Inclusion of Native and Alien Species in Temperate Nature Reserves: an Historical Study from Central Europe

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Abstract: *We studied the establishment and inclusion of native and alien plant species in nature reserves in the Czech Republic. Our aim was to answer the following questions: Do young and old nature reserves contain the same proportion of invasive plant species? Does the time of their introduction affect their representation in these reserves? We obtained recent lists of vascular plant species for 302 reserves established since 1838 and designated the species as native or alien. We divided the latter category into archaeophytes and neophytes, introduced before and after 1500, respectively. The increase in the number of reserves and species was evaluated by inclusion curves. For inclusion curves describing an increase in the number of reserves, the estimated time of 50% inclusion indicated when half the reserves of a particular type were established. For inclusion curves describing an increase in the number of species, the estimated time of 50% inclusion indicated when half the species of a particular category (native species, all aliens, archaeophytes, neophytes), reported from the country, were included in the nature reserves. The forest and dry-grassland reserves were established earlier than those in wetlands and peat bogs, whereas humid-grassland reserves tended to be the most recently established. Half the native species were included significantly earlier (after 25 years) than half of alien species (86 years), and half the neophytes were included later (143 years) than half the archaeophytes (31 years). Early reserves harbor a significantly lower number of alien species than those established later. These reserves include a higher proportion of the Czech Republic's native species and archaeophytes than of its neophytes. There was no difference in the relative rates of inclusion of native species, archaeophytes, and neophytes. However, the fact that the same inclusion rate applies to neophytes, a group with an increasing species pool, as to archaeophytes and native species, which both have constant species pools, suggests that natural vegetation in nature reserves is an effective barrier against the establishment of alien species. On a historical time scale, the early establishment of nature reserves in a given country decreases the probability that the reserve will be invaded by alien plants.*

Inclusión de Especies Nativas y Exóticas en Reservas Naturales Templadas: un Estudio Histórico de Europa Central

Resumen: *Estudiamos el establecimiento e inclusión de especies de plantas nativas y exóticas en reservas naturales en la República Checa. Nuestra meta era contestar las siguientes preguntas: ¿Contienen la misma proporción de especies de plantas invasoras las reservas recientes y antiguas? ¿El tiempo que llevan introducidas afecta su representación en estas reservas? Obtuvimos listas recientes de las especies de plantas vasculares para 302 reservas establecidas desde 1838 y designamos a las especies como nativas o introducidas. Dividimos a esta última categoría en arquefitas y neofitas (introducidas antes y después de 1500, respectivamente). Se evaluó el incremento en el número de reservas y especies mediante curvas de inclusión. Para curvas de inclusión que describían un incremento en el número de especies, el tiempo estimado de 50% de inclusión indicaba cuando se incluyeron la mitad de las especies registradas para el país, de una categoría*

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particular (especies nativas, todas las exóticas, arquefitas y neofitas) en reservas naturales. Las reservas forestales y de pastizales secos se establecieron antes de que se establecieran las de humedales y turberas, mientras que las reservas de pastizales húmedos tendieron a ser las establecidas más recientemente. La mitad de las especies nativas se incluyeron significativamente antes (después de 25 años) que la mitad de las especies exóticas (86 años), y la mitad de las neofitas fueron incluidas después (143 años) que los arquetipos (31 años). Las reservas más antiguas contienen un número significativamente menor de especies exóticas que las establecidas más recientemente. Estas reservas incluyen una mayor proporción de especies nativas y de arquetipos que de neofitas de la República Checa. No hubo diferencia en las tasas relativas de inclusión de especies nativas, arquefitas y neofitas. Sin embargo, el hecho de que la misma tasa de inclusión vale tanto para neofitas, un grupo cuyo número de especies aumenta, como para arquefitas y especies nativas, con números de especies constantes, sugiere que la vegetación natural en las reservas constituye una barrera efectiva contra el establecimiento de especies exóticas. En una escala de tiempo histórico, el establecimiento temprano de reservas naturales en un país determinado disminuye la probabilidad de que la reserva sea invadida por especies exóticas.

Introduction

Biological invasions are a major threat to diversity and have been receiving increasing attention (Drake et al. 1989; Pyšek et al. 1995; Rejmánek 1996, 1999; Williamson 1996; Davis et al. 2000, Richardson et al. 2000*a*, 2000*b*). Although much of the information on plant invasions in temperate zones comes from urban and otherwise disturbed environments harboring high proportions of alien species (Kowarik 1990, 1995; Pyšek 1998), invasions into natural vegetation have always been of special importance (Duffey & Usher 1988; Pyšek et al. 2002*b*). Alien species occur in all nature reserves, and the situation is more disturbing in the Southern Hemisphere (Usher et al. 1988) than in the Northern Hemisphere (Loope 1992). All alien species are potentially dangerous in nature reserves (Cole & Landres 1996), and those that naturalize and are invasive (for terminology see Richardson et al. 2000*b*) may replace native flora or even change ecosystem properties (Vitousek 1990; Gordon 1998) and thus cause management problems (Berger 1993). Reserves are a suitable laboratory for studying the factors that determine the distribution of alien plants and the nature and effectiveness of the barriers alien species must overcome if they are to naturalize and subsequently invade (Richardson et al. 2000*b*). Knowledge of these factors may be used in the management and control of alien plants.

The territory of the Czech Republic is suitable for studies of plant diversity at a wide landscape scale (Kočí 2001; Duchoslav 2002; Pyšek et al. 2002*b*). The region varies in topography, climate, and geology, and a number of habitats can be found even in relatively small areas. Habitat and environmental diversity are associated with a rich flora, and the prevailing climate favors forest (Neuhäuslová & Moravec 1997; Sádlo & Bufková 2002). A long tradition of nature protection in the Czech Republic has resulted in a dense network of nature reserves, including all major vegetation types within a relatively large-scale and diverse region (Maršáková-Němejcová & Mihálik 1977).

