

Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time

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Abstract. The factors that promote invasive behavior in introduced plant species occur across many scales of biological and ecological organization. Factors that act at relatively small scales, for example, the evolution of biological traits associated with invasiveness, scale up to shape species distributions among different climates and habitats, as well as other characteristics linked to invasion, such as attractiveness for cultivation (and by extension propagule pressure). To identify drivers of invasion it is therefore necessary to disentangle the contribution of multiple factors that are interdependent. To this end, we formulated a conceptual model describing the process of invasion of central European species into North America based on a sequence of “drivers.” We then used confirmatory path analysis to test whether the conceptual model is supported by a statistical model inferred from a comprehensive database containing 466 species. The path analysis revealed that naturalization of central European plants in North America, in terms of the number of North American regions invaded, most strongly depends on residence time in the invaded range and the number of habitats occupied by species in their native range. In addition to the confirmatory path analysis, we identified the effects of various biological traits on several important drivers of the conceptualized invasion process. The data supported a model that included indirect effects of biological traits on invasion via their effect on the number of native range habitats occupied and cultivation in the native range. For example, persistent seed banks and longer flowering periods are positively correlated with number of native habitats, while a stress-tolerant life strategy is negatively correlated with native range cultivation. However, the importance of the biological traits is nearly an order of magnitude less than that of the larger scale drivers and highly dependent on the invasion stage (traits were associated only with native range drivers). This suggests that future research should explicitly link biological traits to the different stages of invasion, and that a failure to consider residence time or characteristics of the native range may seriously overestimate the role of biological traits, which, in turn, may result in spurious predictions of plant invasiveness.

Key words: biological traits; cultivation; exotic species; native range; path analysis; plant invasion; propagule pressure; residence time.

INTRODUCTION

Since biological invasions started to be intensively studied in the 1980s (Drake et al. 1989, Richardson and Pyšek 2008), the field has been seeking to describe

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factors that promote invasiveness of species introduced outside their native range. After 30 years of research, predicting which species will become invasive still represents an ultimate goal of invasion ecologists (Daehler and Carino 2000, Rejmánek 2000, Kolar and Lodge 2002, Richardson and Pyšek 2006, Pyšek and Richardson 2007). The complexity of the issue is now fully realized and the problem is being addressed by using sophisticated theoretical frameworks (e.g., van Kleunen et al. 2010a, Gurevitch et al. 2011, Strayer 2012) and statistical models that take interacting factors and spatial or phylogenetic dependence into account in macroecological analyses (e.g., Rouget and Richardson 2003, Thuiller et al. 2006, Wilson et al. 2007, Küster et al. 2008, 2010, Pyšek et al. 2009a, Castro-Diez et al. 2011, Schmidt and Drake 2011). By using various methodological approaches, these studies have identified a number of species' biological and ecological traits that promote invasive behavior in plants (Rejmánek and Richardson 1996, Grotkopp et al. 2002, Pyšek et al. 2009b, Dostál et al. 2013; see Pyšek and Richardson 2007, and van Kleunen et al. 2010b for overviews of such traits).

The application of models that analyze several factors together is crucial to properly address the role of traits promoting species' invasiveness because the context dependence of invasions means that the real effect of traits can be confounded by other factors such as propagule pressure (Rouget and Richardson 2003, Lockwood et al. 2005, Colautti et al. 2006, Ross et al. 2008, Simberloff 2009), time since introduction (Rejmánek 2000, Pyšek and Jarošík 2005, Dehnen-Schmutz et al. 2007), or climate and habitat match between source and target regions (Hejda et al. 2009, Kalusová et al. 2013). At the same time, these factors, which must be included in any proper assessment of the role of species' biological traits, themselves play important roles in contributing to the outcome of particular invasions. Since most studies rarely address these factors in concert, our understanding of how they interact and what is their relative importance is still incomplete.

The process of plant invasion, from a species becoming associated with humans in the native range, usually by being brought into cultivation, to naturalization or invasion in the new range (*sensu* Richardson et al. 2000, Blackburn et al. 2011), can be broken into several parts, each of which is attributable to certain drivers. Here we include, along with information on a wide range of species' biological traits plus geographic traits associated with native range distribution, two factors that are surmised to affect the invasion process. It has been shown that the majority of successful aliens establish in new regions with the help of humans; there is robust evidence in the literature that planting affects invasion (Mack 2000, Hulme 2009, 2011, Pyšek et al. 2011b) and that disproportionately more invaders recruit from species introduced by horticulture (Hanspach et al. 2008, Lambdon et al. 2008, Pyšek et al. 2012). The later

phase of the process, happening in the invaded range, is shaped by residence time, i.e., how much time the species has had to establish and spread in the new region, once it has escaped from cultivation or been unintentionally introduced (Rejmánek 2000, Castro et al. 2005, Pyšek and Jarošík 2005, Williamson et al. 2009, Pyšek et al. 2011a). Propagule pressure and residence time have been repeatedly shown to set the scene upon which the differences in biological traits act in determining the invasion of a species (Colautti et al. 2006, Catford et al. 2009). However, the problem is that in macroecological analyses performed at intercontinental scales, the quality of data that are available for high numbers of species composing whole floras is often low, and some of the factors thus remain unconsidered (Pyšek et al. 2009a, Kueffer et al. 2013).

