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BIODIVERSITY RESEARCH

The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits

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ABSTRACT

Aim Determining which traits predispose a species to become invasive is a fundamental question of invasion ecology, but traits affect invasiveness in concert with other factors that need to be controlled for. Here, we explore the relative effects of biological traits of plant species and their distributional characteristics in the native range on invasion success at two stages of invasion.

Location Czech Republic (for native species); and the world (for alien species).

Methods The source pool of 1218 species of seed plants native to Central Europe was derived from the flora of the Czech Republic, and their occurrence in 706 alien floras all over the world was recorded, distinguishing whether they were listed as an 'alien' or a 'weed' in the latest version of Randall's 'Global compendium of weeds' database. The latter type of occurrence was considered to indicate species ability to invade and cause economic impact, i.e. a more advanced stage of invasion. Using the statistical technique of regression trees, we tested whether 19 biological traits and five distributional characteristics of the species in their native range can be used to predict species success in two stages of invasion.

Results The probability of a species becoming alien outside its native distribution range is determined by the size of its native range, and its tolerance of a wide range of climates acquired in the region of origin. Biological traits play only an indirect role at this stage of invasion via determining the size of the native range. However, the ability of species to become a weed is determined not only by the above characteristics of native distribution, but also directly by biological traits (life form and strategy, early flowering, tall stature, generative reproduction, number of ploidy levels and opportunistic dispersal by a number of vectors). Species phylogenetic relatedness plays only a minor role; it is more important at the lowest taxonomic levels and at the later stage of invasion.

Main conclusion The global success of Central European species as 'weeds' is determined by their distributional characteristics in the native ranges and by biological traits, but the relative importance of these determinants depends on the stage of invasion. Species which have large native ranges and are common within these ranges should be paid increased attention upon introductions, and the above biological traits should be taken into account in screening systems applied to evaluate deliberate introductions of alien plants to new regions.

Keywords

Biological invasions, native distribution, phylogenetic effects, plant invasions, source species pool, species traits, stages of invasion.

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INTRODUCTION

One of the fundamental questions of plant invasion biology is whether it is possible to link success of alien plants to their traits; recent work has shown that some traits can indeed be associated with invasiveness (Pyšek & Richardson, 2007). Biological traits are, however, only a part of invasion success. Other factors are important for determining whether and when a species will succeed as an alien or have an ecological or even economic impact (Vilà *et al.*, 2009). These include residence time (Pyšek & Jarošík, 2005; Wilson *et al.*, 2007; Gassó *et al.*, 2009; Williamson *et al.*, 2009), chance events (Crawley, 1989), and particularly propagule pressure, both in space (by widespread dissemination or abundant plantings) and time (by long history of cultivation), which fundamentally influences the probability of invasions by alien species (Rouget & Richardson, 2003; Kühn *et al.*, 2004a; Lockwood *et al.*, 2005; Richardson, 2006; Catford *et al.*, 2009). Studies that explicitly attempt to filter out confounding effects of propagule pressure have the potential to reveal inherent trait-related determinants of invasibility (Richardson & Pyšek, 2006; Pyšek & Richardson, 2007).

Native ranges have also been identified as important, and large native geographical range is among the best determinants of invasion success in seed plants (Rejmánek, 1996; Goodwin *et al.*, 1999). A large native range may be correlated with invasiveness because it increases the chance that a species is picked up for introduction elsewhere (i.e., increases propagule pressure; Forcella & Wood, 1984; Forcella *et al.*, 1986), or because the traits that allow the species to have a large native range are the same as the ones allowing it to have a large invaded geographical range (Thompson *et al.*, 1995; Booth *et al.*, 2003). Disentangling the relative roles of species traits and native geographical ranges is thus a fundamental question in invasion biology. Knowing the extent to which characteristics of the native range of a species contribute to its potential as a weed could also improve the precision of prediction systems used in weed risk assessment (e.g., Pheloung *et al.*, 1999; Weber *et al.*, 2009).

However, the importance of traits and native distribution characteristics acting in concert has never been rigorously tested using a large set of species and the global scale. In this study, we address this issue by separating the effect of distributional characteristics in the native range from the direct effect of biological species traits. Biological traits can affect invasiveness not only directly, but also indirectly by determining the extent and character of native distribution. Here, we address such indirect effects by using distributional characteristics and biological traits as two groups of explanatory variables, and test the direct contribution of each group to plant invasiveness, as well as the indirect effect of biological traits via their influence on distributional characteristics.

Unlike most studies that focus on alien floras of target regions (see Pyšek & Richardson, 2007 for a review), we use the source-area approach (Prinzing *et al.*, 2002; Pyšek *et al.*, 2004a; van Kleunen *et al.*, 2007), which minimizes the biases associated with the distance to source areas and evolutionary predispositions acquired in various regions of origin. It is based on the assumption that members of the flora of a single biogeographical region have comparable chances to be transported by humans from their native range to other parts of the world. Thus, the differences in their success as aliens can be more unequivocally attributed to their traits, because different chances of species from the source pool to have been introduced elsewhere are reduced (Sol *et al.*, 2008).

Species occurring in the Czech Republic form a representative sample of the Central-European flora because this country is located in the centre of the continent and has a diverse geology and transitional suboceanic-subcontinental climate, which makes its flora rather rich in species that are representative of several floristic regions (Kubát *et al.*, 2002). In this study, these species are used as a source species pool and their non-native occurrence outside Europe as a measure of their performance as aliens elsewhere (Randall, 2002). For historical reasons, the European native flora is very suitable for an analysis of the global patterns of plant invasions, because Europe and Western Asia served as an important donor area of alien species to other regions of the globe (di Castri, 1990; but see Lambdon *et al.*, 2008). European species experienced centuries of testing their invasion potential in a wide range of conditions. We collated information on a wide range of distributional characteristics and biological traits of species, and adopted modelling techniques that correct for problems associated with phylogenetic relatedness. Hence, we were able to assess the role of phylogeny in the invasion process by partitioning the variation into components attributed to species traits, phylogeny and joint influence of these two factors (Desdevises *et al.*, 2003).

