Invasive Plants: Ecological and Agricultural Aspects
Edited by Inderjit

Residence time determines the distribution of alien plants

Petr Pyšek[1,2] and Vojtěch Jarošík[2,]

[1] *Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic*
[2] *Department of Ecology, Faculty of Sciences, Charles University, Viničná 7, CZ-12801 Praha 2, Czech Republic*

Introduction

Determining which biological traits enable a species to become invasive has been a major objective in invasion ecology [1–5]. Part of the theory relies on comparisons of large species sets; such studies attempt to identify the factors that contribute to the probability that a species will be introduced to a region [6] and become naturalized or invasive [7–9]. It has been shown that different factors are of different importance at particular stages of the invasion process [6, 10]. Recently, sophisticated data on alien floras from around the world have become available in the scientific literature [8, 11–16]. Some biological and ecological traits of invading species were identified as contributing to the success of invasive species, e.g., high fecundity [17], efficient dispersal [18], ability to utilize generalist mutualists [19], ability to evade specific natural enemies [20], small genome size [3], relative growth rate [5] or specific leaf area [5, 20].

However, not only species' biological traits are important. Cultural influence has been recognized as an important factor co-determining the fate of species subsequent to their first introduction to a new area [21, 22]. Recently, it has been emphasized that stochastic effects, which depend on initial inoculum size, residence time, and the number of introduction events (propagule pressure) and their spatial distribution [23] co-determine whether a species becomes invasive. One of the robust emerging generalizations of invasion biology is that the probability of invasion success increases with residence time [24], i.e., the time since the introduction of a taxon to a new area. Residence time represents another dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread and the probability of founding new populations increases [25]. As it is usually not known exactly when a taxon was introduced, the term 'minimum residence time' (MRT) has been suggested and used in the literature [24–27].

Herein, we utilize available data to determine the effect of residence time in plant invasions in detail at two temporal scales. First, the phenomenon is analyzed for recent invaders, to explore how species reaching the target areas at different times over the last 2–4 centuries perform as current invaders. Second, a question is raised whether the residence time still affects the current distribution of species that were introduced millennia ago. The results are then discussed in the context of available literature dealing with temporal aspects of plant invasion.

The data

Four data sets representing alien floras or their subsets and containing information on the first record of each species in the area and some measure of their present occurrence were collated: the Azores (38.00 N, 28.00 W; [28]), Czech Republic (49.30 N, 17.00 W; [29, 30]), Hawaiian Islands (22.00 N, 160.00 W; [31]), and New Zealand (41.00 S, 174.00 E; [32]). They were used to assess the effect of minimum residence time (MRT) on the distribution and frequency of species that invaded in the last 2–4 centuries (see Tab. 1 for characteristics of data and how the primary sources were standardized to provide comparable information). In Europe, these species are termed neophytes and defined as aliens that arrived after the year 1500 [33–35].

In addition, information on historical invaders introduced to a target region between the beginning of the Neolithic up to the year c. 1500 (termed archaeophytes, see [35] for definitions) was obtained for two regions: Czech Republic [29] and Great Britain (54.00 N, 2.00 W; [36, 37]). In the New World, a concept analogous to archaeophytes and neophytes is not being consistently used, although early plant introductions are recognized, e.g., by Polynesians to Pacific Islands [31, 38, 39]. These introductions are of minor importance in terms of species number because the vast majority of modern invaders arrived after the discovery of America [40]. In the Mediterranean, the concept of archaeophytes is rather blurred as species that are archaeophytes in other parts of Europe originated in the Mediterranean. Hence in the Azores, Hawaiian Island and New Zealand, all alien species reported in the respective primary sources were considered in analyses, with the exception of early plant introductions to Hawaiian Islands [31].

The present distribution of alien species in studied regions was expressed using two measures: 1) the first measure (termed "range") is related to geographical distribution, expressed by the number of occupied geographical units (mapping squares, islands or regions, Tab. 1) and 2) the second measure (termed "frequency") is related to how frequent the species is in the region regardless of how widespread it is in geographical terms. In original datasets, frequency scales are based on qualitative assessment or estimates of the number of localities (Tab. 1). The number of herbarium specimens given for the New Zealand data was also taken as a measure of frequency as it reflects the number of localities (see [41] for discussion on biases associated with herbarium specimens as sources of data).

Table 1. Summary statistics for regressions of the current distribution of alien plants on minimum residence time (MRT) compiled from the literature. Period indicates MRT of the earliest species' record in the data set. Both the measures of range/frequency and MRT are standardized to zero mean and variance one so that all regression slopes are mutually comparable. For regression slopes, 95% confidence intervals (CI: lower limit – upper limit) are shown; if these overlap, the slopes do not differ significantly at $p = 0.05$. Invasion status follows the definition in Richardson et al. [42] and Pyšek et al. [35]

Region	Measure	Invasion status		R^2 (%)	slope	95% CI	F	P	Period (yrs)	Data	Species set	Source
Azores	frequency	casual [1]	210	4.8	0.073	0.029–0.12	10.58	<0.01	414	frequency scale [2]	complete flora	[28]
Azores	frequency	naturalized	700	15.9	0.42	0.35–0.49	131.99	<0.0001	414	frequency scale [2]	complete flora	[28]
Azores	range	casual	210	14.6	0.22	0.15–0.30	35.61	<0.0001	414	number of islands [3]	complete flora	[28]
Azores	range	naturalized	700	34.9	0.61	0.55–0.67	373.89	<0.0001	414	number of islands [3]	complete flora	[28]
Azores	frequency	all aliens	910	18.7	0.43	0.37–0.49	208.6	<0.0001	414	frequency scale [2]	complete flora	[28]
Azores	range	all aliens	910	35.5	0.60	0.54–0.65	500.58	<0.0001	414	number of islands [3]	complete flora	[28]
Czech Republic	frequency	all aliens [4]	691	29.4	0.54	0.48–0.60	286.7	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	frequency	casual [4]	523	18.0	0.28	0.23–0.33	114.6	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	frequency	naturalized [4]	168	11.8	0.42	0.25–0.60	22.33	<0.0001	202	frequency scale [5]	complete flora	[29]
Czech Republic	range	naturalized [6]	52	23.6	0.49	0.24–0.73	15.47	<0.001	257	number of quadrats	sample of successful aliens	[30]
New Zealand	range	naturalized [7]	32	39.6	0.63	0.35–0.91	19.68	<0.0001	174	number of regions	sample of woody plants	[32]
Hawaiian Islands	frequency	naturalized [8]	786	28.4	0.66	0.58–0.73	310.38	<0.0001	181	number of herbarium specimens	complete flora	[31]

