

Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange

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Abstract

Anthropogenic activities have weakened biogeographical barriers to dispersal resulting in the global spread and establishment of an increasing number of non-native species. We examine the broad-scale consequences of this phenomenon based on an analysis of compositional similarity across urban floras in the northeastern United States and Europe. We test the prediction that homogenization of species composition is uniquely defined within vs. between continents based on the time and place of origin of non-native species. In this case, for archaeophytes and neophytes in Europe (introduced before and after AD 1500, respectively) and non-native species originating from within and outside the United States. More species in urban floras were shared within than between continents. Within Europe, archaeophytes shared more species across urban floras compared with neophytes; strong associations were not observed for non-native species across US urban floras. Between the two continents, non-native species in the United States that originated from outside the United States shared species primarily with archaeophytes but also with European natives and neophytes. These results suggest that the direction of biotic interchange was unidirectional with species moving primarily from Europe to the United States with archaeophytes playing a primary and non-native species originating from outside the two continents a secondary role as a homogenizing source. Archaeophytes, based on combination of biogeographical, evolutionary, and ecological factors in association with a long history of anthropogenic influence, appear to have played a prominent role in the continental and intercontinental homogenization of species composition. This suggests that the uniform homogenization of the Earth's biota is not imminent and is presently directed by a combination of biogeographically defined anthropogenic and historical factors.

Keywords: archaeophytes, biotic homogenization, biotic interchange, compositional similarity, globalization, non-native species, urban floras

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Introduction

Through the influence of anthropogenic-related activities, the Earth's biota has experienced the persistent weakening of biogeographical barriers to dispersal. This has resulted in the spread and establishment of an increasing number of non-native species at increas-

ingly broader scales (Vitousek *et al.*, 1997; Lockwood, 2004; McNeely, 2005). The Earth's biota has experienced many episodes of large-scale biotic interchange whose biogeographical consequences, over geologic time, have been well investigated; however, the consequences for the present period of anthropogenic-related biotic interchange remain poorly understood (Hierro *et al.*, 2005; Vermeij, 2005). Therefore, documenting aspects of this phenomenon at geographical scales will allow us to develop an understanding of its impact on the structure and compo-

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sition of biological communities across space which, ultimately, will allow us to infer the consequences for ecological patterns and processes within the biosphere.

Vascular plants have experienced 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 been one of the primary beneficiaries of anthropogenic-related biotic interchange and thus, when documenting ecological consequences, vascular plants are an appropriate focal group. In addition, urban areas and associated environments stand out as the focal point of biotic interchange of non-native species in general and vascular plants in particular (Sukopp & Werner, 1983; Kowarik, 1990; Pyšek, 1998a; Roy *et al.*, 1999; Wittig, 2004; Chytrý *et al.*, 2005; Tait *et al.*, 2005).

The compilation and study of urban floras was initiated in Europe during the second half of the 20th century (see Pyšek, 1993 and references therein) and the majority of investigations of European urban floras have focused on species numbers (Pyšek, 1998a; Sukopp, 2002) and comparisons of historic and recent floristic compositions within individual cities (Klotz, 1987; Landolt, 2000; Chocholoušková & Pyšek, 2003). In Central European cities, these studies have concluded that species richness over the last one to two centuries has remained at comparable levels but approximately 30–40% of original floras were replaced by, primarily, non-native species (Chocholoušková & Pyšek, 2003).

Therefore, we will focus our investigation on urban areas, the regions containing the greatest proportions of non-native plants and the greatest concentration of long-distance anthropogenic vectors of dispersal for non-native plants. We will examine patterns of compositional similarity across seven urban floras located in western, central and eastern Europe and eight urban floras located in the northeastern United States. These two regions are associated within the same biome – temperate deciduous forest – and contain similar vegetation structures and growth forms in addition to similar climates and physiographic features. Therefore, these two regions differ mainly in geographic location with each region containing unique but inter-related biological and human histories. Any patterns we discern will therefore reflect these influences (Pauchard *et al.*, 2004).