Finally, it has been suggested that different factors potentially influence different stages of the invasion process (Kolar & Lodge, 2001). The factors important at each stage can be different, with socio-economics being generally important initially, biogeography, ecology and evolution later (Williamson, 2006). In our study, we address the stage-dependence of the invasion process by analysing the ability of a species to persist as an alien in the wild in the new region, and its ability to reach a more advanced stage of invasion – becoming a weed.

METHODS

Source species pool and response variables

Seed plants of the Czech Republic (Kubát *et al.*, 2002) were taken as a source species pool to obtain a sample of plant species that are native to Central Europe. Local apomictic taxa of the genera *Rubus* ($n = 38$) and *Hieracium* ($n = 36$) were excluded because of their specific mode of reproduction, and so were subspecies due to their varying taxonomic treatment in different regions. This yielded 1218 seed plant species, for which information on the traits considered was available.

Data on the non-native occurrence of these species outside Europe were gathered from Randall (2002), updated. The database included 706 species lists which contained species from our source pool recorded outside Europe. The data provide reasonable global coverage (Fig. 1), with 13.5% lists of global relevance, 32.5% from North America, 22.6% Australasia and Pacific region, 13.5% Asia, 7.7% Africa, 6.9% South America and 4.4% Central America (based on lists in Randall, 2002). It needs to be noted that the accuracy of Randall's 'Global compendium of weeds' has been criticized (e.g., Richardson & Rejmánek, 2004) for several reasons: some of the reference lists include species that have not become naturalized/invasive in the respective geographical region, but are assumed to possess potential to do so; some of the reference lists are incomplete. Yet, the database represents the best available dataset for the purpose of this study.

In addition to listing species in regions, the database records the alien plant occurrences as a 'weed', defined as having economic impact (Randall, 2002). For our sample of Central European species, we explored separately what we call 'alien success' (the number of regions over the world where a species was reported as an alien), and 'weediness' (proportional number of regions amongst all records where the species has been designated as a 'weed'). Alien success relates to the casual or naturalized stages of the invasion process (in the sense of Richardson *et al.*, 2000). Although the term 'weed' has equivocal meaning in the invasion literature (Pyšek *et al.*, 2004b) and not all invasive species are 'weeds' with economic impact, it follows from the definitions (Richardson *et al.*, 2000) that weediness is closely associated with spread and dominance, which are characteristic of the more advanced stage of the invasion process. Our results can therefore, to a reasonable extent, be interpreted in terms of how species traits and distributional characteristics contribute to invasiveness (Richardson *et al.*, 2000; Pyšek *et al.*, 2004b), but it needs to be borne in mind that the term 'weed' incorporates an indication of human tastes and dislikes and relates to invasions in disturbed rather than natural habitats. We are aware that the distinction between the 'alien success' and 'weediness' as used here is rather vague compared with objective criteria suggested in conceptual studies (e.g., Richardson *et al.*, 2000), yet we link these two characteristics to earlier and later stages of the invasion process, respectively.

Distributional characteristics and biological traits

Information on distributional characteristics and species biological traits was derived from CzechFlor, a working database of national flora held at the Institute of Botany, Průhonice, which was compiled using the monographs of national flora (Hejný & Slavík, 1988–1992; Slavík, 1995–2000; Kubát *et al.*, 2002; Slavík & Štěpánková, 2004) and various papers with primary data, and from the German database BiolFlor (Klotz *et al.*, 2002; Kühn *et al.*, 2004b).

Distributional characteristics in the native range were related to the Czech Republic and included: (1) Number of grid cells from which the species is reported (range 1–679); this system uses a grid of 10′ (longitude) × 6′ (latitude), which at 50°N is 12.0×11.1 km or 133.2 km^2. Species frequencies in the Czech Republic, to a large extent, reflect species frequencies in Europe, as demonstrated by a high correlation of the frequencies in the Czech flora and the digitized Atlas Florae Europaeae (http://www.fmnh.helsinki.fi/english/botany/afe): $r = 0.74$, df = 230, $P < 0.0001$, for species from our dataset for which European distribution is available. (2) Number of habitats in which the species occurs (1–78) out of 88 habitats as defined in Sádlo *et al.* (2007). Comparison with habitat manuals or vegetation monographs of different countries indicates that species growing in many habitats and across a broad altitudinal range in the Czech Republic do so in the whole of Central Europe, as defined by Ellenberg (1988). (3) Mean altitude (150–1450 m a.s.l.) and (4) Altitudinal range (85–1485 m), derived from the occurrence of the species in altitudinal belts. (5) Number of global floristic zones in which the species occurs in the whole of its native range; taken from Klotz *et al.* (2002). Floristic zones are characteristic sequences of plant assemblages reflecting the climate zones from the poles to the equator. For details on variation in response variables see Appendix S1.

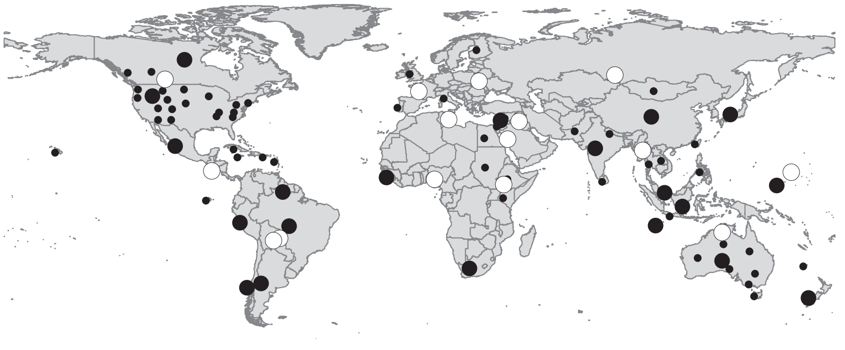

Figure 1 The global distribution of datasets used to infer data on alien success and invasiveness. Empty circles relate to summary data from large geographical regions (e.g. Asia, Australasia, Pacific, Mediterranean), large solid circles to large countries (e.g. Australia, South Africa, USA), small solid circle to individual countries or states. Each circle may represent more than one dataset. Based on datasets listed in Randall (2002).