(Continued on next page)

Table 1. (Continued)

Region	Measure	Invasion status		R^2 (%)	slope	95% CI	F	P	Period (yrs)	Data	Species set	Source
Hawaiian Islands	range	naturalized	786	30.4	0.55	0.49–0.61	341.9	<0.0001	181	number of islands [9]	complete flora	[31]
Great Britain	range	archaeophytes[10]	98	8.3	0.28	0.096–0.48	8.64	0.0041	8000	number of quadrats [11]	complete flora	[36, 37]
Czech Republic	frequency	archaeophytes[10]	136	4.1	0.20	0.038–0.37	5.8	0.0174	7300	frequency scale [5]	complete flora	[29]

[1] Species classified as subspontaneous, casual, and very rare relicts from cultivation by Schäfer [28] where classified as casual, others as naturalized.

[2] Original qualitative frequency scale was transformed as follows: 1 – very rare, 2 – rare, 3 – scattered, 4 – common, 5 – very common. Mean value was used for species with different frequencies on particular islands.

[3] Number of islands on which the species was recorded (n = 9).

[4] Neophytes.

[5] Estimated on a five degree frequency scale of Clement and Foster [60]: 1 = 1–4 localities; 2 = 5–14; 3 = 15–49; 4 = 50–499; 5 = over 500 localities.

[6] A subset of naturalized neophytes with available information on the cumulative number of phytogeographical mapping units (quadrats of 11 × 12 km), from which the species was reported.

[7] One species with zero rate of spread was excluded from the original data.

[8] Species with the first record dated at 1000 A.D. (n = 24) were excluded from the data of Wester [31].

[9] Number of islands on which the species was recorded (n = 9).

[10] Residence time of particular species was taken as the middle of the period from which it is first reported in Great Britain [37] and Czech Republic [29].

[11] Cumulative number of hectads (phytogeographical mapping quadrats of 10 × 10 km) from which the species was reported.

The two measures may be supposed to be closely related because common species tend to be more widespread; this is supported by data from the Azores where both range and frequency are available for the same set of species and they are significantly correlated ($F = 831.6$, df 1, 908, $P < 0.0001$, $R^2 = 47.8\%$). However, they reflect different aspects of the distribution of alien plants: a species may be present in a low number of localities but occupying a large area, or it may be very frequent locally but with restricted overall distribution. For that reason, the two distribution measures were analyzed separately for those regions where data were available. Indeed, the results reported below indicate that using range and frequency, as defined for the purpose of the present paper, provides different results with respect to MRT.

Where information on the invasion status [35] was given or could have been inferred from unequivocal criteria (Tab. 1), alien species were classified into naturalized and casual, using the approach of Richardson et al. [42] and Pyšek et al. [35].

Statistical analysis

Where appropriate, the effect of minimum residence time (MRT) was evaluated by ANCOVAs, using a standardized measure of distribution or frequency (Tab. 1) as the response variable, standardized MRT as a covariate, and region or species group classified according to invasion status (Tab. 1) as factors.

For the Czech flora, where the effect of species traits together with the effect of MRT on the occurrence of alien species was evaluated, the standardized frequency was regressed on four standardized covariates (MRT, maximum plant height, start of flowering and propagule size) and five factors (introduction mode with three levels: accidental and deliberate either for ornamental or utilitary reasons; origin with three levels: America, Asia or Europe; life history with four levels: annual, biennial, perennial or woody plants; Grime's strategy with eight combinations; predominant dispersal mode with four levels: no special vector, water, wind or animals; data taken from [29]). In these analyses, minimal adequate models (MAMs) were determined, where all explanatory variables (factors and covariates) were significantly ($P < 0.05$) different from zero and from one another and all non-significant explanatory variables were removed. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model), and retention of significant terms [43]. To prevent biases to the model structures caused by correlation between variables, model simplifications were made by backward elimination from the maximal models by using step-wise analysis of deviance tables [44]. The results obtained were thus not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification. The appropriateness of the models was checked by plotting standardized residuals against fitted values, and by normal probability plots.

Path analysis [45] was used to explore the inter-relationship between the species distribution, MRT, and the rate of spread. This enabled an assessment of relative direct and indirect effects by which the MRT contributed to the current distribution of alien species through the rate of spread. An appropriate path model was suggested by the regression analysis of the species distribution measures, MRT, and the rate of spread. To achieve a comparable influence in absolute values, as with the minimal adequate models, each parameter was standardized to have a zero mean and variance of one.

Distribution of recent invaders is largely determined by residence time

For the three regions where data on complete alien floras were available (Azores, Czech Republic and Hawaiian Islands), there was a steady influx of alien species over the last two centuries (Fig. 1). Fluctuations in the pattern of increase in species numbers over time among regions usually reflect changes in research intensity or publication of important floral works [31] but sometimes can be interpreted by historical circumstances. That historical events markedly influence the immigration of alien plants into a region was