We considered the inclusion of plant species in nature reserves in the Czech Republic over a historical time scale and sought to answer the following questions: (1) Are reserves of different types established at similar rates or is there an order to the historical designation of different types of reserves? What implications does this have for vegetation types that were protected earlier or later? (2) Are old invaders ecologically distinct from new invaders, and do they differ in their pattern of immigration into reserves? (3) Do reserves pose barriers to invasions—in other words, do reserves of different ages pose different degrees of resistance to invasive species?

Methods

Data

We collected data on the nature reserves in the Czech Republic. The area studied covers 78,854 km^2 (lat. 48°30′–51°05′, long. 12°05′–18°50′. In 1996 there were 1757 small nature reserves in the Czech Republic, covering 823 km^2, or 1.05% of the area of the country (Kos & Maršáková 1997). For 302 (17.2%) of these reserves, there were data suitable for our study. Most of the important, large reserves covering major habitats were included, yielding a total area of 365 km^2 (0.46% of the area of the country and 44.2% of the total area of nature reserves; Pyšek et al. 2002*a*).

We obtained species lists for each reserve from published records and unpublished floristic inventories deposited at the Agency for Landscape Protection. These inventories are carried out regularly by professional botanists who are asked to collect data in a standardized way (Maršáková 1987). We used the most recent species list available for each reserve. Vascular plant species were classified as native or alien. We divided the latter group into (1) archaeophytes (i.e., introduced into the country before 1500 A.D.) and (2) neophytes (introduced after 1500 A.D.). This classification system is widely used in Central European phytogeographical studies (for details: Holub & Jirásek 1967; Schroeder 1969; for comparison with other systems: Pyšek 1995; Pyšek et al. 2002*c*). We did not, however, distinguish between taxa introduced deliberately by humans from those that arrived accidentally. We categorized both these groups as neophytes. The number of species in each of the three groups (native, archaeophytes, neophytes) and the total number of species were recorded for each reserve. When the same species was found in more than one reserve, we counted it only once (in the year when the oldest reserve of those with which it occurred was established). The number of aliens was obtained by summing the numbers of archaeophytes and neophytes.

For each nature reserve, we obtained the following data: year of establishment (from Kos & Maršáková 1997); reserve age (period from year of establishment to present); reserve area (Kos & Maršáková 1997); prevailing vegetation type—that covering most of the reserve area—categorized as pine forest, beech forest, oak forest, hornbeam forest, spruce forest, scree and ravine forests, humid grasslands (meadows, pastures, and saline habitats), wetlands (including pond shores and alder forests), mires, peat bogs, and fens or dry grasslands (steppe vegetation, including scrub in dry habitats) (Chytrý et al. 2001); phytogeographical region in which a reserve is located (Thermophyticum, with dry temperate flora and vegetation; Mesophyticum, with temperate flora and vegetation; or Oreophyticum, with mountain flora and vegetation) (Hejný & Slavík 1988); climatic district (cold, moderately warm, and warm) based on a combination of various climatic characteristics, including number of days with temperature exceeding 10° C (<120; 120–160; >160 days), mean January temperature (<−4°; −4° to −2°; >−2° C), mean July temperature (<15°; 15–18°; >18° C), sum of precipitation in vegetative period (>600; 400–600; <400 mm), and number of days with snow cover (>120; 60–120; 40–60 days) (Quitt 1971); and climax community corresponding to the region in which the reserve is located (based on the map of potential natural vegetation; Neuhäuslová & Moravec 1997).

Statistics

INCLUSION CURVES

We described reserve establishment and species included in the reserves over the period 1931–1996 through inclusion curves. This period was used because only two reserves were established earlier (1838 and 1858). Establishment was determined for individual reserves and classified according to vegetation type, climatic district, climax community, and phytogeographical region (Table 1). The species inclusion was illustrated for native species, archaeophytes, neophytes, and aliens (Table 2).

The inclusion curves consisted of plots of cumulative percentage against increasing numbers for the period 1931–1996. Thus, for reserve establishment, for instance, cumulative percentages of reserves of a particular type were plotted against year (Fig. 1). This enabled us to evaluate differences in the time of establishment of reserves of a different type.

Inclusion curves for native species, archaeophytes, neophytes, and aliens were obtained by plotting the cumulative percentage of species, included in the reserves up to a given year, of the total 2751 native species (Kubát et al. 2002), 248 archaeophytes (Opravil 1980), 1031 neophytes, and 1279 alien species known from the country at the time of the study (Pyšek et al. 2002*c*) (Fig. 2). This provided a relative picture of the percentage of native and alien species and the relative rate at which these species were included in the reserves.

The effects of cumulative number of reserves and reserve area were illustrated by plotting the cumulative percentage of native species, archaeophytes, neophytes, and total aliens against the increasing number of reserves or increasing reserve area included in the reserves up to a given year (Fig. 3). The number and area of reserves were standardized (zero mean, variance one) to achieve, in absolute terms, a comparable influence of their effects. The strength of their effects would not be directly comparable without the standardization because the number and area were measured on different scales (e.g., Sokal & Rohlf 1981).

ANALYSIS OF INCLUSION CURVES

The curves were analyzed with GLIM (version 4; Francis et al. 1994) by specifying binomial errors, logit link function, the response variable, and the explanatory variable over which the numbers were cumulated. The data for the logit link function were stored in two vectors, one to identify the cumulative numbers and the second the total number, giving a binomial denominator. In the case of overdispersion of binomial errors, we applied Williams's adjustment for unequal binomial denominators (Crawley 1993:351–353). The logit, ln (p/1 – p), is a linearization technique that gives in GLIM the link function relating the linear predictor, $b_0 + b_1t$, to the value of the response variable by the expression ln (p/1-p) = $b_0 + b_1t$. In this expression, p is the proportion the cumulative numbers represent of the total number (e.g., for the total number of reserves of particular type) from which p has been drawn, t is the explanatory variable, and b_0

Table 1. Estimated time (t) of 50% inclusion (t_{50}) in the nature reserves in the Czech Republic, classified according to vegetation type, climatic districts, climax community, and phytogeographical region.