Biological traits included: (1) Life history: annual, monocarpic perennial, polycarpic perennial; available for *n* = 1218 species. (2) Life form after Raunkiaer, based on the position of overwintering meristematic tissues (Mueller-Dombois & Ellenberg, 1974): therophyte, hemicryptophyte, geophyte, chamaephyte, phanerophyte, aquatic (hydrophyte); *n* = 1218. (3) Life strategy according to Grime (1979): C – competitor, S – stress-tolerator, R – ruderal and their combinations: CR, CS, SR, CSR; *n* = 1138. (4) Clonality: ability to grow clonally (yes/no); *n* = 1196. (5) Height, calculated as the mean from minimum and maximum height reported in the national flora (0.01–40 m); *n* = 1218. (6) Timing of first flowering, defined as the month in which a plant starts to flower in the native range; *n* = 1218. (7) Flowering period, defined as the number of months over which a plant flowers in the native range (1–9); *n* = 1218. (8) Propagule size is the size of the dispersal unit (seed or fruit; 0.2–45 mm); *n* = 1137. (9) Propagule weight is the weight of the dispersal unit (0.005–1041.9 mg); *n* = 449. (10) DNA content (0.11–155 pg/2C); *n* = 309. (11) Ploidy level refers to the number of homologous copies of chromosomes; *n* = 1152. (12) Number of ploidy levels reported for the species. (13) Type of reproduction: only by seed (s); mostly by seed and rarely vegetatively (ssv); both by seed and vegetatively (sv); mostly vegetatively and rarely by seed (vvs); exclusively vegetatively (v); *n* = 1216. (14) Self-compatibility, defined as the ability to produce viable zygotes after selfing (yes/no). (15) Dicliny, describing the spatial separation of genders with male and female organs on different flowers or plants, thus reflecting whether a single individual is capable of generative reproduction or not: hermaphrodite (all flowers bisexual), monoecious (male and female flowers on the same plant), gynomoecious (female and bisexual flowers on the same plant), andromonoecious (male and bisexual flowers on the same plant), trimonoecious (bisexual, female and male flowers on the same plant), male sterile (only female flowers), dioecious (male and female flowers on different plants), gynodioecious (female and bisexual flowers on different plants or female and monoecious flowers on different plants), androdioecious (male and bisexual flowers on different plants or male and monoecious flowers on different plants), trioecious (female and male and bisexual and/or monoecious, gynomonoecious or andromonoecious flowers on different plants); *n* = 1185. (16) Pollen vector: insects, wind, water, no specific vector needed; *n* = 1199. (17) Number of pollen vectors by summing up the above mentioned dispersal vectors of one species; *n* = 1199. (18) Dispersal mode describes the vectors which disperse generative propagules (seeds or fruits), i.e. wind, water, self, epizoochory (on the fur or feathers of animals), endozoochory (through the intestine system of animals), ants; *n* = 1179. (19) Number of dispersal vectors of the above mentioned occurring in one species; *n* = 1179.

Statistical analysis

Regression trees (Breiman *et al.*, 1984; Steinberg & Colla, 1995; De'ath & Fabricius, 2000) were used to explain alien success and weediness of Central European species as response variables. As weediness is a proportional number from all cases when the species was recorded, data on weediness were weighted by the total number of alien records in each region, to avoid too strong influence of the proportions calculated from species-poor records (see e.g., Crawley, 1993, p. 265–290; Pyšek *et al.*, 2003). Following De'ath & Fabricius (2000), to describe how the average number of alien species and the average proportional representation of weeds depend on all the explanatory variables, distributional characteristics and biological traits were first used jointly in the same analysis as explanatory variables. Then, to describe the indirect effects of biological traits via their influence on distributional characteristics, the individual distributional characteristics were used as the response variables and the biological traits as explanatory variables.

The trees were constructed by repeatedly splitting the species into two subgroups based on the values of response variables using binary recursive partitioning in CART® v. 5.0 (Breiman *et al.*, 1984; Steinberg & Colla, 1995). This method uses the most reliable pruning strategy of over-growing trees, ensuring that no important tree structure is overlooked. To find the best tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was grown, and their resubstitution relative errors, corresponding to residual sums of squares, were estimated. Ten-fold cross-validation was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the tree with the smallest number of terminal nodes was selected as the best tree in such a way that its estimated cross-validated relative error was within one standard error of the minimum (1-SE rule; Breiman *et al.*, 1984). Following De'ath & Fabricius (2000), a series of 50 cross-validations was run, and the modal (most likely) single tree chosen for description. Total variance explained by the best single tree was calculated as $r^2 = 1 -$ resubstitution relative error. To prevent predictor variables with missing values to have an advantage as splitters, the variables with missing values were penalized in proportion to the degree in which they were missing, and treated by back-up rules that closely mimicked the action of the primary splitters (Breiman *et al.*, 1984; Steinberg & Colla, 1995). To check appropriateness of the trees, residuals were plotted against predicted values of their terminal nodes (Quinn & Keough, 2002).

