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Czech alien flora and the historical pattern of its formation: what came first to Central Europe?

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Abstract Temporal patterns of immigration to the country were analysed using 668 alien species in the flora of the Czech Republic for which the dates of the first record were available (64.8% of the total number of 1031 so-called neophytes, i.e. aliens introduced after the year 1500). After a period of initial slow increase lasting to the 1840s, the accumulation of neophytes over time could be best fitted by a linear model that explained 97% of the variance. The intensity of floristic research, which varied between periods, did not significantly affect the overall increase in the number of aliens. The effect of species traits on the year of introduction was evaluated, with continent of origin, introduction type (deliberate or accidental), life history, Grime's life strategy, onset of flowering, mode of dispersal and propagule size as explanatory variables. Species of European origin and CSR strategists arrived earlier than those with other origins and strategies. Deliberately introduced species appeared earlier than accidental arrivals, and those cultivated for utilitary reasons on average arrived earlier than ornamentals. Species capable of early flowering were remarkably more prevalent among early newcomers. A separate analysis of accidentally introduced American species also identified life history as a significant predictor of immigration time, with annuals being introduced earlier than biennials and perennials. The data contribute to an understanding of a crucial stage of the invasion process that has received little attention in the literature. The model "early alien" to Central Europe is a European species with a CSR strategy deliberately brought for cultivation as a utilitary plant. Once it escaped from cultivation, its establishment in the wild was favoured by its ability to flower early and, therefore, complete the life cycle.

Keywords Alien flora · Immigration pattern · Invasion history · Origin · Species traits · Year of introduction

Introduction

Studies attempting to identify which biological and ecological characters as well as historical and geographical determinants support species invasiveness are vital driving forces of contemporary research into plant invasion (Roy 1990; Perrins et al. 1992; Richardson and Cowling 1992; Rejmánek 1995, 1996, 1999; Pyšek et al. 1995; Crawley et al. 1996; Rejmánek and Richardson 1996; Williamson 1996). Features associated with competitive ability, perennial life form, vegetative reproduction and clonality (Pyšek 1997; Kolar and Lodge 2001), as well as dispersal abilities/possibilities and fecundity (e.g. Baker 1965; Ashton and Michell 1989; Noble 1989; Mitchell and Gopal 1991; Saxena 1991; Richardson et al. 2000a) appear as key characteristics improving the potential of a species to increase in abundance in a new area and spread with considerable speed, i.e. become naturalized or invasive (Richardson et al. 2000b). Several studies have demonstrated that species invasiveness is correlated with size of primary geographic range (Forcella and Wood 1984; Rejmánek 1995, 1996, 1999; Starfinger 1998), abundance in native habitats (Williamson 1996), and early introduction into the secondary area (Rozenfelds and Mackenzie 1999; Rejmánek 2000; Kolar and Lodge 2001). The latter indicates that the time of introduction is a crucial feature principally affecting not only the fate of particular species but also composition of whole alien floras and interaction of newcomers with native taxa.

As pointed out by Williamson (1996), while much has been written about invasions, most of it is case histories, surveys of case histories, and statistically weak generalizations. Although there has been remarkable progress in

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the last 5 years, the post hoc nature of research on plant invasions still remains one of the weak links of the field. Most studied are invasions that have already started and, thus, proved worthy of attention, be it for scientific or practical reasons. The very beginning of the process, i.e. introduction to the target area, which is the crucial step of any invasion, is the least understood part of the process because of a marked lack of data. The introduced woody plants documented by the careful records of foresters and gardeners in Brandenburg, Germany are a remarkable exception to this rule; analysis of such data has yielded valuable and novel insights into the problematics of plant invasion (Kowarik 1995a). However, apart from woody plants, dates of introduction are rarely known for many alien species (Esler 1987; Rejmánek 2000).

Even where such data are available, the focus is usually on the relationship between residence time and species invasiveness, evaluated after the invasion process have been running for decades or centuries. No attention has been paid to the sequence in which species immigrated to their secondary distribution areas. It can be assumed that such an immigration/invasion pattern is determined by the interplay of humans acting as vectors (Kowarik 2003) and the biological and ecological properties of invading species, namely those related to establishment in a new area.

The present paper focuses on this first step of invasion (in fact the very start of any invasion is the moment a propagule attaches to a human vector, about which there are virtually no data). The project attempted to identify those species that overcame the first (geographical) barrier (Richardson et al. 2000b) easier than other species and were, therefore, the first to arrive. It uses data from a well-known territory with a remarkable knowledge of plant history. The Czech Republic has one of the strongest floristic traditions of any European country. The earliest accounts of the complete flora of the territory date from the beginning of the 19th century (Pohl 1809–1814; Presl and Presl 1819). Since then, there is a satisfactorily continuous record of high-quality floras (Opiz 1823, 1852; Čelakovský 1867–1881; Polívka 1900–1904) complemented by numerous herbarium collections, the extent of which (5.21 million specimens) is also above the European average (Mihulka and Pyšek 2001). Such accumulated knowledge provides a good opportunity for studying the onset of invasions and the temporal patterns of alien species arrival.