Classification	t_{50}[a] *(years)*	*CI of* t_{50}[b]	*Inclusion curves (±SE)*[c] b_0	b_1
Vegetative type				
forest	32.51 a	31.42–33.57	−3.00 ± 0.13	0.092 ± 0.0036
steppe	34.74 a	33.45–36.00	−3.28 ± 0.17	0.094 ± 0.0044
wetlands and peatbogs	39.84 b	38.42–41.27	−3.26 ± 0.17	0.082 ± 0.0041
grasslands	48.58 c	47.07–50.16	−6.03 ± 0.69	0.12 ± 0.0082
Climatic district				
cold	36.25 a	34.88–37.61	−3.17 ± 0.17	0.087 ± 0.0043
moderate	35.94 a	34.81–37.05	−3.23 ± 0.14	0.090 ± 0.0036
warm	37.68 a	36.08–39.27	−3.13 ± 0.19	0.083 ± 0.0047
Climax community				
oak	32.99 a	31.65–34.29	−2.60 ± 0.14	0.079 ± 0.0036
spruce	35.62 ab	33.85–37.34	−3.00 ± 0.21	0.084 ± 0.0052
elder	37.11 b	35.50–38.70	−3.13 ± 0.19	0.084 ± 0.0048
beech	37.14 b	35.94–38.34	−3.47 ± 0.17	0.093 ± 0.0041
hornbeam	38.36 b	36.91–39.81	−3.52 ± 0.20	0.092 ± 0.0049
Phytogeographical region				
Mesophyticum	36.05 a	34.87–37.21	−3.15 ± 0.15	0.087 ± 0.0037
Oreophyticum	36.48 a	34.96–37.97	−3.35 ± 0.20	0.092 ± 0.0051
Thermophyticum	37.04 a	35.53–38.54	−3.14 ± 0.18	0.085 ± 0.0045

[a] *Time of inclusion is calculated from the cumulative number of reserves of each type between 1931 and 1996. Values with the same letter overlap in confidence interval (CI) and do not differ significantly at* $p = 0.05$.
[b] *Confidence Interval of* t_{50} *is 95% of the estimated time of 50% inclusion.*
[c] *Inclusion curves are fitted by linear regression* $g = b_0 + b_1 t$, *where* g *is logit, expressed as* $\ln(p/1 - p)$, *and* p *is the cumulative number as a proportion of the total number of reserves of a particular type.*

and b_1 are the regression coefficients. The logits of each inclusion curve were weighted by the total number to prevent the logits that were estimated from small numbers having an undue influence on the values of the statistical models. We determined the curvilinearity of the curves by stepwise addition of powers to the explanatory variable and by checking if the addition caused a significant ($p < 0.05$) reduction in deviance.

To compare the inclusion curves, we calculated the estimated time of 50% inclusion, t_{50}, with the 95%

Table 2. Estimated time (t) of 50% inclusion (t_{50}) in nature reserves in the Czech Republic of native and alien species, calculated from cumulative numbers of native and alien species included between 1931 and 1996.

Species types	*Species types plotted against*	t_{50}[a]	*CI of* t_{50}	*Inclusion curves (±SE)*[b] b_0	b_1
	Years				
Native		25.13 a	21.43–28.23	−0.54 ± 0.071	0.022 ± 0.0018
Aliens total[c]		91.93 b	85.70–99.91	−1.94 ± 0.062	0.021 ± 0.0014
Archaeophytes		31.36 a	26.99–35.16	−0.66 ± 0.095	0.021 ± 0.0023
Neophytes		142.90 c	131.7–157.3	−2.84 ± 0.057	0.020 ± 0.0012
	Standardized number of reserves				
Native		−0.72 a	−0.99–−0.52	0.27 ± 0.036	0.37 ± 0.037
Aliens total[c]		3.22 b	2.79–3.81	−1.15 ± 0.028	0.35 ± 0.028
Archaeophytes		−0.37 a	−0.68–0.12	0.13 ± 0.045	0.35 ± 0.047
Neophytes		6.32 c	5.51–7.40	−2.09 ± 0.026	0.33 ± 0.025
	Standardized reserve areas				
Native		−0.76 a	−1.08–−0.52	0.27 ± 0.040	0.35 ± 0.042
Aliens total[c]		3.46 b	2.92–4.23	−1.14 ± 0.032	0.33 ± 0.031
Archaeophytes		−0.40 a	−0.77–−0.10	0.13 ± 0.049	0.32 ± 0.051
Neophytes		6.92 c	5.88–8.40	−2.09 ± 0.03	0.30 ± 0.028

[a] *Time of inclusion is years for species types plotted against years, and standardized values of time for species types plotted against standardized number of reserves and standardized reserve area. Values with the same letter overlap in confidence interval (CI) and do not differ significantly at* $p = 0.05$.
[b] *Inclusion curves as in Table 1.*
[c] *Total alien species is divided into archaeophytes (introduced before 1500 A.D.) and neophytes (introduced later).*

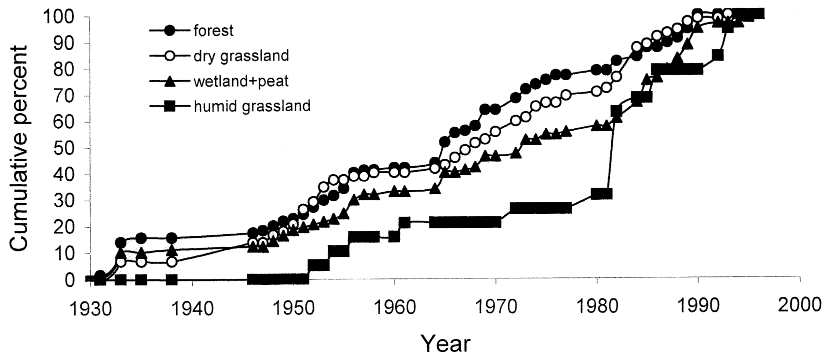


Figure 1. Cumulative percentage of forest, steppe, wetland plus peatbog, and grassland reserves established from 1931 to 1996.

confidence interval, CI, for each curve using Fieller's theorem (Collett 1991; Crawley 1993:275–278). When t_{50} of inclusion curves overlapped in the CI of t_{50} (lower limit to upper limit), the curves did not differ significantly in the time it took for half the available species pool to appear in reserves. For inclusion curves relative to reserve establishment (Table 1), the estimated time of 50% inclusion was when half the reserves of a particular type were established. For inclusion curves describing the inclusion of species in the nature reserves (Table 2), the estimated time of 50% inclusion indicated when 50% of the species in the country were included in the nature reserves. Regression slopes of these inclusion curves (i.e., the values of b_1 in Table 2) indicate the relative rates at which natives, aliens, archaeophytes, and neophytes approached their inclusion points. For comparable rates, the intercepts of inclusion curves (i.e., the values of b_0 in Table 2) indicated the proportional representation of natives, archaeophytes, and neophytes in nature reserves.