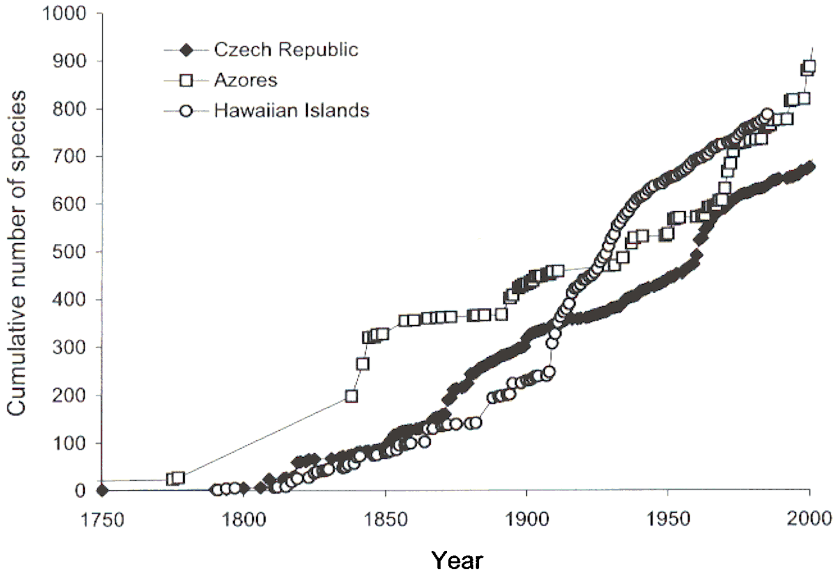

Figure 1. Temporal pattern of invasion into the three regions analyzed in the present study. Cumulative number of species reported up to a given year is shown for the Czech Republic (n = 691; time scale: 1750–2001, data: [27]), Azores (n = 910; 1589–2001; [26]) and Hawaii (n = 786; 1791–1985; [29]). See Table 1 for details on data sets.

documented for Taiwan. In this country, there was a clear acceleration of records of alien species about ten years after political events in 1940s to 1960s, which were associated with massive immigration of Chinese from the mainland [27].

Of the three regions shown in Figure 1, the increase in records of alien species is most regular for the Czech Republic. A previous paper [6] showed that the record of cumulative species numbers over time in this country was not significantly affected by research intensity which has been quite high since the beginning of the 19th century and fairly steady over the last 50 years or so [29, 46]. In any case, Figure 1 documents that alien species differ in their residence time and that the three data sets provide a reasonable basis for evaluating the effects of residence time on the current distribution of alien species in these regions.

Range and frequency

For all data sets, a significant relationship between the range/frequency of aliens and their MRT was found, and most models are highly significant. The percentage of variation in the data explained by MRT varies between 4.1 and 39.6, with higher values reached where complete data sets including both groups of aliens, i.e., naturalized and casual, were considered (Tab. 1). This can be regarded as strong evidence that residence time is an important factor affecting the range and frequency of alien species in various regions, including examples of continental (Czech Republic) and island floras (Azores, New Zealand, Hawaii) from Old (Azores, Czech Republic) and New World (Hawaii, New Zealand). The same relationships are indicated for complete alien floras and their subsets (Tab. 1). Additional evidence for a close relationship between the number of reported localities of alien species and MRT comes from literature data on naturalized grasses in Venezuela ($R^2 = 63\%$, $n = 111$, $P < 0.001$; [23]) and naturalized taxa of Fabaceae in Taiwan ($R^2 = 23\%$, $n = 48$, $P < 0.01$; [26]). The latter result can be compared with those obtained for alien representatives of the same family in the Czech Republic, where the number of current localities is also significantly related to MRT ($R^2 = 50\%$, $n = 56$, $P < 0.0001$; data from Pyšek et al. [29]). Rejmánek et al. [23]), using the data on alien plant species recorded in five north-western states of the USA, also found a significant dependence of the number of occupied counties on the minimum residence time ($R^2 = 18\%$, $n = 132$, $P < 0.001$). Finally, even for as few as seven invading plants in Kenya [47], the number of herbarium specimens highly significantly depended on the species' residence time ($R^2 = 82\%$, $n = 7$, $P < 0.01$).

Available data are too scarce to allow a rigorous statistical analysis of detailed patterns, but some conclusions can be drawn from comparing the statistical parameters of regressions summarized in Table 1. Before this can be done, some theoretical considerations need to be outlined, that is what can be inferred from the statistical regression relationships and how do they relate to residence time? Three parameters of the regression can be used for comparisons. First, the slope of the regression line indicates how suitable the recipient region is for invasions; the higher the slope, the more distributed alien species with the same MRT will be. Since all slopes were standardized (zero mean, variance one; Tab. 1), the slopes obtained for different group of taxa and regions are mutually comparable. Second, the proportion of explained variation (R^2) is another parameter and indicates how important MRT is in determining the outcome of invasions. R^2 parameters from linear regression models with the same number of explanatory variables and the same transformation can be directly compared with each other [48]. Whether an invading species will be successful in a new region depends on a complex interplay of numerous factors, that include traits of invading species, interaction with native biota, constraints imposed by existing communities, environmental variables such as climate and disturbances, but also chance and timing [19, 49–51]. The more important MRT is relative to other factors, the higher the proportion of variation it explains. A non-significant effect of MRT would indicate the completely overwhelming effect of the other factors, hence when the species was introduced would not affect its chances to become naturalized or invade. Third, the intercept with y axis for MRT = 0 refers to the start of the spread; the higher it is, the earlier the invasion started.

The data summarized in Table 1 allow for comparison with respect to the invasion status (Pyšek et al. [35]) and invaded region. First, it is plausible to compare the subsets of naturalized and casual species within each data set as the measures used to express the species' occurrence are the same. In the Azores using the range as a measure (Fig. 2), naturalized species invaded earlier than casuals, as indicated by a significant difference ($F = 114.0$; $df = 1, 907$; $P < 0.001$) between intercepts, and their range increased with MRT at a faster rate than that of casuals since the slopes were significantly higher for naturalized than casual species ($F = 36.62$; $df = 1, 907$; $P < 0.001$). Minimum adequate model (MAM) describing this pattern explained 43.1% of variance ($F = 228.7$; $df = 3, 906$; $P < 0.001$). Lower values of regression slopes for casuals compared to naturalized species reflect the fact that the latter generally occupy a wider range. If frequency is used as a measure, the results are the same, i.e., naturalized species invading earlier ($F = 190.4$; $df = 1, 908$; $P < 0.001$) and increasing their frequency with increasing MRT faster ($F = 117.1$; $df = 1, 908$; $P < 0.001$) than casuals (MAM: 29.7%; $F = 192.1$; $df = 2, 907$; $P < 0.001$). However, unlike the former model, casuals do not increase their frequency with MRT, as indicated by the slope from this relationship not being significantly different from zero ($F = 1.34$; $df = 1, 907$; NS). Comparison of the two measures available for the Azores, i.e., the number of occupied islands (as a proxy for range) and species frequencies, seems to indicate that while in naturalized species both range and frequency increase with MRT, for casual aliens this is true only for range but not for frequency. This is in accordance with the characteristics of both species groups; casuals are often

