Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a Temperate Region

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Abstract: *We studied 28 alien tree species currently planted for forestry purposes in the Czech Republic to determine the probability of their escape from cultivation and naturalization. Indicators of propagule pressure (number of administrative units in which a species is planted and total planting area) and time of introduction into cultivation were used as explanatory variables in multiple regression models. Fourteen species escaped from cultivation, and 39% of the variance was explained by the number of planting units and the time of introduction, the latter being more important. Species introduced early had a higher probability of escape than those introduced later, with more than 95% probability of escape for those introduced before 1801 and <5% for those introduced after 1892. Probability of naturalization was more difficult to predict, and eight species were misclassified. A model omitting two species with the largest influence on the model yielded similar predictors of naturalization as did the probability of escape. Both phases of invasion therefore appear to be driven by planting and introduction history in a similar way. Our results demonstrate the importance of forestry for recruitment of invasive trees. Six alien forestry trees, classified as invasive in the Czech Republic, are currently reported in nature reserves. In addition, forestry authorities want to increase the diversity of alien species and planting area in the country.*

Keywords: alien forestry trees, Czech Republic, invasive trees, species naturalization

Historia de Siembra y Presión de Propágulos como Predictores de la Invasión de Especies Leñosas en una Región Templada

Resumen: *Estudiamos 28 especies de árboles no nativos que actualmente están sembrados con fines forestales en la República Checa para determinar la probabilidad de su escape del cultivo y naturalización. Utilizamos indicadores de la presión de propágulos (número de unidades administrativas en que una especie está sembrada y área total de siembra) y del tiempo de introducción al cultivo como variables explicativas en modelos de regresión múltiple. Catorce especies escaparon del cultivo, y 39% de la varianza fue explicada por el número de unidades de siembra y del tiempo de introducción, con mayor importancia del último. Las especies introducidas temprano tuvieron una mayor probabilidad de de escapar que las introducidas posteriormente, con más de 95% de probabilidad de escapar las introducidas antes de 1801 y < 5% las introducidas después de 1892. La probabilidad de naturalización fue más difícil de pronosticar, y 8 especies fueron clasificadas erróneamente. Un modelo sin las 2 especies de mayor influencia sobre el modelo produjo predictores similares de la naturalización y de la probabilidad de escapar. Por lo tanto, ambas fases de la invasión parecen ser dirigidas de manera similar. por la historia de siembra y de introducción. Nuestros resultados demuestran la importancia de la silvicultura en el reclutamiento de árboles invasores. Actualmente, seis árboles forestales no nativos, clasificados como invasores en la República Checa, son reportados en reservas naturales.*

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Adicionalmente, las autoridades forestales desean incrementar la diversidad de especies no nativas y el área de siembra en el país.

Palabras Clave: árboles forestales no nativos, árboles invasores, naturalización de especies, República Checa

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Introduction

Invasions of alien tree species resulting from commercial planting began on a large scale in the twentieth century (Richardson 1998), but these invasions represent a serious problem in many areas (Richardson & Rejmánek 2004). Alien woody species represent a substantial proportion of the most noxious alien species worldwide (Weber 2003), and even intact forests are not resistant to invasion (Rejmánek 1996). Many exotic trees introduced for commercial exploitation, wind protection, or ornamental purposes subsequently became invaders (Zalba & Villamil 2002), and some change the character, condition, form, or nature of ecosystems (transformers sensu Richardson et al. 2000). Impacts of invasive tree species are diverse (Versfeld & van Wilgen 1986; Simberloff et al. 2003) and include suppression of native plants (Richardson et al. 1989), reduction of wildlife habitat (Zavaleta 2000), increased water loss (Zavaleta 2000), increased fuel loads and altered fire regimes (Brooks et al. 2004), and nutrient enrichment (Vitousek & Walker 1989; Richardson & Higgins 1998). The phenomenon of alien tree invasions has serious economic consequences (Zavaleta 2000; van Wilgen et al. 2001; Taylor & Irwin 2004) that can negate advantages gained from their commercial use (Richardson et al. 2004).

Among invasive alien plants, the most severe effects result from those intentionally introduced and cultivated to serve human needs (Kowarik 2005). This is especially so in the case of woody plants because under certain conditions any widely planted alien tree species may become naturalized and invade natural ecosystems (Richardson 1998). Forestry is an important pathway of introduction of alien tree species into new areas: 443 tree species are planted in forests around the world and 282 of them are invasive (sensu Richardson et al. 2000). In Europe, 12 species are naturalized and another 12 are invasive (Haysom & Murphy 2003).

Predicting which species will invade is a fundamental challenge in invasion ecology (Daehler et al. 2004). Studies of woody plants based on natural experiments created by centuries of deliberate planting in various parts of the world (Rouget & Richardson 2003; Richardson & Rejmánek 2004) have to date provided the best predictive framework (Rejmánek & Richardson 1996; Rejmánek et al. 2005). Information not only on species traits but also on environmental determinants and propagule pressure substantially improves predictions of the outcome of invasions (Rouget & Richardson 2003). Human-induced propagule pressure in particular is a crucial factor in plant invasions (Lonsdale 1999; Leung et al. 2004, Chytrý et al. 2005).