ALIEN PLANTS AND RESERVE AGE

The relationship between reserve age and the number of archaeophytes and neophytes present was first evaluated by analysis of covariance. The number of aliens in each reserve, square-root transformed appropriate for count data (e.g., Sokal & Rohlf 1981:421–423), was the response variable. We divided this into archaeophytes and neophytes, which were levels of a factor, and regressed the number of aliens on reserve age. The model was simplified by deletion tests (e.g., Crawley 1993). We confirmed the adequacy of the fitted statistics by plotting standardized residuals against fitted values and through the normal probability plots of the fitted values. No effort was made to remove other factors that affect the numbers of aliens.

As a second step, we used general linear models to identify the effects of reserve age on representation of alien species unbiased by other factors. This evaluation was carried out using a newly developed approach (Pyšek et al. 2002*a*) based on Lonsdale (1999). This method evaluates the effects of particular factors, independent of other variables, by identifying minimal adequate models. A previous study performed on the same nature reserves as the ones we analyzed here (Pyšek et al. 2002*a*) identified the factors determining the proportion of reserve flora made up of alien species. Standardized residuals of minimal adequate models, obtained by removing the three explanatory variables with the largest effect on proportional representation of aliens (i.e., elevation, climatic district, and number of native species) (Pyšek et al. 2002*a*), were regressed for total aliens, neophytes, and archaeophytes on age of reserves.

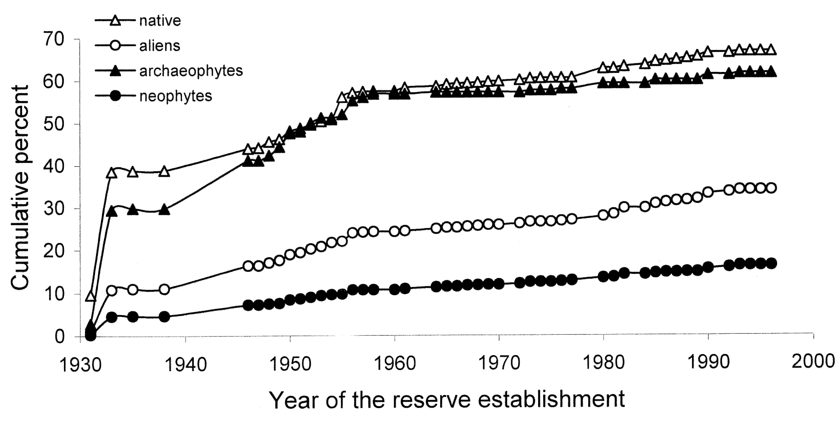
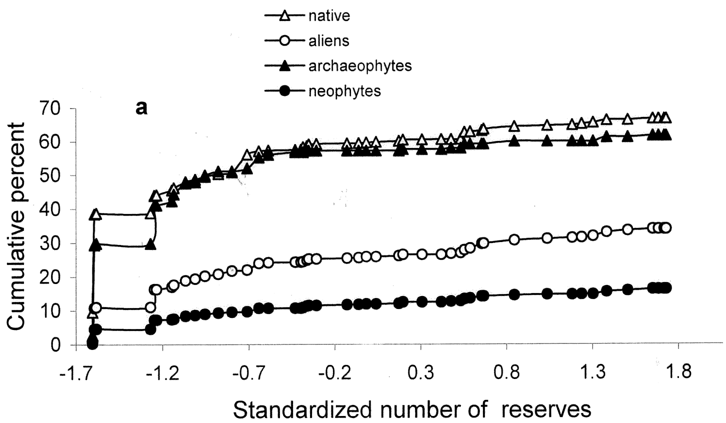


Figure 2. Cumulative percentage of native, archaeophyte, neophyte, and total alien species in the Czech flora included in nature reserves from 1931 to 1996.



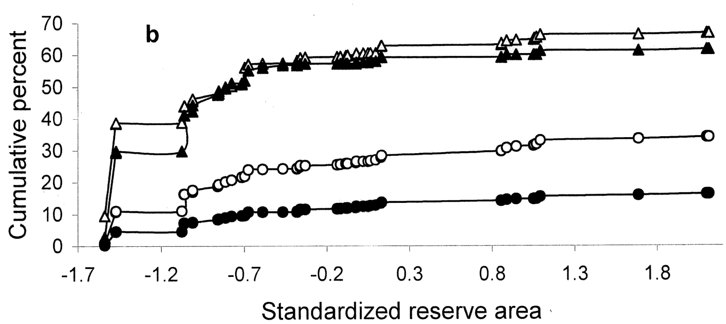


Figure 3. Cumulative percentage of native, archaeophyte, neophyte, and total alien species in the Czech flora included in nature reserves from 1931 to 1996 relative to (a) the standardized number of reserves and (b) the standardized area of reserves. The number and area were standardized because they were measured on different scales. The standardization enables a direct comparison of their relative effects.

Results

Reserve Establishment

The number and area of nature reserves in the Czech Republic has grown exponentially since the establishment of the first reserve in 1838 (Fig. 4). The pronounced exponential character of the curve reflects the fact that only two reserves were established in the nineteenth century. Since the 1930s, the establishment of reserves proceeded at a remarkable rate. However, there was an obvious decrease in the rate of reserve establishment in the 1990s in terms of number and area.

