyšek *et al.*, 2003). Thus, it is conceivable that the biogeographical position currently occupied by archaeophytes could be replicated by neophytes but at a much broader geographical and ecological scale.

Evidence from this and other studies suggests that neophytes have not achieved this state, with regional anthropogenic and historical factors delineating continental and intercontinental associations (La Sorte *et al.*, 2007). Nevertheless, relative to archaeophytes, neophytes have a greater range and extent of anthropogenic opportunities, which is likely to result in greater biological impacts if they develop biogeographical patterns similar to archaeophytes. Alternatively, the level of regional distinctiveness for neophytes in urban areas could represent a long-term pattern maintained by anthropogenic activities. The introduction of new species and the maintenance of regional, non-self-sustaining populations, might outpace the adaptation and geographical expansion of neophytes, thus maintaining high β diversity. Losses in β diversity, therefore, would be more evident in non-urban regions or at coarser resolutions, where introduction pressure would be weaker and anthropogenic activities

less prevalent. Alternatively, if a species benefits from anthropogenic activities, both occupancy and abundance are likely to respond in a positive fashion (the abundance–occupancy relationship; see Gaston *et al.*, 2000 for review). Within urban areas, therefore, assessments that include abundance estimates might provide a more comprehensive representation of how non-native species have impacted upon β diversity (La Sorte & McKinney, 2007).

This study reaffirms the conclusion that, at present, the uniform homogenization of the Earth's continental biota is not imminent (La Sorte *et al.*, 2007). What this study also indicates is that patterns documented among urban areas will not capture all the possible outcomes for β diversity. Urban areas provide one perspective or inferential framework for assessing this complex global phenomenon. The impact that anthropogenic activities will have on β diversity is determined by a combination of biotic and abiotic factors including human demographic, cultural, economic and social factors (Cassey *et al.*, 2007; La Sorte *et al.*, 2007). Nevertheless, in an increasingly urbanized world, the effect of urban environments will expand, not only within urbanized regions but outside them as well. Ecological patterns within and among urban areas, therefore, will play an increasingly important role in defining how biological diversity will be configured by human activities in the future.

In summary, if biological patterns within urban areas represent the consequences of intensive anthropogenic activities, and if archaeophytes represent the long-term and broad-scale consequences of successful associations with anthropogenic activities, we have a model to assess how expanding anthropogenic activities are likely to impact upon biological diversity in the future. At present, broad-scale losses in β diversity are driven primarily by non-native species with strong regional and historical associations with human activities. As new non-native species develop similar associations, they are likely to develop similar geographical patterns. The long-term and broad-scale consequences of the spread and establishment of non-native species, however, might not be evident within urban areas alone, where anthropogenic activities could inadvertently foster high β diversity. Examining patterns outside urban areas, or at coarser resolutions, would overcome this limitation (e.g. Qian & Ricklefs, 2006; Castro *et al.*, 2007). In addition, the inclusion of estimates of abundance, derived from empirical data or inferred from established ecological relationships, would provide a broader perspective on how β diversity has changed (La Sorte & McKinney, 2007). However, urban areas are growing in extent and influence and are likely to remain an important indicator of the impact of intensive anthropogenic activities on biological diversity.

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BIOSKETCH

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