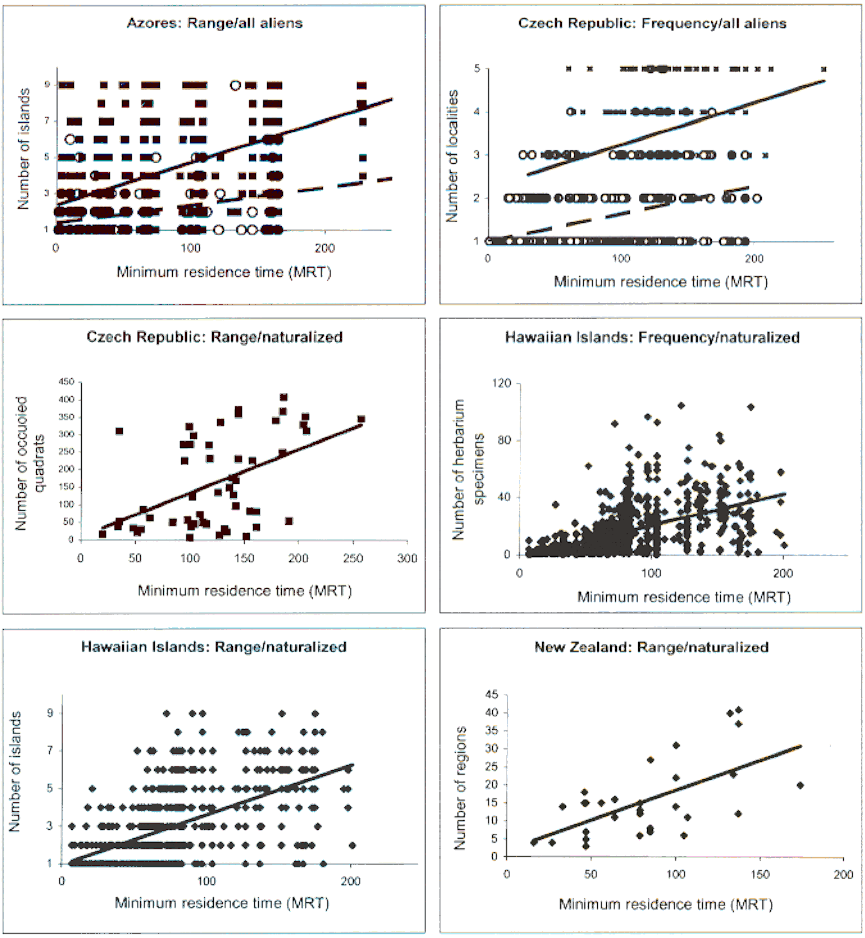

Figure 2. Examples of relationships between frequency and distribution range of alien species and minimum residence time (MRT, in yrs). See Table 1 for parameters of standardized relationships. Empty circles and dashed line refers to casual, solid squares and solid line to naturalized species on figures referring to all aliens.

rare species that do not persist in the wild without repeated input of diaspores by human activities [42]. Obviously, the longer the casuals are present the more islands they colonize but the propagule pressure might have been too low to ensure simultaneous increase in frequency; regardless of how long they have been present, their frequency is on average the same. This suggests that for casuals “being at the right place at the right time”, i.e., earlier than others, manifests primarily into a better chance to achieve a wide range but not to become more frequent.

The pattern is different in the Czech Republic, where only frequency is available as a measure. Naturalized species again invaded significantly earlier than casuals (F = 250.9; df = 1, 688; P < 0.001) and the number of localities they occupy increased with MRT at a faster rate than that of casuals (F = 250.9; df = 1, 688; P < 0.001). In total, 54.6% of variance is explained by MAM (F = 275.0; df = 3, 687; P < 0.001). Unlike in the Azores, casual species that are present for a long time have higher frequencies than those that arrived early. As the measures of frequency are very similar for both regions (Tab. 1), the difference does not seem to be an artefact of the way the data were recorded. It may be hypothesized that differences between both regions, namely in propagule pressure, which is higher in a densely populated mainland region with intensively managed landscape and developed industry [46], are responsible for the observed difference. That might explain why casuals increased their frequency with increasing MRT in the Czech Republic but not in the Azores.

Second, two comparisons are possible *among regions*. Four data sets provide information on the range of naturalized taxa (Tab. 1), which significantly increased with increasing MRT (MAM: 32.9%, F = 872.0; df 1, 1778; P < 0.001). In the Azores, Czech Republic, Hawaii and New Zealand (the latter based on a subset of woody plants only), neither the start of invasion (F < 0.01; df = 3; 1775; NS) nor the rate of increase in range with MRT (F = 0.67; df = 3, 1778; NS) significantly differed among these regions.

Measures of frequency are available for complete alien floras (including casual species) of the Azores and the Czech Republic (Tab. 1). Both regions were invaded at the same time (F < 0.01; df = 1, 1598 P < 0.001) but the rate of increase in frequency was significantly (F = 6.09; df = 1, 1599; P < 0.05) higher for the Czech Republic than the Azores.

Invasion status

Residence time affects not only the range and frequency of an alien species but also its invasion status, i.e., whether it persists as casual or becomes naturalized or invasive [42]. These two measures, distribution and status, are closely related (naturalized and invasive species are usually distributed over a wider range and exhibit higher frequencies than casuals) but not necessarily; many alien species are naturalized only locally [29, 52] and some casuals may be quite distributed, but still relying on repeated input of diaspores [35]. Table 2 shows the difference in the mean MRT between alien species classified with respect to invasion status. The pattern is consistent for the three floras (Azores, Czech Republic and New Zealand) and corresponds to that found for the range/frequency. Casual species have significantly shorter mean MRT than naturalized aliens in both the Azores and the Czech Republic, and within the latter region, invasive species have a tendency for a longer MRT than those that are classified as naturalized but not invasive (Richardson et al. [42] and Pyšek et al. [35]). The same holds for New Zealand, where the difference between naturalized and invasive species appears significant (Tab. 2).

Table 2. Mean minimum residence time (MRT) for species with different invasion status in regional floras. Means bearing the same letter within a region are not significantly different at $p = 0.05$ in ANOVA or LSD test. Invasion status follows the definition in Richardson et al. [42] and Pyšek et al. [35].