The trees were presented graphically, with the root Node 1, standing for undivided data, at the top, and the terminal nodes, describing homogeneous groups of species, at the bottom of the hierarchy. Following Steinberg & Colla (1995), the quality of each split was assessed by the improvement, corresponding to the proportion of the total sum of squares explained by the split; these improvements were used to compare proportion of variance explained by the distributional characteristics and biological traits in regression trees. Surrogates of each split, describing splitting rules that closely mimicked the action of the primary split, were assessed and ranked according to their association values, with the highest possible value 1.0 corresponding to the surrogate producing exactly the same split as the primary split; these association values were used to evaluate alternative splits in regression trees.

To account for phylogenetic effects, we partitioned the variance in alien success and weediness into a part strictly due to ecological characteristics (i.e., distributional characteristics plus biological traits), a part strictly due to phylogeny, a part due to a joint influence of these two factors (i.e., phylogenetically structured variation of ecological characteristics) and the unexplained part of the variation. First, a patristic distance matrix (i.e. the sum of branch lengths on a path between a pair of taxa) was derived from a phylogenetic supertree (Durka, 2002) containing all species with alien records, considering each branch length to be equal to one unit (e.g. Prinzing *et al.*, 2002). A principal coordinate analysis was then performed on this matrix, using the function *cmdscale* in R package version 2.3.1 (R Development Core Team, 2006). Each principal coordinate (called PC hereafter) of the matrix represented the relative amount of phylogenetic variance proportional to the associated eigenvalue (Diniz-Filho *et al.*, 1998). The PCs were listed in decreasing order of explained variance, from PC1 to PC1181, omitting a few last axes having negative eigenvalues. We then incorporated phylogenetic information into the statistical analysis following Desdevises *et al.* (2003); see Appendix S2). As the phylogenetic corrections calculated by variance partitioning of alien success and weediness, unlike the analyses on regression trees, do not allow for using missing values, they were assessed using the species with complete information on traits available. To verify that the same predictors of distributional characteristics and biological traits used in the phylogenetic corrections, which were determined by the best trees based on the whole dataset, remain valid for the subsets used in the calculations of variance partitioning, the analyses on regression trees were repeated on the subsets used for the phylogenetic corrections, and the best trees, determined from the whole dataset and from the subsets, were compared.

Variance components analysis (restricted maximum likelihood estimation method in S-Plus v. 6.2) for all species from genera represented by at least two species in the dataset (81.3% of the data) was used to describe how total variations in alien success and weediness are distributed among taxonomic levels. In this method, the larger the variance at a particular taxonomic level, the larger the possible lack of statistical independence below this level, due to a likely phylogenetic relatedness of species within the taxa (Harvey & Pagel, 1991).

RESULTS

Alien success

The best regression tree (Fig. 2) explained 45.2% of variability in alien success. This was completely accounted for by only two distributional characteristics of the species: number of grid cells from which the species is reported in the Czech Republic, and number of floristic zones in which it occurs in its native range, with an explanatory power of the former about 2.5 times higher than that of the latter. The lowest average alien success (20.2 records) was predicted if the species occurred in < 52.0% of grid cells and four floristic zones, and the highest (144.8 records), if the native distribution exceeded 78.8% of grid cells and seven floristic zones (Fig. 2).

The number of habitats in which the species grows in the Czech Republic was positively correlated with the number of grid cells ($r = 0.80$, df = 1187, $P < 0.0001$), for which it was a surrogate. The alternative model in which the number of habitats replaced the number of grid cells produced a splitting rule that closely mimicked the action of the primary split, with an association value of 0.545 and its effect was about 3.4 times smaller than that of the number of grid cells.

Biological traits of species were only indirect predictors of their alien success (Table 1), via their effect on distributional characteristics: 9.3% of variance in the number of grid cells was explicable by flowering period and plant height (Table 1,

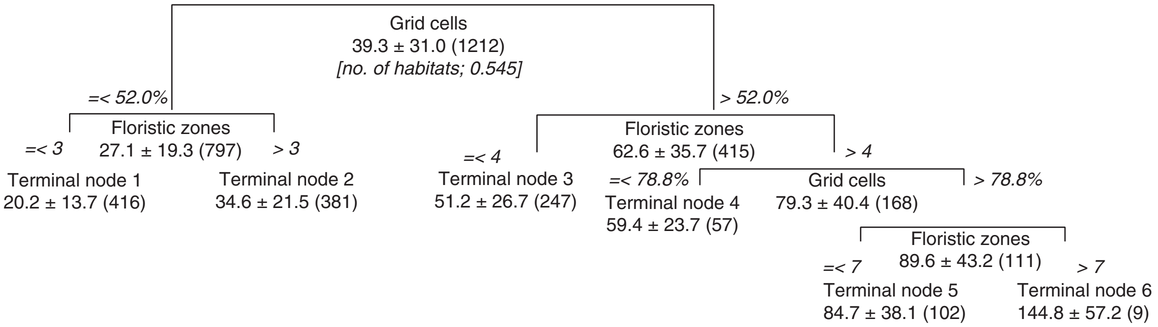

Figure 2 Regression tree analysis of alien success of Central European species, expressed as the number of records as alien in floras outside Europe, using distributional characteristics and biological traits as explanatory variables. Each node shows the splitting variable, splitting criteria, mean ± standard deviation for alien success and number of species in parentheses. Branch lengths are proportional to the improvement value that corresponds to explained variance at each node. Surrogate of the primary split Grid cells, describing splitting rule that closely mimics the action of the primary split, and its association value, ranking this similarity at the scale 0 – 1, is in square brackets. Grid cells = number of grid cells occupied in the Czech Republic; Floristic zone = number of floristic zones in the native range.

Table 1 Summary of the biological traits of Central European species having effects on their occurrence as aliens in other parts of the world in regression trees. Alien success is expressed as the number of records as alien outside Europe, weediness as the proportion of records as a weed. Indirect effects are manifested via the effect of traits on distribution in native range. Life history, dispersal vectors and number of ploidy levels appeared only in alternative regression tree models; annual life history closely mimicked therophytic life form, and dispersal vectors and number of ploidy levels appeared as new explanatory variables when dropping number of grid cells from the best regression tree (see text for details).