Significant differences in the time of reserve establishment were found for different vegetation types. The first reserves were mainly in forest and dry grassland areas, later in wetlands and peat bogs, and the focus on humid grasslands has been more recent (Table 1, Fig. 1).

Reserves in all three climatic districts and phytogeographical regions were established evenly over time (Table 1). The differences in climax communities of the area in which the reserves were located were also minor, indicating slightly earlier establishment in the regions with oak and spruce forests. However, the time of establishment of the latter did not significantly differ from that for areas with alder, beech, and hornbeam Table 1).

Species Included in the Nature Reserves

Inclusion curves (Fig. 2) and their parameters (Table 2) indicate that half the native flora was included in the nature reserves in the first 25 years (i.e., significantly before half the alien species). The predicted time for the inclusion of 50% of alien species was 86 years (i.e., shorter than the 143 years for neophytes). The corresponding period for archaeophytes (31 years) did not significantly differ from that for native species.

Inclusion curves of species, taking into account the number (Fig. 3) and area (Fig. 3) of reserves established at a particular time, did not differ. This was supported by the similar shapes of the curves in Fig. 3 and that their parameters in Table 2 were not significantly different. Also, the shapes of the curves were similar whether reserve number and area were considered (Fig. 3) or not (Fig. 2). As a result, the differences in inclusion of particular species categories, expressed in Table 2 by t_{50} values with nonoverlapping confidence intervals, were the same regardless of whether the species types were plotted against standardized number of reserves and areas or against years (Table 2). Native species differed significantly from aliens and number of reserves, and area needed to include half the archaeophytes was lower than that needed to include 50% of the neophytes. When the standardized values of the time of 50% inclu-

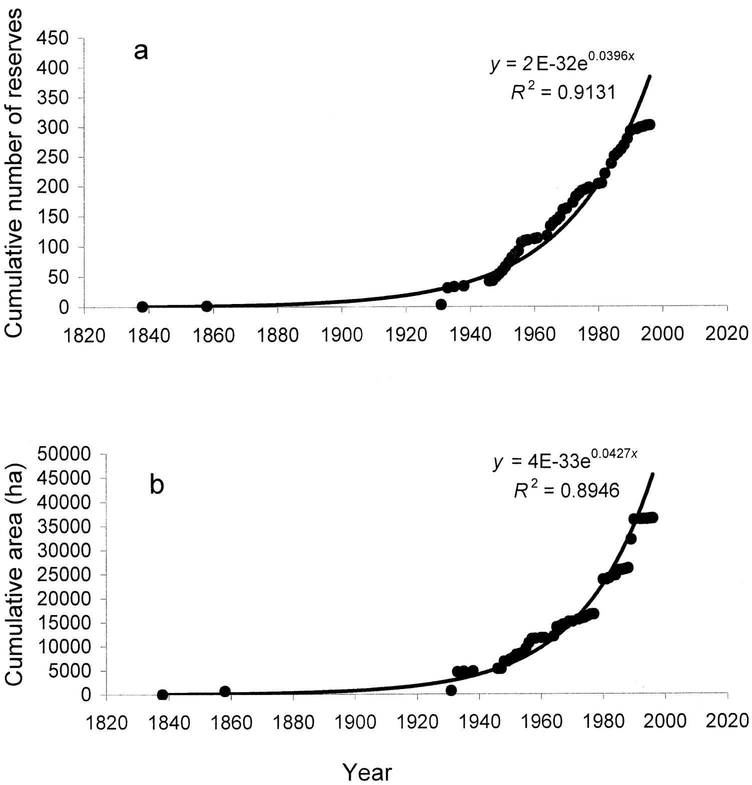


Figure 4. Cumulative growth in the (a) number and (b) area of nature reserves established from 1837 to 1996 in the Czech Republic.

sion were back-transformed to the original scales, the number of reserves needed for 50% inclusion (with 95% confidence interval) of native species, archaeophytes, aliens, and neophytes was 93 (70–111), 124 (96–147), 445 (406–497), and 720 (648–816) and of area was 8,975 (5,591–11,522), 12,641 (8,611–15,817), 52,805 (47,058–61,083), and 88,521 (77,564–104,378) ha, respectively.

The confidence intervals of the three different measures used to express the rate of inclusion (nonstandardized values with the species types plotted against years and the species types plotted against standardized reserve numbers and areas) overlapped for native species, archaeophytes, and neophytes (Fig. 5). This indicates that, relative to the total flora, native species, archaeophytes, and neophytes did not differ in their rate of inclusion in the nature reserves.

However, the confidence intervals of the intercepts of the inclusion curves followed the same pattern as the predicted times for 50% inclusion in Table 2: they overlapped for native species and archaeophytes, respectively (for nonstandardized values, −0.68 to −0.40 and −0.77 to −0.55; for standardized cumulative numbers of reserves, 0.20−0.34 and 0.042−0.220; for standardized cumulative areas of reserves, 0.19−0.35 and 0.034−0.230), but differed from neophytes, which had much lower intercepts (for nonstandardized values, −2.95 to −2.73; for standardized numbers of reserves, −2.14 to −2.94; for standardized areas of reserves, −2.15 to −2.03). This means, relative to the total flora, the proportion of native species and archaeophytes included in nature reserves was significantly higher than for neophytes.

Alien Species and Age of Reserve

Before other factors that influence the numbers of alien species present were removed, the age of a reserve had only a marginal effect on the number of alien species ($F = 3.04$; df = 1, 602; $p = 0.08$). There were fewer alien species in reserves established early on, and there was no difference between archaeophytes and neophytes in this respect (deletion test for different regression slopes: $F = 0.043$; df = 1, 601; $p = 0.84$).

After effects other than reserve age were removed, the residuals for the proportion of alien species were higher in the more recently established nature reserves (standardized residuals of aliens = −11.67 + 0.0059 year of establishment, $F = 4.51$; df = 1, 300; $p = 0.034$). The results were significant for neophytes as well (standardized residuals of neophytes = −12.23 + 0.0023 year of establishment, $F = 4.97$; df = 1, 300; $p = 0.026$) but not for archaeophytes (standardized residuals of archaeophytes = −9.34 + 0.0047 year of establishment, $F = 2.87$; df = 1, 300; $p = 0.091$).