The null hypothesis tested in this paper is that, over the last 500 years, all alien species arriving in the Czech Republic had the same chance to reach their target area and the temporal pattern of their arrival was random and independent of their biological and ecological properties and origin. Further, by studying a large data set, we attempted to analyse how the intensity of floristic research affects the usability of historical data.

Materials and methods

The Czech Republic and its alien flora

The Czech Republic is located between 48°33’ and 51°03’ latitude and 12°06’ and 18°52’ longitude. It has diverse climatic and geographic conditions, covers an area of 78,864 km^2, and has 10.3 million inhabitants, with a human population density of 131 inhabitants per km^2. The network of roads (0.71 km per km^2) and railways (0.11 km per km^2) is rather dense. Besides railways and roads, traffic on the River Elbe, the River Donau and their tributaries has contributed significantly to the richness of the present alien flora (Jehlík 1998). Due to its geographical location in the very centre of the continent, the country has been a crossroad between West and East, and South and North Europe since early times, and intensive movement of people and goods has contributed to plant introductions (Pyšek et al. 2002; Pyšek and Prach 2003). Many species of Asian and East European origin entered the central part of the European continent at a large railway station of the East-West oriented railway system in the Slovak part of former Czechoslovakia (Jehlík and Hejný 1974; Jehlík 1998).

Once introduced, an alien species has a relatively high chance to establish itself because the diverse Czech landscape forms a fine-scale mosaic of various habitats. The landscape is intensively used and fragmented by the long-term effect of human activities; large undisturbed areas are virtually absent. The country has relatively well-developed industry (from the late 18th to the middle of the 20th century, it was one of the most industrialized parts of Europe) and a long gardening tradition, which was responsible for the introduction of many ornamental plants (Pyšek and Prach 2003).

The alien flora of the Czech Republic consists of 1364 taxa (see Pyšek et al. 2002 for the complete list of species and analysis of its composition and structure), of which 1031 (i.e. 75.6%) are so-called neophytes. In traditional Central European phytogeographical classification systems (Holub and Jirásek 1967; Schroeder 1969), this term is used for taxa introduced by humans after the discovery of America. In original sources, it was applied only to species introduced inadvertently, but at present it is often used, for the sake of simplicity, without taking the means of introduction into account (see Pyšek et al. 2002 for discussion). This approach was followed in the present paper and all alien species assumed to have been introduced after ca. 1500 AD were considered as neophytes, regardless of accidental or deliberate introduction.

Data analysed

The year of the first report of occurrence in the wild (i.e. excluding planted species of alien origin not escaping from cultivation) in the Czech Republic was sought for each neophyte listed in historical floral works (Pohl 1809–1814; Presl and Presl 1819; Opiz 1823, 1852; Čelakovský 1867–1881; Polívka 1900–1904) and in primary literature (see Pyšek et al. 2002 for bibliography). These data were acquired only for neophytes because, for the remaining 333 representatives of the alien flora (so-called archaeophytes, introduced before 1500), no exact records are available as to the date of introduction and only rough classification to historical periods is possible (Pyšek et al. 2003). The data were obtained for 668 neophytes (i.e. 64.8% of the total); this subset of species was used to carry out statistical analyses. The date of the first report in the Czech Republic is further termed “year of introduction”. The term “introduction” is used in the present paper without any connotations as to the mode of introduction. Species that arrived not solely for human purposes still reached their secondary ranges because of humans and were thus indirectly “introduced”. Dates of introduction of particular species can be found in a previous paper by Pyšek et al. (2002).

Of the 1031 neophyte species, 252 (i.e. 24.4%) are considered extinct. These are species for which no records have been found for a long period and it was considered unlikely that they would appear again. These taxa were included in the analysis (if the year of introduction was known) because this paper investigates the ability of an alien plant to get to the territory of the country and establish there to an extent necessary for it to be recorded. The analysis presented in this paper does not go beyond this stage and does not consider the further fate of a species in the area. The "extinct" species, therefore, also provide relevant information.

