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Extra-regional residence time as a correlate of plant invasiveness: European archaeophytes in North America

FRANK A. LA SORTE[1,4] AND PETR PYŠEK[2,3]

[1]*Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive, MC 0116, La Jolla, California 92093 USA*
[2]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic*
[3]*Department of Ecology, Faculty of Science, Charles University Prague, Viničná 7, CZ-128 43 Prague, Czech Republic*

Abstract. Human activities have degraded biogeographical barriers to dispersal resulting in the spread and naturalization of increasing numbers of nonnative invasive species. One correlate of invasiveness within a region is residence time or time since introduction. Plant species that were introduced into Europe prior to AD 1500 (European archaeophytes) that were subsequently introduced into North America provide a unique opportunity to examine the effect of extra-regional residence time (i.e., residence time that occurred in a nonnative region before a species was introduced into a new region). Here, we examine how nonnative species with extensive extra-regional residence times have affected beta diversity among states in the contiguous United States of America based on an analysis of occupancy and distance decay of similarity. State floras contained an average of 3106 ± 922 species (mean ± SD) with 2318 ± 757 species classified as native, 180 ± 43 species as European archaeophyte, and 608 ± 236 species as other exotic with no European archaeophyte association. For European archaeophytes, 42% were identified as noxious weeds in the United States with 8% identified as agricultural and 14% as natural-area weeds (20%, 2%, and 13% for other exotics, respectively). In strong contrast to natives and other exotics, European archaeophytes were more widespread and presented weaker distance-decay patterns. Thus, European archaeophytes were more likely to become noxious weeds, particularly within agricultural areas, and were associated with significant losses in beta diversity. We suggest that this outcome is a consequence of extra-regional residence time, which allowed for the selection of species or the evolution of traits that favored the colonization of arable habitats associated with early agricultural activities in Europe, habitats that are widespread, resource rich, and uniformly distributed in the United States. Our findings suggest that a long-term trajectory can be established, with residence time in one region building biological and geographical potential, often in direct association with anthropogenic activities, for invasions in new regions. When predicting or managing for potential invaders within a region, identifying extra-regional residence time and its consequences is critical when assessing a species' long-term invasive potential.

Key words: beta diversity; biotic homogenization; compositional similarity; distance decay; European archaeophyte; invasiveness; nonnative species; North America; plant species invasion potential; residence time; vascular plants.

INTRODUCTION

Human activities have degraded biogeographical barriers to dispersal, thereby promoting the spread and naturalization of species beyond their historic ranges, resulting in the increased globalization of the earth's biota (Elton 1958, McNeely 2005). One outcome of this process of human-mediated biotic interchange is the phenomenon of biological invasion, where introduced species rapidly proliferate in new regions, resulting, in many cases, in significant ecological and economic consequences (Vitousek et al. 1997, Mack et al. 2000). Numerous biotic and abiotic factors to explain or predict invasiveness have been proposed and tested (Rejmánek et al. 2005, Richardson and Pyšek 2006, Pyšek and Richardson 2007, Hayes and Barry 2008). One historical factor, also referred to as a stochastic factor, that is often considered is residence time, or time since first introduction into a nonnative region (Rejmánek 2000, Richardson and Pyšek 2006). Residence time has been found to be an important correlate of invasiveness and range extent where nonnative species with a longer residence time within an invaded region tend to be more widely distributed (Rejmánek 2000, Castro et al. 2005, Hamilton et al. 2005, Pyšek and Jarošík 2005, Rejmánek et al. 2005, Wilson et al. 2007, Küster et al. 2008; but see Thuiller et al. 2006). Due to the lack of historical data for many nonnative species, however, residence time is often difficult to quantify and must be estimated indirectly, in many cases based on the

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[4] E-mail: flasorte@ucsd.edu

species' first known record (minimum residence time). In addition, residence time is typically seen as a confounding factor whose effect must be removed to assess more relevant biological factors that determine invasiveness (Pyšek and Jarošík 2005).