An important feature of our study is that we employed the source-area approach (Prinzing et al. 2002, Pyšek et al. 2004b, 2009a, Thuiller et al. 2005, van Kleunen et al. 2007, Blumenthal et al. 2009, Bucharová and van Kleunen 2009, Mitchell et al. 2010, Dostál et al. 2013), which is based on delimiting a source pool of species native to a certain region and following their post-introduction performance in another region. By focusing on this specific trajectory, we minimize confounding variation that arises when considering multiple source areas of introduction, both in terms of evolutionary predispositions acquired in disparate regions of origin, as well as various historical contingencies that shape introduction dynamics. Specifically, the source-area approach is based on the assumption that, all else being equal, members of the flora of a single biogeographic region have comparable chances to be transported by humans from their native range into other parts of the world (in this case from Europe to North America) because they are exposed to the same historical, socioeconomic, and biogeographic factors (Pyšek et al. 2009a, 2014). The differences in the success as aliens can be thus more reliably attributed to their traits if the source-area approach is applied (Sol et al. 2008). Moreover, there are historical reasons why Europe is a major donor of introduced plants into other parts of the world, including the North American continent (di Castri 1990, Stohlgren et al. 2011), making this direction of intercontinental introductions an appropriate model (van Kleunen and Johnson 2007, Blumenthal et al. 2009, Mitchell et al. 2010).

In this paper we used one of the most complete databases on plants invading from Europe into North America to explore the following: (1) which factors determine whether some plant species native to central Europe become naturalized and widespread in North America, (2) whether species' biological traits play a role in this process, and if so, (3) how their effect is modified by factors associated with human activities and the time since introduction. Our approach to exploring these issues was (1) to test, by using confirmatory path analysis, whether a conceptual model developed a priori

from ecological knowledge is supported by a statistical model inferred from a comprehensive database, and (2) to identify the importance of the direct effects of biological traits on several important drivers of the conceptualized invasion process.

MATERIAL AND METHODS

Conceptual model of invasion

The statistical approach we adopted is based on previous studies that identified several important drivers of invasion (e.g., Wilson et al. 2007, Gravuer et al. 2008, Küster et al. 2008, Pyšek et al. 2009a, b, 2014, McGregor et al. 2012) including species' biological traits, ecological and geographic characteristics (habitats in which the species occurs in the native range and how widely it is distributed), propagule pressure (captured by factors reflecting association with humans, such as cultivation in both ranges), and residence time. We assumed a sequential dependence (path) among the different drivers. Specifically, we hypothesized that residence time in the invaded range is predicted by the other suites of traits, and consequently, predicts the dependent (or response) variables, which comprise various measures of invasion. Therefore, we tested whether the following path structure, representing the invasion process broken into a sequence of "drivers" based on a priori knowledge, is supported by the data: biological traits → range of occupied habitats in the native range → regional frequency in the native range → cultivation in the native range → cultivation in the invaded range → residence time in the invaded range → number of regions where naturalized. We also tested whether the biological traits are an important predictor of each driver of the invasion process or affect the process just at the beginning by determining the range of occupied habitats. The steps of the statistical analysis are presented in Appendix A: Fig. A1.

Source species pool, and response and explanatory variables

Vascular plants of the Czech Republic (Danihelka et al. 2012) were used to obtain a sample of plant species that are native to central Europe (as defined by Ellenberg 1988). Local apomictic taxa with a small distribution range, e.g., the genera *Rubus*, *Hieracium*, and *Taraxacum*, were excluded, and so were the infraspecific taxa (Pyšek et al. 2009a). The screening yielded 1218 seed plant species that represent the source species pool.

Data on the occurrence of central European species in North America (excluding Mexico) were taken from the North American Vascular Flora database (Biota of North America Program [BONAP]; Kartesz 2010), which is an updated and expanded version of the Synthesis of North American Flora (Kartesz and Meacham 1999). The North American data cover species occurring in the United States (we included Alaska, but excluded Hawaii), Canada, Greenland, Puerto Rico, and other smaller islands ($n = 66$ distinct

geographic units at the state/province level, hereafter termed regions). Of alien species introduced to North America (see Plate 1), the North American Vascular Flora covers those that are naturalized (established) in at least one region, forming a permanent component of local floras (corresponding to the definition of Richardson et al. 2000, Pyšek et al. 2004a, Blackburn et al. 2011). The data thus reflect the naturalization of central European species in North America. The screening yielded 466 species native to central Europe that are currently naturalized in North America, forming populations that escape and reproduce in the wild; these species were analyzed in the present paper (see Appendix B).

To describe the species' naturalization in North America, we employed two metrics as response variables (taken from Kartesz 2010): (1) the number of regions in North America ($n = 66$ U.S. states and Canadian provinces and other regions specified in the previous paragraph) where the species is naturalized; and (2) the latitudinal and longitudinal range in North America (based on a maximum distance between regions in a north–south and east–west direction, respectively).

Species' biological traits used include (see Appendix C for a detailed description and data sources): (1) life history (annual, monocarpic perennial herb, polycarpic perennial herb, shrub, tree); (2) life strategy (competitive, ruderal, and stress tolerant); (3) plant height, as reported in the national flora; (4) clonality, scored from 2–7, with annuals scored as 0 and non-clonal perennials as 1; (5) ploidy level (diploid, polyploid, and diploidized polyploid); (6) nuclear genome size (C-value); (7) length of the flowering period, defined as the number of months over which the plant flowers in the native range; (8) relative importance of seed reproduction on a semi-quantitative scale 1–4; (9) sex type, describing whether one or two plants are needed for sexual reproduction; (10) pollen vector (insects, wind, selfing); (11) number of pollen vectors; (12) propagule size, as the length of the dispersal unit (seed or fruit); (13) seed bank persistence, coded 0 for transient, 0.5 for short-term, and 1 for long-term persistent; (14) dispersal vector (ants, other animals [epizoochory, endozoochory], wind, water, and self); (15) the number of dispersal vectors. Two physiological measures adopted include (16) specific leaf area (SLA), and (17) leaf dry matter content (LDMC).

