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Planting intensity, residence time, and species traits determine invasion success of alien woody species

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Abstract. We studied the relative importance of residence time, propagule pressure, and species traits in three stages of invasion of alien woody plants cultivated for about 150 years in the Czech Republic, Central Europe. The probability of escape from cultivation, naturalization, and invasion was assessed using classification trees. We compared 109 escaped–not-escaped congeneric pairs, 44 naturalized–not-naturalized, and 17 invasive–not-invasive congeneric pairs. We used the following predictors of the above probabilities: date of introduction to the target region as a measure of residence time; intensity of planting in the target area as a proxy for propagule pressure; the area of origin; and 21 species-specific biological and ecological traits. The misclassification rates of the naturalization and invasion model were low, at 19.3% and 11.8%, respectively, indicating that the variables used included the major determinants of these processes. The probability of escape increased with residence time in the Czech Republic, whereas the probability of naturalization increased with the residence time in Europe. This indicates that some species were already adapted to local conditions when introduced to the Czech Republic. Apart from residence time, the probability of escape depends on planting intensity (propagule pressure), and that of naturalization on the area of origin and fruit size; it is lower for species from Asia and those with small fruits. The probability of invasion is determined by a long residence time and the ability to tolerate low temperatures. These results indicate that a simple suite of factors determines, with a high probability, the invasion success of alien woody plants, and that the relative role of biological traits and other factors is stage dependent. High levels of propagule pressure as a result of planting lead to woody species eventually escaping from cultivation, regardless of biological traits. However, the biological traits play a role in later stages of invasion.

Key words: alien plants; biological invasions; Czech Republic; naturalization; propagule pressure; species traits; woody species.

INTRODUCTION

One of the fundamental questions in invasion biology is which traits predispose a species to becoming naturalized (reproducing in the wild independently of humans; see Richardson et al. 2000, Pyšek et al. 2004) or invasive in the region to which it is introduced. This issue has been debated since the field became established as a distinct branch of contemporary ecology (Baker 1965, Roy 1990, Rejmánek 1996, 2000). Many studies have attempted to profile successful invaders (see Pyšek et al. 2006, Pyšek and Richardson 2007 for reviews). In the last decade, however, it has been recognized that the traits of a species are only part of any explanation for invasion success, and that other factors such as residence time (Crawley et al. 1996, Mulvaney 2001, Pyšek and Jarošík 2005, Křivánek et al. 2006) and propagule pressure (Rejmánek 2000, Mulvaney 2001, Brown and Peet 2003, Rouget and Richardson 2003, Foxcroft et al. 2004, Kühn et al. 2004, Daehler 2006) codetermine whether a species will successfully naturalize in a new region. This recognition has led to the application of models that analyze several groups of factors at the same time; several studies have recently addressed the role of traits in plant invasions in relation to other potentially confounding factors that co-determine invasiveness (Hamilton et al. 2005, Thuiller et al. 2006, Wilson et al. 2007). It follows that because of this context dependence, the role of traits in plant invasions can only be assessed properly when the main confounding factors are controlled for (Mulvaney 2001, Pyšek and Jarošík 2005).

It has also been suggested that the factors that are important at each stage of an invasion, such as introduction vs. naturalization or naturalization vs. invasion, are different, with socioeconomic factors being generally important initially, and biogeographical, ecological, and evolutionary factors increasing in importance in later stages (Williamson 2006). This implies that different traits are important at different stages of the invasion process (Kolar and Lodge 2001,

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2002, Pyšek et al. 2003, Marchetti et al. 2004), but this has not been rigorously tested using real data.

Studies on woody species have contributed substantially to our understanding of the invasion process (Rejmánek and Richardson 1996, Richardson and Rejmánek 2004, Křivánek and Pyšek 2006, Křivánek et al. 2006, Herron et al. 2007, Essl 2007, Mácová 2008). The availability of very good data on traits and detailed information about planting history in many parts of the world (Richardson et al. 2004) makes woody plants a suitable model for testing the role of factors determining the probability of naturalization, and for separating the influence of biological traits from that of confounding factors. In addition, many woody plants are among the most important invasive species with serious impacts on invaded ecosystems (transformers sensu Richardson et al. 2000; Carmen and Brotherson 1982, Richardson et al. 1989, Vitousek and Walker 1989, Richardson and Higgins 1998, Lowe et al. 2001). Moreover, they are the most important group in terms of forestry, ornamental gardening and landscape architecture (Lambdon et al. 2008). The need for a compromise between commercial use and environmental protection has made them the subject of risk-assessment schemes aimed at separating species with a high likelihood of post-introduction naturalization and spread, from those that can be safely introduced (Reichard and Hamilton 1997, Pheloung et al. 1999, Daehler et al. 2004, Křivánek and Pyšek 2006).