		Minimum residence time			
Region	Invasion status	Mean	S.D.		Source
Azores	casual	57.5 a	65.1	210	[28]
Azores	naturalized	102.8 b	69.8	700	[28]
Czech Republic	casual	76.3 b	51.4	523	[29]
Czech Republic	invasive	140.0 a	41.5	54	[29]
Czech Republic	naturalized (excl. invasive)	126.3 a	47.8	114	[29]
Czech Republic	naturalized	130.7 a	46.2	168	[29]
New Zealand	invasive	106.1 a	31.3	11	[32]
New Zealand	naturalized	63.0 b	37.3	22	[32]

Importance of the residence time relative to other factors

The probability of invasion success increases with residence time [24] but in particular floras, a long minimum residence time does not always correlate with more localities. For example, among Fabaceae in Taiwan several genera have more than one naturalized species with similar MRTs and these species differ in invasion success; some occupy many habitats whereas others have never spread out. Four of the six naturalized species of the genus *Crotalaria* have similar MRTs but the numbers of recorded localities range from four to 70. Wu et al. [26] suggested two explanations: i) the species with more localities might have been spread more efficiently by human activities or, ii) they differ in their invasiveness. As pointed out above, the higher the variation in invasiveness of individual species and the more important the effect of local conditions and recipient vegetation, the less important residence time will be for determining the result of invasion.

To obtain an insight into the role residence time plays relative to other factors, current frequency of alien species in the Czech Republic was related to several life history characteristics that were used as explanatory variables and so was MRT of each species in the data set. The minimal adequate model explained 52% of variance in the frequency of alien species (F = 7.40; df = 28, 197; $P < 0.001$). Grime's life strategy, area of origin and dispersal mode had a direct effect on the number of localities, while life history and height significantly contributed to the explained variation in interactions with other variables (Tab. 3). MRT did not exhibit a direct effect on the number of localities but significantly interacted with both life strategy and life history. Compared to other factors, the effect of MRT was very strong. Its interaction with Grime's life strategy and species' life history explained 35.9% of variance

Table 3. Significance (F, df, P) of explanatory variables in the minimal adequate model of the frequency of alien species in the Czech Republic when regressed on the minimum residence time together with other species traits (factors are in *italics*, other traits are standardized covariates).

Explanatory variable	F	df	P
Grime life strategy	2.47	6, 203	<0.05
Origin	5.18	2, 199	<0.01
Dispersal mode	3.59	3, 200	<0.05
(*Grime life strategy*) × (minimum residence time)	2.49	6, 203	<0.05
(*Life history*) × (minimum residence time)	4.03	3, 200	<0.01
(*Grime life strategy*) × (height)	2.86	7, 204	<0.01

($F = 14.52$; $df = 10, 207$; $P < 0.001$), while all species traits not including MRT together explained only 16.1% of variance ($F = 3.62$; $df = 18, 215$; $P < 0.001$). This can be considered as a robust evidence of the overwhelming effect of the residence time on current pattern in the distribution of alien species. It must be kept in mind that the results reported here concern a single region, but given that the simple regression of frequency on MRT for this data set is well within the range of values found for other models summarized in Table 1, it might be of general validity.

Data on naturalized aliens of the Czech Republic allow another view on the relative importance of MRT. Williamson et al. [30] give the maximum rate of spread for a subset of species that were found to have a straight section on a logarithmic plot of the cumulative number of quadrats over time. The rate of spread of an alien species in the invaded region is constrained by environmental factors, biological and ecological barriers as well as the resistance of local plant communities to invasion; hence the variation in this parameter reflects the relative importance of these factors. Multiple regressions, relating the distribution range to both explanatory variables yielded a significant relationship ($F = 7.39$; $df = 2, 24$; $P < 0.01$) and explained 38.1% of the variance. Both explanatory variables, i.e., the MRT ($F = 14.16$; $df = 1, 25$; $P < 0.001$; $R^2 = 36.5\%$) and the rate of spread ($F = 8.87$; $df = 1, 25$; $P < 0.01$; $R^2 = 22.9\%$) were significant and contributed to the current distribution range of naturalized aliens. Path analysis, a convenient tool for evaluating the relative effect of these two factors (Tab. 4), revealed strong direct effects of MRT, a positive one on range (b_2) and negative on the rate of spread (a_1). The earlier the species arrived, the wider range it occupies, and the later it arrived, the more slowly it has been spreading. When summing the positive direct and negative indirect effect of MRT (the latter manifested via the rate of spread) on range ($b_2 + a_1b_1$), the total effect of MRT on the current distribution appears to be weaker than the total effect of the rate of spread (Tab. 4).

Residence time is therefore less important than the rate of spread in determining the present distribution range of naturalized Czech aliens. This result

Table 4. Path and effect coefficients of the path model of the distribution range of naturalized aliens in the Czech Republic (expressed as the number of phytogeographical mapping quadrats) as a function of MRT and rate of spread (data from [30]). Path coefficients a_1, b_1 and b_2 represent direct effects; a_1 is the regression slope for standardized variables rate of spread and MRT; b_1 and b_2 are standardized regression slopes from multiple regression of range as a function of MRT and rate of spread. Indirect effects are calculated as a product of path coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects.

Path coefficients:	
a_1, effect of MRT on the rate of spread (direct)	–0.63
b_1, effect of the rate of spread on range (direct)	0.62
b_2, effect of MRT on range (direct)	0.78
a_1b_1, effect of MRT on range (indirect)	–0.39
Effect coefficients:	
$b_2 + a_1b_1$, MRT on range (total)	0.39
b_1, rate of spread on range (total)	0.62

is in a seeming contradiction with the results provided by the minimal adequate model using species traits, discussed above (Tab. 3). A comparison of these two models indirectly indicates the importance of landscape features and recipient communities [30]. In the minimal adequate model, including species characteristics, some proportion of variation remains unexplained – a part that can be related to environmental variables. Residence time therefore seems to be more important than species traits on their own but if the rate of spread, which can be viewed as a proxy for the complex effect of all factors related to invasions, is included, those factors explain the distribution range of aliens better than the time of their arrival.