Geographic characteristics refer to the distribution in the native range (see Appendix C for a detailed description and data sources) and include: (1) regional frequency in central Europe, expressed as the number of grid cells $\sim 12 \times 11$ km from which the species is reported in the Czech Republic and Germany; (2) number of habitats in which the species occurs in the Czech Republic; (3) number of global floristic zones in which the species occurs in the whole of its native range, representing a proxy for climatic versatility; (4) altitudinal range in the Czech Republic, another proxy for

climatic versatility; (5) cultivation in the native range reflects the intensity of planting in the Czech Republic using a semiquantitative scale 0–3 (0, not planted; 1, planted for horticultural purposes in gardens, parks, and so on; 2, planted in the wild outside gardens; 3, subject to breeding processes to enhance their performance, and planted in the wild).

Finally, we collated information on drivers that may mediate the effect of the above mentioned variables on naturalization in the invaded range: (1) year of introduction to North America, which made it possible to derive a minimum residence time (with the term “minimum” referring to it being an estimate inferred from the earliest known record; Rejmánek 2000) on this continent (see Appendix C for estimation details and Appendix D for information sources); and (2) cultivation in the invaded range, as a proxy for propagule pressure, based on BONAP data (Kartesz 2010) classifying species by whether they are used in horticulture, economically important, or used by humans for other purposes, on a scale of 0 to 3.

Statistical analysis

Data imputation.—Several variables in the data set presented between 0.2% and 36% of missing values. To manage missing values we used imputation rather than case-wise deletion of incomplete entries because case-wise deletion results in information loss (in our case reducing the taxa available for analysis from 466 to just 176), reduced statistical power, and potentially biased parameter estimates (Rubin 1976). We performed imputation and model diagnostics in R 2.15.2 (R Development Core Team 2012) using the Amelia II package (Honaker et al. 2011). Imputation involves estimating m values for each missing cell in the data set, and creating m complete data sets where the observed values are the same but the missing values are filled using a distribution of values that reflects the uncertainty around those missing values. Amelia II performs imputation using an expectation–maximization algorithm. Full details of the imputation procedure and model diagnostics are given in Appendix E. The results suggest that the algorithm converged successfully and the imputed values were generally adequate as they fell within the range of the measured data. Thus, one imputed data set was selected at random for further analysis.

Regression trees.—The objective of this analysis was to select the most important biological traits as predictor variables to explain variation in the response variables and drivers. The regression trees were fitted with the *rpart* package in R. For each variable, an overfitted regression tree was “grown” by specifying a complexity parameter of zero. At each split, a relative error was calculated using tenfold cross validation. The trees were “pruned” (to generate parsimonious trees that balance fit and complexity) by selecting a set of three trees whose number of splits minimized the relative error. Assump-

tions of the model, that the residuals are “white noise,” were verified. First, a visual inspection of the plots of residuals vs. fitted values ensured that no pattern was present. Second, the phylogenetic autocorrelation in the residuals was calculated. The phylogenetic tree was obtained from DaPhnE (Durka and Michalski 2012), and the cophenetic distance was calculated with the package *ape*. From the set of three regression trees, the final tree was selected by ensuring that the autocorrelation was always smaller than 0.2 and was not significant up to lag 10 (after correction for multiple testing with Bonferroni adjustment, $0.05/10 = 0.005$, for a P value obtained by simulation with 500 resamples). This implies that the residuals of the regression tree model contained no information. The final regression trees were always ecologically plausible and as a measure of fit of the parsimonious model the R^2 of the regression tree was calculated.

Path analysis.—The objective of this analysis was to (1) test the conceptual model of invasion defined above in the section *Conceptual model of invasion*, and (2) test the hypothesis that biological traits have a direct effect on each driver of invasion. Path analysis allows the modeling of dependencies among a set of variables, and is associated with the use of several multiple regressions, using partial regression coefficients. It is similar to performing several regressions among the different nodes (here, steps between drivers of the invasion process). Using this approach, not only the variance, but also the covariance among the variables is modeled. To achieve objective (1), a simple model based on a priori knowledge (see the *Conceptual model of invasion* section) was fit. Each driver in the conceptual model was taken as a node in the path analysis, which started with the ecological and geographic characteristics to explain variation in the range of occupied habitats, which then explains the variation in regional frequency in the native range, and so on, until the variation in the response variable is explained by the residence time in the invaded range. This represents the simplest model possible based on a priori knowledge. To achieve objective (2), a saturated model was fit with regressions (i.e., arrows) to explain the variation in the range of occupied habitats based on ecological and geographic characteristics. Then the number of occupied habitats *and* the traits were used to explain variation in the regional frequency in the native range, and so on; each node was explained by the preceding node *and* all the traits. This represents the most complicated model possible based on a priori knowledge. Models of intermediate complexity were also built by adding regressions only between certain nodes and the traits. The different models were compared based on ecological plausibility, fit, and parsimony. Final models were selected and further refined by removing some of the biological traits that were not significant (at Type I error rate of 0.05) and testing whether there was feedback (bidirectional arrow) between the drivers of the invasion process.