The approach used in this paper allowed us to reduce some of the biases that constrain analyses of the determinants of naturalization in plants. We use woody plants cultivated in the Czech Republic, Central Europe, to address the above issues in a complex model including major factors known to codetermine invasion success: (1) propagule pressure, using a proxy of planting intensity; (2) residence time in the target region, i.e., the amount of time the species has been present in (Central) Europe; and (3) a wide range of species' biological traits. By explicitly considering the above factors, as well as traits, we aim to reveal the direct effects of biological traits unbiased by propagule pressure and residence time. By using the congeneric approach (Pyšek and Richardson 2007), we eliminated the role of phylogenetic relatedness which has been shown to bias the effect of traits on invasion (Crawley et al. 1996, Pyšek 1997, Hamilton et al. 2005, Lloret et al. 2005, Cadotte et al. 2006). Further, the stage dependence of the role of traits and other factors (Kolar and Lodge 2001, Marchetti et al. 2004, Williamson 2006) is addressed by comparing the three stages of the invasion process (sensu Richardson et al. 2000).

Material and Methods

Species data and variables

Alien woody plants escaping from cultivation in the Czech Republic were used as the data set (see Plate 1). Only neophytes (species introduced to Europe after the discovery of America; see Pyšek et al. [2004] for the full definition) were considered. Species were classified according to their invasion status into (1) escaping from cultivation but only occurring as casuals in the wild (further referred to as "escaped"), (2) naturalized, i.e., forming self-reproducing populations in the wild, and (3) invasive, i.e., quickly spreading at considerable distances from source populations. The categories of invasion status were as defined in Richardson et al. (2000) and Pyšek et al. (2004) and classification of species followed that in Pyšek et al. (2002*b*).

Using the DAWIS database held at the Institute of Botany, Průhonice, Academy of Sciences of the Czech Republic (Křivánek and Pyšek 2007; database *available online*),[5] which contains information on 1691 alien trees, shrubs, and woody vines (with a mean height of over 0.5 m) grown in garden centers and commonly cultivated in this country, each alien species occurring in the wild (escaped, naturalized, or invasive) was paired with an alien congener not escaping from cultivation (termed "not escaped"). Congeners were chosen so as to be phylogenetically as close as possible, based on the most recent taxonomical treatments. Where an alien congener is not cultivated in the Czech Republic, the phylogenetically closest relative was used (Appendix A). This approach was adopted to eliminate phylogenetic bias in the data set.

This screening yielded (1) 109 escaped–not-escaped congeneric pairs, (2) 44 naturalized–not-naturalized congeneric pairs, and (3) 17 invasive–not-invasive pairs (Appendix A). The data sets were used to analyze the probability of escape from cultivation (Model I), the probability of naturalization (Model II) and that of invasion (Model III).

The information obtained for each species from the DAWIS database (Křivánek and Pyšek 2007) can be divided into introduction variables and trait variables (see Appendix B for details). The introduction variables included time (date) of introduction to cultivation in the Czech Republic and in Europe, as a measure of minimum residence time; if the date for the Czech Republic was the earliest record for the continent, the first record outside this country was used as the date of introduction to Europe; intensity of planting in the Czech Republic expressed as the number of garden centers and botanical gardens selling the species; type of use (ornamental, landscaping, forestry); area of origin (Asia, Europe, Mediterranean, North America); species of a hybrid origin were a separate category.

Trait variables included life form (tree, shrub, vine); leaf persistence (deciduous, conifers); height (m); duration of the juvenile period, expressed as the age at first flowering (years); beginning and duration of the flowering period in the Czech Republic (months); breeding system (hermaphrodite, monoecy, dioecy); fruit type (dry, fleshy); seed weight (mg); fruit size (cm); beginning and duration of fruit maturity (months);

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[5] ⟨http://www.ibot.cas.cz/invasions/projects.htm#dawis⟩

TABLE 1. Effect of traits described as continuous variables on the probability that an alien woody species cultivated in the Czech Republic (CR) escapes from cultivation or becomes naturalized or invasive.

Probability of escape			Probability of naturalization		
Trait	*P*	Associated $\alpha = 0.05$	Trait	*P*	Associated $\alpha = 0.05$
High propagule pressure	0.0000312	0.003938	**High propagule pressure**	0.00150	0.003938
Early introduction to CR	0.000864	0.00423	**Early introduction to Europe**	0.00200	0.00423
Heavy seed	0.0219	0.00465	Early introduction to CR	0.0392	0.00465
Early introduction to Europe	0.0236	0.00512	Large fruit	0.0442	0.00512
Extended flowering	0.0271	0.00568	Early fruit maturity	0.185	0.00568
Large fruit	0.0656	0.00639	Minimum precipitation	0.208	0.00639
Early flowering	0.0967	0.00730	Extended flowering	0.246	0.00730
Minimum precipitation	0.179	0.00851	Height	0.342	0.00851
Height	0.267	0.0102	Minimum temperature	0.383	0.0102
Short juvenile period	0.293	0.0127	Early flowering	0.404	0.0127
Minimum temperature	0.362	0.0170	Short juvenile period	0.473	0.0170
Early fruit maturity	0.574	0.025	Seed weight	0.671	0.025
Extended fruit maturity	0.643	0.050	Extended fruit maturity	0.712	0.050