The age of reserve had a significant effect on the occurrence of alien species. The earlier the reserve was established, the fewer alien species it harbored.

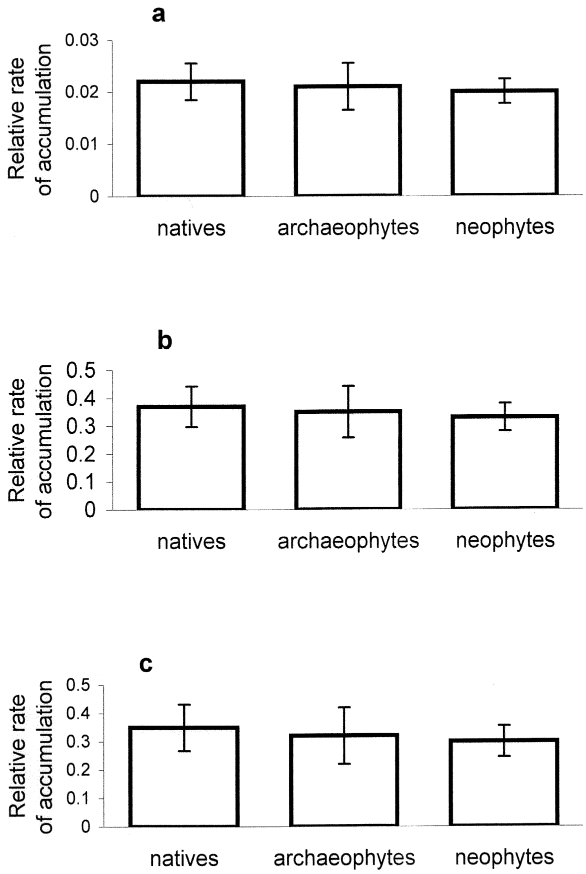


Figure 5. The relative rate, with 95% confidence interval, of the inclusion of native, archaeophyte, and neophyte species calculated (a) without considering reserve number and area and (b) considering standardized cumulative number of reserves and (c) area of reserves. The relative rates of inclusion are the regression slopes of the inclusion curves.

Discussion

Pattern of Reserve Establishment in the Czech Republic

Our data indicate that the various types of Czech nature reserves were established at an even rate in climatic districts and phytogeographical regions. Early on, however, the focus was on creating forest and dry grassland reserves; only later was it on wetlands and much later on humid grassland reserves. This can be explained by land use and rate of deterioration of particular vegetation types (Moravec 1995; Pott 1996). In the Central European temperate landscape, forests, as the climax communities (Neuhäuslová & Moravec 1997), were the first to be threatened, as were the floristically rich, fragmented dry grasslands (steppe). The protection of wetlands and humid grasslands was triggered when extensive soil amelioration and large-scale landscape changes resulted in the rapid loss of such habitats. The remarkable deceleration in reserve creation in the 1990s was a consequence of political changes in the country in 1989. The new political system resulted in changes in land ownership and increased interest in economic issues. Consequently, nature conservation became less important.

In theory, our study indicates the total area and the total number of reserves needed if the complete flora of the region is to be included in reserves. Based on a linear regression, it can be estimated that, given the rate of species inclusion for the period 1931–1996, all native species would be in nature reserves in the year 2032. Not all the reserves were included in the analysis, however, so it is necessary to qualify the prediction by including their number and area. In this case, 463 reserves (49,655 ha) would be needed to include all the native species, an objective already achieved by the current network of nature reserves. In theory, all native species of plants should already be within one or other of the reserves, with two reservations. First, the sample we analyzed was not random, and it focused on reserves that are unique and vegetationally diverse. Second, any prediction based on regression is valid only if the future creation of reserves follows the same rules as in the past. For instance, the prediction would be invalid if the decrease in the rate of reserve establishment, indicated in the 1990s (Fig. 4), continued. Based on the rate of species inclusion from the 1990s, the linear regression predicts that all native species would be included no earlier than 2317. A realistic prediction thus needs to be based on reliable assumptions about future reserve establishment, which has to take into account many complex circumstances, such as the political situation, society's view on ecological issues, and the availability of economic resources. Factors like these make such predictions hazardous.

Barriers to Inclusion of Native and Alien Species in Nature Reserves

Considerable knowledge of the global pattern of invasion into nature reserves has been accumulated from studies conducted in national parks, biospheric reserves, and small nature reserves (Duffey & Usher 1988). This research has yielded some generalizations: nature reserves all over the world contain about half the number of non-native species contained by sites outside reserves (Lonsdale 1999); the number of alien species that occur in a nature reserve is closely related to the number of human visitors (Macdonald et al. 1988; Usher 1988; Lonsdale 1999; Pyšek et al. 2002*a*); tropical and arid subtropical reserves seem to have fewer alien species because of their more equitable environments (Holdgate 1986); reserves situated on islands have more aliens than those located on the mainland (Brockie et al. 1988; Holt 1992); and reserves within large protected sections of landscape (i.e., national parks, landscape protected areas) have fewer neophytes than those surrounded by unprotected landscape (Pyšek et al. 2002*a*). However, these studies do not indicate whether the low occurrence of aliens in reserves is a consequence of their nonrandom inclusion in nature reserves or a consequence of a higher resistance of nature reserves to the establishment of non-native plants. These studies thus do not indicate whether the natural vegetation of nature reserves may act as a barrier to the establishment of alien species.

Our results suggest that the number of alien species is lowest in areas that have been reserves for the longest time; the number of alien species increased with decreasing reserve age. This result was only marginally significant because other important variables affect alien numbers in nature reserves. Elevation, climatic district, and number of native species each explained more than 10% of the variation in the proportional occurrence of alien species in reserves (Pyšek et al. 2002*a*). When these factors were filtered out, the relationship between age and the proportional extent to which reserves were invaded by alien plants was significant for all aliens and neophytes. However, the tendency for there to be fewer alien species in reserves established early on was only an evidence that old reserves harbor fewer alien species than nature reserves in comparable environments that have been established more recently. It does not indicate, however, which of two possible scenarios may apply: (1) old reserves had a more intact and thus more resistant flora at the time of establishment or (2) they were more specifically managed and less disturbed (e.g., no building activity, visitors were only allowed to walk on paths), and consequently it was more difficult for alien species to invade.