For all path analyses, continuous variables were standardized to improve convergence. Several semi-quantitative variables were used so that the assumption of multivariate normality was not met. This prevented the use of maximum likelihood estimation and a diagonally weighted least square with robust standard error estimation algorithm was used in the package *lavaan* (Rosseel 2012) in R. This estimation method is known to offer more accurate parameter estimates when the data are highly non-normal (here not completely continuous) and performs better than maximum likelihood in small sample size for large models (Mindrila 2010). Model fit was assessed with the standardized root mean square residuals (RMSR). The RMSR is a function of the Euclidean distance between the measured variances and covariances and the predicted variance and covariance from the model. A value of zero is ideal, and values of 0.08 or less are desired (Tabachnik and Fidell 2007). The parsimony of the models was assessed with the parsimony goodness of fit index (PGFI), which penalizes models with several parameters that do not increase the fit by a large amount. A value of 1 is ideal. In addition, a visual assessment of the residuals in the covariance matrix confirmed that the parsimonious models explained the main patterns in the database (Tabachnik and Fidell 2007). For all models, convergence was usually achieved with <1000 iterations.

RESULTS

Regression trees

There were initially three dependent variables: the number of regions in North America in which the plant is naturalized, longitudinal range invaded, and latitudinal range invaded. These dependent variables were strongly correlated and often resulted in similar trees, so further analyses were performed only with the number of regions.

When using biological traits and geographic characteristics, as well as the drivers supposed to mediate their effects, to predict the number of regions invaded, minimum residence time, cultivation in the invaded range, and soil seed bank persistence were identified as important variables by the parsimonious tree (Appendix A: Fig. A2). Since an objective of the work was to test whether biological traits have an impact on each driver of invasion included in the conceptual model, cultivation in the invaded range was further explored by fitting a regression tree with all the variables except cultivation in the native range, minimum residence time, and regional frequency in the native range (Appendix A: Fig. A3). Similarly, important predictors of cultivation in the native range were selected based on all biological traits, but excluding cultivation in the invaded range, minimum residence time, and regional frequency in the native range. Collectively the three regression trees (Appendix A: Figs. A2–A4) suggested that shrub life history, stress-tolerant life strategy, propagule size, specific leaf area, leaf dry matter content, plant height, number of

dispersal vectors, wind pollination, length of the flowering period, and clonality were important biological traits acting on several drivers of the naturalization process. The holoploid genome size was selected in the regression trees, but since a high percentage of the variable was imputed (36.4%), and it correlated with other variables, it was not included in further analysis.

Of the geographic characteristics, the number of habitats was most important, as it appeared in both regression trees explaining cultivation in both ranges (Appendix A: Figs. A3 and A4).

Path analysis

The direct effect of the number of habitats in the native range on the number of regions invaded in North America was included along with minimum residence time in all models since these effects were found to be important by the regression trees and are part of the conceptual model. In contrast, the variables wind dispersal, number of dispersal vectors, and shrub life history were often nonsignificant, and therefore, were not considered in the path analyses.

Fig. 1 shows that the simplest path diagram estimated from the database supported the conceptual model (objective 1) since the diagram was parsimonious and most paths were significant (see Appendix A: Table A1 with coefficients of the regressions in the path diagram for more details). However, with a RMSR = 0.10, the fit could be improved. Keeping the structure, but adding some paths, resulted in a highly parsimonious model with better fit (Fig. 2; Appendix A: Table A2), and we hereafter used this model to make biological interpretations of the data. This model indicated that biological traits had a direct effect, not only on the number of habitats occupied by a species in the native range, but also on the probability that it will be cultivated there (objective 2; see also Appendix A: Fig. A5 of the most complex [saturated] model illustrating that biological traits had direct effects on each driver of invasion, but some of these effects were rather negligible [$P < 0.05$]). Although some of the traits such as life strategy other than stress-tolerance, height, and propagule size contributed to both a wide range of occupied habitats and the probability of being cultivated in the native range, other traits acted on these two drivers of the naturalization process differently. For example, seed bank persistence was an important explanatory variable of the variation in the number of habitat types occupied in the native range, but not of cultivation in the native range. The same held true for other traits with smaller effects such as the length of flowering period and clonality. Conversely, specific leaf area did not appear among the important explanatory variables for the number of habitats, but it had a small negative effect on the probability of cultivation in the native range; this effect was, however, not significant at the 0.05 level. The covariances were less directly relevant to our objectives, but it is worth mentioning that several were highly