We will categorize species of vascular plants into two classes: native and non-native. We will further classify non-native species based on their place of origin for US floras – originating from within or outside the United States – and their time and place of origin for European floras – originating before AD 1500 and from within Europe and after AD 1500 and from outside Europe.

The year AD 1500 signifies the discovery of the New World and the initiation of relatively rapid and substantial changes in human demography, agriculture, commerce, and industry. We will explore how each category is compositionally represented within and among floras within each continent and across continents.

It was initially predicted that, with the degradation of biogeographic barriers to dispersal through global human commerce, species composition of regional biotas would become more homogenous over time through the introduction and establishment of non-native species (Elton, 1958). However, investigations suggest that, at least with recent patterns, this prediction is not always met. Specifically, there is evidence that non-native species originating from within a continent play an initial role increasing similarity in species composition across communities. For example, there is evidence that species composition of avian assemblages (La Sorte & Boecklen, 2005) and fish assemblages (Rahel, 2000, 2002; McKinney, 2005a) in North America and assemblages of vascular plants (McKinney, 2005a; Kühn & Klotz, 2006) in North America and Europe have become more similar through the introduction and colonization of species originating from within each continent. Conversely, there is evidence that non-native species originating from outside a continent play an initial role in decreasing similarity in species composition across communities (McKinney, 2004, 2006; Kühn & Klotz, 2006; La Sorte & McKinney, 2006). This is related, at least in some cases, to the greater prevalence of geographically rare species which tend to promote reduced levels of compositional similarity across communities (McKinney, 2004; La Sorte & McKinney, 2006). These contrasting associations suggest two predictions for our present investigation: (1) assemblages of non-native species originating from within the United States and originating from within Europe will share more species in common within each continent vs. between the two continents; and (2) assemblages of non-native species originating from outside the United States and from outside Europe will share fewer species in common within each continent but more across the two continents. Testing these two predictions will allow us to assess the broad-scale ecological consequences of anthropogenic-related biotic interchange; specifically, the spatiotemporal scope and structure of patterns of homogenization of species composition within and between continents.

Materials and methods

Floras for eight United States cities including Boston, Chicago, Detroit, Minneapolis, New York, Philadelphia,

Saint Louis, and Washington DC and native or non-native status within each flora were acquired from original sources compiled by Clemants & Moore (2003). We used the PLANTS database (USDA, NRCS, 2006) to identify species that had been introduced into the United States. Floras for seven European cities including Berlin (West), Brno, Brussels, Leipzig, Pilsen, Prague, and Warsaw and native or non-native status were acquired from original sources (Kunick, 1974; Sudnik-Wójcikowska, 1987; Gutte, 1989; IBGE, 1999) or, in the case of Czech cities, classified according to a recent checklist of non-native plant species (Pyšek *et al.*, 2002). European florae were based on long-term systematic research and included both naturalized and casual species (*sensu* Richardson *et al.*, 2000).

Using these databases, we first combined all varieties and subspecies into single species. We then standardized taxonomic nomenclature across the 15 urban florae using the Missouri Botanical Garden's TROPICOS database and the program TaxonScubber, version 1.2 (Boyle, 2004). This resulted in a total of 4152 unique species in United States florae, 3176 in European florae, and a grand total of 6154 unique species for all 15 florae combined. We then designated each species as native (indigenous) or non-native (nonindigenous, alien, exotic) and each non-native species as originating from either within or outside the United States for US florae or originating either before or after AD1500 for European florae (Pyšek *et al.*, 2004b; McKinney, 2005a). We placed each US species into one of three origin classes: (1) species that were only identified as native within the eight florae (native); (2) species that were native to the United States and identified as non-native in at least one flora (extralimital native); and (3) species that were non-native to the United States (exotic). We then placed each European species into one of three origin classes traditionally used in investigations of European florae: (1) evolved in central, western, and eastern 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 central, western, and eastern Europe before AD1500 (archaeophyte); and (3) introduced into this region of Europe after AD1500 (neophyte). Archaeophytes are typically associated with rural environments or intermediate levels of anthropogenic activities and originate primarily from the Mediterranean Basin; neophytes, in contrast, are typically associated with urban environments or more intensive anthropogenic activities and originate primarily from North America and Asia (Sukopp & Werner, 1983; Weber, 1997; Pyšek, 1998a; Pyšek *et al.*, 2002). Species in European florae were classified as archaeophytes if they were designated as an archaeophyte in at