Given the overall increase of aliens in the Central European landscape in the twentieth century (Kowarik 1990; Pyšek et al. 2003), the later a reserve was established the higher the number of aliens it is likely to have harbored at the time of establishment. However, nature reserves have always been selected with one goal in mind: to obtain the most representative example of an intact natural community of a given kind. Therefore, reserves established at the end of the twentieth century may nevertheless have had relatively few alien species because the selection process focused on intact communities. A comparison of recent species lists of new and old reserves shows that this is not the case. Recently established reserves have higher numbers of alien species than those established more than a half century ago, probably because completely natural sites are no longer present in the modern landscape. Further, it is possible that old reserves harbor fewer aliens because they are more pristine. The most valuable communities are likely to be conserved first and not primarily because they are old. Even if vegetation is important in the selection, it would not invalidate the relationship between reserve age and representation of aliens because the kind of vegetation in a reserve does not affect the representation of alien species (Pyšek et al. 2002*a*). Thus, it is possible to claim that there is an unbiased effect of reserve age.

Therefore, the conclusion that old reserves had fewer aliens initially is rather robust, and the question now becomes whether it is more difficult for an alien species to invade a nature reserve than a corresponding section of "normal landscape." If the answer is yes, the low initial representation of aliens in old reserves becomes more marked with the passage of time.

True accumulation over time cannot be measured using a data set like the one we used in this study. For this, it is necessary to know the number of alien species at the time each reserve is established. Unfortunately, neither records of the initial flora in the reserves nor many records going back decades or centuries exist. Nevertheless, our study offers indirect evidence that nature reserves are resistant to the establishment of alien plants. The intercepts of the inclusion curves indicate that, since 1931, the reserves had proportionally fewer neophytes than natives and archaeophytes. That the inclusion curves have similar slopes, which measure relative rates of incorporation, indicates that the rates of incorporation of alien species did not differ for particular species categories. Most important, incorporation was not faster for neophytes than for archaeophytes and native species. That is, the more recently established reserves did not contain proportionally more neophytes. Because the relative rates of species inclusion are related to current species pools, and thus include neophyte species that may have arrived after reserve establishment, the relative rates are not biased by the fact that some neophytes could have appeared (and actually did) in the reserves after their establishment.

The unchanging proportions of native and alien species during the process of reserve accumulation indicate similar relative rates of inclusion, which suggests that natural vegetation acts as a barrier against alien species. During the period of measurement of the inclusion curves, the pool of alien species rapidly increased (Pyšek et al. 2002*c*, 2003), whereas the pool of native species and archaeophytes remained the same. By definition, all native species and archaeophytes were present in the landscape at the time of establishment of the first reserve. In contrast, only 10.8% of the presently known neophytes in the flora of the Czech Republic occurred in the country in 1838, when the first reserve was established. The corresponding figure for 1931, when the analysis started, is 55.4% (Pyšek et al. 2003). Given this, the positive slopes of the native and archaeophyte inclusion rates are due to gradual inclusion into reserves, whereas the similar slope of the neophytes is most likely due to the increased pool of these species relative to that of archaeophytes or natives.

Not All Aliens are the Same

We found that native species are present in nature reserves as a result of a different set of circumstances than those for neophytes but under the same circumstances as those of archaeophytes. Archeophytes, typically weeds from arable land of mostly Mediteranean origin (Opravil 1980; Pyšek et al. 2002*c*), have shared the same environment with native taxa since the Neolithic period (for some 5000–7000 years). It appears that archaeophytes are omnipresent in the landscape, with sites established as nature reserves being no exception. They are highly represented, even when the first nature reserves were established in areas dominated by natural communities, which are the focus of nature conservation. In Central Europe, large sections of undisturbed landscape are rare, and archaeophytes survive because of small-scale disturbances. This indicates the importance of the time of arrival in the perception of alien taxa. In Central Europe, treating as a single category the two distinct groups of aliens, which differ in their time of arrival, ecology, and relation to the native flora (Pyšek et al. 2002*a*), may result in important relationships remaining hidden.

There are few invasive archaeophytes in the Czech flora (Pyšek et al. 2002*c*), and their impact is almost exclusively on agriculture. Consequently, neophytes is the group of alien plants that should be taken seriously by conservationists. We did not find any difference between the inclusion of native species and archaeophytes, but with neophytes there is an important message for nature conservation. The earlier that nature reserves are established in a country, the easier it is to find undisturbed landscape to protect: the intensively managed Central European landscape deteriorated continuously over the period 1931–1996. In addition, older nature reserves are less likely to be invaded. Given the high number of species that may become invasive in the future (Rapoport 1991), the only possible approach to nature reserves, where the ultimate goal is pristine communities, is to prevent the entrance of all aliens. The later a reserve is created, the more difficult it is to achieve this goal.

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Literature Cited

Berger, J. J. 1993. Ecological restoration and nonindigenous plant species: a review. Restoration Ecology **1:**74–82.

Brockie, R. E., L. L. Loope, M. B. Usher, and O. Hamann. 1988. Biological invasions of island nature reserves. Biological Conservation **44:** 9–36.

Chytrý, M., T. Kučera, and M. Kočí, editors. 2001. Habitat catalogue of the Czech Republic. Agency for Nature Conservation and Landscape Protection of the Czech Republic, Prague (in Czech).

Cole, D. N., and P. B. Landres. 1996. Threats to wilderness ecosystems: impacts and research needs. Ecological Applications **6:**168–184.

Collet, D. 1991. Modelling binary data. Chapman and Hall, London.

Crawley, M. J. 1993. GLIM for ecologists. Blackwell Scientific Publications, London.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88:**528–534.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. 1989. Biological invasions: a global perspective. Wiley, Chichester, United Kingdom.

Duchoslav, M. 2002. Flora and vegetation of stony walls in East Bohemia (Czech Republic). Preslia **73:**1–25.