	Alien success		Weediness	
Biological trait	Direct effect	Indirect effect	Direct effect	Indirect effect
Flowering period	–	Long	Long	Long
Height	–	Tall	–	Tall
Life form	–	Aquatic	Therophyte	Aquatic
Life history	–	–	Annual	–
Life strategy	–	–	CR	–
Reproductive type	–	–	Generative	–
Dispersal vectors	–	–	Diverse	–
Ploidy levels	–	–	Diverse	–

Fig. 3A), and 8.1% of variance in the number of floristic zones by life form (aquatic vs. all terrestrial forms) and flowering period (Table 1, Fig. 3B). The highest number of grid cells is predicted for species with the flowering period longer than four months, or, if shorter, for species taller than 1.9 m. Species recorded in the lowest number of grid cells are those with the flowering period shorter than five months and height below or equal to 0.3 m (Fig. 3A). The number of floristic zones occupied was higher for aquatic plants than for terrestrial species, for which it increased with the increasing length of the flowering period (Fig. 3B).

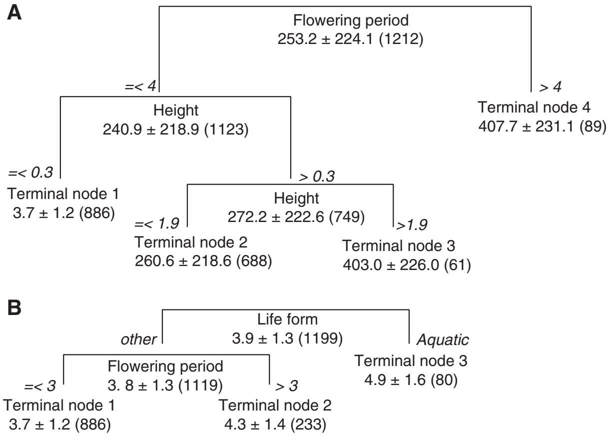

Figure 3 Regression tree analysis of the number of grid cells (A) and the number of floristic zones (B) of Central European species occupied in the native range, based on biological traits. Each node shows the splitting variable, splitting criteria, mean ± standard deviation for number of grid cells (A) and that of floristic zones (B) and number of species in parentheses. Vertical depth of each node is proportional to its improvement value that corresponds to explained variance at each node. Flowering period in months; Height = mean plant height (m); Life form after Raunkiaer (see text).

Weediness

The best tree explained a similar amount of variability in weediness (43.6%) as was the case for alien success. However, the variability in weediness was directly explicable both by distributional characteristics and biological traits (Fig. 4). Explanatory distributional characteristics were the same as for alien success, i.e. number of grid cells occupied in the Czech Republic (with the number of habitats as a surrogate) and that of floristic zones, and so was their relative contribution to the total improvement in the best tree. Of the four biological traits with explanatory power, two also contributed indirectly to alien success, namely flowering period and life form. Other traits with a direct effect on weediness were life strategy and reproduction type (Fig. 4, Table 1). Altogether, the contribution of the direct effects of distributional characteristics to the total explained variance was 65.1% and that of biological traits 34.9%. The most invasive species occurred in more than 70.4% of grid cells, their native distribution spanned over more than four floristic zones and they had Grime's competitor/ruderal (CR) life strategy (Fig. 4). The alternative model (not shown) indicated two more biological traits: the number of dispersal vectors and the number of ploidy levels. Species which are dispersed by more than two vectors and occur as both diploids and polyploids were most weedy.

Phylogenetic effects

Explanatory variables, improvement values and proportion of explained variance were very similar between the best regression trees of alien success and weediness, calculated for the whole dataset, and those run on subsets of data that were used for calculating the phylogenetic corrections (98.8 and 93.1% of the whole dataset for alien success and weediness, respectively, due to missing cells). Hence the results on the role of phylogenies are representative for the whole dataset.