We explored the role of forestry in tree species invasions in the temperate zone of Europe. We considered the following questions: What is the relative importance of spatial (extent of planting) and temporal (history of planting) factors in determining the probability of naturalization? Do these factors affect the probability of escape from cultivation and of subsequent naturalization in the same way?

Methods

Study Area

The Czech Republic is at the geographical center of Europe, and the intensive movement of people and goods through this area since early times has contributed to the introduction of many alien species (Pyšek et al. 2002*b*; Mandák et al. 2004). The landscape is intensively used and rather fragmented due to the long-term effect of human activities, and large undisturbed areas of landscape are virtually nonexistent (Pyšek & Prach 2003).

Planting aimed at forest recovery in the Czech Republic started in the second half of the eighteenth century (Blaščák 2003). Since the second half of the nineteenth century, many alien trees, previously only grown for horticultural purposes, have been in experimental forest plantations (Beran & Šindelář 1996). Now approximately 90% of forests in the country consist of nonindigenous trees, either of foreign provenances of native species or of alien species (Hynek & Dorňák 2003). Up to now, 127 alien woody species have been reported from the wild (occurring outside cultivation), 37 of which are naturalized and 17 are invasive (Pyšek et al. 2002*b*). Eleven species affect ecosystems and are considered transformers (Křivánek et al. 2004).

Data

We collated data for all 28 tree species alien (non-native, exotic) to the Czech Republic that are planted currently for forestry purposes (Table 1). Based on Pyšek et al. (2002*b*) and following the terminology of Richardson et al. (2000), we classified the species into (1) not escaping from cultivation, (2) escaping from cultivation but only occurring as casuals, and (3) naturalized. Casual species

Table 1. Alien tree species planted in the Czech Republic for forestry purposes and included in the study.

Species	*Origin*[a]	*Status*[b]	*Year of introduction*	*Planting area (ha)*	*Number of planting units*	*Number of localities outside cultivation*
Abies concolor (Gord.) Engelm.	Nam	no	1910	0.89	5	1
Abies grandis Lindl.	Nam	no	1879	733.32	39	5
Abies nordmanniana (Stev.) Spach.	As	no	1845	1.80	8	0
Abies procera Rehd.	Nam	no	1865	0.04	1	0
Acer negundo L.	Nam	nat[c,e]	1835	337.06	21	133
Aesculus hippocastanum L.	Eu As	cas[e]	1576	551.87	38	181
Ailanthus altissima (Mill.) Swingle	As	nat[c,e]	1813	12.79	6	17
Castanea sativa Mill.	Eu Af As	cas	1562	24.64	11	21
Fraxinus americana L.	Nam	no	1835	53.35	4	6
Juglans nigra L.	Nam	cas	1835	679.08	9	20
Juglans regia L.	As	nat[e]	1852	84.13	18	48
Padus serotina	Nam	nat[c,e]	1852	12.36	18	22
Picea engelmanni (Parry) Engelm.	Nam	no	1879	10.77	7	0
Picea glauca (Moench) Voss	Nam	no	1835	584.86	20	0
Picea mariana (Mill.) Britt., Sterns et Poggenb.	Nam	no	1835	18.27	10	0
Picea omorika (Pančic) Purkyně	Eu	no	1906	200.25	25	1
Picea pungens Engelm.	Nam	no	1910	9885.50	40	33
Pinus banksiana Lamb.	Nam	no	1912	257.99	31	22
Pinus cembra L.	Eu	no	1852	2.23	6	5
Pinus contorta Dougl.ex Loud.	Nam	no	1965	89.51	6	2
Pinus nigra Arnold	Eu	nat[e]	1824	3688.56	39	175
Pinus strobus L.	Nam	nat[c,e]	1812	3089.89	41	114
Platanus × hispanica Mill.	h	cas	1835	3.48	11	1
Populus cult.[d]	h	nat[c,e]	1852	1933.97	24	58
Pseudotsuga menziesii (Mirbel) Franco	Nam	nat[e]	1842	4369.83	41	96
Quercus palustris Muenchh.	Nam	no	1835	5.98	7	3
Quercus rubra L.	Nam	nat[c,e]	1852	4379.97	40	194
Robinia pseudoacacia L.	Nam	nat[c,e]	1835	14190.12	36	615

[a] *Abbreviations: Af, Africa; As, Asia; Eu, Europe; Nam, North America; h, hybrid (taken from Rehder 1940; Koblížek 2000; Pyšek et al. 2002*b*).*

[b] *Abbreviations: no, not escaped; cas, casual; nat, naturalized (see text for definitions).*

[c] *Classified as invasive (Pyšek et al. 2002*b*).*

[d] *Various cultivars of the hybrid* Populus ×canadensis *Moench (=* P. nigra × P. deltoides*) are used in forestry.*

[e] *Recorded in nature reserves (based on Pyšek et al. 2002*a*).*

are defined as alien plants that do not form self-replacing populations and rely on repeated introductions for their persistence. Naturalized plants reproduce consistently and sustain populations over many life cycles without direct intervention by humans. Invasive plants are a subset of naturalized plants that have the potential to spread over a considerable area (Richardson et al. 2000; Pyšek et al. 2004).

For species escaping from cultivation, the total number of localities reported from the Czech Republic (i.e., frequency) was determined based on the national database of published floristic records (FLDOK) deposited at the Institute of Botany, Průhonice.