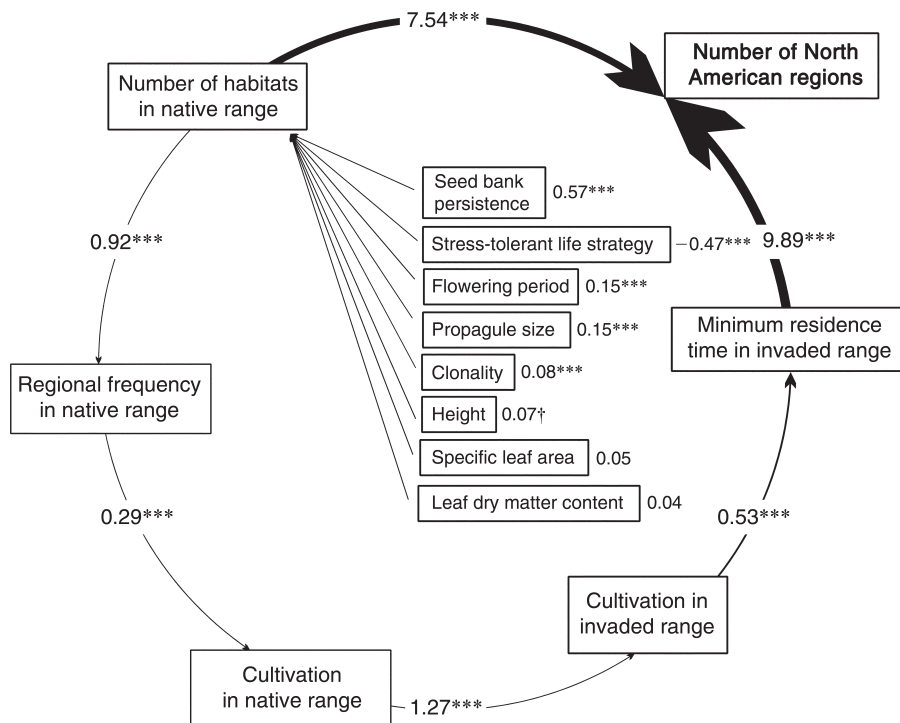


FIG. 1. The simplest path analysis fitted to predict the number of North American regions in which central European species have become naturalized (standardized root mean square residuals [RMSR]=0.10, parsimony goodness of fit index [PGFI]=0.40). This confirms that the conceptual model is supported by the data but the fit can be improved. The width and magnitude of an arrow showing the relationships between drivers is proportional to the value of the coefficient. Coefficients following trait names indicate the effects on the number of habitats in the native range. Boldface type distinguishes the response variable (number of North American regions) from explanatory ones. See Appendix A: Table A1 for statistics.

† $P < 0.1$; *** $P < 0.001$.

significant and ecologically plausible (for example, taller plants have larger propagules; Leishman et al. 1995: Table 1).

Finally, we built a model with a feedback between the regional frequency in the native range and cultivation in the native range, and a direct link between cultivation in the invaded range and the number of North American regions invaded (Fig. 3; Appendix A: Table A3). The feedback and direct link existed, as indicated by the coefficients significantly different from zero, but did not increase the fit sufficiently to justify their inclusion. This yielded a slightly less parsimonious model (compared to that shown in Fig. 3), but illustrates the existence of an important ecological effect of propagule pressure on naturalization.

Overall, the path analyses suggested that invasion of central European plants in North America, in terms of the number of North American regions invaded, increased with increasing residence time and frequency of cultivation there, but was also directly affected by the number of habitats occupied by the species in its native range, which in turn, was directly modified by species' biological traits. The effects of minimum residence time and native range habitats were the strongest of these three variables. Other, less strong relationships among determinants of invasion included a weak positive link

between cultivation in both ranges: The probability of cultivation in the native range, directly determined by biological traits, resulted in more frequent cultivation in the invaded range (Fig. 2; Appendix A: Table A2).

DISCUSSION

Toward a general model of plant species invasiveness

Decades of search for determinants of plant species invasiveness have indicated that factors contributing to post-introduction success are more likely to be identified within certain taxonomic or ecologically defined groups rather than within sets of all vascular or seed plants (Pyšek and Richardson 2007). Here we demonstrate how a general model can be built for a complete flora of a region, providing insights into the relationships between the drivers of the naturalization process and their relative importance. By using the most complete database of plants invading from central Europe to North America available to date, we elucidated the complex interplay between plant species' biological traits, their distribution characteristics in their native range, and human activities (which influence propagule pressure and residence time in the new region) in determining invasion in novel environments. Since the traits determine which species will successfully pass through ecological filters to establish in the new range,