Notes: Traits are listed from low to high *P* values, top to bottom. The differences in traits between escaped vs. not escaped, naturalized vs. not naturalized, and invasive vs. not escaped, respectively, were tested by nonparametric paired comparisons of congeners, with significance assessed at 5% level using sequential Bonferroni tests with the associated experiment-wise error rate α based on the Dunn-Šidák method. *P* values of individual traits are non-adjusted values of type I error in the paired comparisons, arranged in descending order of significance. Only *P* values of traits in boldface type, which are smaller than their sequentially increasing associated α's, are significant at the 5% level of significance.

germination (%); type of reproduction (only generative, also vegetative); nitrogen fixation (yes/no); minimum mean annual temperature at which the species is planted in the Czech Republic, a measure of the tolerance to frost; and minimum mean annual precipitation at which the species is planted in the CR, a measure of the drought tolerance.

Statistical analysis

For each trait described as a continuous variable (Table 1), paired comparisons of the congeners were carried out separately on the probability of escape from cultivation (Model I), naturalization (Model II), and invasion (Model III). Because not all the data could be transformed to assume a normal distribution, paired *t* tests assuming normal distribution could not be used. Paired tests were therefore first determined by calculating the difference in each pair, and then by using the nonparametric, one-sample, Wilcoxon's signed rank test, which compares the mean of the differences among the congeners with the null hypothesis that this difference is equal to zero (Crawley 2002:178–179). Because this procedure involved repeated tests of different traits of the same set of species and it was therefore necessary to adjust the values of the type I error α at the 5% level, sequential Bonferroni tests with the associated experiment-wise error rate α based on the Dunn-Šidák method were applied (Sokal and Rohlf 1995:241–242).

The effects of species traits on the probability of escape, naturalization, and invasion (Model I, II, and III, respectively) were assessed by classification trees (Breiman et al. 1984, De'ath and Fabricius 2000, Bourg et al. 2005). The invasion status groupings (Model I, escaped vs. not escaped; Model II, naturalized vs. not naturalized; Model III, invasive vs. not invasive) were the response variables; other variables, including the identity of congeners, were explanatory. Classification trees are deemed an appropriate statistical method for this analysis, since many explanatory variables had missing values and some had nonnormal distribution. These features of the data precluded two alternative methods, namely, binary logistic regression (e.g., Grotkopp et al. 2002) which could be used for all the explanatory variables, and discrimination analysis (Rejmánek and Richardson 1996, Muth and Pigliucci 2006) which could be used for the continuous variables. The classification trees were constructed by binary recursive partitioning, with the default "Gini" index impurity measure used as the splitting index, in CART v. 6.0 (Breiman et al. 1984, Steinberg and Colla 1995). This approach uses the most reliable pruning strategy of over-growing trees, ensuring that any important tree structure is not overlooked (see Chytrý et al. 2008). To determine the optimal tree, a sequence of nested trees of decreasing size, each of them being the best of all trees of its size, were constructed, and their resubstitution relative errors were estimated. Ten-fold cross validation was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the optimal tree chosen both based on the minimum-cost tree rule, which minimizes the cross-validated error (the default setting in CART v 6.0; Steinberg and Colla 1995:43), and based on the 1 − SE rule, which minimizes cross-validated error within one standard error of the minimum (Breiman et al. 1984). Following De'ath and Fabricius (2000), a series of 50 cross validations were run, and the modal (most likely) single optimal tree chosen for description. In the case that each rule produced another optimal tree, the overall single optimal tree was chosen following Bourg et al. (2005), i.e., based on the lower overall misclassification

Table 1. Extended.

	Probability of invasion	
Trait	P	Associated $\alpha = 0.05$
Early introduction to CR	0.0282	0.003938
High propagule pressure	0.031	0.00423
Minimum temperature	0.0479	0.00465
Early introduction to Europe	0.0547	0.00512
Height	0.0636	0.00568
Minimum precipitation	0.0902	0.00639
Early fruit maturity	0.1703	0.00730
Extended fruit maturity	0.1703	0.00851
Short juvenile period	0.241	0.0102
Extended flowering	0.37	0.0127
Large fruit	0.5948	0.0170
Early flowering	0.9552	0.025
Seed weight	1	0.050

rate (comparing the misclassification rate of the two models with misclassification rate of the null model), and based on the higher values of sensitivity (i.e., true positive rate, defined as proportion of observations correctly identified as suitable) and specificity (i.e., true negative rate) of the chosen single optimal tree.