Within regions typically studied by invasion ecologists, the earliest possible introduction date is often the date of European discovery, after which the majority of introductions would have occurred. Despite intensive research (Pyšek et al. 2008), historical information on invasions before European discovery is often available but poorly delineated. Consequently, residence times considered in studies outside Europe are confined to a few hundred years and tend to be relatively similar. This fact has limited the ability of investigators to determine the long-term effect of residence time. One exception is Europe itself, where nonnative species of vascular plants are distinguished as having either an ancient (European archaeophyte) or a modern (neophyte) origin. "European archaeophytes" are defined as plant species that were intentionally or unintentionally introduced into regions of Europe between the initiation of agricultural activities during the Neolithic period (ca. BC 4000) and the European exploration of the Americas (ca. AD 1500; Preston et al. 2004, Pyšek et al. 2004*a*; see Plate 1). Plant species introduced into Europe after AD 1500 are here termed "neophytes." Both categories of nonnative plants in Europe are found in greatest numbers in disturbed, anthropogenic habitats with herbaceous vegetation and fluctuating resources (Sádlo et al. 2007, Chytrý et al. 2008*a*, *b*). European archaeophytes were introduced as admixture to crops translocated by Neolithic people, and their affinity to agricultural habitats is still obvious in Europe after millennia of invasions, with archaeophytes tending to be associated with older crops and neophytes with more recently introduced crops (Pyšek et al. 2005).

Nonnative species can affect biological diversity in a variety of ways including altering species richness at a locality (α diversity) and turnover in species composition among localities (β diversity; Whittaker 1972). Changes in β diversity have been forwarded as an objective measure of the ecological impact of biological invasions, particular when examined at broader spatial scales (McKinney and La Sorte 2007). Interest in how nonnative species influence β diversity is also related to the concern that the naturalization and spread of nonnative species could lead to declines in the distinctiveness of native assemblages (McKinney and Lockwood 1999). In Europe, archaeophytes have wide geographic distributions (Pyšek and Jarošík 2005) and are associated with losses in β diversity among urban areas across Europe (La Sorte et al. 2008) and among urban and rural areas in Germany (Kühn et al. 2003, Kühn and Klotz 2006). Work in North America suggests that nonnative species have promoted losses in β diversity (Qian and Ricklefs 2006). The impact of European archaeophytes on native plant assemblages in North America, however, has not been determined. There is evidence that European archaeophytes are associated with losses in β diversity among urban areas in the northeastern United States (La Sorte et al. 2007); however, it is unclear if these patterns are valid at broader spatial scales. The goal of this study, therefore, is to determine if losses in β diversity observed for archaeophytes in Europe are replicated by European archaeophytes in North America.

The distinction between European archaeophytes and neophytes provides a unique historical and geographical perspective for the study of residence time. Most European archaeophytes originated from the Mediterranean Basin (comprising southeastern Europe, western Asia, and northern Africa) and their native distributions are confined primarily to the Eurasian continent (Preston et al. 2004, Pyšek et al. 2004*a*). Consequently, European archaeophytes were introduced into North America primarily as neophytes after AD 1500 and likely originated from European anthropogenic habitats, in particular agricultural habitats. Beyond strong historical and economic ties, Europe and North America share similar climates, vegetation structure, and growth forms that, in total, have likely facilitated the exchange of nonnative species among the two continents.

This study develops insights into the relative roles of residence time in defining invasiveness within and among Europe and North America, something that cannot be readily distinguished in studies restricted to Europe (Pyšek et al. 2005). That is, within Europe, questions related to effects of residence time can be explored (Pyšek and Jarošík 2005, Chytrý et al. 2008*a*), and outside of Europe, questions related to the added effect of extra-regional residence time (residence time that occurred in a nonnative region before a species was introduced into a new region) can be addressed (Pyšek et al. 2004*b*). These contrasting spatiotemporal scenarios provide the opportunity to evaluate the associations between different forms of residence time, with implications for the prediction and management of invasive species. Observed differences in patterns of occupancy and β diversity in North America can therefore be attributed to differences in residence time, extra-regional residence time, and associated differences in ecology and habitat affinities that evolved in association with or independent of anthropogenic activities.