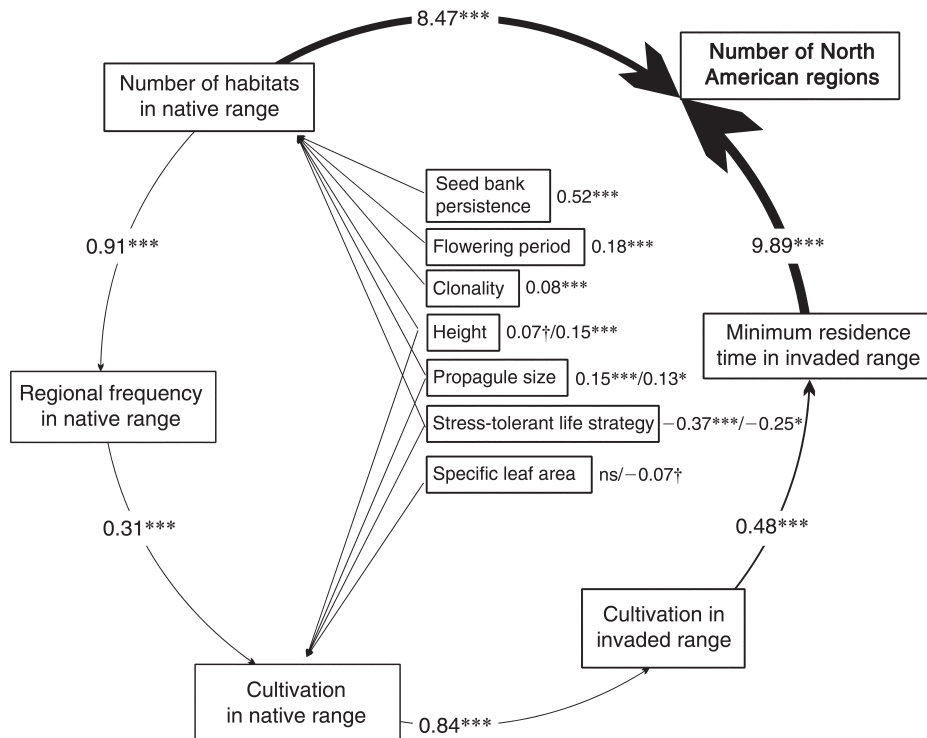


FIG. 2. A highly parsimonious model of the naturalization process with improved fit over the simplest model (Fig. 1). This model uses only biological traits whose parameter estimates are different from zero (RMSR = 0.09, PGFI = 0.39). The width of an arrow showing relationships between drivers is proportional to the value of the coefficient. Coefficients following trait names indicate the effects on the number of habitats/cultivation in native range. See Appendix A: Table A2 for statistics.

† $P < 0.1$; * $P < 0.05$; *** $P < 0.001$; ns, not significant.

as well as the geographic distribution in the native range and the types of habitats the species occupy, they have both direct and indirect effects on invasion (Pyšek et al. 2009a). We build on the conceptual framework of comparative approaches for assessing the determinants of invasiveness suggested by van Kleunen et al. (2010a), by asking whether invasive species differ in their traits from noninvasive species *before* they are moved outside their native range (see, e.g., Jeschke and Strayer 2006, Schlaepfer et al. 2010). Specifically, we ask which species are likely to naturalize and establish over a wide geographic range, without being necessarily invasive. This provides a direct test of the recently emphasized importance of the naturalization stage of the invasion process (sensu Richardson et al. 2000, Blackburn et al. 2011), a better understanding of which is crucial for prediction, because all naturalized species are potential invaders (Richardson and Pyšek 2012).

Residence time, propagule pressure, and habitat legacy interact in setting the scene for the trait game

Extensive travel and trade exchanges between Europe and North America have created one of the most intensive bidirectional exchanges in the history of biological invasions (di Castri 1990). Focusing on this specific invasion route and the direction from Europe to North America allowed us to assign information on

residence time in the target region for each species considered, and include it in the same model with measures of propagule pressure. Residence time, in this case, the time a species has been present in the wild (outside cultivation) in North America, is generally accepted as a crucial driver of invasion (e.g., Castro et al. 2005, Pyšek and Jarošík 2005, Williamson et al. 2009, Gassó et al. 2010). However, this variable is rarely included in large-scale macroecological studies (but see, e.g., Wilson et al. 2007, Lavoie et al. 2013). This is so because, in addition to the widespread lack of good data on times of introduction, it is only possible to assign this variable to species introduced to a geographically defined area. Additionally, we were able to employ a more direct measure of propagule pressure for each species by estimating the intensity of its cultivation in the invaded range. Horticulture is generally acknowledged as the main pathway in plant invasions (Mack 2000, Dehnen-Schmutz et al. 2007, Hanspach et al. 2008, Hulme et al. 2008, Lambdon et al. 2008, Hulme 2011, Pyšek et al. 2011b), which makes it a more proper measure than usual proxies derived from indicators of general human activity (see, e.g., Richardson and Pyšek 2006, Chytrý et al. 2008). Our results clearly indicate the overwhelming role of these factors in determining invasion, with minimum residence time having about

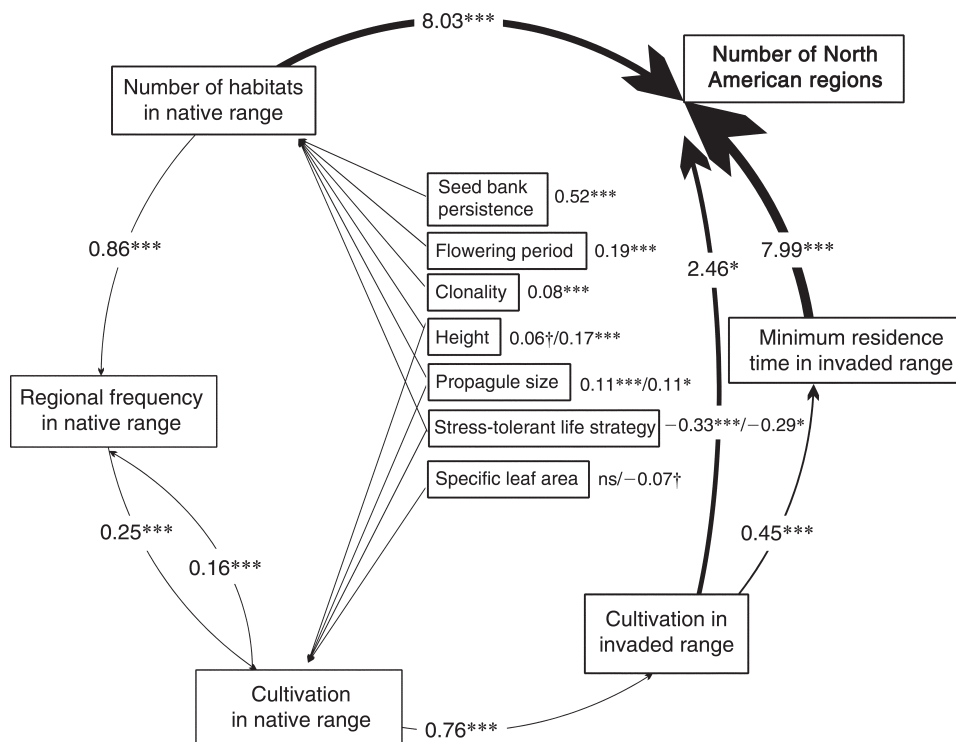


FIG. 3. A model with added feedback between regional frequency and cultivation in the native range and a direct link between cultivation in the invaded range and the number of North American regions invaded (RMSR = 0.09, PGFI = 0.37). The feedbacks generate coefficients that are different from zero but result in a decrease in parsimony (i.e., increase in PGFI). Coefficients following trait names indicate the effects on the number of habitats/cultivation in native range. See Appendix A: Table A3 for statistics.