The optimal trees were represented graphically, with the root standing for undivided data at the top, and the terminal nodes, describing the most homogeneous groups of data, at the bottom of the hierarchy. The quality of each split was expressed by its improvement value, corresponding to the overall misclassification rate at each node, with high scores of improvement values corresponding to splits of high quality. Surrogates of each split, describing splitting rules that closely mimicked the action of the primary split, were assessed and ranked according to their association values, with the highest possible value 1.0 corresponding to the surrogate producing exactly the same split as the primary split. Because it is easier to be a good splitter on a small number of records, to prevent missing explanatory variables from having an advantage as splitters, the explanatory variables were penalized in proportion to the degree to which they were missing, and treated by back-up rules, based on the surrogates specific to each split, that closely mimicked the action of the primary splitters. To reduce the splitting power of high categorical explanatory variables (the identity of congeners with 109, 44, and 17 categories in Model I, II, and III, respectively), these were also adjusted to have no inherent advantage over continuous explanatory variables, following penalization rules of Steinberg and Colla (1995).

Results

Paired comparisons of congeners for all continuous variables (Table 1) showed that the probabilities of both escape and naturalization most significantly increased with increasing planting intensity, used as a surrogate for propagule pressure. The probability of escape significantly increased with early introduction to the Czech Republic, while that of naturalization with early introduction to Europe. No variable had a significant effect on the probability of invasion in pair-wise comparisons (Table 1).

The classification tree, which incorporated all variables including categorical, revealed that the probability of escape (Model I) depends exclusively on planting intensity; none of the biological traits had a significant effect. A higher probability of escape from cultivation was predicted if the species was planted in at least three garden centers (Fig. 1). The misclassification rate of the model was 34.4%, compared to 50% for the null model.

Unlike the probability of escape, the probability of naturalization (Model II) and invasion (Model III) depends not only on planting intensity, but also on other variables such as biological traits. The best classification trees for the probability of naturalization and invasion had misclassification rate of 19.3%, and 11.8%, respectively, i.e., substantially lower than that for escape. Regarding naturalization, species originating in Asia are less likely to naturalize in Central Europe than those from North America or other parts of Europe, including the Mediterranean. Within the latter group, the probability of naturalization depends on planting intensity. If it is low, as for species planted in less than three garden centers, it depends on fruit size whether or not a species becomes naturalized. Those with fruits smaller than 1.1 cm are less likely to naturalize than those with fruit size exceeding this threshold (Fig. 2).

The probability of invasion is, in the first place, determined by the date of introduction into the Czech Republic; species introduced before 1823 were more likely to invade than those brought to the country after that date. The species introduced early were further differentiated by their ability to tolerate low temperatures, with those capable of growing in areas with local minima below 6.5°C being most invasive (Fig. 3).

Importantly, the identity of congeners did not significantly affect any of the resulting trees. It only appeared as a surrogate, with the highest association value of 0.89 at node 3 of the probability of naturalization tree (Fig. 2), but its improvement value was only 6% of that of the primary splitter, i.e., fruit size. For invasion, the identity of congeners appeared as a surrogate of minimum temperature at node 2 (Fig. 3), with association value 0.5 corresponding to improvement only 3% comparing to the primary splitter minimum temperature. This indicates that the traits identified as important in the analyses are generally valid for the data set used, unbiased by the phylogenetic relatedness of the species.

Discussion

Determinants of invasion act in concert and are context dependent

Despite increasing awareness of factors that determine naturalization success of alien species, invasion biology