METHODS

Data sets

Floras for each of the 48 contiguous states were acquired (USDA NRCS 2008) and three groups of species were distinguished with respect to their origin and invasion status in the United States. The groups include native species and two groups of nonnative species introduced to the USA after AD 1500. "Nonnative" status refers to the whole of the United States; i.e., species native to a part of this continent and exotic to another (see Lambdon et al. 2008 for the concept) were not considered. The first were nonnative species identified as archaeophytes in Europe, termed here "European archaeophyte"; it needs to be emphasized that they are not archaeophytes in America in terms of the conventional definition (Pyšek et al. 2004*b*). A list of 449 European archaeophytes was compiled based on archaeophytes recorded in Germany (Kühn and Klotz 2002), the Czech Republic (Pyšek et al. 2002), and Great Britain (Preston et al. 2004). The second were nonnative species introduced to the United States that did not occur as archaeophytes in Europe, termed here "other exotic." Last, we acquired lists of species identified as noxious weeds in the United States (USDA NRCS 2008), a list of 126 globally significant agricultural weeds (Holm et al. 1997), and a list of 820 globally significant natural-area weeds (Weber 2003). Here noxious weed implies substantial ecological and economic damage within an invaded region.

Lists of European archaeophytes were combined and all subspecies, varieties, and synonyms were merged into single species. The same procedure was applied to native and noxious weed species. The taxonomic nomenclature across European archaeophytes and other exotics was standardized using TaxonScubber, version 2.0 (Boyle 2006). From a total of 19 137 species, 3786 species were classified as nonnative within the United States (USDA NRCS 2008). From these, 327 species were identified as European archaeophytes and 3459 as other exotic.

Statistical analysis

Compositional similarity for native, other-exotic, and European-archaeophyte floras were estimated for pair-wise combinations of states and presented as a function of the distance between state geographic centers. State centers were estimated based on each state's center of mass if the state was a flat surface, and the distance between state centers was estimated based on geodesic distance. A total of 1128 unique pair-wise combinations of states were available for analysis. States centers were separated by 1916 ± 1355 km on average (mean ± SD) with an average surface area of $1.7 \times 10^5 \pm 1.3 \times 10^5$ km^2. Compositional similarity for paired floras was estimated using two dissimilarity measures: the complement of the Jaccard index (Jaccard 1900) and the Beta-sim index (Lennon et al. 2001, Koleff et al. 2003). The Jaccard dissimilarity between two assemblages is defined as

$$d_{\mathrm{J}} = \frac{b+c}{a+b+c}$$

where a is the number of species shared, b is the number of species unique to the first assemblage, and c is the number of species unique to the second assemblage. The Beta-sim dissimilarity between two assemblages is defined as

$$d_{\mathrm{B}} = \frac{\min(b,c)}{\min(b,c)+a}.$$

The Beta-sim is an alternative to the Jaccard that minimizes the influence of species richness gradients or nestedness between paired assemblages (Lennon et al. 2001). For the Jaccard index, species richness gradients tend to promote stronger dissimilarity between paired assemblages because a can only be as large as the smaller of the two assemblages. The Beta-sim index accounts for this bias by only considering the smaller of the two assemblages based on the number of unique species. The Jaccard index therefore considers the combined effect of compositional similarity and species richness gradients, whereas the Beta-sim index considers the effect of compositional similarity after controlling for the effect of species richness gradients. Including both indices provides a broader perspective and allows for comparisons with studies where only the Jaccard index was used.