least one flora; 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 seven European urban florae, any species that were not designated exclusively as native were placed into one of the two non-native classes with archaeophyte taking precedence over neophyte. We defined the origin classes in this manner to promote a regional assessment within the United States and Europe that was consistent across the two continents and treated each class in the same manner spatially independent of local classifications within cities. This applies primarily to species classified as extralimital native or archaeophyte. Species in these two classes originated from within the United States or from within European but displayed the ability to become established outside of their native ranges and thus influence spatial patterns of compositional similarity within these regions. Therefore, to be consistent within and between these two regions, species identified in one of these classes in at least one flora was classified as such across all florae within the region.

We estimated the level of compositional similarity between pairs of florae 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). This index was chosen because it has better properties when strong species richness differences exist between paired assemblages. In this case, substantial differences in species richness existed between United States and European florae. From the 15 urban florae, 201 unique pair-wise combinations of florae were available for analysis. We separated these 201 pairs into three groups for analysis: the first group contained paired European florae ($n=21$), the second contained paired US florae ($n=28$), and the third contained European florae paired with US florae ($n=56$). Using these three groups, we examined the level of compositional similarity within each continent and across the two continents for species identified within each flora and species identified within each of the six origin classes.

We used, because of heterogeneity of variance across samples and non-normality within samples, randomization procedures developed by Wilcox (2005) to test for differences in the β -sim dissimilarity index across florae. We used the function *t1waybt* to test for similarity across sample means and the function *linconb* for multiple testing that retained a simultaneous α -level of 0.05. All procedures were based on the application of the bootstrap-*t* method using untrimmed means and 10 000 bootstrap samples. The test statistic for *t1waybt* was reported as F_t which, when the means are not trimmed, has an approximate *F* distribution using Welch's (1951) adjusted degrees of freedom. All ana-

lyses were conducted using the statistical software R, version 2.3.0 (R Development Core Team, 2006).

Results

European cities contained 0.979 million inhabitants on average (SD=0.660) and US cities contained 1.908 million inhabitants on average (SD=2.606; Table 1). European cities were separated by 451 km on average (SD=254) and US cities were separated by 907 km on average (SD=484). Urban floras in European cities contained, on average, 1220 species (SD=468) with 575 classified as native (SD=271), 398 as neophyte (SD=219), and 247 as archaeophyte (SD=51; Table 1). Urban floras in the United States contained, on average, 2042 species (SD=455) with 1217 classified as native (SD=207), 555 as exotic (SD=213), and 269 as extralimital native (SD=56; Table 1). Based on average proportions, urban floras in Europe contained 46% native

species, 32% neophyte, and 22% archaeophyte. With neophytes and archaeophytes combined, European urban floras contained 54% non-native species. Based on average proportions, urban floras in the United States contained 61% native species, 26% exotic species, and 13% extralimital native species. With extralimital native and exotic species combined, urban floras contained 39% non-native species.