For each species, year of the first report of cultivation in the country was considered ("time of introduction") (Svoboda 1976, 1981). Information on the extent of planting was obtained from the Forest Management Institute, Brandýs nad Labem (Czech Republic), which is based on the administrative system of 41 so-called natural forest areas. These areas are administrative units defined on the basis of geography, geomorphology, and climate, which are the main determinants of the identity of planted tree species (Plíva & Žlábek 1986). They vary in size (range 1,453–256,378 ha), with an average of 59,008 ha. Based on the data in 2000, we used the following measures of the extent of planting: (1) total area (termed "planting area") and (2) number of areas (termed "planting units") in which the species was planted (Table 1). The planting area was obtained as a sum of the sizes of planting units in which a species was planted.

Statistical Analysis

We analyzed the data with multiplicative regression models that included interactions between explanatory variables (Quinn & Keough 2002). The response variables were the probability of escape, the probability of naturalization, and frequency, and explanatory variables were planting area ($\log_{10}$ transformed), time of introduction, and number of units (ln transformed).

Because the explanatory variables were measured on different scales, they were standardized to zero mean and unit variance to achieve comparable influence for all. The standardization enabled direct comparisons of variable effects because steeper regression slopes directly indicated larger effects. Using the standardized values, we checked collinearity with a matrix of correlation coefficients and by calculating tolerance values. To achieve the latter, we compared the regression of the explanatory variable in question against all the remaining explanatory variables in the model. The tolerance values for each explanatory variable were considered unacceptably low if their values in the expression $1 - r^2$ (where r^2 is the variance explained by the remaining explanatory variables) were <0.1 (Quinn & Keough 2002). These low tolerance values, indicating a high correlation, can negatively affect the estimates of model parameters.

Through our analysis we sought to determine the minimal adequate model in which all explanatory variables and their interactions were significantly ($p< 0.05$) different from zero and from one another and all nonsignificant terms were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model (containing all explanatory variables and their interactions) and then proceeding with elimination of nonsignificant terms (through deletion tests from the maximal model) and retention of significant terms (e.g., Pyšek et al. 2002*a*). To prevent biases to model structures caused by correlation between variables, we applied a backward elimination from the maximal models with stepwise analysis of deviance tables (Crawley 1993). Thus the results were not affected by the order in which the explanatory variables were removed in the stepwise process of model simplification. We checked appropriateness of the models by plotting standardized residuals against fitted values and by normal probability plots (e.g., Crawley 1993).

Following Quinn and Keough (2002), we analyzed interactions among the explanatory variables by using centered variables (i.e., variables rescaled by subtracting their mean from each observation). Significant interaction between two explanatory variables was examined with simple slopes of the multiplicative models at varying values of the interacted variables. We used simple slopes of one variable on another to arrive at three specific values of the changing variable: mean and mean plus and minus its sample standard deviation (Quinn & Keough 2002).

Successful escape and naturalization events were modeled in logistic regressions by specifying binomial error distributions and logit link functions, with escape and naturalization outcomes (success or failure) as response variables. We evaluated overall significance of the logistic regressions by a G^2 test on likelihood ratio chi-square statistic (i.e., as the deviance of the maximum likelihood model). First we evaluated the individual parameters of logistic regressions and their interactions by deletion tests based on the G^2 statistic, and then we evaluated the same parameters by a maximum likelihood version of a t test. This test (Wald statistic) is based on asymptotic standard errors (ASEs) of the parameter estimates. Odds and their confidence intervals (CI) were used as a measure of how the odds change with the one-unit change of the parameters and to predict the >95% and the <5% probability of escape or naturalization (see e.g., Crawley 1993). An overall goodness of fit of the models to the data was assessed with the Hosmer and Lemeshow (1989) test. Frequency was square-root transformed and modeled with the ordinary least square regression (OLS) with a normal distribution of errors and identity link function.

To determine which species had the largest influence on the established minimal adequate models, we assessed points with the largest influence on the statistics with either the distribution of Cook's distances (Cook 1977) (in OLS regression) or $\Delta\beta$ (the analog of Cook's statistic in logistic regression [Hosmer & Lemeshow 1989]). Data points with the largest Cook's distances or $\Delta\beta$ were sorted in descending order and weighted out of the analysis one after another (Gilchrist & Green 1994; Jarošík et al. 2002). We refitted parameter values after weighting out each data point and assessed the significance of changes in their parameters through deletion (logistic regressions) or t (OLS regression) tests. If the refitted parameters changed significantly, the points weighted out were assumed to have caused this change. Standardized residuals (i.e., the standardized differences between the observed and fitted values for each species) were also inspected. However, the inspection of the residuals themselves is not enough to reveal significant changes in parameter estimates, because extreme values often have the smallest residuals (Crawley 1993). Therefore, the use of Cook's distances or $\Delta\beta$, combining leverage and residuals in a single statistic of absolute values of weighted standardized deletion residuals, appeared to be a more appropriate method for examining influential data points than the residuals themselves.