To evaluate the determinants of species arrival, we needed to identify the basic properties of each particular species, with the limitation that for large species sets the availability of data is the most limiting factor. The following characteristics were selected:

1. Origin: This was classified with respect to the continent (Africa, America, Asia, Australia, Europe); where a species' primary distribution area included Europe, it was classified as of European origin, regardless of other continents it covered. North, Central, and South America were grouped together. Of the 615 species classified according to the area of origin, 348 species (56.6%) were of European origin, 158 (25.7%) from America, 85 (13.8%) from Asia, 13 (2.1%) from Africa, and 11 (1.8%) from Australia. For 53 species, the origin was obscure or they were hybrids originating in the country (Pyšek et al. 2002).
2. Introduction: Deliberate (brought into the country by humans for a purpose) and accidental introduction was distinguished. If a species was introduced by both means, it was classified as deliberate. Having been brought in by both means does not constitute an advantage for a species in terms of the present paper: The mean year of introduction for species introduced both ways was 1892.1 ± 44.4 (mean ± SD, *n*=54), while in those introduced only deliberately the mean year was 1898.4 ± 57.1 (*n*=304). Since there is obviously no difference in mean year of introduction, the deliberate/accidental category was included into deliberate and not analysed separately. Within the 361 deliberate introductions in the data set (54 of the total), two subgroups were distinguished, i.e. species brought in as utilitary plants (37.7%, with food, spice, medical use, fodder and landscaping being most frequent; see Pyšek et al. 2002for details) or as ornamentals (62.3% of all deliberately introduced taxa).
3. Life history: Annual, biennial, perennial and woody life histories were distinguished. Species exhibiting more than one life history were included into that which is most common for them in the Czech Republic. Semi-shrubs, shrubs and trees were grouped into the woody category.
4. Life strategy: The strategies followed those of Grime (1979) (C, CR, CS, CSR, R, S, SR) and were taken from Grime et al. (1988) and Frank and Klotz (1990). Data were available for 417 taxa (i.e. 62.4% of species within the analysed subset).
5. Propagule size: This was determined for seeds or fruits, depending on which part of the reproductive structure serves for dispersal of the species (Pyšek et al. 2002) (classified into categories 0.25–0.99, 1.00–1.49, 1.50–2.19, 2.20–3.29, 3.30–4.99, 5.00–7.39, 7.40–10.99 and 11.00–60.00 mm).
6. Flowering time: The month (1–10) during which the species initiates flowering in the Czech Republic.
7. Dispersal: Prevailing mode of dispersal (none, water, wind, zoo).

The data on species characteristics were compiled using flora of the Czech Republic (Hejný and Slavík 1988–1992; Slavík 1995–2000), the determination key to the flora (Kubát et al. 2002), and other sources (Frank and Klotz 1990).

The arbitrary date dividing neophytes from archaeophytes is related to the discovery of North America by Europeans. For that reason, special attention was paid to the group of American species introduced accidentally (*n*=71), as for these the zero time point is unambiguously defined (strictly speaking, for neophytes from Eurasia, earlier introduction cannot be completely excluded). By excluding the deliberate introductions, a further source of variation was removed, since all remaining species within the subset had to cross an ocean or other geographical barrier without direct human intervention and, thus, their appearance in the target territory can be considered as more directly dependent on biological and ecological properties than is the case for primarily cultivated taxa.

Statistical analysis

Data on the increase in number of neophytes were analysed by regression models, using cumulative numbers of neophytes as a response variable and the year of introduction as the explanatory variable. The adequacy of linear, power and logarithmic models was checked by comparing explained variance and also by plotting standardized residuals against fitted values and ordered residuals against expected order statistics (Crawley 1993). To test for additional non-linear components in the linear model, increasing powers of the explanatory variable were calculated and added to the model one after another. If the addition caused significant ($P<0.05$) increase in explained variance, the power was kept in the model (Sokal and Rohlf 1995). To determine which years gave results that caused additional non-linear components of linear increase, points with the largest influence on statistics were assessed by the distribution of Cook's (1977) distances. Data points with the largest Cook's distances were sorted in descending order and weighed out of the analysis one after the other (Gilchrist and Green 1994). Parameter values were refitted after weighing out each data point and significance of non-linear components was re-assessed. If the refitted parameters indicated linear increase without additional non-linear components, the points weighed out were assumed to cause the violation. The analysis was repeated on smoothed data, with cumulative numbers of neophytes summed by decades. Calculations were made using general linear modelling in GLIM, version 4 (Francis et al. 1994).

The effect of species traits on the year of introduction was evaluated by one-way ANOVAs, with significance assessed at the 5% level with Bonferroni's correction. The year of introduction of each species was a response variable and the species traits, continent of origin, introduction type, life history, Grime's life strategy, month of flowering initiation, mode of dispersal and propagule size, were factors. Multiple comparisons of differences among species traits were made by LSD tests, except the a priori notion that annuals should invade earlier than biennials and perennials, which was tested by orthogonal contrast. The effects of flowering start and propagule size were also analysed by simple linear regressions. Interactions between all traits, which were available for individual species, were analysed by a fixed effect factorial ANOVA with disproportional and unequal sample sizes. The analysis was made by an iterative approximate estimation technique in S-PLUS (S-PLUS version 4 Guide to Statistics 1997). The analyses were repeated for the subset of accidentally introduced species of American origin.