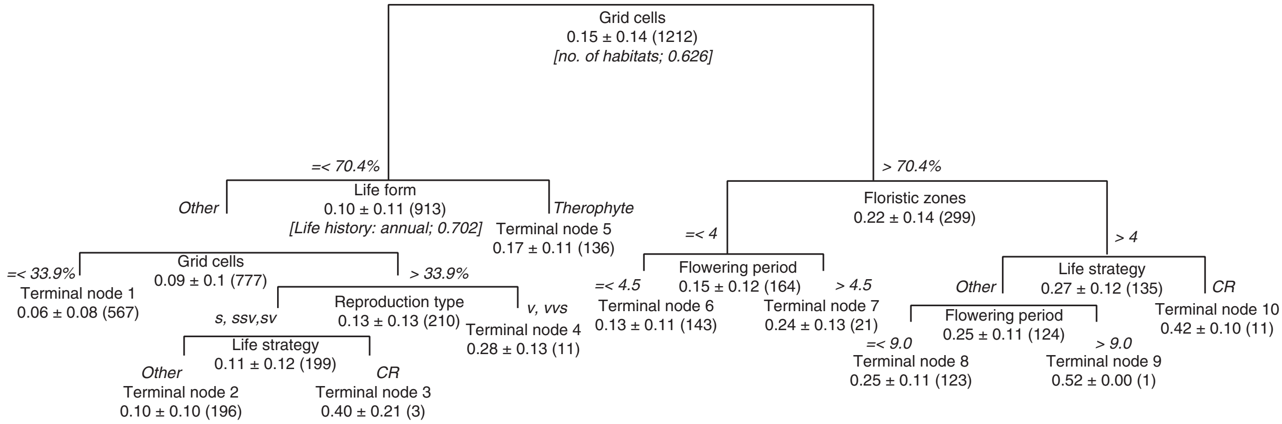

Figure 4 Regression tree analysis of weediness of Central European species, expressed as proportional representation of occurrences as 'weed' among all records in alien floras outside Europe, using distributional characteristics and biological traits as explanatory variables. Each node shows splitting variable (with surrogates in brackets where applicable), splitting criteria, mean ± standard deviation for weediness and number of species in parentheses. Surrogates of the primary splitters Grid cells and Life form, describing splitting rules that closely mimic the action of the primary splitters, and their association values, ranking these similarities at the scale 0 – 1, are in square brackets. Branch lengths are proportional to the improvement value that corresponds to explained variance at each node. Grid cells = number of grid cells occupied in the native range; Floristic zone = number of floristic zones; Life form according to Raunkiaer; Flowering period in months; Reproduction type = s, ssv, sv, vvs, v: only by seed, mostly be seed and rarely vegetatively, both by seed and vegetatively, mostly vegetatively and rarely by seed, and exclusively vegetatively, respectively; Life strategy according to Grime (1979).

The fractions of variation related to biological traits that include the embedded parts of phylogenetically structured variation (fractions [a + b] in Fig. 5) were highly significant for both alien success ($F = 84.56$; df = 15, 1171; $P < 0.0001$) and weediness ($F = 27.21$; df = 38, 1117; $P < 0.0001$), and explained 51.4 and 46.3% of variation in these two response variables, respectively (Fig. 5). The corresponding regression trees that also included embedded parts of the phylogenetic structure of biological traits (Figs 2 and 4) explained similar amount of variance (45.2 and 43.6% for alien success and weediness, respectively).

When ascertaining phylogenetically related fractions of variation that included the embedded parts of phylogenetically structured variation of biological traits (fractions [b + c] in Fig. 5), 28 and 29 principal coordinates (PCs) were significant and retained in models for alien success ($F = 7.35$; df = 28, 1154; $P < 0.0001$) and weediness ($F = 9.81$; df = 29, 1117; $P < 0.0001$), respectively. The sums of their eigenvalues represented 14.4 and 22.0% of the total variances of patristic distance matrices and explained 13.1 and 18.3% of the variations in alien success and weediness, respectively (Fig. 5). Essentially, differences at relatively small phylogenetic scales (i.e., among species within genera and among genera within families) were important, as indicated by PCs being significant only if higher than PC3. This interpretation is strongly supported by the results of variance component analyses among taxonomic levels. The variance components were the greatest among species within genera, much smaller among genera within families, and negligible (< 0.0001%) for the highest taxa, subclasses and classes (Fig. 6).

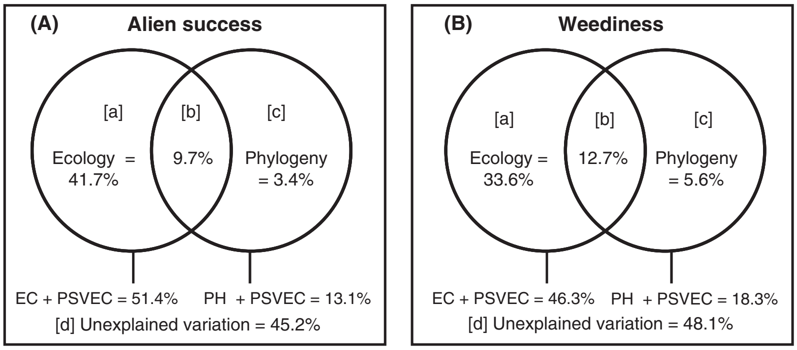

Figure 5 Partitioning of the variation in alien success (A) and weediness (B) among ecological characteristics (EC, parts [a + b] of the Venn's diagrams), phylogeny (PH, parts [b + c]) and PSVEC (phylogenetically structured variation of ecological characteristics, the intersections [b]). The rectangles represent 100% of the variations, of which [d] are the unexplained parts. Ecological characteristics include both significant distributional characteristics and biological traits.

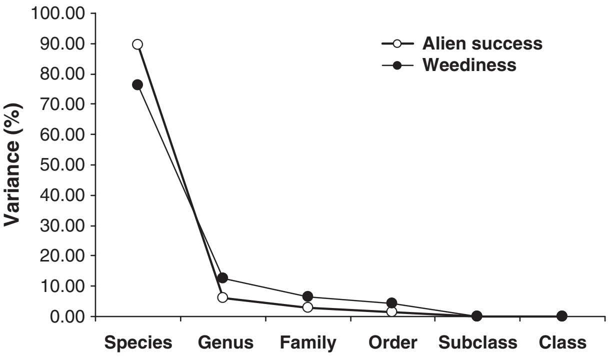

Figure 6 Taxonomic distributions of variance in alien success (number of records as alien outside Europe) and weediness (proportion of records as a 'weed') among 986 Central-European plant species (81.3% of the dataset), estimated by the variance component analysis. Variance components are percentages of total variance accounted for at successive taxonomic levels. Data for weediness were angular transformed prior to analysis.

The part of variation strictly due to phylogeny (fractions [c] in Fig. 5) was small but significant for both alien success (3.4%: $F = 4.18$; df = 28, 1142; $P < 0.0001$) and weediness (5.6%: $F = 5.36$; df = 29, 1016; $P < 0.0001$). Overall, the fractions of variation simultaneously related to both biological traits and phylogeny (fractions [a + b + c] in Fig. 5) explained 54.8% of variation in alien success ($F = 34.46$; df = 43, 1143; $P < 0.0001$) and 51.9% of variation in weediness ($F = 19.89$; df = 68, 1117; $P < 0.0001$).

The effect of phylogeny was systematically higher for weediness than alien success. This is indicated by a larger part of variation due to phylogeny and due to phylogenetically structured variation in ecological traits (parts [c] and [b] in Fig. 5, respectively) for weediness than alien success, and by smaller variance components among species within genera, but larger for higher taxa (Fig. 6) for weediness than alien success.