Based on complete urban floras, several patterns were evident across the three groups of 105 paired floras (Table 2; Fig. 1). Similarity differed on average across the three groups ($F_t=217.167$, $P \leq 0.001$) and was greatest for paired US floras and paired European floras and weakest for paired US/European floras. Therefore, United States and European urban floras had more species in common within each continent and fewer species in common across the two continents. In addition, similarity did not differ on average between paired United States and paired European floras suggesting similar

Table 1 Summary of the data used in the study with the geographic location of the seven European cities and eight United States cities, the number of inhabitants in each city, and the total number of species in each flora and the number of species classified in each of three origin classes

City	Latitude/ longitude	Inhabitants (million)	Total species	Neophyte/ exotic	Archae- ophyte/ extralimital native	Native	Source
<i>Europe</i>							
Berlin, West (Germany)	52.31 N/13.24 E	1.930	975	323	217	435	Kunick (1974)
Brno (Czech Republic)	49.11 N/16.36 E	0.388	770	301	249	220	Grüll (1979)
Brussels (Belgium)	50.51 N/4.21 E	0.970	714	186	169	359	IBGE (1999)
Leipzig (Germany)	51.20 N/12.23 E	0.539	1745	823	292	630	Gutte (1989)
Pilsen (Czech Republic)	49.46 N/13.24 E	0.165	1034	247	215	572	Pyšek & Pyšek (1988), Nesvadbová & Sofron (1997), Chocholoušková & Pyšek (2003)
Prague (Czech Republic)	50.05 N/14.27 E	1.212	1890	548	320	1022	Špryňar & Münzbergová (1998)
Warsaw (Poland)	52.14 N/21.01 E	1.650	1410	356	268	786	Sudnik-Wójcikowska (1987)
<i>United States</i>							
Boston	42.22 N/71.20 W	0.589	2315	759	328	1228	Clemants & Moore (2003) and references therein
Chicago	41.59 N/87.54 W	2.896	1766	439	266	1061	
Detroit	42.25 N/83.10 W	0.951	1616	391	203	1022	
Minneapolis	44.53 N/93.13 W	0.383	1400	247	168	985	
New York	40.47 N/73.58 W	8.008	2527	738	282	1507	
Philadelphia	39.53 N/75.15 W	1.518	2546	795	301	1450	
Saint Louis	38.45 N/90.23 W	0.348	1756	379	283	1094	
Washington DC	38.51 N/77.20 W	0.572	2407	694	321	1392	

The classes neophyte, archaeophyte, and native correspond to European floras and the classes exotic, extralimital native, and native correspond to United States floras. See text for description of origin classes.

Table 2 Results from the bootstrap-*t* multiple testing procedure examining differences in average β -sim dissimilarity index for different combinations of European and United States urban floras and origin classes (see text for descriptions of origin classes)

	<i>n</i>	Mean β -sim (SD)
<i>Complete floras</i>		
Europe	21	0.311 (0.096)*
United States	28	0.263 (0.061) [†]
Europe/United States	56	0.635 (0.104)*, [†]
<i>European classes</i>		
Native	21	0.260 (0.080)*, [‡]
Archaeophyte	21	0.136 (0.047)*, [†]
Neophyte	21	0.450 (0.102) [‡] , [‡]
<i>United States classes</i>		
Native	28	0.262 (0.090)
Extralimital native	28	0.301 (0.062)*
Exotic	28	0.211 (0.081)*
<i>European Native vs. United States classes</i>		
Native	56	0.910 (0.024)*, [‡]
Extralimital native	56	0.965 (0.011)*, [†]
Exotic	56	0.784 (0.065) [‡] , [‡]
<i>European Archaeophyte vs. United States classes</i>		
Native	56	0.986 (0.002)*, [‡]
Extralimital native	56	0.977 (0.006)*, [†]
Exotic	56	0.446 (0.125) [‡] , [‡]
<i>European Neophytes vs. United States classes</i>		
Native	56	0.933 (0.022)*
Extralimital native	56	0.933 (0.022) [†]
Exotic	56	0.765 (0.063)*, [†]

The β -sim index estimates the level of compositional similarity among *n* paired urban floras and has a range from 0 to 1, high similarity to low similarity, respectively.

*,[†],[‡]Average β -sim values with identical symbols differed based on a simultaneous α -level = 0.05.

compositional structures were present within each continent.