Results

Pattern of increase in alien species numbers

Increase in the number of neophytes over time was best fitted by a linear model explaining 97% of the variance. There was also a significant non-linear component of increase (deletion test: F=74.54; df=2, 162; $P<0.001$; R^2=1.4%), with statistically significant quadratic (F=14.60; df=1, 161; $P<0.001$; R^2=0.14%) and cubic (F=13.53; df=1, 161; $P<0.001$; R^2=0.13%) terms (Fig. 1A). Non-linear components of increase are caused by a slow increase of neophytes in the initial decades between the 1750s and 1840s (Fig. 1B), which had the highest values of Cook's distance. Since the 1850s, the highest Cook's distances appeared in the 1880s (Cook's distance 0.12) and 1970s (distance 0.14), reflecting the more intensive floristic research in these periods.

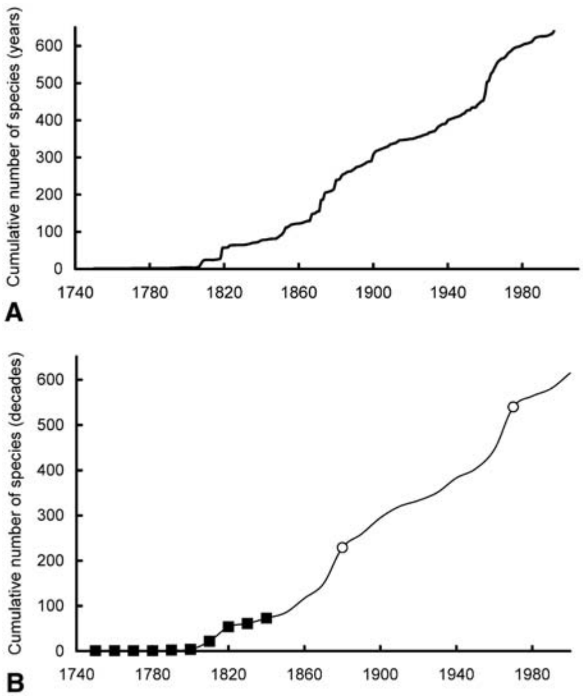

Fig. 1 Cumulative number of neophytes (*y*) plotted against time of invasion (*x*) in years (**A**) and decades (**B**). **A** Non-linear increase is y=218890−341.2x+0.18x^2−0.000030x^3 (F=3372.0; *df*=3, 160; P<0.001; R^2=98.4%). **B** *Squares* indicate decades from 1750 to 1840 that violate linear increase. Linear increase from 1850, indicated by the line, is y=1824+0.3x (F=736.4; *df*=1, 14; P<0.001; R^2=98.1%). *Empty circles* have the largest Cook's distances and correspond to decades 1870–1880 and 1960–1970

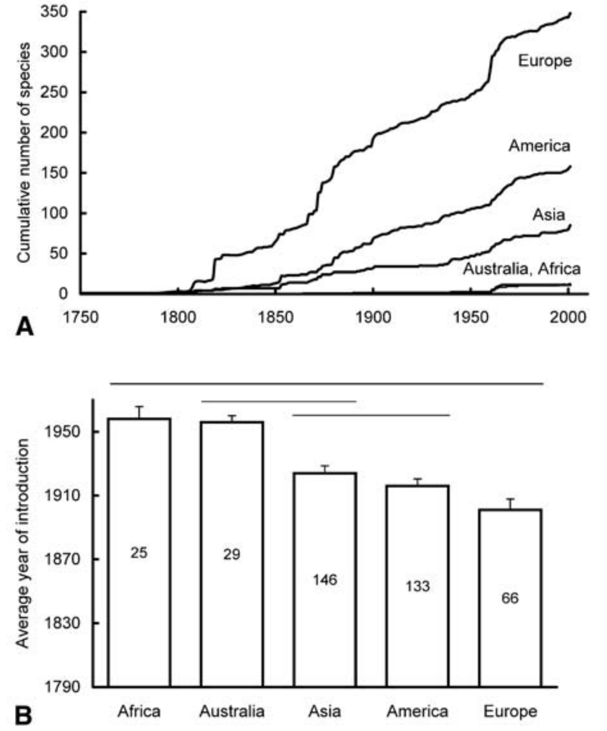

Fig. 2 **A** Increase with time in the cumulative number of species originating from particular continents. Note that the cumulative curves for Australia and Africa follow basically the same pattern because of the low number of species. **B** Average year of introduction (± standard error) shown for the continents. *Horizontal lines* show groups not significantly different by using least significant differences (LSD). *Numbers inside the bars* are sample sizes

Factors affecting the time of introduction

All interactions between traits of individual species, determined by the iterative approximate estimation technique, appeared insignificant at P=0.13. From the main effects of the species traits, as determined by the one-way ANOVAs with Bonferroni's correction, only dispersal mode and propagule size appeared insignificant (Table 1).