DISCUSSION

Controlling for confounding factors

Our results suggest that success of particular species in early stages of invasion can be predicted by characteristics of their native distributions, whereas their biological traits are important for determining success levels at later stages, when they co-determine, along with the native-range distributional characteristics, which species become serious invaders. Our analyses did not explicitly include data on propagule pressure, which are hardly available in invasion biology (Richardson & Pyšek, 2006; Chytrý *et al.*, 2008; Pyšek *et al.*, 2009). However, the effect of distributional characteristics in the native geographical range and the absence of direct effects of species traits on species establishment outside its native range can be interpreted as a strong indication of the importance of propagule pressure for invasion. The results also indicate the importance of species tolerance to a wide range of climates, which was represented by the number of floristic zones in our analysis. This implies that unless factors such as propagule pressure and climatic tolerance are taken into account, the results of studies searching for invasive plant traits can be confounded and the importance of traits overestimated. Another important confounding variable, minimum residence time (Rejmánek, 2000), which was shown to explain a substantial part of variation in invasion success (Castro *et al.*, 2005; Thuiller *et al.*, 2006; Wilson *et al.*, 2007) could not be accounted for in this study. Our data include 37,085 records of alien success and 5883 records of weediness of the source species pool in various parts of the world, but the information on the time of introduction is not available in most cases. Nevertheless, the models for both alien success and weediness explained 45 and 36% of variation in the data, respectively, indicating that important explanatory variables were taken into account in our study.

Several studies recently addressed the role of traits in plant invasions (e.g., Herron *et al.*, 2007; van Kleunen & Johnson, 2007; Gravuer *et al.*, 2008; Küster *et al.*, 2008), but none of those that considered potentially confounding factors co-determining invasiveness, at the same time, (i) used a global dataset, (ii) attempted to analyse different stages of invasion process and (iii) took distributional characteristics into account together with species traits [see recommendations by Sol *et al.* (2008)]. Thuiller *et al.* (2006) based their analysis on the invading species pool in the target region of South Africa, and their results cannot be used in a predictive framework. Hamilton *et al.* (2005) analysed several traits on different spatial scales and accounted for phylogenetic effects, but disregarded the different steps of the invasion process and did not consider distributional characteristics in native ranges. Van Kleunen *et al.* (2007), in a study based on global horticultural usage of species of *Iridaceae*, analysed introduction to horticulture and naturalization separately, and employed distributional characteristics together with some species traits. Gravuer *et al.* (2008) considered human and biogeographic factors as well as traits and three invasion stages, but only for a single genus (*Trifolium*). Küster *et al.* (2008) considered distributional characteristics but used a target area approach of one invasion step and focused on important interactions among ecological characteristics. Hence, none of the available studies shows the importance of the distribution of species in their native range and its relationship to biological species traits. In addition, none of them apply to all seed plants of the source area and global scale.

Propagule pressure, climatic tolerance and habitat versatility

The analysis of variables used to characterize the native range of Central European species revealed three important features of native distribution: (i) regional frequency expressed as the number of grid cells occupied, (ii) the ability to grow in various habitats and (iii) climatic tolerance reflected by the number of climatic zones in which the species occurs in its native range.

Regional frequency has the most pronounced effect on the invasion process and is related to propagule pressure: widespread species are more likely to be dispersed by humans because they occur in more locations (Booth *et al.*, 2003). Similarly, species occurring in more habitats have a higher chance to be introduced to the areas outside their native range. Indeed the regional frequency and habitat range are positively correlated and their effects cannot be easily separated: regionally abundant or widely distributed species encounter a wider range of habitats than species with restricted regional frequency or smaller ranges. In larger or more densely occupied ranges species interact with more diverse assemblages of native biota, which may lead to better adaptation to a wider range of conditions (Booth *et al.*, 2003). This positive feedback between regional abundance (or range size) and habitat range can thus result in the evolution of invasiveness (Sax & Brown, 2000).

This is supported by evidence in the literature that preadaptation to a wide range of climates acquired through evolutionary history contributes to success of a species as an invader (Thuiller *et al.*, 2005). Also in our current analysis, the significant effects of the number of floristic zones in the native range on both alien success and weediness indicate that the tolerance to a wide range of climates is crucial for both naturalization and invasion in the new region.

Relative importance of distributional characteristics and biological traits at different stages of invasion

By analysing two separate stages of the invasion process (Richardson *et al.*, 2000; Williamson, 2006), we show that the relative importance of native-range distributional characteristics and biological traits is stage-dependent and that the latter is more important in later, more advanced stages of invasion. Biological species traits have only an indirect effect on the probability that a species will become introduced or naturalized in the new region (via their effect on distributional characteristics in the native range). By contrast, biological traits directly affect weediness. Additional evidence for these conclusions comes from a study of invasive woody plants in the Czech Republic, in which the effects of biological traits, residence time and planting extent (a measure of propagule pressure) on three stages of the invasion process were considered, and biological traits only played a role in later stages (Pyšek *et al.*, 2009). Still, the direct effect of biological traits on weediness in this study was 32.3% and that of the distributional characteristics 67.7% of the total variation explained. This indicates that the distributional information from the species native range can be used as the most important predictor of its invasion success (Rejmánek, 1996; Goodwin *et al.*, 1999).