Duffey, E., and M. B. Usher, editors. 1988. Biological invasions of nature reserves. Biological Conservation **44:**1–135.

Francis, B., M. Green, and C. Payne, editors. 1994. The GLIM system. Release 4 manual. Clarendon Press, Oxford, United Kingdom.

Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications **8:**975–989.

Hejný, S., and B. Slavík, editors. 1988. Flora of the Czech Republic. 1. Academia, Prague (in Czech).

Holdgate, M. W. 1986. Summary and conclusions: characteristics and consequences of biological invasions. Philosophical Transactions of the Royal Society of London, Series B **314:**733–742.

Holt, R. A. 1992. Control of alien plants on nature conservancy preserves. Pages 525–535 in C. P. Stone, C. W. Smith, and J. T. Tunison, editors. Alien plants invasions in native ecosystems of Hawaii: management and research. University of Hawaii Press, Honolulu.

Holub, J., and V. Jirásek. 1967. Zur Vereinheitlichung der Terminologie in der Phytogeographie. Folia Geobotanica & Phytotaxonomica **2:**69–113.

Kočí, M. 2001. Subalpine tall-forb vegetation (Mulgedio-Aconitetea) in the Czech Republic: syntaxonomical revision. Preslia **73:**289–331.

Kos, J., and M. Maršáková. 1997. Protected areas of the Czech Republic. Agency for Nature Conservation and Landscape Protection of the Czech Republic, Prague (in Czech).

Kowarik, I. 1990. Some responses of flora and vegetation to urbanization in Central Europe. Pages 45–74 in H. Sukopp, S. Hejný, and I. Kowarik, editors. Urban ecology. SPB Academic Publishing, The Hague.

Kowarik, I. 1995. On the role of alien species in urban flora and vegetation. Pages 85–103 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Kubát, K., L. Hrouda, and J. Chrtek Jr., Z. Kaplan, J. Kirschner, J. Štěpánek, and J. Zázvorka, editors. 2002. Key to the flora of the Czech Republic. Academia, Prague (in Czech).

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

Loope, L. L. 1992. An overview of problems with introduced plant species in national parks and biospherical reserves. Pages 3–28 in C. P. Stone, C. W. Smith, and J. T. Tunison, editors. Alien plants invasions in native ecosystems of Hawaii: management and research. University of Hawaii Press, Honolulu.

Macdonald, I. A. W., D. M. Graber, S. DeBenedetti, R. H. Groves, and E. R. Fuentes. 1988. Introduced species in nature reserves in mediterranean type climatic regions of the world. Biological Conservation **44:**37–66.

Maršáková, M. 1987. Methods of research on inventories of nature reserves. State Institute of Nature Protection, Prague.

Maršáková-Němejcová, M., and Š. Mihálik, editors. 1977. National parks, nature reserves and other nature protected areas in Czechoslovakia. Academia, Prague (in Czech).

Moravec, J., editor. 1995. Red list of plant communities of the Czech Republic and their endangerment. 2nd edition. Severočeskou Přírodou, Příloha **1995:**1–206 (in Czech).

Neuhäuslová, Z., and J. Moravec, editors. 1997. Map of potential natural vegetation of the Czech Republic. Academia, Prague.

Opravil, E. 1980. The history of synanthropic vegetation 1–6. Živa, Prague **28:**4–5, 53–55, 88–90, 130–131, 167–168, 206–207 (in Czech).

Pott, R. 1996. Biotoptypen: Schutzenswerte Lebensräume Deutschlands und angrenzender Regionen. Verlag Eugen Ulmer, Stuttgart.

Pyšek, P. 1995. On the terminology used in plant invasion studies. Pages 71–81 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Pyšek, P. 1998. Alien and native species in central European urban floras: a quantitative comparison. Journal of Biogeography **25:**155–163.

Pyšek, P., K. Prach, M. Rejmánek, and M. Wade, editors. 1995. Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam.

Pyšek, P., V. Jarošík, and T. Kučera. 2002*a*. Patterns of invasion in temperate nature reserves. Biological Conservation **104:**13–24.

Pyšek, P., T. Kučera, and V. Jarošík. 2002*b*. Plant species richness of nature reserves: the interplay of area, climate and habitat in a Central European landscape. Global Ecology And Biogeography **11:**279–289.

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

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

Quitt, E. 1971. Climatic regions of Czechoslovakia. Studia Geographica **1971/16:**1–84.

Rapoport, E. H. 1991. Tropical versus temperate weeds: a glance into the present and future. Pages 441–451 in P. S. Ramakrishnan, editor. Ecology of biological invasion in the tropics. International Scientific Publications, New Delhi.

Rejmánek, M. 1996. A theory of seed plant invasiveness: the first sketch. Biological Conservation **78:**171–181.

Rejmánek, M. 1999. Invasive plant species and invasible ecosystems. Pages 79–102 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. Invasive species and biodiversity management. Kluwer Publishers, Dordrecht, The Netherlands.

Richardson, D. M., N. Allsopp, C. D'Antonio, S. J. Milton, and M. Rejmánek. 2000*a*. Plant invasions: the role of mutualisms. Biological Review **75:**65–93.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000*b*. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6:**93–107.

Sádlo, J., and I. Bufková. 2002. Vegetation of the Vltava river alluvial plain in the Šumava Mts (Czech Republic) and the problem of relict primary meadows. Preslia **73:**67–83 (in Czech).

Schroeder, F. G. 1969. Zur Klassifizierung der Anthropochoren. Vegetatio **16:**225–238.

Sokal, R., and F. J. Rohlf. 1981. Biometry. Freeman, San Francisco.

Usher, M. B. 1988. Biological invasions of nature reserves: a search for generalisation. Biological Conservation **44:**119–135.

Usher, M. B., F. J. Kruger, I. A. W. Macdonald, L. L. Loope, and R. E. Brockie. 1988. The ecology of biological invasions into nature reserves: an introduction. Biological Conservation **44:**1–9.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos **57:**7–13.

Williamson, M. 1996. Biological invasions. Chapman and Hall, London.