Typically, as distance or geographical separation increases, the level of compositional dissimilarity increases between paired assemblages—a phenomenon commonly referred to as "distance decay in similarity" (Nekola and White 1999, McKinney 2004, Soininen et al. 2007). We examine distance-decay patterns for each of the three categories of species based on bivariate plots of dissimilarity by distance between paired states. Permutation tests were used to estimate the probability of distance-decay patterns for European archaeophytes occurring by chance alone. Initially, ordinary least-square regression was used to estimate the slope and intercept for European archaeophyte distance-decay patterns based on the Beta-sim index. The three categories—native, other exotic, and European archaeophyte—were then permutated without replacement across the 19 137 species. The Beta-sim index was then recalculated for all pair-wise combinations of states. The same regression model was then applied to species identified as European archaeophytes in the state floras based on the permutated classification. This routine was implemented 4999 times. Where the values of the observed intercept and slope occurred within the distributions of permutation-derived values provided a measure of the probability of the European archaeophyte distance-decay patterns occurring by chance alone.

RESULTS

The 48 state floras of the contiguous United States contained an average of 3106 ± 922 species (mean ± SD) with 2318 ± 757 species classified as native, 608 ± 236 species as other exotic, and 180 ± 43 species as European archaeophyte. Based on average percentages, 74.4% of species in state floras were identified as native, 19.5% as other exotic, and 6.1% as European archaeophyte. Out of the 327 European archaeophytes, 136 species or 41.6% were identified as noxious weeds in the United States. Out of the 3459 other exotics, 680 species or 19.7% were identified as noxious weeds in the United States. Based on the 126 species identified as globally significant agricultural weeds, 31 species were not identified in any of the state floras, 14 species were identified as native, 54 species as other exotic, and 27 species as European archaeophyte. Thus, 1.6% of other exotics and 8.3% of European archaeophytes were considered significant agricultural weeds. From the 820 species considered globally significant natural-area weeds, 261 species were not identified in any of the state floras, 53 species were identified as native, 459 species as other exotic, and 47 species as European archaeophyte. Thus, 13.3% of other exotics and 14.4% of European archaeophytes were considered significant natural-area weeds. In total and relative to other exotics, European archaeophytes were twice as likely to be identified as noxious weeds in the United States, 5 times as likely to be identified as noxious weeds within agricultural areas, and equally likely to be identified as noxious weeds in natural areas.

Occupancy of species within states suggested similar distributions for native and other-exotic species, which diverged substantially from the patterns observed for European archaeophytes (Fig. 1). Native and other-exotic species had positively skewed distributions with the majority of species occurring in very few states (median = 3 states for both native and other exotics). European archaeophytes had a nearly uniform distribution with a minor peak associated with the most widespread species (median = 27 states). The greatest proportion of United States noxious weeds was found with the most widespread other exotic and the most widespread European archaeophyte species (Fig. 1).

Similar distance-decay patterns were displayed within each category for the Jaccard and the Beta-sim indices, and the patterns diverged in a similar fashion among the three categories within each index (Fig. 2). The effect of species richness gradients, as represented by the Jaccard index, resulted in higher overall values of dissimilarity across the three categories of species. Native species presented the strongest distance-decay patterns with a well-defined asymptote for the Jaccard and a poorly defined asymptote for the Beta-sim index. Native species had the highest levels of dissimilarity, particularly at greater distances, for both indices. Other-exotic species presented intermediate distance-decay patterns with poorly defined asymptotes that showed higher dissimilarity relative to native species at shorter distances and lower dissimilarity relative to native species at greater distances. European archaeophytes presented virtually no distance-decay patterns and the lowest levels of dissimilarity for both indices.