$^\dagger P < 0.1$; $^* P < 0.05$; $^{***} P < 0.001$; ns, not significant.

three times as strong an effect as the propagule pressure resulting from the cultivation in the invaded range.

The interpretation of the parsimonious models suggests that native species are typically brought into cultivation in their home range and/or brought as a horticultural commodity to the invaded range, escape from cultivation and after some period of time in the wild become naturalized and incorporated into the local flora (Mack 1991). For several species, this is a simplified scenario, as not all of them followed the horticultural pathway and some cultivated species may have also been brought unintentionally. Nevertheless, only 6% of species in the analyzed data set became established without being used in some way by humans in North America, which makes our results generally valid. Such a high proportion of species used by humans among the naturalized aliens in North America, compared to previous studies (e.g., Lambdon et al. 2008), may be explained by the comprehensive treatment of human use in the BONAP database (Kartesz 2010).

The number of habitats the species occupies in the native range is the driver with the second most important direct effect on naturalization in North America, of comparable importance as that of the minimum residence time (note that the effects of habitat were also consistently important in the regression trees). The results also indicate that a wider range of habitats

results in a greater regional frequency in the native range. However, we note that it is impossible to disentangle which of the two factors is a primary driver as they act in concert. The range of occupied habitats also increases with larger distribution, suggesting that the more widespread a plant species is, the more habitats it occupies. Nevertheless, previous studies have also shown that the range of habitats occupied by a plant species was a more important factor influencing the diversity of insect pollinators than the species' distribution (Pyšek et al. 2011a).

This key role of habitat legacy in shaping invasion dynamics accords with recently published studies in which the habitat affinities of plant species in their native range were shown to play an important role in their invasion (Hejda et al. 2009, Kalusová et al. 2013). The strong direct effect of the breadth of habitat niche on invasion suggests that abundant, widely distributed species are superior competitors due to their ability, acquired over evolutionary history, to tolerate a wide range of abiotic conditions, use a broad spectrum of resources, and resist a large number of potential enemies (Sax and Brown 2000). They are hence ecologically highly versatile, which enables them to colonize different environments. Although originally put forward to explain invasion of continental species on islands, this hypothesis can be applied to the habitat niche breadth



PLATE 1. Invasion of the European oxeye daisy, *Leucanthemum vulgare* subsp. *vulgare*, in Nyack, close to the Glacier National Park, Montana, USA. Photo credit: K. Štajerová.

given the close relationship between habitat range and distribution.

The results further point to a link between regional frequency and probability of cultivation in the native range, although the link is three times weaker than that between habitat range and regional frequency. Given that cultivated native species were originally taken by horticulturalists from the wild, it seems likely that common species are more frequently cultivated, mainly because they are easier to grow than rare species.

Biological traits: important players once the scene is set

Although the best fit model (i.e., most complex or saturated, yet least parsimonious; Appendix A: Fig. A5) indicates that a few biological traits have some direct effects on all drivers, the majority of these effects are negligible and should be treated with caution. This agrees with a previous study that reported direct effects of biological traits on the global invasion of central European species only during the most advanced, post-naturalization stage of invasive spread, while the effects of traits on the probability of a species becoming naturalized were indirect (Pyšek et al. 2009a).

The suite of predictive biological traits indirectly promoting naturalization of central European species in North America, identified by the highly parsimonious best-fit model (Fig. 2), is therefore a much more robust result. It includes traits that have been repeatedly demonstrated to promote invasion, such as ability to flower over extended periods of time, vigorous clonal growth, and tall stature (see Pyšek and Richardson 2007 for a review and references therein). Generally, the

important traits can be mapped along a plant's life cycle, with some of them acting at each stage, being related to reproduction (flowering, seed bank), growth and persistence at a site (specific leaf area, clonality, height, life strategy, seed bank), and dispersal (seed bank, propagule size). This corresponds to the results of a previously published meta-analysis where invasive species were found to have higher performance in traits spanning all categories of plant performance such as physiology, leaf-area allocation, shoot allocation, growth rate, size, and fitness (van Kleunen et al. 2010b).

Two traits with the strongest indirect effects on naturalization are stress-tolerant life strategy and seed bank persistence; still they are orders of magnitude weaker than residence time, number of habitats in the native range, and propagule pressure. As slow growers, stress-tolerant species are at a disadvantage as invaders because of their lower capacity in terms of resource capture and use (Blumenthal et al. 2009, Mitchell et al. 2010, Dostál et al. 2013). They are frequently found in ecologically extreme habitats and are poor competitors (Grime 2001). Additionally, our results suggest that slow growth also decreases the probability of a species being promoted by frequent cultivation; horticulturalists generally prefer fast-growing plants and good competitors are usually easy to maintain. The ability to form a persistent seed bank only affects the number of occupied habitats in the native range, but this effect is the strongest of all the traits examined, having complex and multiple effects on each stage of the life cycle. Soil seed banks are considered to be "dispersal in time" (Thompson et al. 1997) and play a major role as reservoirs of

species and genetic diversity and allow for the persistence of a species at a site, buffering environmental changes that may occur over time (Harper 1977). Their importance in invasions has only started to be recognized and tested recently (Gioria et al. 2012). Because of this, as well as a general lack of data (Gioria et al. 2014), seed banks do not routinely appear among traits highlighted in studies addressing species invasiveness. Our results nevertheless suggest that for colonization and naturalization, dispersal in time by soil seed banks is as important as dispersal in space.