The level of compositional similarity for origin classes within paired United States and paired European floras presented several relevant patterns (Table 2; Fig. 2). On average, similarity differed across the three origin classes for European floras ($F_t=86.164$, $P\leq 0.001$) and similarity differed across the three origin classes for US floras ($F_t=10.845$, $P\leq 0.001$). In European floras, archaeophytes had the highest and neophytes the lowest levels of shared species. In US floras, the differences were less substantial with only exotics presenting evidence of more shared species relative to extralimital natives.

The level of compositional similarity across the nine unique combinations of US and European classes present several relevant findings (Table 2; Fig. 3). The level of similarity differed across the three US classes when

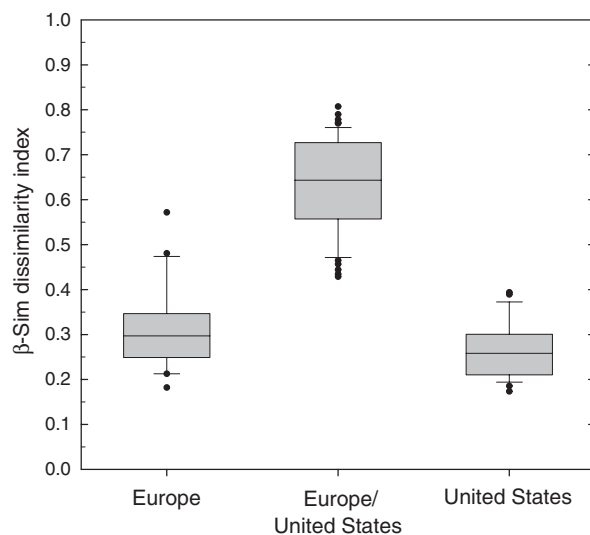


Fig. 1 Box plots of the β -sim dissimilarity index examining levels of compositional similarity among urban floras in Europe ($n = 7$), the United States ($n = 8$), and across the two continents. Each box delineates the 25th and 75th percentiles with the median represented by the horizontal line. The whiskers delineate the 10th and 90th percentiles and the points represent outliers. See text for definition of origin classes.

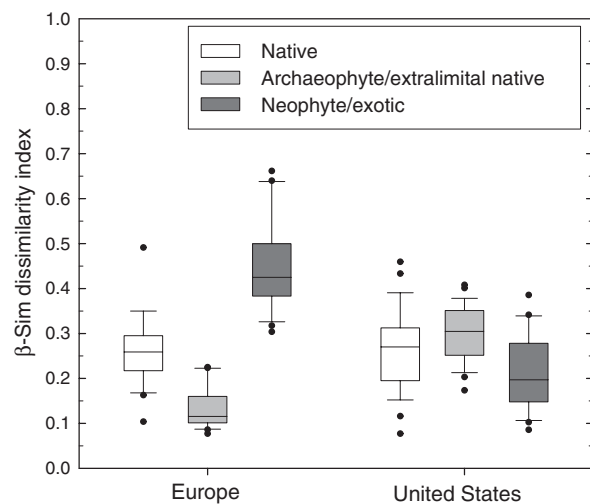


Fig. 2 Box plots of the β -sim dissimilarity index examining levels of compositional similarity within three European origin classes (Europe) and within three United States origin classes (United States). Seven urban floras were considered in Europe and eight in the United States. The European origin classes include native, archaeophyte, and neophyte and the US origin classes include native, extralimital native, and exotic. Each box delineates the 25th and 75th percentiles with the median represented by the horizontal line. The whiskers delineate the 10th and 90th percentiles and the points represent outliers. See text for definition of origin classes.