The regression coefficients based on the Beta-sim index indicated that European archaeophyte distance-decay patterns had the smallest intercept (0.135) relative to native (0.252) and other-exotic (0.316) distance-decay patterns and the weakest slope (2.10×10^{-6}) relative to native (1.30×10^{-4}) and other-exotic (2.78×10^{-5}) distance-decay patterns. Based on permutation tests, the probability of the observed pattern occurring for European archaeophytes by chance alone was very small ($P \leq 0.001$; Fig. 3). This was particularly the case for the slope coefficient, with the observed slope for European archaeophytes being much smaller and occurring well outside the distribution of permutation regression lines (Fig. 3). Hence, there was little turnover in European archaeophytes across state floras, and this pattern was unlikely to have occurred by chance alone if European archaeophytes were selected randomly from all available species in the state floras.

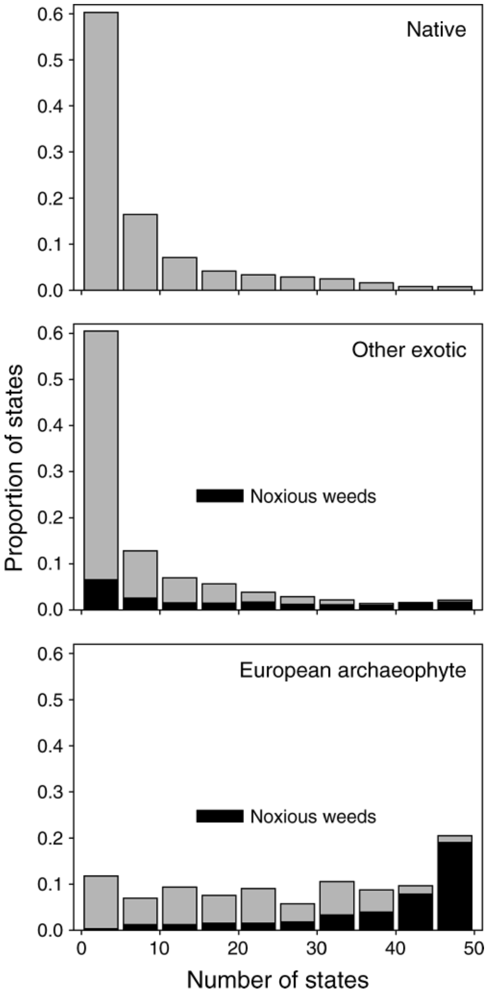

FIG. 1. The proportion of states ($n = 48$) within the contiguous United States containing species of plants identified in three categories: native to the region (Native), nonnative to the region and not identified as a European archaeophyte (Other exotic), and identified as a European archaeophyte. The black portion of the histogram bars identifies the frequency of species in each distribution category that were identified as noxious weeds in the United States.

DISCUSSION

European archaeophytes promote compositional similarity in the United States

In this study, European archaeophytes were found to occur consistently in state floras across the contiguous