The time of introduction was affected by the species origin, type of introduction and its purpose, flowering start and Grime life strategy (Table 1). In the separate analysis of accidentally introduced American species, life history also significantly affected the year of introduction, as annuals were introduced earlier (1924 ± 6.83, mean ± SE) than biennials and perennials (1960 ± 5.00) (F=16.36; *df*=1, 102; P<0.05).

Considering the significant effect of the species origin (Table 1), European species reached the Czech Republic on average significantly earlier than those from America, Asia, and Australia. American species were introduced significantly earlier than Australian species. Species of African origin did not differ in the year of introduction from other neophytes (Fig. 2).

Deliberately introduced species appeared earlier (1879 ± 2.91) than accidental arrivals (1930 ± 2.86). Within the former group, taxa cultivated for utilitary reasons arrived earlier on average (1883 ± 4.34) than ornamentals (1906 ± 3.75) (Table 1).

The year of introduction was significantly affected by Grime life strategies (Table 1). Species with the CSR strategy, although less represented in terms of absolute

Table 1 Summary of ANOVAs showing the effect of particular explanatory variables on the year of introduction between 1750 and 2001 of 668 alien species into the Czech Republic (*df* degrees of freedom, F F-statistic, P significance level with Bonferroni's correction, R^2 explained variance; %)

Explanatory variable	df	F	P	R^2
Origin	4, 160	9.47	<0.05	5.8
Mode of introduction: accidental versus deliberate	1, 666	61.56	<0.05	8.5
Deliberate introduction: utilitary versus ornamental	1, 359	15.24	<0.05	4.1
Life history	3, 660	0.43	NS	–
Grime life strategy	6, 409	3.42	<0.05	4.8
Start of flowering	9, 519	2.21	= 0.1	3.7
Propagule size	7, 336	1.31	NS	–
Dispersal mode	3, 583	1.47	NS	–

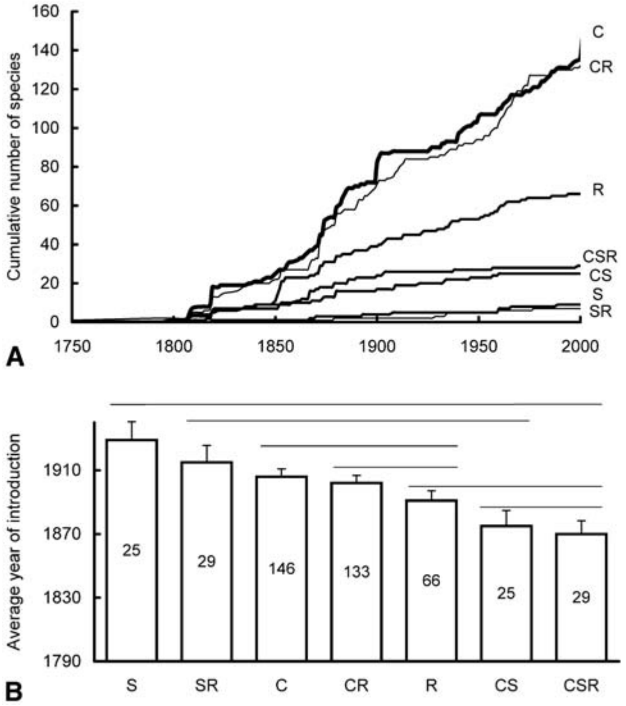

Fig. 3 **A** Increase with time in the cumulative number of species of various life strategies. **B** Average year of introduction (± standard error) displayed for particular strategies for the whole data set. *Horizontal lines* show groups not significantly different by

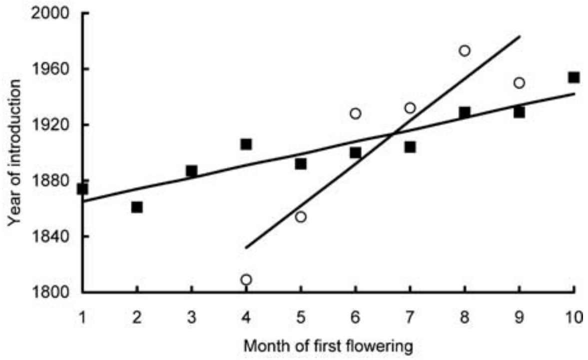

Fig. 4A, B Effect of the start of flowering expressed in months (x) on the year of introduction (y) expressed for the whole data set (*solid squares*) and for accidentally introduced American species (*empty circles*). **A** y=1856+8.6x (F=51.3; df=1, 8; P<0.05; R^2=86.5%). **B** y=1710+30.3x (F=18.6; df=1, 4; P=0.06; R^2=82.3%); B is only marginally significant due to Bonferroni's correction

numbers (n=29) (Fig. 3A), were on average introduced as early as 1870, i.e. significantly earlier than SR, C and CR strategists. Species with the CS strategy were introduced earlier than those with C or CR strategies (Fig. 3B).