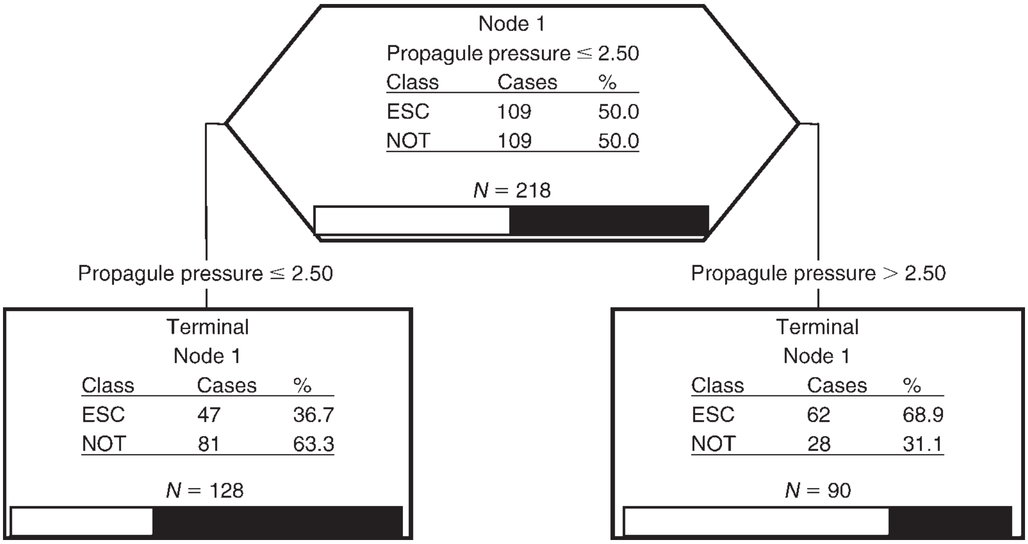

FIG. 1. Classification tree analysis of the probability of alien woody plants grown in the Czech Republic escaping from cultivation, based on the comparison of 109 escaping and not-escaping congeneric pairs (see *Material and methods: Species data and variables* for details). Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion, and number of cases (N) of escaped (ESC) and not-escaped (NOT) species expressed by numbers in each class (cases, %) and by horizontal bars. The same optimal tree was chosen based on the minimum-cost tree and the 1 − SE rule; see Appendix C for a full classification tree and cross-validation process of the optimal tree, and Appendix D for summary and diagnostic information on the optimal tree. The intensity of planting in the target area, expressed as the number of garden centers and botanical gardens selling the species, was used as a proxy for propagule pressure.

is still at the phase of developing robust generalizations (Richardson and Pyšek 2006). This is because many biological, environmental, and anthropogenic factors interact to determine the distribution of alien species and because many analyses have been flawed by not considering fundamental issues such as residence time (e.g., how much time a species has had to spread), availability of suitable habitats, and propagule pressure. Including residence time and potential range always significantly increases the explanatory power of the models and whether or not they are taken into account can also affect which factors emerge as significant determinants of invasiveness (Pyšek and Jarošík 2005, Wilson et al. 2007). These issues were recently addressed in several studies. Thuiller et al. (2006) used environmental factors, land use, life-history traits of the invaders, residence time, origin, and human use to examine the spatial pattern of invasive alien plant species in South Africa, and showed that after accounting for environmental factors, the pattern of invasions was driven by human uses, life forms, and reproductive traits. Hamilton et al. (2005) compared life-history correlates of invasion success between regional and continental spatial scales among nonnative plants of eastern Australia. After controlling for residence time and cross-correlation with other life-history traits, small seed mass and high specific leaf area were correlated with invasion success, but the results varied with scale (Hamilton et al. 2005). The outcome of such studies depended on which factors were included as explanatory variables. Overall their results indicate that the major determinants of invasion success are complex and need to be investigated in concert.

The approach used in this paper allowed us to assess, for woody plants cultivated in Central Europe for about 150 years, a complex of effects of crucial determinants of naturalization and invasion: (1) residence time in the target region, (2) propagule pressure expressed as the intensity of planting in the target area (3) area of origin, and (4) a wide range of species biological traits. The low misclassification rate of the models, 19.3% for naturalization and 11.8% for invasion, indicates that the variables used included major determinants of these processes. Further, by analyzing the probability of escape from cultivation and that of naturalization and invasion as three separate stages of the invasion process (Richardson et al. 2000, Richardson and Pyšek 2006, Williamson 2006), we showed that the relative role of biological traits and other factors is stage dependent (Kolar and Lodge 2001, 2002, Marchetti et al. 2004, Gravuer et al. 2008) and that the traits only play a role in later, more advanced stages of invasion. More importantly, the biological traits of species had no effect on the probability that a species would escape from cultivation. If propagule pressure, due to planting, is high enough, woody species eventually escape from cultivation no matter what their biological traits are.

Residence time matters

The results indicate that the effect of residence time interacts with scale. Whereas the probability of escape is associated with the time of introduction to the Czech