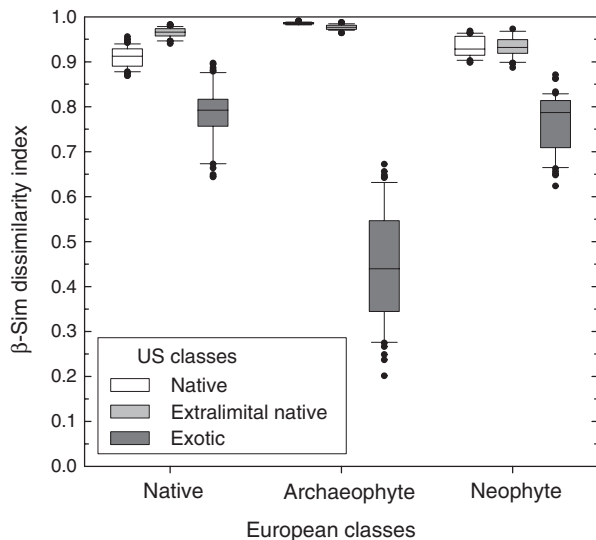


Fig. 3 Box plots of the β -sim dissimilarity index examining levels of compositional similarity between nine unique combinations of three European origin classes and three United States origin classes within seven European and eight United States urban floras. Each box delineates the 25th and 75th percentiles with the median represented by the horizontal line. The whiskers delineate the 10th and 90th percentiles and the points represent outliers. See text for definition of origin classes.

contrasted with European natives ($F_t=255.719$, $P \leq 0.001$), archaeophytes ($F_t=504.707$, $P \leq 0.001$), and neophytes ($F_t=183.173$, $P \leq 0.001$). United States exotics presented the highest levels of compositional similarity with each of the three European classes. More specifically, United States exotics shared more species in common, relative to US natives and extralimital natives, with European natives and neophytes but primarily with European archaeophytes.

Discussion

Our results suggest that our initial predictions were unable to capture the associations found both within and among urban floras in the United States and Europe. Patterns documented for non-native species within each continent were distinct and followed our predictions for European but not for US floras. Patterns found across the two continents suggested a very different association from the predicted one. Overall, our findings suggest a role for human history as a significant factor in defining patterns of biotic interchange and its ecological consequences.

Differences in compositional similarity across origin classes were more substantial in European floras which, in general, followed our predictions. That is, archaeophytes displayed the highest and neophytes the lowest

level of compositional similarity across floras. Thus, non-native species originating from within Europe promoted homogenization of species composition and non-native species originating from outside Europe promoted differentiation of species composition. However, US floras lacked substantial differences across origin classes with evidence contrary to our predictions with exotics playing a greater role promoting homogenization relative to extralimital natives. A possible explanation for these outcomes might include the age, size, and spatial location of cities in Europe vs. the United States. Specifically, relative to US cities, European cities are older, smaller, and more tightly clustered in space which likely benefited European archaeophytes over United States extralimital natives by providing abundant habitat in close proximity and the time necessary to spread and become established in these areas. However, these factors fail to explain the patterns observed with US exotics. Our analysis of composition patterns across the two continents suggests a possible explanation for US exotics.

Across the two continents, US exotics shared species in common with both native and non-native European species but primarily with species that originated in European floras as non-native before AD1500. That is, US exotics shared the majority of species in common not with European neophytes, as was predicted, but with European archaeophytes. Several conclusions are evident based on these findings. First, higher levels of compositional similarity displayed by US exotics when compared with United States extralimital natives and European neophytes can be interpreted as a consequence of the presence of European archaeophytes in United States floras. In other words, archaeophytes appear to be a primary source for US exotics thus promoting, in a similar fashion to archaeophytes in European floras, higher levels of compositional similarity. Therefore, our results suggest archaeophytes have played a prominent role in promoting homogenization of species composition within Europe, within the United States, and between the two continents. In addition, an examination of native species across the two continents suggests European natives are a greater source of non-natives in the United States relative to US natives as a source of non-natives in Europe. Therefore, our results suggest that the direction of biotic interchange is unidirectional with European natives and archaeophytes playing a primary role as non-natives in the United States (di Castri, 1989). Our analysis also found higher levels of compositional similarity between European neophytes and US exotics suggesting a secondary role for non-native species originating from outside the two continents as a homogenizing source.