The onset of flowering was only marginally significant in ANOVA (Table 1) but had a very significant effect on the year of introduction in the regression test. Species starting to flower early in the season were more likely to have been introduced earlier than those starting to flower later in the season. Expected time of introduction was 1882 ± 1.20 for a plant starting to flower in March while for a species starting to flower in October it was 1942 ± 1.20. The relationship was even more pronounced in American species introduced accidentally (Fig. 4).

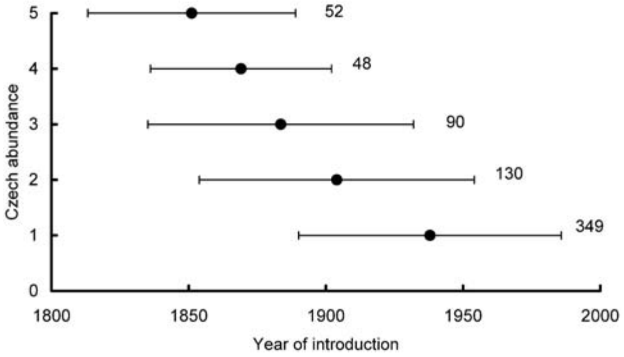

Fig. 5 Relationship between the maximum abundance reached by a species in the 20th century and the year of its introduction (mean, standard deviation and sample size are given). The scale of Clement and Foster (1994) was used to express the abundance in the Czech Republic: *1*=1–4 localities; *2*=5–14, *3*=15–49, *4*=50–499, *5*=over 500. Above *15*, the number of localities is an estimate. Pearson's correlation coefficient r=0.986, P<0.001

Discussion

The nature of the data

One possible criticism of the data presented in this paper is the reliability of the year of introduction, i.e. the time of the first report. This date in fact means the minimal year of introduction and indicates that the species has been present at least since the given year. Actual presence may have been and, in a number of cases, most likely was longer. At present we have no better data and probably never will have for the given geographic region, time scale and number of species involved. However, there are two reasons justifying the use of the available data for the present purpose. First, the year of introduction was obtained using the same data sources for all species, which makes the results comparable (Pyšek and Prach 1993; Pyšek et al. 2002). Second, there is an accepted relationship for plants between early introduction to an area and species high abundance and/or invasiveness (Scott and Panetta 1993; Rozefelds and Mackenzie 1999; Rejmánek 2000; Kolar and Lodge 2001). This relationship holds for the data set analysed in the present paper. There was a highly significant correlation between the maximum abundance reached by a species in the territory of the Czech Republic in the course of the 20th century and the year of introduction (Fig. 5). Hence the problem of lack of reliable records for the period between the end of Medieval and the second half of the 18th century, when the first records appear in our data set, can be overcome.

Where there is a positive relationship between number of localities and year of introduction, we can assume, even if our records start as late as two centuries after the arbitrarily stated zero time point for the so-called neophytes (± 1500), that species appearing as the earliest newcomers in our data set really arrived sooner than the others. Since the same sources were used for each species, creating an even chance for them to be recorded (Pyšek and Prach 1993), species that were more common then should have been recorded with higher probability, i.e. earlier. Furthermore, because of the positive relationship between abundance and year of introduction, those that were recorded immediately after the onset of floristics were probably true early newcomers.

Another argument supporting the relevance of the data for the present purpose is the past character of the landscape in the Czech Republic. Although the landscape was gradually colonized by humans from the Neolite (starting in 5300 BC) to the Medieval, depending on local conditions (proceeding from floodplains in warm regions to colder highlands), the higher mountain areas were colonized as late as the 17th–19th century (Ložek 1999). Given the high original proportion of forest cover, there were large portions of closed forests until the Late Medieval and these acted as barriers to migration. It may, therefore, be hypothesized that the steady influx of neophytes, as recorded by our data, did not start immediately after 1500 but much later. As indicated by analyses of very old regional floras for which the local data are available (Schwenckfelt 1600, analysed by Hendrych 2001), there had been no remarkable plant invasions up to 1600.