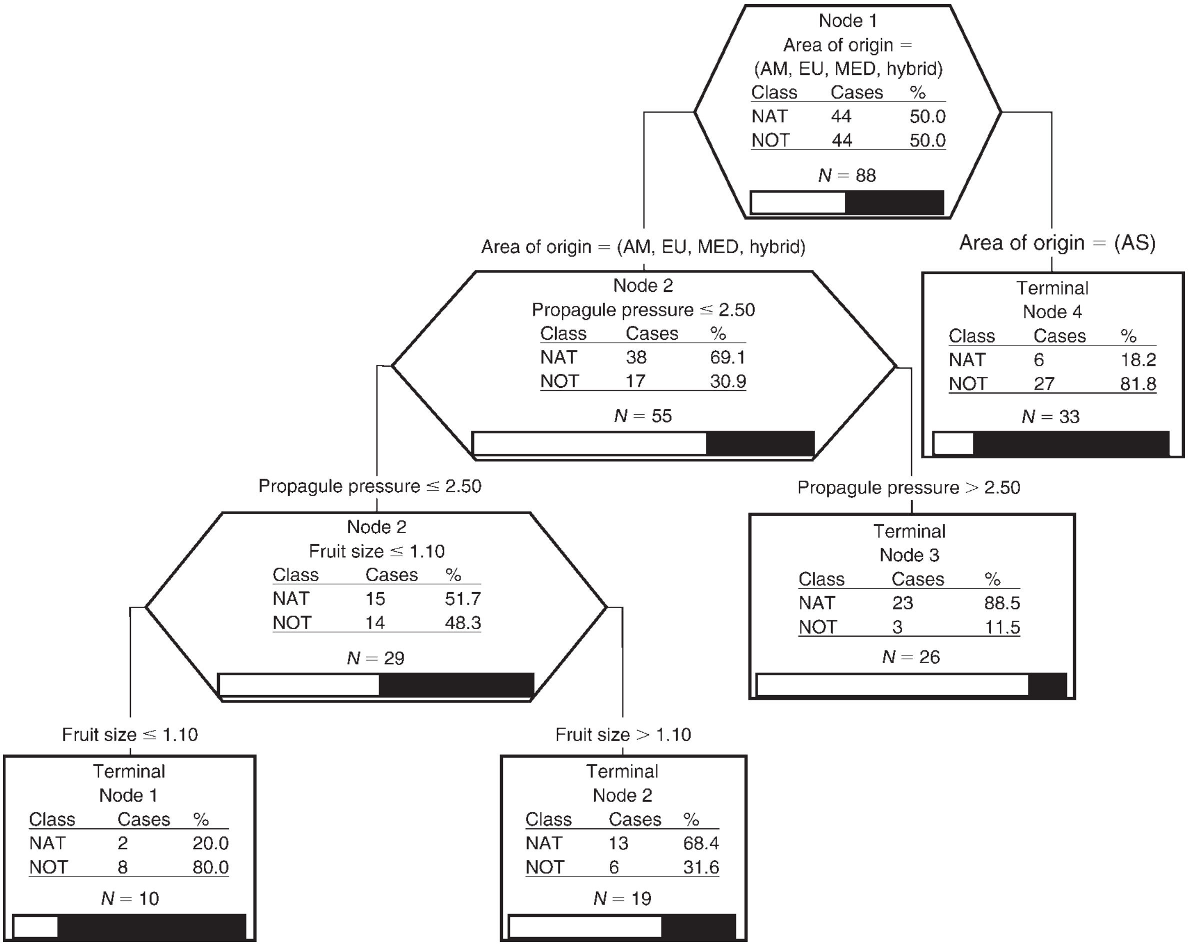

FIG. 2. Classification tree analysis of the probability of an alien woody plant species cultivated in the Czech Republic becoming naturalized, based on the comparison of 44 naturalized and not-naturalized congeneric pairs (see *Material and methods: Species data and variables* for details). The probability of naturalization significantly depends on geographic origin, planting intensity, and fruit size. Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion, and number of cases (N) of naturalized (NAT) and not-naturalized (NOT) species expressed by numbers in each class (cases, %) and by horizontal bars. The optimum tree differed under the minimum-cost tree and the 1 – SE rule. However, the depicted overall optimal tree, chosen based on the minimum-cost tree, had a lower misclassification rate (19.3%) compared to that based on the 1 – SE rule (26.1%) and higher value of sensitivity (0.795 vs. 0.614), while specificity of both trees was high and similar (minimum-cost tree, 0.818; 1 – SE rule, 0.864). Abbreviations are: AM, North America; EU, Europe; MED, Mediterranean. See Appendix C for the full classification tree and cross-validation process of the optimal tree and Appendix D for summary and diagnostic information on the optimal tree.

Republic, that of naturalization depends on the time of introduction to a wider area of Europe. This can be interpreted in terms of interaction between residence time and propagule pressure. Residence time integrates aspects of propagule pressure: the longer the species is present in the region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and the founding of new populations (Rejmánek et al. 2005). The first stage of invasion, which is in planted woody species, represented by an escape from cultivation, is sooner or later reached if there is a high enough planting intensity even if many of the escapees fail to naturalize (Křivánek et al. 2006, Křivánek and Pyšek 2007). A long history of cultivation in a wider geographical region at the continental scale of Europe, however, reflects that some species may have been already adapted to European conditions when introduced to the Czech Republic. Compared to Europe, woody species were introduced to the Czech Republic (CR) with an average delay of almost 80 years (average time of introduction to CR, 1828 ± 71 years [mean ± SD], $n = 158$; to Europe, 1752 ± 105 years, $n = 138$), which means several generations later, depending on the length of juvenile period. This point emphasizes the importance of studying the naturalization process independently of state borders as national data may have limited potential.