For logistic models, we compared the original (with all species included) and refitted (with some species omitted one after another based on $\Delta\beta$) minimal adequate models. We made this comparison by calculating the number of misclassified species and by comparing G^2, Wald statistics, odds and their CI, and the values of Hosmer and Lemeshow tests of these models. In addition, we assessed the value of $r^2{}_L$ (i.e., the explained variance for logistic models suggested by Menard [2000]) and the value of the Akaike information criterion (AIC) for the best model (i.e., one that provides the maximum fit of the logistic model for the fewest number of explanatory variables [Quinn & Keough 2002]). We considered the refitted models better than the original ones if they explained more variance and had lower values of AIC (because a low value of AIC suggests a better fit for the lower number of parameters). We performed calculations in software packages GLIM (version 4, Francis et al. 1994) and SPSS (version 12, SPSS, Chicago, Illinois).

Results

Probability of Escape

Of the 28 species analyzed, 14 escaped from cultivation (Table 1). The probability of escape was significantly affected by the time of introduction and by the number of units (Fig. 1; Table 2). This minimal adequate model was highly significant ($G^2 = 23.53$; df $= 2$; $p < 0.0001$) and explained 39% of variance ($r^2_L = 0.39$). This model also had a high information value (AIC = 209.66), with no evidence of a lack of fit (Hosmer and Lemeshow test: $\chi^2 = 5.59$; df $= 7$; $p = 0.59$) (Table 3).

Species that were introduced early had a higher probability of escape than those that were introduced later. The odds ratio for each year of introduction was estimated as 0.885, with 95% CI from 0.997 to 0.785 (Table 2). That is, holding the ln of the number of units constant and starting with the first record of introduction in 1562, each species in each year had a 0.885 chance of escaping, with >95% probability of escape in 1801 and <5% probability in 1892 (Fig. 1).

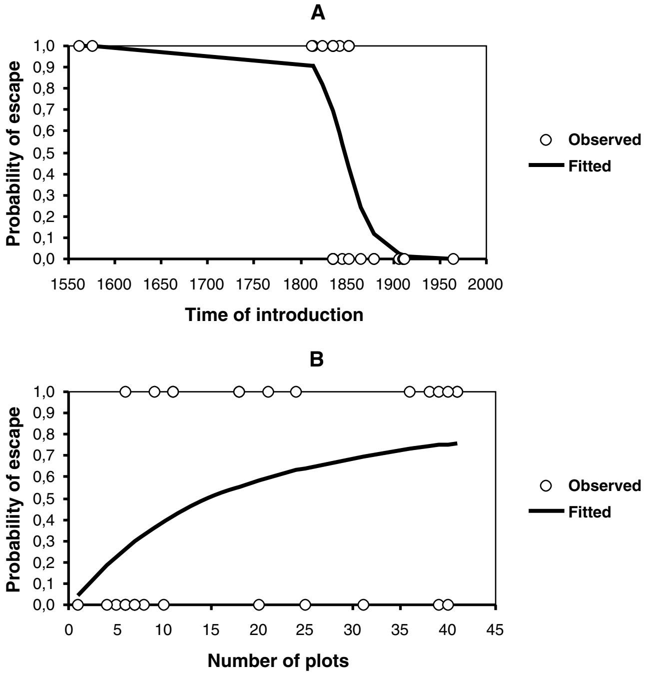

Figure 1. The probability that an alien tree species will escape from cultivation in the Czech Republic based on (A) the time of introduction for cultivation and (B) number of units (plots) in which it is planted. The figure is based on simple logistic regressions. Parameters of this model, based on multiple logistic regression, are given in Table 2, statistics are given in Table 3.

Table 2. Parameters in logistic regression of the minimal adequate model of the probability of escape of the introduced woody species.

Parameter	*Estimate*	*ASE*[a]	G^{2b}	*df*	p	*Odds ratio*[c]	*95% CI of odds ratio*	*Standardized estimate*	*ASE*[a]	*Tolerance values*[d]	*Wald statistic*[e]	*df*	p
Intercept	218.2	108.5						1.214	0.8084		2.239	1	0.135
Time of introduction	−0.1227	0.06055	17.92	1	<0.0001	0.885	0.785–0.997	−10.24	5.054	0.98	4.050	1	0.044
Ln (number of units)	3.155	1.595	9.591	1	0.0019	23.466	1.010–545.014	2.950	1.492	0.98	3.867	1	0.049

[a] *Asymptotic standard errors.*

[b] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum-likelihood model).*

[c] *Odds and their confidence intervals (CI) measure how the odds change with the one unit change of the parameters.*

[d] *Tolerance values measure collinearity of the parameters (i.e., the impact of correlation of the parameters on their estimates).*

[e] *Wald statistic is a maximum likelihood version of a t test.*

Table 3. Statistics of the minimal adequate models for the probability of escape and the probability of naturalization of alien forestry species in the Czech Republic.

							Hosmer and Lemeshow test[d]		
Event	*Omitted species*	G^{2a}	*df*	p	r^2_L[b]	*AIC*[c]	χ^2	*df*	p
Escaped	none	23.53	2	<0.0001	0.39	209.66	5.59	7	0.59
Naturalized	none	11.48	5	0.043	0.31	603.10	4.64	7	0.70
	Castanea sativa	14.54	5	0.012	0.41	426.10	6.25	7	0.511
	Castanea sativa and *Aesculus hippocastanum*	20.23	2	<0.0001	0.58	185.94	2.883	6	0.823

[a] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum likelihood model).*

[b] *Explained variance for logistic models as suggested by Menard (2000)*

[c] *Akaike information criterion for the best model (i.e., one that provides the maximum fit of the logistic model for the least number of predictors).*

[d] *Describes an overall goodness of fit of the models to the data.*

The model also predicted an increase in the probability of escape with increasing number of units. Holding the time of introduction constant, the odds ratio per the ln of one unit was 23.466 (95% CI: 1.010–545.014) (Table 3). This corresponded to <5% probability of escape for one unit and, approximating beyond the range of the number of units under the study, to >95% probability for 200 units (Fig. 1).