Residence time not only represents another dimension of propagule pressure [25] but also integrates culturally-determined processes [53]. With increasing time since the first introduction, the probability also increases that safe sites for establishment appear as a result of natural disturbances and human-made changes in site conditions that both may facilitate invasions. For example, *Ailanthus altissima* in central Europe started to spread vigorously only after rubble sites appeared in destroyed cities after World War II. With increasing time since the first introduction, the probability also increases that the introduced species is propagated by various modes of secondary releases by humans (e.g., deliberate planting or sowings in the wild) that may overbridge gaps between suitable, but not accessible sites [54]. It should be therefore borne in mind that the rate of spread also integrates spreading resulting from ongoing human activities.

Historical invaders: the effect of residence time still detectable

One might expect that in archaeophytes, historical invaders that were arriving for several millennia since the beginning of Neolithic agriculture until the end of Medieval, the effect of the time of arrival would be no longer obvious. The opposite is true: for both data sets providing the information on approximate dates of the first records ([29, 37]; Tab. 1), the current frequency or range of archaeophytes in the region increases with MRT, indicating that the earliest newcomers are more common than those that arrived later (Fig. 3). The rather low proportion of explained variation (4.1 and 8.3%, Tab. 1) reflects that residence time is, compared to other factors affecting the present distribution, of lower importance in archaeophytes than in most data sets covering recent newcomers.

Archaeophytes in the Czech Republic and Great Britain do not differ in the rate at which their distribution increases with MRT (F = 0.41; df = 1, 232; NS). This means that in both regions, MRT has the same effect on the invasion by archaeophytes and neither of the regions appears to have been more suitable for invasion by this group of species. The reason might be that arable land, a typical habitat of archaeophytes [33, 37, 55], is to a large extent similar in different regions and so it is the management that affects the occurrence of archaeophytes [43].

Interestingly, the mean MRT for British archaeophytes is highly significantly lower than that of Czech archaeophytes. On average, the invasion of

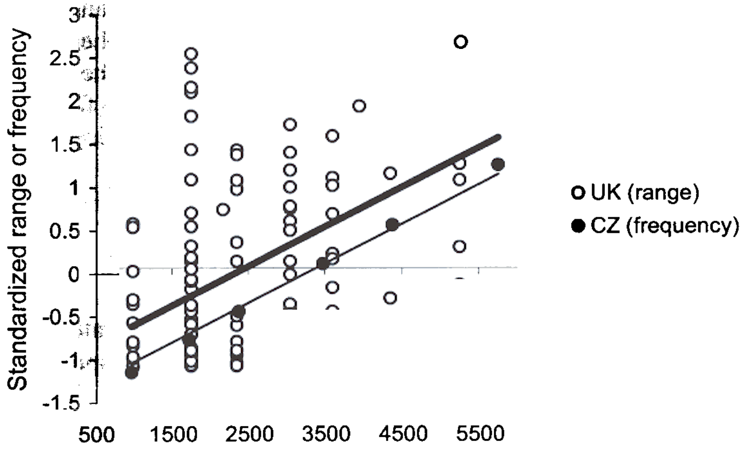

Figure 3. The relationship between standardized current range (UK) and frequency (Czech Republic) of archaeophytes and their non-standardized MRT (yrs). Note that for the average standardized range and frequency (having a zero mean) the MRT is 2,461 years for UK but 3,388 years for the Czech republic; this difference is statistically significant (F = 23.25; df = 1, 232; P < 0.001). The slopes are not statistically different (F = 0.42; df = 1, 232; NS); their values for both range (UK) or frequency (CZ) and MRT standardized are in Table 1.

archaeophytes reached the area of the present Czech Republic by nearly thousand years earlier than that of Great Britain (Fig. 3). This primarily reflects that the onset of Neolithic agriculture in Great Britain (c. 6,000 yrs B.P. [37]) was postponed compared to Central Europe (c. 7,300 yrs B.P. [29]). One might expect the different geographical distances of these regions from the Mediterranean, the area where archaeophytes originated, to play a role. Britain is located further to the northwest, i.e., more distant, but the results do not suggest that there was a delay in invasion by archaeophytes in this region due to the time needed for reaching it. They rather indicate that as Neolithic people brought about not only crops but also weeds [43], the invasion by archaeophytes in both regions started immediately with the beginning of agriculture.

Discussion

The data analyzed above provide firm evidence that residence time is an important factor that should be considered in studies on plant invasions. Our study confirms the conclusions of previous papers; so far, the effect of residence time was highlighted in the literature namely by papers of Rejmánek and his collaborators [23–27]. More evidence is available from New Zealand, where the most widespread invaders are those which were introduced early [24], and Tasmania [23]. Rejmánek et al. [23] concluded that the suggestions made recently by some ecologists, that there is some constant proportion of invasive taxa recruiting from the pool of introduced taxa [40, 56, 57] is unlikely to hold. Rejmánek et al. [23] suggest that the reasonably constant proportion of alien taxa that invade across a wide range of systems is, at least partly, a result of the similar mean residence times of species in alien floras.

It should be noted that the dates of first species records are not in fact the exact dates of invasion, i.e., time at which the species first occurred in the wild after it has been unintentionally introduced or escaped from cultivation. That it is usually not known exactly when this happened is why the term of "minimum" residence time was suggested [24–26]. Nevertheless, this approach is justified: It can be reasonably expected that the more common a species is the more often it is recorded by floristic surveys, hence that common species were first recorded earlier than less common species. For multi-species analyses, the comparability increases if the information on all species in the set is derived from the same primary sources [30, 46]. In general, potential for generalization based on floristic records increases if biases associated with such data are taken into account. In some papers attempts have been made to control for the increasing intensity of floristic research over analyzed periods by involving the information on the dynamics of native species under the same scenario [41, 47] or on the increasing quantity of herbarium collections [57].

The present overview extends the view that residence time is important. We showed that in modern invasions on the time scale of centuries, the longer the alien species are present in the territory the higher their chance 1) to pass successfully through the stage of casual occurrence and become naturalized, and 2) to become more distributed and invade over a larger range. The former is documented by higher mean MRT found in naturalized than in casual species (see also [25]), the latter by a significant positive relationships between measures of invasive species distribution and MRT.