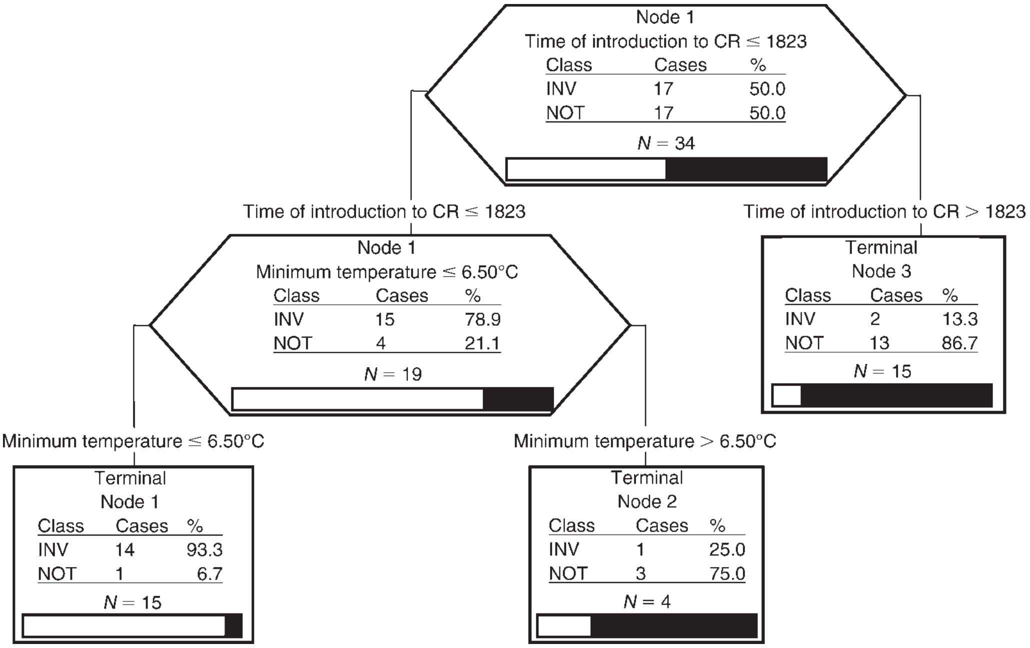

FIG. 3. Classification tree analysis of the probability of an alien woody plant species cultivated in the Czech Republic (CR) becoming invasive, based on the comparison of 17 naturalized and not-escaped congeneric pairs (see *Material and methods: Species data and variables* for details). The probability of invasion significantly depends on the date of species introduction into the Czech Republic and its tolerance of low temperatures. Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion, and number of cases (N) of invasive (INV) and not-escaped (NOT) species expressed by numbers in each class (cases, %) and by horizontal bars. The same optimal tree was chosen based on the minimum-cost tree and the 1 − SE rule; see Appendix C for a full classification tree and cross-validation process of the optimal tree and Appendix D for summary and diagnostic information on the optimal tree.

The above-mentioned interaction between residence time and propagule pressure can also explain why residence time in the Czech Republic (not in Europe), turned out to be the most important factor determining success at the most advance stage of the process (i.e., invasion and associated spread). This stage is associated with the "propagule pressure aspect" of residence time; if it is expressed for the specific region of the Czech Republic in which invasion occurs, it appears to be more informative than that reflecting the situation at the larger scale of the whole continent.

Propagule pressure and area of origin matter

The pairwise analyses revealed that planting intensity was more a important determinant of escape from cultivation and naturalization than residence time. Mulvaney (2001) found naturalization success of 2000 woody species cultivated in Australia to be significantly correlated with each of these two predictors separately, with the intensity of planting yielding higher significance levels. Furthermore, residence time in our study was no longer significant in complex models when the region of origin was introduced as a variable. It is, however, likely that the effect of residence time in our data was partly manifested via the area of origin since species from different continents were introduced to Central Europe at different times (Pyšek et al. 2003). Like the effect of traits and residence time, the effect of origin was also stage-dependent; the region of native distribution only becomes important during naturalization.

Propagule pressure is defined as "a composite measure of the number of individuals released into a region to which they are not native" (Lockwood et al. 2005). This definition incorporates estimates of the absolute number of individuals involved in a release event (propagule size) and the number of discrete release events (propagule number). As these figures are rarely available in plant invasion ecology (unlike for example, studies of birds and fish where number of introduction events and site of stock is often known; Jeschke and Strayer 2005), plant ecologists use proxies such as human population density in a region and number of visitors to nature reserves (see Richardson and Pyšek 2006 for an overview). Neither the propagule size nor the propagule number as defined by Lockwood et al. (2005) can be identified directly in studies relying on historical data. We suggest that the number of botanical gardens and parks where the species was cultivated is a reasonable measure of the total reproductive output. It is also a reasonable proxy of the amount of propagules dispersed into the surroundings by humans and natural means, from the site of cultivation over the whole period of cultivation.

In general, studies that explicitly filter out confounding effects of propagule pressure have the potential to reveal inherent trait-related determinants of naturalization and invasibility (Pyšek and Richardson 2007). That propagule pressure, both in space (by widespread dissemination, abundant plantings) and/or time (by long history of cultivation), fundamentally influences the probability of invasions by alien species has been convincingly demonstrated (Rejmánek 2000, Brown and Peet 2003, Rouget and Richardson 2003, Richardson 2006). A previous paper using planting intensity as a surrogate of propagule pressure for woody species in the Czech Republic (Křivánek et al. 2006) showed that not only overall planting intensity is important, but also its spatial distribution: species planted over a wider geographic range, hence sampling a more diverse suite of environmental conditions, were more likely to naturalize (see also Wilson et al. 2007).