The minimal adequate model misclassified 3 of the 28 species. *Picea glauca* and *P. omorica* are not escaped but were classified as escaped, and the escaped *Juglans nigra* was classified as not escaped. These three species also had the largest differences between the observed and fitted values (the largest standardized residuals) and caused the largest changes in the parameters of the model after being deleted from the model (they had the largest values of $\Delta\beta$). Results did not change, however, if *Picea glauca*, the species with the largest $\Delta\beta$, was omitted. That is, the misclassified species did not cause significant changes in the structure or the explanatory power of the minimal adequate model.

The estimates of the parameters were highly significant when evaluated by G^2 test (time of introduction: $G^2 = 17.92$, df $= 1$, $p < 0.0001$; ln of the number of units: $G^2 = 9.591$, df $= 1$, $p = 0.0019$) and still significant when evaluated by the Wald statistic (time of introduction: $G^2 = 4.050$, df $= 1$, $p = 0.044$; ln of the number of units: $G^2 = 3.867$, df $= 1$, $p = 0.049$). Because the parameters were not correlated, there was no negative impact on their estimates due to collinearity (tolerance values = 0.98) (Table 2).

Probability of Naturalization

Of the 28 species analyzed, 10 were considered naturalized (Table 1). The original minimal adequate model for all species indicated a significant interaction between the time of introduction and the ln of the number of units ($G^2 = 4.007$, df $= 1$, $p = 0.045$) and between the time of introduction and the log of planting area ($G^2 = 4.057$, df $= 1$, $p = 0.044$) (Table 4). This suggests that the time of introduction alone cannot be used for the prediction of the probability of naturalization, because it is differentially affected by low and high number of planting units and by small and large extent of planting area. This model was significant ($G^2 = 11.48$, df $= 5$, $p = 0.043$, $r^2_L = 0.31$) and gave no evidence for a lack of fit (Hosmer and Lemeshow test: $\chi^2 = 5.59$, df $= 7$, $p = 0.59$); however, it had a low information value (AIC = 603.10) (Table 3). Moreover, the confidence intervals of the odds ratio of all parameters included one, indicating that changes in these parameters do not allow prediction of the probability of a species being naturalized. The tolerance value for the standardized log of area was unacceptably low, indicating a possibility of detrimental effects on the estimated regression parameters (Table 4). Eight of the 28 species were misclassified, and when the species with the largest $\Delta\beta$, *Castanea sativa*, was omitted, the parameters of the model changed significantly (Tables 3 & 4).

The refitted minimal adequate model without *Castanea sativa* explained more variance ($r^2_L = 0.41$) and had larger information value (AIC = 426.10) than the original one with all species included (Table 3). Most importantly, the confidence interval of the odds ratio of the interaction between time of introduction and ln of the number of units did not include one (Table 4), which enabled prediction of the probability of naturalization against time of introduction for different values of the ln of the number of units. With a low number of units (mean + 1 SD of the ln of the number of units), regression of the number of years since introduction did not change the probability of naturalization ($G^2 = 0.125$, df $= 1$, $p = 0.72$). However, with a high number of units (mean – 1 SD), the regressed years marginally decreased the probability of naturalization ($G^2 = 3.698$, df $= 1$, $p = 0.054$). This indicates that, similar to the probability of escape (Table 2), but only for a high number of units, the probability of naturalization increases for species introduced early. However, 6 of the 27 species remained misclassified, and when the species with the largest $\Delta\beta$, *Aesculus hippocastanum*,

Table 4. Parameters of the minimal adequate models of the probability of naturalization of alien forestry species in the Czech Republic

Omitted species	*Parameter*	*Estimate*	*ASE*[a]	G^{2b}	*df*	p	*Odds ratio*[c]	*95% CI of odds ratio*	*Standardized estimate*	*ASE*	*Tolerance values*[d]	*Wald statistic*[e]	*df*	p
None	intercept	166.137	128.588						−0.8484	0.5440		2.424	1	0.428
	log(planting area)	111.557	79.585	1.812	1	0.18	2.81E+48	0.000–1.55E+116	1.449	1.102	0.096	1.727	1	0.189
	time of introduction	−0.093	0.07	1.694	1	0.19	0.911	0.794–1.046	−1.511	1.296	0.711	1.334	1	0.248
	ln (number of units)	−132.657	94.497	0.228	1	0.63	0.000	0.000–6.7E+22	0.4946	1.054	0.218	0.220	1	0.639
	(time of introduction) × (ln[number of units])	0.073	0.051	4.007	1	0.045	1.075	0.972–1.189	5.292	3.6792	0.194	2.030	1	0.154
	(time of introduction) × (log[area])	−0.060	0.043	4.057	1	0.044	0.942	0.865–1.025	−6.615	4.629	0.198	2.001	1	0.157
Castanea sativa	intercept	654.637	358.437						−0.7191	0.6178		1.346	1	0.246
	log(planting area)	119.029	83.055	0.341	1	0.56	4.94E+51	0.000–2.46E+122	0.699	1.193	0.199	0.342	1	0.559
	time of introduction	−0.360	0.196	5.638	1	0.017	0.698	0.475–1.025	−7.499	4.188	0.525	3.161	1	0.075
	ln (number of units)	−273.507	134.622	1.388	1	0.24	0.000	0.000–0.000	1.451	1.339	0.217	1.168	1	0.280
	(time of introduction) × (ln[number of units])	0.150	0.074	7.63	1	0.0057	1.162	1.006–1.342	11.68	5.715	0.207	4.141	1	0.42
	(time of introduction) × (log[area])	−0.065	0.045	4.36	1	0.037	0.938	0.858–1.024	−7.482	5.225	0.190	2.047	1	0.152
Castanea sativa and *Aesculus hippocastanum*	intercept	204.0	108.3						0.3707	0.7362		0.251	1	0.616
	time of introduction	−0.1163	0.06085	12.64	1	0.00038	0.89	0.789–1.005	−9.710	5.079	0.99	3.561	1	0.059
	ln (number of units)	3.792	1.809	12.54	1	0.00040	44.361	1.223–1609.011	3.545	1.692	0.99	4.286	1	0.038