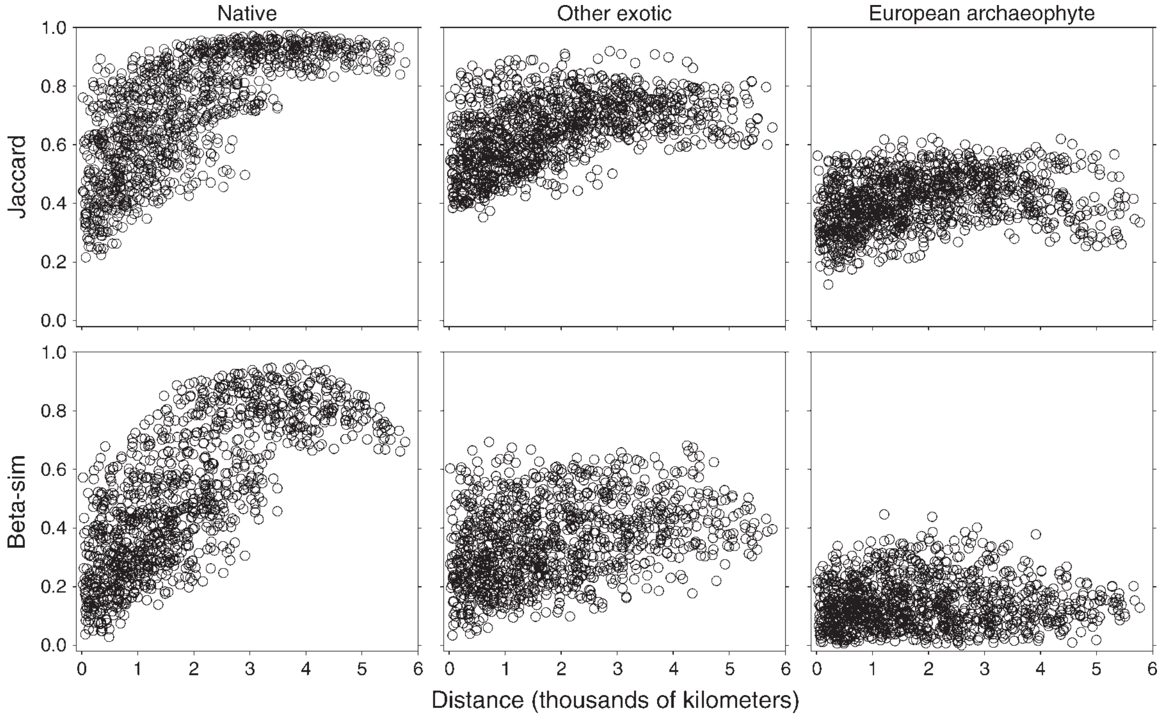

Fig. 2. Distance decay of similarity patterns for three categories of plant species: native to the region (Native), nonnative to the region and not identified as a European archaeophyte (Other exotic), and nonnative to the region and identified as a European archaeophyte. The first row of panels is based on the Jaccard dissimilarity index, and the second row on the Beta-sim dissimilarity index. Plant species were identified in 48 state floras in the contiguous United States, and distance was estimated using the geodesic distance between state centers.

United States. As a consequence, European archaeophytes promoted strong patterns of compositional similarity among state floras, with little evidence for spatial variation in these associations. Thus, each state contained a large proportion of European archaeophytes from the available pool with little turnover in species composition among states. These patterns were consistent when species richness gradients were included in the assessment and when the gradients were controlled for. Therefore, relative to other-exotic species, European archaeophytes were associated with substantial losses in β diversity. In addition, European archaeophytes were more likely to become noxious weeds in the United States, with the greatest influence associated with agricultural areas.

This study expands upon earlier investigations where European archaeophytes were found to be associated with higher compositional similarity among urban areas in the northeastern United States and Europe (La Sorte et al. 2007) and among urban and rural areas in Europe (Kühn et al. 2003, Kühn and Klotz 2006, La Sorte et al. 2008). Our findings suggest the impact of European archaeophytes on β diversity in North America is a continent-wide phenomenon, which expands upon the findings of Qian and Ricklefs (2006). The compositional patterns documented by these authors were based on the Jaccard index, which does not control for species

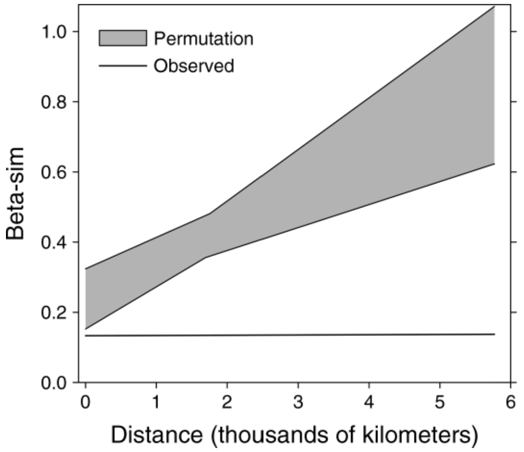

Fig. 3. Plot of the distribution of ordinary least-square regression fits to European archaeophyte distance-decay patterns based on the Beta-sim dissimilar index for 4999 permutations (gray region) of three categories (native, other exotic, and European archaeophyte), and the observed regression fit for European archaeophytes (horizontal solid line). Plant species were identified in 48 state floras in the contiguous United States, and distance was estimated using the geodesic distance between state centers.

richness gradients. Thus, their findings of higher compositional similarity for nonnative species in North America would likely be stronger if these differences were accounted for. Moreover, our findings suggest that the compositional patterns documented for nonnative species were driven, at least in part, by the presence of European archaeophytes.