A further discussion point about the data used is that a first introduction to the Czech Republic does not mean, in many cases, an arrival directly from the place of original distribution; it might have been from neighbouring countries. The location of the Czech Republic in the very centre of the continent makes this assumption even more probable. However, it can be assumed that, on a historical time scale, the chance of a particular species to establish and spread was similar across Europe, and for its central part in particular, and that there were no striking differences between the countries. An early appearance in the Czech Republic can be assumed to correlate with the time of the species arrival to other countries. Support for this assumption can be drawn from the repeatedly documented importance of the performance of alien taxa elsewhere (Williamson and Fitter 1996; Starfinger 1998). This knowledge is among the best predictors of species invasiveness in the new area (Webb 1985; Reichard and Hamilton 1997) and provides crucial information for correct invasion prediction (Daehler and Carino 2000). Quantitative evidence for this relationship can be provided by comparing abundances of alien floras of the British Isles (Clement and Foster 1994; Ryves et al. 1996) and the Czech Republic (Pyšek et al. 2002), assessed using the same scale. For the 751 species present in both alien floras, the relationship was highly significant and demonstrates that even such distant regions, in terms of geography, climate, and history, have quantitatively similar alien floras as far as abundance is concerned (Fig. 6). Alien species abundant in one European country tend to be abundant in other countries too and the more abundant they presently are, the earlier they were introduced. Thus, it can be supposed that, on the time scale studied in this paper, the pattern of gradual enrichment of the Czech flora is not dramatically different from the pattern valid for the whole continent. Whether the species was introduced via neighbouring countries or directly should not, therefore, dramatically affect the rather robust results.

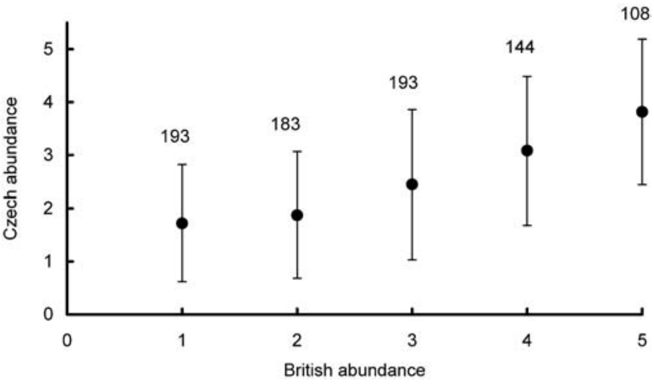

Fig. 6 Relationship between the abundance of alien species in the Czech Republic (data from Pyšek et al. 2002) and UK (data from Clement and Foster 1994; Ryves et al. 1996). The same scale was used to estimate the abundance in each country (mean, standard deviation and sample size are given). Pearson's correlation coefficient r=0.97, P<0.01

From a statistical point of view, evaluation of the effect of species traits on the year of introduction by one-way ANOVAs supposes no interactions between the species traits. However, significant interactions between the traits cannot be excluded completely, for two reasons. First, the analysis of interactions by the fixed effect factorial ANOVA with disproportional and unequal sample sizes was not based on an orthogonal design. Consequently, the solutions were only approximate. Second, data for individual species traits were not available for all species in the data set. Consequently, only subsamples of different species could be analysed for different interactions. However, since all interactions analysed appeared insignificant, it seems improbable that significant interactions were overlooked.

The pattern of increase in neophyte numbers

The present data show that, after the initial period of slow accumulation of neophytes lasting until the 1840s, their consequent influx into the country was steady and best fitted by a linear model. Two periods with disproportionately high contribution to the number of species were detected. The first is the one of Čelakovský (1867–1881) who paid remarkable attention to alien species and summarized the knowledge available up to his time in extensive floral works. The second one is the 1970s, reflecting the establishment of a research division at the Institute of Botany specializing in vegetation of disturbed habitats (Pyšek and Prach 2003). However, the pattern of species accumulation with time is not significantly affected by the intensity of floristic research in the area, which makes the data unbiased for inferring conclusions on the temporal course of alien species introductions into the area. Using species numbers accumulated over decades to detect periods with the highest contribution to the data set is justified, since on a historical time scale such contribution reflects the work of remarkable personalities or research groups focussed on a study subject, whose activities used to be spread over longer periods of time.

The temporal sequence of alien species arrivals

The temporal sequence of arrivals can be summarized as follows. European species arrived before newcomers from other continents. However, those from Asia (i.e. the same Eurasian mainland, not separated by the sea) were as late as those from other, more distant continents. This indicates that geographical proximity only operates, and provides an advantage, up to a certain distance. Probably more important, an interplay of geographical distance with climatic match, an important predictor of invasiveness (Pannetta and Dodd 1987), plays a role since species growing in closer latitudes are adapted to a similar climate.

Deliberate introductions for utilitary purposes preceded deliberate introductions of ornamentals, and accidental arrivals were the latest. This pattern is hardly surprising and indicates that, in the early days of modern plant invasions into Central Europe, alien plants were necessary associates of basic living requirements of humans. Joy of gardening started to take its toll later.