[a] *Asymptotic standard errors.*

[b] *G^2 test on likelihood ratio χ^2 statistic (i.e., the deviance of the maximum likelihood model).*

[c] *Odds and their confidence intervals (CI) measure how the odds change with the one unit change of the parameters.*

[d] *Tolerance values measure collinearity of the parameters (i.e., the impact of a correlation of the parameters on their estimates).*

[e] *Wald statistic is a maximum likelihood version of a* t *test.*

was omitted from this refitted model, the parameter estimates again changed dramatically (Tables 3 & 4).

The refitted minimal adequate model with both *Castanea sativa* and *Aesculus hippocastanum* omitted was highly significant ($G^2 = 20.23$, df $= 2$, $p < 0.0001$), explained most variance ($r^2{}_\mathrm{L} = 0.58$), had the largest information value (AIC $= 185.94$), and gave the largest overall goodness of fit to the data (Hosmer and Lemeshow test: $\chi^2 = 2.88$, df $= 6$, $p = 0.82$) (Table 3). Only 4 of the remaining 26 species were misclassified: *Picea glauca* as naturalized and *Ailanthus altissima*, *Juglans regia*, and *Padus serotina* as not naturalized. These species had the largest standardized residuals and $\Delta\beta$, but when these species were deleted from this refitted minimal adequate model, the model's parameters did not change significantly.

Predicting the probability of naturalization based on the refitted minimal adequate model with two omitted species (Fig. 2) yielded results very similar to the model predicting the probability of escape (Fig. 1). Both models differed only by inclusion of *Castanea sativa* and *Aesculus hippocastanum* in the original minimal adequate model for escape. These two species were missing from the refitted model for naturalization. Similar to the model predicting the probability of escape, the probability of naturalization in the refitted model was significantly affected by the time of introduction ($G^2 = 12.64$, df $= 1$, $p = 0.00038$) and by the ln of the number of units ($G^2 = 12.54$, df $= 1$, $p = 0.00040$). As before, the estimates were not negatively affected by collinearity (tolerance values $=$ 0.99) (Table 4), suggesting that both the temporal (time of introduction) and the spatial (the number of units) factors were estimated reliably.

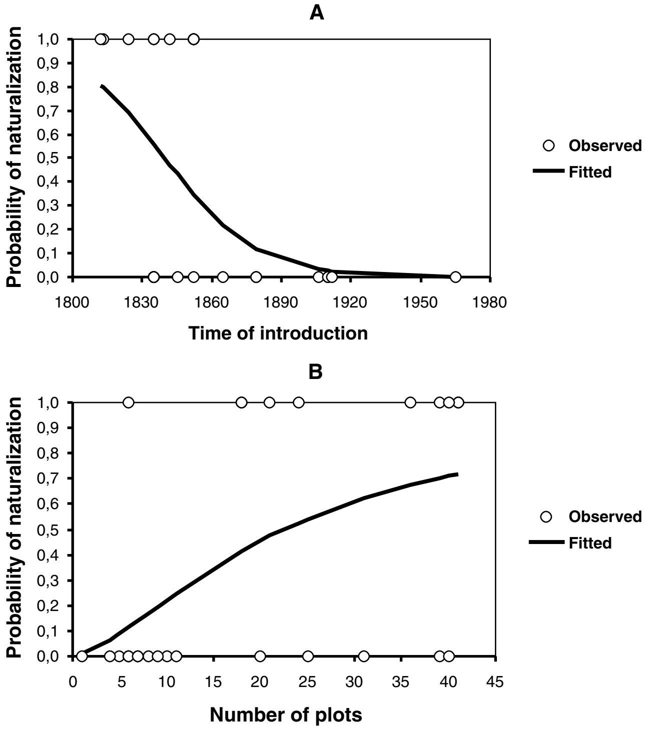

Figure 2. The probability of naturalization of alien tree species planted in the Czech Republic based on (A) the time of introduction for cultivation and (B) the number of units (plots) in which they are planted. The figure is based on simple logistic regressions. Parameters for this model, based on multiple logistic regression, are given in Table 4, statistics are given in Table 3. Castanea sativa *and* Aesculus hippocastanum *were omitted (see text for details).*