Another potentially important trait is genome size. This trait was not included in our path analysis models because of a high fraction of missing values and correlation with other variables, but had a consistent effect in regression trees. Small genome size has been suggested to contribute to plant species invasiveness in theoretical frameworks because it allows a species to reproduce more quickly, hence, having a shorter generation time and higher propagule pressure (Rejmánek 1996, Rejmánek et al. 2005). The importance of this trait was later confirmed in studies comparing invasive with noninvasive species (Kubešová et al. 2010, Pandit et al. 2014), as well as in a study of central European species invading globally (Pyšek et al. 2009a).

In summary, our results suggest that habitat legacy, propagule pressure, and residence time in the invaded range are the main driving forces of naturalization in North America, the effect of which is mediated by specific biological traits acting differently on these drivers.

What can we improve: gaps in the data

Given that species' biological traits scale up to shape habitat breadth, propagule pressure, and residence time, it is surprising that their predictive power was rather weak overall. Factors affecting the outcome of invasions are of different importance during particular stages and the role of biological traits is stage dependent (Williamson 2006, Dawson et al. 2009, Pyšek et al. 2009a, 2011a, Richardson and Pyšek 2012, Moodley et al. 2013). The traits that confer an advantage at one stage of the process and in a particular habitat may be neutral or even detrimental at another phase and/or in a different habitat. For example, while small genome size played a role in the naturalization of alien species in the Czech Republic, it did not separate invasive species from those that do not invade (Kubešová et al. 2010; see also Küster et al. 2008). In the present study, we also identified stage-dependent effects of several traits, as exemplified by seed banks, flowering period, and clonality mediating native habitat breadth (Fig. 2). This highlights the need for research that is explicitly linked to particular stages of the invasion process to generate more predictive information. Additionally, the general lack of data describing intraspecific genetic variation in traits among distinct invading populations may diminish their predictive power. A worthy future goal is to treat

populations, rather than species, as the smallest unit of dispersal and spread.

A further issue is that the criteria for classifying a species as invasive, as opposed to naturalized but not invasive, are rather vague and differ among authors and regions (e.g., Colautti and MacIsaac 2004). The threshold to consider a species naturalized, i.e., with sustained self-reproduction in the wild for a period of time accounting for extreme events (Richardson et al. 2000, Blackburn et al. 2011), is a more rigorous criterion than measures of the rate of spread on which the classification of invasiveness is usually based, and for which there is a great variation in how it is measured (Pyšek and Hulme 2005, Williamson et al. 2009). The resulting message is that we need a more consistent application of current definitions that would result in better measures, standardized among regions, of what is labeled as an invasive species.

Implications for predicting invasion

The results of the present study point to the potential use of similar analyses for improving predictions of future invaders, but also to gaps in data, the closing of which would further improve the predictive value of such models. First, despite our model being comprehensive by current research standards, information on some traits that are known to influence invasion is still missing. This concerns mainly some reproductive traits that are logistically difficult to estimate and ideally should be collected in a comparative manner (i.e., using designed biogeographic comparisons) rather than taken from opportunistic observational data, because they heavily depend on habitat, region, and other contexts, and hence, frequently show larger within-species variation than among-species variation (see Kattge et al. 2011). For example, fecundity expressed as the amount of seed produced, based on data taken in a comparative manner, was one of the most important traits discriminating naturalized and invasive species in the Czech flora (Moravcová et al. 2010). More detailed information on seed bank longevity beyond the simple categorization based on whether the species builds a persistent seed bank (Kleyer et al. 2008), such as the amount, density, and survival times of seed in the soil, is also still largely not available (Gioria et al. 2012, 2014), yet the results of our study suggest that this trait is of great importance and predictive power. The potentially great explanatory power of genome size, as noted, is also restricted by data availability.

Unlike comparisons of differences in traits between alien species with different success in the introduced range, where it cannot be inferred whether the differences were already present at the moment of introduction or reflect post-invasion evolution, our approach points to differences that were present at the moment of introduction (van Kleunen et al. 2010a). Therefore, the traits identified in our study may be considered of robust predictive value for introductions from Europe to North

America. This value is further enhanced by the fact that a large fraction of species do not need to undergo evolutionary change for invasion (Parker et al. 2013, Colautti et al. 2014) and behave the same way abroad as at home. For such species, studies like ours can identify traits that increase the likelihood of an alien species becoming invasive elsewhere (Jeschke and Strayer 2006, Schlaepfer et al. 2010, van Kleunen et al. 2010a). These studies could be particularly informative for risk assessment, because the traits can be assessed in organisms that have not been introduced elsewhere yet, but are considered for intentional introduction (van Kleunen et al. 2010a). Finally, one important message from the present analysis is that studies that do not include effects of habitats in the native range or that of the minimum residence time on species' invasion may seriously overestimate the role of biological traits, which, in turn, may result in spurious predictions.

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SUPPLEMENTARY MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-1005.1.sm>