Relative to other-exotic species, more European archaeophytes are considered noxious weeds in the United States. Therefore, by definition, in localities where European archaeophytes occur, they are likely to be found in high abundance. And due to their greater abundance, they are likely to dominate community structure and function (Hillebrand et al. 2008). Thus, the occurrence information used in this assessment provides a partial and likely conservative representation of the ecological impact of European archaeophytes on the North American flora (La Sorte and McKinney 2007).

Habitat for time substitution in filling geographic range

Although both groups were introduced as neophytes into North America, European archaeophytes are widely distributed and, unlike other exotics, seem to have fulfilled their potential geographic ranges. Residence times for other exotics in North America are typically shorter when contrasted with European archaeophytes, and this has likely limited the opportunity for these species to expand their ranges to include all areas with suitable habitat (Pyšek and Jarošík 2005, Chytrý et al. 2008*a*). There is evidence from Europe that almost all naturalized neophytes are still expanding their ranges in Europe, and estimates indicate a time of around 150–300 years for neophytes to fill their potential ranges. Archaeophytes likely had more opportunities for earlier introductions into North America and, based on our findings, appear to have completely filled their potential range. For archaeophytes in Europe, the process of filling potential ranges has been more or less completed and they have range sizes slightly larger than native species in Europe (Williamson et al. 2009).

Part of the explanation for these patterns is related to the habitat preferences of both groups. The wide distribution of European archaeophytes is likely the result of their special habitat requirements (Williamson et al. 2009). Neophytes occur in a wide range of habitats, approximately those of natives, but with a different spectrum of abundances (Williamson et al. 2009), and are most common in human-disturbed ruderal and riparian habitats (Chytrý et al. 2005, 2008*a*, *b*, Sádlo et al. 2007). In contrast, European archaeophytes are primarily weeds of arable soils. When compared to natural habitats in the United States, arable soils represent a uniform and widespread habitat that is likely, due to the nature of agricultural commerce, to be subject to stronger propagule pressure from nonnative species. That explains why European archaeophytes became widely distributed and filled their geographical ranges in a relatively limited period of time: it can be hypothesized that lack of time was compensated for by availability of suitable habitats and dispersal opportunities.

The role of invasion history: residence times from different regions sum up

The invasion of archaeophytes into Europe was initiated with Neolithic agricultural activities (Pyšek et al. 2005). Although by definition only species that invaded by the end of the Middle Ages are considered archaeophytes in Europe, it does not mean that introductions of propagules of these species from their native range did not continue after that date. It has been assumed that over the millennia of ongoing invasion, some archaeophytes in Europe went through a peak of high abundance and distribution, which subsequently retreated (so-called "post-invasive species"; see Pyšek et al. 2002). Current distribution patterns observed in Europe resulted from adaptation of archaeophytes to local climatic and habitat conditions, as well as from the selection for agricultural practices (Pyšek et al. 2005). This selection process was likely accelerated by the presence of pre-adaptations (or exaptations sensu Gould and Vrba 1982); specifically, preexisting characteristics (e.g., an affinity for open habitats with frequent disturbance) that happened to be well suited to conditions associated with early agricultural activities. Furthermore, many European archaeophytes (~20% among German archaeophytes) are only associated with anthropogenic habitats and have no known native distributions (anecophytes; Scholz 1995, 2007). These species evolved in situ within their European nonnative range, and extra-regional residence time represents the period during which speciation occurred. Therefore, European archaeophytes that have invaded other continents as neophytes exhibit a strong and in many cases an exclusive affinity for agricultural lands, and the capability to survive and thrive as agricultural weeds.