With the two species omitted and mutually comparable standardized values of the parameters, the estimates for escape (Table 1) and naturalization (Table 4) overlapped widely in their asymptotic standard errors (ASE, Tables 2 and 4). However, the ASEs for the time of introduction in the naturalization model were only marginally significant (Wald statistic $= 3.561$, df $= 1$, $p = 0.059$). Consequently, the prediction of naturalization based on the odds ratio of the time of introduction included zero (Table 4); hence, only the ln of the number of occupied units could be used to predict the probability of naturalization. Species planted at four units had >5% probability of naturalization and, approximating beyond the range of the number of occupied units under study, those planted at 200 units would have >95% probability of naturalization (Fig. 2). However, species planted at one unit had >5% probability of escape. That is, this refitted minimal adequate model predicted the 5% probability of naturalization for more units than the minimal adequate model for escape, but the same 95% probability of escape and naturalization was predicted for species planted at 200 units.

The planting area had no significant effect on either the probability of naturalization or the probability of escape.

Frequency of Species Escaped from Cultivation

Planting area had a significant effect on the number of localities recorded in natural and seminatural vegetation (Fig. 3). For the 14 species escaped from cultivation (Table 1), the minimal adequate model indicated a significant effect of the log of planting area ($\sqrt{\text{number of localities}} = -1.169 + 4.096\log(\text{planting area})$, df $= 1, 12$, $F = 19.68$, $p = 0.00081$, $r^2 = 0.62$). Neither the time of introduction nor the number of units appeared significant. *Robinia pseudoaccacia* (Fig. 3) caused the largest change in the regression slope of the number of localities on planting area after deleting this species from the minimal adequate model (Cook's distance $= 0.94$). However, the decrease in the regression slope was not significant ($t = 1.12$, df $= 12$, $p = 0.14$), suggesting that inclusion of this species did not cause significant changes in the structure and explanatory power of the model.

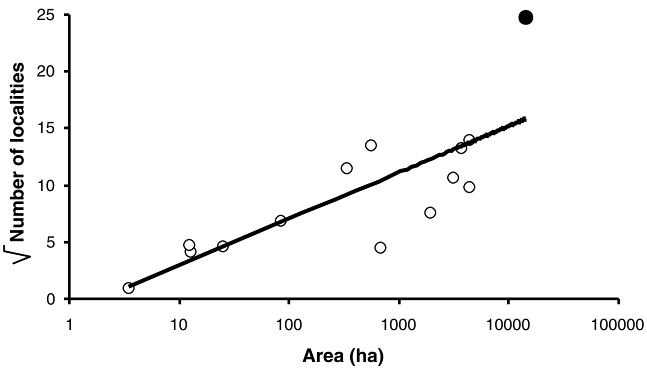

Figure 3. Relationship between the number of localities of alien tree species reported from natural and seminatural habitats in the Czech Republic and the planting area. Fitted values are given in the text. The black point is Robinia pseudoaccacia.

Discussion

Extent of Planting as a Surrogate for Propagule Pressure

Propagule pressure is a crucial determinant of invasion success (Lonsdale 1999; Rejmánek et al. 2005). It can fundamentally influence the probability of invasions by alien species in both space (widespread dissemination, abundant plantings) and time (long history of cultivation) (e.g., Kowarik 1995; Richardson 1996; Rouget & Richardson 2003). Unfortunately, it is difficult to measure and express quantitatively, particularly on a large scale (Rouget & Richardson 2003). Quantitative surrogates for propagule pressure such as number of visitors to nature reserves (Lonsdale 1999), human population size (McKinney 2002), or economic activity (Taylor & Irwin 2004) have been used.

In studies of tree invasions, information on the extent and character of planting can be used as a surrogate for propagule pressure. Forestry records often provide reliable estimates of planting area and time of introduction. In addition, longevity of trees and their easy mapping allow for determining dispersal foci, the distance from which can be used as another surrogate for propagule pressure (Rouget & Richardson 2003).

The data we used on planting are recent and may have varied over several centuries of species invasions, thus exerting different effects during the analyzed period. Nevertheless, historical data available for individual species (Blaščák 2003) indicate that changes over time in the relative extent of their planting were not so dramatic as to affect the robust results of our models.

Planting History and Propagule Pressure as Triggers of Invasion

The probability of escape increased with the time since introduction and the number of planting areas, with the former predictor being more important than the latter. A rather high proportion of explained variation indicates that these predictors determined to a large extent whether the invasion started or not. Unexplained variation may be attributable to species-specific traits and habitat conditions.

For species introduced to cultivation before the beginning of the nineteenth century, there was a 95% probability that they had escaped from cultivation, whereas those introduced after the end of the nineteenth century had the same probability that they had not escaped up to now. Such predictions must be interpreted in the present context: time acts as an important driver of invasion and species not escaped yet may start to invade in the future (Kowarik 1995). Effects of global warming (e.g., Bengtsson 1997) may play an important role in this respect because invasions of many alien species in Central Europe are constrained by low temperatures (Pyšek et al. 2003).

Interpreting the other significant predictor of the probability of escape, number of planting units, is more difficult. With 41 planting units recognized by the forestry classification system in the Czech Republic, a linear approximation beyond the range of data does not account for a possible threshold number of units between 42 and 200, above which the character of the relationship may change unpredictably. Nevertheless, it indicates that the number of available units is too low to ensure that a species will escape from cultivation just because it is widely planted, regardless of planting history.