The only biological trait that confers establishment of a wide distribution in the native range and at the same time directly contributes to the weediness in new regions is an extended flowering period. However, the weediness is determined by a more complex suite of traits, most of which do not have any effect on the distribution in the native range. This allows us to draw some conclusions on the reasons for the positive correlation between native and invaded distribution range sizes previously reported in literature (Rejmánek, 1996; Goodwin *et al.*, 1999). There are two explanations why large native ranges should lead to successful invasion. It has been suggested that invading capacity is high in widespread species, which simply have a higher probability of being moved by humans to other regions than less widely distributed species (Forcella & Wood, 1984; Forcella *et al.*, 1986; Jäger, 1988). The second explanation is based on the assumption that traits that allow the species to have a large native range are the same as the ones allowing it to have a large invaded geographical range (Thompson *et al.*, 1995; Booth *et al.*, 2003). Our results indicate that the former explanation is more likely and points to the importance of propagule pressure. The theory of the same traits playing role in both ranges seems to be only partly valid, as indicated by exceptions to this rule reported for individual species (Richardson & Bond, 1991). Nevertheless, both explanations are obviously not mutually exclusive (Scott & Pannetta, 1993; Rejmánek, 1996).

Tall stature, another strong predictor of native distribution, does not appear among traits directly increasing weediness in our study. Plant height has been repeatedly identified as a trait associated with invasiveness in congeneric comparisons and multispecies comparative studies (Crawley *et al.*, 1996; Goodwin *et al.*, 1999; Pyšek & Richardson, 2007), but our results indicate that its effect may be manifested through more complex traits, such as life strategy. Plants with the CR strategy are tall, efficient users of resources combining fast growth with a high reproductive output (Grime, 1979) and experience a stronger enemy release in invaded range (Blumenthal *et al.*, 2009). Generally, reproductive and dispersal characteristics (long period of flowering, annual life form and generative reproduction, use of a variety of dispersal vectors) were crucial for a species to become weedy in our study. The fact that species known to occur as both diploids and polyploids tend to be more weedy than those having only one ploidy level suggests the importance of phenotypic plasticity, genetic variation and hybridization in the colonization by invasive species (Ellstrand & Schierenbeck, 2000) as well as the role of the evolution of polyploidy in facilitating invasions (Hurka *et al.*, 2003; Abbot & Lowe, 2004). It can be assumed that plasticity in terms of ability to be dispersed by a variety of vectors increases the chance of long-distance dispersal, which has been shown to control the rate of spread (Higgins & Richardson, 1999).

Phylogenetic effects

When analysing large comparative datasets, potentially confounding effects of phylogenetic relatedness should be taken into account to distinguish between ecological and evolutionary explanations (Harvey & Pagel, 1991). Only a few studies looking at traits associated with invasiveness have applied phylogenetic correction (Crawley *et al.*, 1996; Prinzing *et al.*, 2002; Kühn *et al.*, 2004a; Hamilton *et al.*, 2005; van Kleunen &

Johnson, 2007; Küster *et al.*, 2008). Nevertheless, the small proportion of variation strictly due to phylogeny and its association with lower taxonomic levels contradicts some previous studies (Daehler, 1998; Pyšek, 1998), which suggested that invasive alien plants are non-randomly distributed within higher taxonomic groups. However, these studies did not rigorously test phylogenetic partitioning of variation in invasiveness. So far the robust evidence for invasiveness being phylogenetically related at lower taxonomic levels only comes from a study of gymnosperms (Richardson & Rejmánek, 2004). Therefore, both phylogenetic eigenvector filtering as well as variance component analysis indicate that large-scale phylogenetic trends are less important than small-scale phylogenetic autocorrelation in the strict sense. This result has important implications for monitoring and prediction of plant invasions. The fact that for high taxonomic levels there is very weak, if any at all, phylogenetic component of invasion success implies that we cannot predict that a species belonging to a particular family, order or class would be more predisposed to invasions than other species belonging to other taxa at the same hierarchical level. The variation in weediness in our study was primarily associated with species level. This is important practical message (e.g. for nursery industry, which primary deals with individual species and varieties), stressing that pest risk assessment should be performed at the level of species and genera, while generalizations based on higher taxonomic levels can be misleading. However, the systematically higher effect of phylogeny on weediness than alien success indicates that at the later stages of invasion, when biological traits co-determine the outcome of the process in concert with distributional characteristics, the role of phylogeny increases as alien species proceed from the stage of casual and naturalized to that of invasive and pest.

CONCLUSIONS

Searching for 'invasive traits' is partly practically motivated. There is growing evidence that some species are inherently better equipped to become invasive after being moved to new areas by humans (Pyšek & Richardson, 2007). If so, we can identify species with potential to become weedy and consider management options to prevent or at least reduce the damaging effects of biological invasions. Finding a set of traits associated with invasiveness that applies to all seed plants has been until recently considered an unrealistic aim (Williamson, 1999). However, our study suggests that rigorous statistical approaches which account for confounding factors and the use of large datasets with information on global success of species originating from a single area can result in identification of a suite of traits that are associated with success of plant invaders in modern landscapes. Potential use of these results in the management of invasive species is not constrained by the fact that traits identified in our study mostly relate to invasions in disturbed habitats; vast majority of invasions start in such habitats and species establish there before they invade habitats that are more natural (di Castri, 1990; Essl *et al.*, 2009). Our results may therefore be useful for improving screening systems designed to identify potentially noxious invaders before introduction to a new region (Pheloung *et al.*, 1999). This could be performed by including information on how widespread a species is in its native range and how the distribution interacts with other factors such as traits; by identifying their relative importance, our study provides the first quantitative basis for such an assessment. Nevertheless, the minor and only indirect role of traits in early stages of invasion process, i.e. in determining whether a species can become casual or naturalized, but not invasive or weedy alien (Richardson *et al.*, 2000) advocates for a precautionary approach to the management. Species which have large native ranges, within which they are common and occupy many habitat types, and possess traits which were identified as contributing to weediness in this study, should be paid increased attention upon introductions. From a scientific point of view, future studies searching for invasive traits need to take into account confounding factors associated with propagule pressure to avoid misleading conclusions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Variation in response variables.

Appendix S2 Partitioning the variance in alien success and weediness.