Species possessing the most opportunistic CSR strategy (Grime 1979) appear to have arrived first, and those with a CS-type strategy were also present rather early. This indicates that tolerance to stress is an important prerequisite for species reaching new target habitats after translocation from more or less distant areas. There is support for this statement at the taxonomic level; among the Caryophyllales, there are a number of successful aliens in global terms because of their increased ability to withstand adverse conditions (Pyšek 1998a). Previous studies searching for life-strategy determinants of invasiveness identified species possessing S or S-combined strategy as poor invaders (Pyšek et al. 1995). This is only a seeming contradiction; instead, it suggests that a different life strategy is advantageous at different steps of the invasion process. Several factors determine the probability that a species will pass particular stages of the invasion process successfully, so it is probable that species characteristics important for completing those stages will be different (Kolar and Lodge 2001). For the initial phase, stress-tolerance represents good equipment for an unknown environment to which the species has not yet been adapted. Later on, if the species has the capability to survive in a new region, competitive ability becomes crucial for successful performance. As shown previously on a limited data set, Grime's life strategies (Grime 1979; Grime et al. 1988) are a convenient predictor of invasion success because of the complexity of biological and ecological features they reflect (Prach and Pyšek 1999). The possible caution that the use of Grime's strategies for similar purposes, i.e. to explain species performance and success, brings the danger of circular reasoning is not justified here, since the ability to immigrate and establish in a new region is based on an interaction of strategies, with both the capability to survive in disturbed and stressed habitats (typical of R- and S-strategy) and to compete successfully (favoured by C strategy). The question of which kind of life strategy favours immigration is, therefore, legitimate because the classification of species into particular strategies made by Grime et al. (1988) has not been a priori affected by species capability to immigrate.

Early flowering appears to be a very important prerequisite for successful immigration (Goodwin et al. 1999; Rejmánek and Reichard 2001). One of the major constraints to alien plants in Central Europe is late flowering associated with incapability to set seed, caused by an imperfect climatic match between the source and target areas. This is usually manifested by a decisive influence of altitude on representation of alien species (Mihulka 1998; Pyšek et al. 2002b) and the role of large cities acting like "heat islands" (Gilbert 1989; Wittig 1991; Kowarik 1995b, Pyšek 1998b). Environment match affects potential invaders in two basic respects. The first, ability to flower and set seed, can be studied quantitatively using data sets like those reported in the present paper. The second is seedling resistance or sensitivity to frost, eliminating potential introduction at a very early stage. Unfortunately, no data are available to evaluate the latter phenomenon in quantitative terms. Even if assessed experimentally, the results do not contribute much to the question of how large a proportion of species (and of which features) is eliminated by climate at a very early stage of immigration. The species that need to be tested to answer this question, i.e. the members of a potentially invasive group, remain largely unknown because they do not germinate or survive the seedling stage for later recording.

Climatic match operates with a phenology that can be separated into several aspects. The highly significant effect of flowering on the date of introduction was manifested through the onset of flowering and not the end (F=0.17; df=1, 527; NS). Duration of flowering, which is the combination of both, was less important (variance explained by flowering duration was R^2=1.7% compared with R^2=86.5% explained by its onset) but still significant (F=9.02; df=1, 527; P<0.01). These results indicate that the end of flowering is determined by the late-season physical limits of the environment that cannot be overcome. Late start of flowering cannot be compensated, in temperate conditions, by shifting phenology to the autumn because of early frosts. An immigrating plant has to be able to flower early, which is the only possibility to ensure proper seed set or storage of necessary reserves (Reichard and Hamilton 1997; Goodwin 1999).

The fact that annuals were the earliest newcomers among accidentally introduced American species indicates the difference between planted and inadvertently introduced species. On the global scale, humans tend to translocate clonal perennials at a higher rate than non-clonal plants, which are often garden annuals (Pyšek 1997). The early arrival of plants with CSR strategy documented for the whole data set, including planted species, illustrates the frequent occurrence of this kind of strategy among cultivated plants (19 of 29 species with a CSR strategy were introduced deliberately, i.e. 65% and well above the whole data set average). On the other hand, annuals possess attributes that favour their ability to accompany humans, such as large seed set and ability to form seed banks (Thompson et al. 1997; Baskin and Baskin 1999).

In the studies to date, the time of introduction was used as a predictor of invasive success (Rozefelds and Mackenzie 1999; Rejmánek 2000). Moreover, few reviews have separated results of different transitions, i.e. transportation, release, establishment and spread (Kolar and Lodge 2001). In the present study, we analysed the time of introduction as a response variable, explained by available species traits. It appears that species do not reach their secondary distribution areas by chance but some of them are predestined to be more successful than others in the early step of the invasion process. A model "early alien" of the Czech flora is a European species with CSR strategy deliberately brought into cultivation as a utilitary plant. Once it escapes from cultivation, its establishment in the wild is favoured by its ability to flower early and, therefore, complete its life cycle.

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