The role of biological traits overestimated?

Within the scientific community, opinions on whether or not it is possible to link invasiveness to plant traits range from "relative agnosticism to sanguine confidence" (Cadotte et al. 2006). Nevertheless, a recent review of literature revealed that there is a strong support for height, vigorous vegetative growth, early and extended flowering, and reproductive characteristics as traits universally associated with invasiveness in vascular plants (Pyšek and Richardson 2007). Studies reporting these findings are fairly robust, as they were tested in different regions of the world and based on different floras (Crawley et al. 1996, Cadotte et al. 2006, Richardson 2006). Yet, the direct effect of biological traits on invasion success of woody species in the Czech Republic is minor once we control for confounding factors, and is only detectable for later stages of the invasion process, i.e., naturalization and invasion (sensu Richardson et al. 2000). This is somewhat surprising, considering that there are several papers demonstrating the role of traits for woody plants specifically. The well-established theory of determinants of invasiveness in woody plants posits that invasiveness is associated with early flowering and fruit maturity, small seed mass, short period between mast years, and capacity for dispersal of fruits/seeds by vertebrates (Rejmánek and Richardson 1996, Richardson and Rejmánek 2004).

We suggest several explanations for this result. First, our data set included representatives of a single life form, which reduces overall variation in traits, and life form itself has often been identified as an important trait associated with invasiveness (Crawley et al. 1996, Herron et al. 2007, see Pyšek and Richardson 2007 for a review). Second, classical studies on invasiveness of woody plants (Rejmánek and Richardson 1996) did not explore the role of species traits in relation to that of confounding factors, which can result in overestimating of the importance of traits (Richardson et al. 1994, Pyšek and Jarošík 2005, Wilson et al. 2007). Third, the information on planting history is very detailed for woody species, hence the planting intensity used in our study is probably a more precise surrogate of propagule pressure (see also Mulvaney 2001) than human popula-

Plate 1. Invasion of *Syringa vulgaris* (Oleaceae, lilac native to southeastern Europe) at a basal rock outcrop, Andělská hora, in the western Czech Republic. This shrub (top) spreads vegetatively by root sprouts, (center) penetrates into seminatural vegetation, and (bottom) forms extensive stands. Photo credit: P. Pyšek.

tion density or economic parameters commonly used for his purpose (e.g., McKinney 2001, Pyšek et al. 2002*a*, Taylor and Irwin 2004, Thuiller et al. 2005). Therefore, its crucial effect may be more obvious and explain a larger proportion of variation in our study than was the case in other studies.

Fruit size was the only important biological trait that appeared marginally significant in pair-wise comparisons and significant in the naturalization model accounting for the effect of confounding factors. We found that under low propagule pressure, species with fruits smaller than 1.1 cm in diameter are significantly less likely to naturalize than those with fruit size exceeding this threshold. This indicates that in woody plants, advantages of having large fruits, which are generally thought to be better for establishment (Pyšek and Richardson 2007), prevail over limited seed output associated with large fruits. The size of the propagule seems to be more important than its character (i.e., whether the fruit is dry or fleshy). This trait was also included in the analysis but was not significant. However, the type of fruit is closely associated with its size, fleshy fruits being significantly larger than dry fruits (one-way factorial ANOVA on log fruit size, $F = 21.30$; df = 1, 198; $P < 0.001$) which indirectly supports previous results that in woody species, vertebrate and human-mediated dispersal associated with large fleshy fruits is an important factor contributing to invasiveness (Rejmánek 1995, Richardson and Rejmánek 2004). Another trait associated with successful invasion is ability to tolerate low winter temperatures. Frost is an important factor constraining distribution in the temperate zone of Europe and species able to cope with it during the invasion are at advantage in terms of regions that can be invaded.

Our results indicate that a relatively simple suite of factors determines, with high probability, the invasion success of alien woody plants. This potentially has practical implications, namely, residence time and factors associated with propagule pressure play an important role throughout the entire invasion process. In the beginning stage, they could be used as the only predictors of the escape from cultivation. At later stages, however, the pattern of success and failure is fine tuned by the biological traits of an invading species, and needs to be taken into account.

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APPENDIX A

List of tested species (*Ecological Archives* E090-193-A1).

APPENDIX B

List of tested variables (*Ecological Archives* E090-193-A2).

APPENDIX C

Full trees for the models of the probability of escape from cultivation of alien woody plants grown in the Czech Republic and cross-validation process for selection of the optimal classification trees (*Ecological Archives* E090-193-A3).

APPENDIX D

Terminal node information tables, misclassification by class of the response variable tables, and prediction success classification and probability tables (*Ecological Archives* E090-193-A4).