In general, what our findings suggest is that, at the present time, European urban floras, with their longer history of human habitation, have developed substantially different patterns from US urban floras. In addition, the exchange of species across continents appears to be geographically more limited than initially predicted. Species that were shared across the two continents do not reflect a substantial global influence but instead a strong regional influence reflecting the close historical ties between the two continents.

Therefore, there is little evidence that homogenization of urban floras is being driven by shared non-native species originating from outside the two continents. Rather, homogenization of floras was driven primarily by the presence of shared archaeophytes. An explanation for these findings can be formulated based on a variety of basic insights gained from other investigations. First, by the early 19th century, evidence suggests that non-native species in the United States were derived from floras found in association with agricultural areas in Western Europe (Mack & Erneberg, 2002; Mack, 2003). It is likely these early non-native species contained a large proportion of archaeophytes, which are typically associated with agricultural or ruderal areas.

Second, non-native species from outside the two continents – neophytes and exotics – are more recent inhabitants and likely not as well adapted to the environmental, ecological, and anthropogenic conditions in their introduced ranges (Pyšek *et al.*, 2004c). Third, the level of propagule pressure associated with neophytes and exotics are likely not as substantial due to the close proximity of long-established propagule sources and the presence of consistent dispersal vectors for archaeophytes both within and across continents. Consistent propagule pressure across spatial scales has been found to be a critical factor in the naturalization and broad-scale establishment of non-native species (Kolar & Lodge, 2001; Lockwood *et al.*, 2005; Von Holle & Simberloff, 2005; Pauchard & Shea, 2006).

Fourth, there is evidence that the distribution of geographic range size is weighted towards geographically rare species for exotic and neophyte species and towards geographically common species for extralimital native and archaeophyte species (Pyšek *et al.*, 2004c; La Sorte & McKinney, 2006). Further, there is evidence that, in general, successful invasive plants are characterized by large native geographical distributions (Forcella & Wood, 1984; Rejmánek, 1995, 2000; Williamson & Fitter, 1996); more specifically, there is evidence European species with large geographical distributions in Europe are more likely to be successful invaders in North America (Rejmánek, 1996; Goodwin *et al.*, 1999). Finally, Europe appears to be, at least at present, the

primary source of non-native species globally, particularly for regions that share similar environmental conditions and post AD 1500 human histories (Crosby, 1972, 1986; di Castri, 1989; Pyšek, 1998b; Lonsdale, 1999).

Therefore, archaeophytes contain a variety of ecological, evolutionary, and biogeographical characteristics that have promoted their successful colonization and dispersal within Europe, North America, and likely other continents. Chief among these characteristics are broad geographic distributions, well-developed adaptations to regional environmental and ecological conditions, associations with environments formed through anthropogenic activities, and a long history of human mediated biotic interchange both within Europe and within the United States and from Europe to other continents.

Our findings suggest that, at least at the present time across these two continents, biotic interchange has not been uniform but appears to reflect the influence of unique geographically defined human histories. Nevertheless, the patterns documented in this study will likely continue to develop as globalization of biotas and human commerce continues to expand in geographic scope and regional intensity (Vermeij, 2005). Importantly, our results do suggest that the complete globalization (uniform homogenization) of the Earth's biota is not as yet imminent (Collins *et al.*, 2002; Heger & Trepl, 2003; McKinney, 2005b). In addition, our results suggest that homogenization is not driven by the presence of non-native species alone but by the ability of these species to become widespread. However, continuing biotic mixing within the biosphere will likely create greater opportunities for these species to become widespread, which appears to be underway with evidence that archaeophytes have declined in prevalence (Pyšek & Mandák, 1997; Pyšek, 1998a; Pyšek *et al.*, 2004a, 2005) and neophytes and exotics have increased in prevalence in rural and urban floras (Pyšek, 1998a; Wittig, 2004; Pyšek *et al.*, 2005; La Sorte & McKinney, 2006). Nevertheless, at present, continental, and intercontinental patterns of homogenization appear to be directed by geographically restricted and taxonomically selective anthropogenic factors that reflect human bias in dispersal, trade, and cultivation.

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