Since the end of the Middle Ages, European archaeophytes have been introduced to other continents in conjunction with European exploration, settlement, and commerce. Within Europe, there is evidence that residence time, even after thousands of years since initial introductions, can still be detected in the extent of archaeophyte distributions (Pyšek and Jarošík 2005). The residence time for species that started their invasion as archaeophytes in Europe is much shorter in other continents, to which they arrived as neophytes. European archaeophytes would likely have been some of the first nonnative species introduced into North America, and they are likely to have accrued longer residence times relative to other nonnative species. However, this fact alone does not appear sufficient to explain the magnitude of their success in North America. Factors related to the consequences of extra-regional residence time appear to provide, at least in this particular case, an important if not critical component. Specifically, the

PLATE 1. (Upper left) An abandoned field in Central Europe serves as a typical habitat for commonly occurring archaeophytes, first introduced to this region before the end of the Middle Ages. These include (top right) *Arctium tomentosum*, (middle right) *Silene latifolia* ssp. *alba*, (lower right) *Convolvulus arvensis*, and (lower left) *Viola tricolor*. All these species were subsequently introduced into North America and became widespread weeds. Photo credits: P. Pyšek.

long period of residence time in Europe allowed for the selection of species or the evolution of traits that favored the colonization of early agricultural habitats. These same characteristics selected for in European agricultural areas subsequently promoted the early introduction of European archaeophytes into North America and their rapid and thorough invasion of the continent. Thus, longer residence time within North America (which allowed for plentiful introduction and dispersal events) and an extensive period of extra-regional residence time in Europe (which allowed for prolonged evolutionary activity) likely determined the broadscale success of European archaeophytes in North America.

Our study suggests that nonnative species with longer histories as aliens are in a better position to become invasive and widespread when introduced into new regions, and that residence time need not necessarily relate exclusively to the target region invaded. Our ability to predict invasiveness—a task that has often resulted in context-dependent generalizations with limited taxonomic and geographic predictive power (Williamson 1999, Daehler 2003)—can therefore be expanded to include considerations of extra-regional residence time and impact on β diversity. This perspective can be viewed as an approach for quantifying aspects of a species' invasion history. Invasion history outside the target region has been used as a factor to explain or predict invasiveness (Kolar and Lodge 2001, Hayes and Barry 2008) and, in many ways, is an obvious correlate of invasiveness. Nevertheless, invasion history is typically defined by subjective criteria on an ordinal scale (e.g., Parker et al. 2007). The findings from this study suggest that invasion history and invasive potential can be quantified on a continuous scale of potential impact based on extra-regional residence time and some measure of β diversity. Hence, the longer a nonnative species' history as an alien and the broader its impact on spatial patterns of diversity within a region, the greater its invasive potential in new regions

In summary, human-mediated biotic interchange has led to an expanding influx of nonnative species. Once these species have developed associations with anthropogenic activities (specifically, increased resource availability, dispersal opportunities, and altered disturbance regimes) they will be in a position to outcompete native species and become invasive (Daehler 2003, Colautti et al. 2006). As more species are added to the pool of nonnatives and residence time grows, inherent latency periods will be overcome and more species will become invasive (Kowarik 1995). The findings from this study suggest that once a species has developed its invasive potential within a region, it will be in a better position to become invasive in other regions. Hence, a cycle of expanding geographic consequences can be established, driven by human-mediated biotic interchange, environmental change, selection, and adaptation—a cycle that can develop over thousands of years, as witnessed for archaeophytes in Europe (Pyšek and Jarošík 2005). Therefore, trajectories established in the recent past could contain long-term momentum that cannot be easily altered by humans, except possibly in regions where the species has yet to be introduced. When predicting or managing for potential invaders within a region, identifying invasion history in other regions based on residence time and impact on β diversity is critical when assessing a species' long-term invasive potential.

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