Unlike the number of units, the total planting area did not affect the probability of a species escaping from cultivation. It is likely that the high number of units exposed the species to a wide range of geographical conditions and increased the chance that a species would encounter conditions suitable for escape from cultivation or for naturalization. That a large area itself did not contribute to the invasion success possibly reflects that planting of a species, however extensive, may be concentrated to a limited region where the escape from cultivation may be prevented by factors beyond propagule pressure, such as climate constraints, lack of dispersal vectors, or lack of disturbance.

Planting area was the only significant predictor of the frequency of occurrence of casual and naturalized tree species outside cultivation. Neither the number of units nor time since introduction played a role in frequency of occurrence. This indicates that factors affecting the dynamics of spread of these species in the landscape are different from those that determine whether the process of invasion starts or not. It appears that the amount of propagules supplied by planted stands has an overwhelming effect on species frequency in the landscape, regardless of how these propagules are distributed over a wide range of geographical conditions. In addition, once a species becomes naturalized (10 of the 14 escaping species in the data set are naturalized), it creates additional propagule pressure from wild, reproducing populations. The effect of these propagules on the species' population dynamics may be more important than what would correspond to their proportional amount because they increased the propagule pressure under the conditions that were sampled and proved suitable by maternal populations (i.e., where the species became naturalized).

Are Naturalization and Escape Driven by the Same Forces?

The minimal adequate model for escape provided better results than that for naturalization. That the prediction for the latter, more advanced stage of invasion was less reliable than that for the beginning of invasion is not surprising because naturalization is driven by a more complex array of factors than mere escape from cultivation (Kowarik 1995; Rejmánek et al. 2005). To become naturalized, a species must overcome reproductive barriers in the area of introduction (Richardson et al. 2000). Once this has happened, its occurrence is less dependent on short-lasting opportunities, including chance (Crawley 1989). Variation in species traits and the effect they have on the probability of naturalization thus makes predicting naturalization more difficult than predicting escape. The number of species planted for forestry purposes was too low to allow for the statistical analysis of species traits. Nevertheless, some insight can be gained by exploring species that were misclassified by the predictive models, whether they have some specific features responsible for them not fitting the statistical patterns.

The two species that caused the difference between the minimal adequate models of escape and naturalization with all species included (*Castanea sativa* and *Aesculus hippocastanum*) are reported as first introduced in 1562 and 1576, respectively. The introduction of the remaining species did not start before 1812. Both these species were introduced early, have escaped from cultivation, but are not naturalized. That is why their inclusion changed the prediction of naturalization but not that of escape. Omitting the earliest introduced species (*Castanea sativa*) yielded results similar to those of the escape model and indicated the increasing probability of naturalization for species introduced early, although only when they were planted at a high number of units. With both species omitted, the probability of naturalization depended on the same predictors as that of escape. The only difference was that the 5% probability of naturalization was predicted for a higher number of units than the probability of escape. That more planting units are needed for a species to naturalize than to escape from cultivation results from the character of the invasion process, with progressively fewer species overcoming subsequent barriers (Richardson et al. 2000).

Forestry as a Pathway for Alien Tree Species

Some alien woody species potentially represent a significant threat to biodiversity worldwide because of their high invasiveness and impact on invaded vegetation (Binggeli 1998; Haysom & Murphy 2003; Richardson & Rejmánek 2004). Forestry introduces individuals from provenances suitable for a particular climate and implements large-scale planting, creating massive propagule pressure (Rouget & Richardson 2003). This makes forestry a very efficient pathway for invasions (Richardson 1998; Haysom & Murphy 2003). Compared with horticulture, fewer species are introduced via forestry but proportionally more naturalize or invade. Of 4360 alien woody species introduced into the Czech Republic for horticultural purposes and 1358 alien species frequently planted in parks and gardens (M. K., unpublished), only 127 are thought to have escaped from cultivation (Pyšek et al. 2002*b*). The effect of forestry, however, acts on a large scale. In 2000 the 28 tree species we analyzed in this study were planted on 45203 ha, representing 1.77% of the total forest area in the country (available from http://www.uhul.cz/slhp3/defaultA.htm). Knowledge of factors determining the probability of alien trees escaping from cultivation or becoming naturalized is therefore crucial for minimizing impacts of future invasions associated with forestry and conserving biodiversity. In addition, the number of invaders in the future will likely increase due to the lengthy lag phases in invasions of woody species even if new introductions ceased (Kowarik 1995), which is improbable because more species are planted over larger areas (Richardson & Rejmánek 2004). In the Czech Republic, the threat is enhanced by forestry practices. The area used for plantations of alien trees could increase up to 7% of the total forest area and currently there are 24 other tree species being planted and tested as potential candidates for future introductions into the landscape (ÚHÚL 1994; Beran & Šindelář 1996).

The data documenting a link between forestry-mediated invasions and nature conservation are also available. Of the 28 species planted for forestry purposes, 6 that are classified as invasive in the Czech Republic (Table 1) occur in nature reserves. Although they do not currently invade massively in the reserves studied in a previous paper (Pyšek et al. 2002*a*), their occurrence represents a potential threat to the biodiversity of protected areas in this country.

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