In Europe, the effect of residence time is still obvious after several millennia of plant invasions. Not surprisingly, it is less pronounced in archaeophytes than in neophytes but statistically detectable, even though the data used to reconstruct the history of invasions on a time scale of millennia must be necessarily less precise and more biased than reconstructions based on herbaria and published records that are available for neophytes.

Can we compare the effect of residence time between these two distinct groups of European alien species, i.e., archaeophytes and neophytes (historical invaders *versus* recent newcomers)? Simple comparison along the lines of the present paper would suggest investigation of the current distribution of both groups. That archaeophytes are more common than neophytes has been repeatedly documented using the Czech flora [29, 55] and the same can be shown for Great Britain. Number of quadrats (hectads) from which the species is reported from the period 1987–1999 in Preston et al. [36] is significantly higher ($F = 173.3$; $df = 1, 1751$; $P < 0.001$) for archaeophytes (as classified in Preston et al. [37], $n = 231$) than for neophytes ($n = 836$). However, this pattern cannot be interpreted as a consequence of different residence times only. Archaeophytes, mostly weeds of arable land recruited from the Mediterranean area, represent an ecologically distinct group with specific features and differ from neophytes in many respects: life form and strategy and habitat requirements in particular [55]. That they are more common than neophytes is certainly, at least in part, associated with their long-term presence in invaded regions – there is no reason to expect that the principles valid for archaeophytes and neophytes separately, on two different time scales, do not apply for the entire history of plant invasions in Europe. However, given the pronounced difference in habitat affinities of both groups, to decouple the effect that residence time might have had on archaeophytes and neophytes from other factors, both groups should be compared in a habitat where their occurrence overlaps, i.e., arable land. Such analysis is available and shows that the historical associations are very subtle, yet clearly detectable at present: Pyšek et al. [43] found that archaeophytes are common in old crops introduced with the beginning of agriculture, such as cereals, but poorly represented in relatively recently introduced crops (rape, maize), where neophytes are most numerous. These patterns reflect the history of plant invasions in Central Europe. Neolithic agriculture, introduced from the Near East in the 6th millennium BC, brought archaeophytes with crops and, by creating intense and continuous propagule pressure and imposing new agricultural management, facilitated their invasion. By contrast, the crops introduced during the past five centuries and their specific agrotechnical management has supported spreading of other weed species, mainly invaders from overseas. In addition, archaeophytes respond like neophytes to some variables (climate, seasonal development of crop) and, alternatively, like native species to other variables (increasing agricultural intensification through time, human population density). This indicates that the identity of crop and its introduction history are important factors determining the current distribution of archaeophytic weeds and acting in concert with the residence time of associated weeds.

Finally, a question may be raised: what is the effect of residence time at spatial scales other than those considered in the present paper? For individual invading species residence time is usually not known at local scale. An exception is the study of Müllerová et al. (Institute of Borany, Průhonice, Czech Republic; unpublished observation), who documented, by using historical aerial photographs, 40 years of invasion by *Heracleum mantegazzianum* in the Czech Republic. Knowing when this species appeared in particular localities allowed quantification of the relative importance of the rate of spread and residence time for the outcome of invasion. Both residence time and the rate of spread significantly contributed to the resulting size of invading populations, and the direct effect of the residence time was four times smaller than that of the rate of invasion. However, since the residence time affected the rate of invasion (which was faster in sites where the invasion started later), it exerted an indirect effect on the size of invading populations. Consequently, the total effect of the residence time was about the same as that of the rate of spread (Müllerová et al., unpublished observation).

This is different from the results of path analysis performed on a number of naturalized species of the Czech flora discussed above (Tab. 4) where the rate of spread turned out to be more important than residence time. Both analyses can be only compared with the awareness of the differences in data in mind. Nevertheless, the higher relative importance of residence time found in the study on *H. mantegazzianum* might reflect that 1) the rate of spread is closely associated with a species' invasion potential and *H. mantegazzianum* is one of the most successful European invaders [59]. It is likely that other, less competitive alien species would be more limited by local constraints which would accordingly increase the average importance of the rate of spread on behalf of the residence time. 2) For *H. mantegazzianum*, the rate of invasion was directly measured from aerial photographs capturing the area invaded at particular time intervals which is a more exact measure of the rate of spread than estimation from cumulative increase in distribution over time [30, 32]. Unfortunately, data that would make it possible to compare the patterns at different scales and among species are not available.

Lack of data is a major obstacle to disentangling the intriguing phenomenon of residence time in plant invasions. High quality data sets, using the same classification criteria of the species' invasion status [35] and based on detailed historical information are unfortunately rare. To proceed further, more data are needed to allow for analyses that would make it possible to relate the effect of residence time to environmental characteristics and local conditions of invaded regions.

Acknowledgments
Four anonymous reviewers are acknowledged for the comments on the manuscript. We thank Ivan Ostrý for technical support. This study was supported by the European Union within the FP 6 Integrated Project ALARM (GOCE-CT-2003-506675) by grant no. 206/03/1216 from the Grant Agency of the Czech Republic, by the institutional long-term research plan no. AV0Z60050516 funded by the Academy of Sciences of the Czech Republic and by grant MSMT 0021620828 from the Ministry of Education of the Czech Republic.

References

1 Noble IR (1989) Attributes of invaders and the invading process: terrestrial and vascular plants. In: JA Drake, HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek, M Williamson (eds): *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK, 301–313

2 Rejmánek M (1995) What makes a species invasive? In: P Pyšek, K Prach, M Rejmánek, M Wade (eds): *Plant invasions: general aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands, 3–13

3 Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. *Biol Conserv* 78: 171–181

4 Goodwin BJ, McAllister AJ, Fahrig J (1999) Predicting invasiveness of plant species based on biological information. *Conserv Biol* 13: 422–426

5 Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *Amer Nat* 159: 396–419

6 Pyšek P, Sádlo J, Mandák B, Jarošík V (2003) Czech alien flora and a historical pattern of its formation: what came first to Central Europe? *Oecologia* 135: 122–130

7 Daehler CC (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biol Conserv* 84: 167–180

8 Prinzing A, Durka W, Klotz S, Brandl R (2002) Which species become aliens? *Evol Ecol Res* 4: 385–405

9 Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105: 229–238

10 Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16: 199–204

11 Lonsdale M (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536

12 McKinney M (2001) Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biol Conserv* 100: 243–252

13 McKinney M (2004) Measuring floristic homogenization by non-native plants in North America. *Global Ecol Biogeogr* 13: 47–53

14 Sax DF (2000) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J Biogeogr* 28: 139–150

15 Sax DF, Gaines SD, Brown JH (2002) Species invasions exceeds extinctions on islands worldwide: a comparative study of plants and birds. *Amer Natur* 160: 766–783

16 Thébaud C, Simberloff D (2002) Are plants really larger in their introduced ranges? *Amer Natur* 157: 231–236

17 Richardson DM, Cowling RM (1992) Why is mountain fynbos invasible, and which species invade? In: B van Wilgen, DM Richardson, FJ Kruger, BJ van Hensbergen (eds): *Swartboskloof – fire in South African mountain fynbos*. University of Cape Town, 161–179

18 Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77: 1655–1661

19 Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions – the role of mutualisms. *Biol Rev* 75: 65–93

20 Lake JC, Leishman MR (2003) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117: 215–226

21 Kowarik I (1995) Time lags in biological invasions with regards to the success and failure of alien species. In: P Pyšek, K Prach, M Rejmánek, M Wade (eds): *Plant invasions: general aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands, 15–38

22 Crawley MJ (1989) Chance and timing in biological invasions. In: JA Drake, HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek, M Williamson (eds): *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK, 407–423

23 Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) *Ecology of invasive plants: state of the art*. In: HA Mooney, RM Mack, JA McNeeley, L Neville, P Schei, J Waage (eds): *Invasive alien species: searching for solutions*. Island Press, Washington, DC, 104–161

24 Rejmánek M (2000) Invasive plants: approaches and predictions. *Austral Ecol* 25: 497–506

25 Rejmánek M, Richardson DM, Pysˇek P (2005) Plant invasions and invasibility of plant communities. In: E van der Maarel E (ed.): *Vegetation ecology*. Blackwell Science, Oxford, UK, 332–355

26 Wu S-H, Chaw S-M, Rejmánek M (2003) Naturalized Fabaceae (Leguminosae) species in Taiwan: the first approximation. *Bot Bull Acad Sin* 44: 59–66

27 Wu S-H, Hsieh C-F, Chaw S-M, Rejmánek M (2004) Plant invasions in Taiwan: insights from the flora of casual and naturalized alien species. *Diver Distrib* 10: 349–362

28 Schäfer H (2003) Chorology and diversity of the Azorean flora. *Diss Bot* 374: 1–128

29 Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186

30 Williamson M, Pyšek P, Jarošík V, Prach K (2005) On the rates and patterns of spread of alien plants in the Czech Republic and Britain. *EcoScience*; *in press*

31 Wester L (1992) Origin and distribution of adventive alien flowering plants in Hawaii. In: CP Stone, CW Smith, JT Tunison (eds): *Alien plant invasions in native ecosystems of Hawaii: management and research*. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, 99–154

32 Bellingham PJ, Duncan RP, Lee WG, Buxton RP (2004) Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. *Oikos* 106: 308–316

33 Holub J, Jirásek V (1967) Zur Vereinheitlichung der Terminologie in der Phytogeographie. *Folia Geobot Phytotax* 2: 69–113

34 Schroeder FG (1969) Zur Klassifizierung der Anthropochoren. *Vegetatio* 16: 225–238

35 Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143

36 Preston CD, Pearman DA, Dines TD (2002) *New atlas of the British and Irish flora*. Oxford University Press, Oxford, UK

37 Preston CD, Pearman DA, Hall AR (2004) Archaeophytes in Britain. *Bot J Linn Soc* 145: 257–294

38 Florence J, Waldren S, Chepstow-Lusty AJ (1995) The flora of the Pitcairn Islands: a review. *Biol J Linn Soc* 56: 79–119

39 Waldren S, Weisler MI, Hather JG, Morrow D (1999) The non-native vascular plants of Henderson Island, South-Central Pacific Ocean. *Atoll Res Bull* 463

40 di Castri F (1989) History of biological invasions with special emphasis on the Old World. In: JA Drake, HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek, M Williamson (eds): *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK, 1–30

41 Delisle F, Lavoie C, Jean M, Lachance D (2003) Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *J Biogeogr* 30: 1033–1042

42 Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity Distrib* 6: 93–107

43 Pyšek P, Jarošík V, Chytrý M, Kropác Z, Tichý L, Wild J (2005) Alien plants in temperate weed communities: Prehistoric and recent invaders occupy different habitats. *Ecology* 86: 772–785

44 Crawley MJ (1993) *GLIM for ecologists*. Blackwell Scientific Publications, Oxford, UK

45 Sokal R, Rohlf FJ (1995) *Biometry. 3rd edition*. Freeman, New York

46 Pyšek P, Prach K (2003) Research into plant invasions in a cross-roads region: history and focus. *Biol Invas* 5: 337–348

47 Stadler J, Mungai G, Brandl R (1998) Weed invasion in East Africa: insights from herbarium records. *Afr J Ecol* 36: 15–22

48 Anderson-Sprecher R (1994) Model comparisons and R^2. *Amer Statist* 48: 113–117

49 Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. *Plant Ecol* 135: 79–93

50 Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88: 528–534

51 Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67–70

52 Williamson M (1993) Invaders, weeds and the risk from genetically modified organisms. *Experientia* 49: 219–224

53 Kowarik I (2003) *Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa*. Verlag Eugen Ulmer, Stuttgart, Germany

54 Kowarik I (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. *Biol Invas* 5: 293–312

55 Pyšek P, Richardson DM, Williamson M (2004) Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. *Diver Distrib* 10: 179–187

56 Williamson M (1996) *Biological invasions*. Chapman and Hall, London, UK

57 Williamson M, Fitter A (1996) The varying success of invaders. *Ecology* 77: 1661–1666

58 Mihulka S, Pyšek P (2001) Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *J Biogeogr* 28: 597–609

59 Weber E (2003) *Invasive plant species of the world. A reference guide to environmental weeds*. CABI Publishing, Wallingford, UK

60 Clement EJ, Foster MC (1994) *Alien plants of the British Isles. A provisional catalogue of vascular plants (excluding grasses)*. Botanical Society of the British Isles, London, UK