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Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits

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Abstract Many woody plants have been recently recognized as major invasive species with serious impacts on species diversity and functioning of invaded ecosystems. We evaluated the global invasion success of temperate trees and shrubs with native ranges in central Europe and explored the role of their native distribution and that of biological traits in determining whether they have become invasive in other parts of the world. Of the 94 species forming the source-area species

pool, 27 % are known to be invasive in at least one region of the world. Generalized linear models on phylogenetically non-informed analyses revealed that tall woody plants flowering early in the season, and occupying many grid cells in the native range are significantly more likely to become successful invaders than species not possessing these traits. However, other traits can partly reduce the disadvantages resulting from low regional frequencies in the native range and consequent lower probability of them being introduced elsewhere. Species that do not depend for reproduction on another individual, those pollinated by wind and dispersed by animals are likely to become invasive even if they do not have extensive native distributions. However, of these traits only the regional frequency in

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the native range remained significant when phylogenetic relationships were taken into account. This indicates that the effect of the regional frequency is generic, valid across all woody species, and fine-tuned by advantageous biological traits inherited from common ancestors, shared by groups of phylogenetically-related species. Traits that only appeared significant in the phylogenetically non-informed analyses should be considered as specific for shrubs and trees of central Europe. Mode of reproduction was only significant in the phylogenetically-informed analysis, indicating that reproduction exclusively by seed favours invasiveness of woody species. From the management perspective, however, the predictive value of some traits is not diminished by them being phylogenetically constrained since we are not interested whether the behaviour of particular species is a result of evolutionary history but how we can treat specific cases of invasion.

Keywords Central Europe · Dispersal · Distribution · Invasiveness · Native range · Pollination · Reproduction · Shrubs · Source area approach · Tree invasions

Introduction

Some woody plants have been recently recognized as major invasive species, and many of them have naturalized or became invasive in many parts of the world (Richardson and Rejmánek 2011; Rejmánek and Richardson 2013). This is reflected in their coverage by various lists of “worst invaders” (e.g., DAISIE 2009), as well as by the fact that among the most intensively studied invasive plants globally, there are 20 % of woody species (Pyšek et al. 2008). Although the representation of woody species may not be disproportionately high in terms of species numbers, compared to other growth forms, many woody plants have serious impact on species diversity and functioning of invaded ecosystems (e.g. Carmen and Brotherson 1982; Richardson et al. 1989; Vitousek and Walker 1989; Higgins and Richardson 1998; DAISIE 2009; Pyšek et al. 2012c). The increasing interest in studying woody plant invasions since the late 1990s (e.g. Reichard and Hamilton 1997; Henderson 1998; Barton et al. 2004) came with realization that they not only have considerable impact on invaded ecosystems but also represent an ideal model

group of invaders (Richardson 1998, 2006; Richardson and Rejmánek 2004; Kueffer et al. 2013).

Efforts have been made to predict invasions by alien trees and shrubs (e.g. Reichard and Hamilton 1997; Bellingham et al. 2004; Richardson and Rejmánek 2004; Křivánek and Pyšek 2006; Křivánek et al. 2006; Herron et al. 2007), identify traits and factors associated with their invasiveness (Richardson et al. 1994; Rejmánek and Richardson 1996; Widrlechner 2001; Grotkopp et al. 2002; Pyšek et al. 2009b) and model their invasion dynamics (Richardson and Bond 1991; Higgins and Richardson 1998). In general, studies of invasions by woody plants have shed light on many crucial aspects of invasion ecology. Centuries of introductions all over the world have provided us with natural experiments in various biogeographical settings. Still, as new naturalizations are continuing at steady pace, and woody plant invasions are rapidly increasing in importance, thorough and objective assessment of naturalized and invasive woody plant species around the world is urgently needed; first steps towards this goal have been made recently (Richardson and Rejmánek 2011).

Decades of search for the “holy grail” of plant species invasiveness proved that factors contributing to invasiveness are more likely to be identified within certain taxonomic or ecologically defined groups rather than by studies addressing all vascular plants (Pyšek and Richardson 2007). In this respect, woody plants represent a unique and promising group thanks to good historical data on times and magnitudes of introductions documented by forestry and horticulture records in many parts of the world (Richardson and Rejmánek 2004; Pyšek et al. 2009b). In terms of data quality and comprehensiveness of information on introductions and subsequent spread, trees and shrubs provide the best information of all plant life forms. Indeed, woody species are the only plant group for which there is a global database of invasive species. This database, based on exhaustive survey of regional and national databases, contains the data on presence of 622 species of trees and shrubs identified as invasive in at least one of 15 broad biogeographical regions of the world (Richardson and Rejmánek 2011).

In this paper we made use of this unique data set to evaluate the global invasion success of temperate woody plants with native range in central Europe, and explain it using a wide range of plant traits. We use the source-area approach (Prinzing et al. 2002; Pyšek et al. 2004b, 2009a; Thuiller et al. 2005; van Kleunen et al.

2007; Bucharová and van Kleunen 2009), i.e. delimiting a source pool of species native to certain region and following their post-introduction performance in other regions. In this way, we minimize the differences associated with the distance to source areas and evolutionary predispositions acquired in various regions of origin. The approach is based on the assumption that members of the flora of a single biogeographical region have (at least theoretically) comparable chances to be transported by humans from their native range to other parts of the world (Pyšek et al. 2009a), because they are exposed to the same historical, socioeconomic and biogeographical factors. Still we are aware that species from the same source area have different introduction histories which can have important effects on invasion success (Bucharová and van Kleunen 2009). Unfortunately, this data is not available and hence our approach seems to be the most appropriate among the ones reviewed by van Kleunen et al. (2010). This means that the variation in probability that they would become a subject of intentional export from the region, or get into contact with humans for unintentional translocation, is lower than in analyses of alien floras of target regions where alien plants come from various regions that may be historically, socioeconomically and culturally very different. Thus, the differences in the success as aliens can be less critically attributed to their traits by using the source-area approach (Sol et al. 2008).

In the last decade it has been realized and illustrated by quantitative models that invasions are complex processes, driven by various interactions of traits of invading species (Küster et al. 2008) and other factors such as propagule pressure, residence time and correspondence of climates between source and target regions. This recognition has led to the application of models that analyse several groups of factors at the same time; this is especially important for properly addressing the role of traits that can be confounded by other factors contributing to invasiveness (e.g. Mulvaney 2001; Rouget and Richardson 2003; Kühn et al. 2004; Hamilton et al. 2005; Pyšek and Jarošík 2005; Thuiller et al. 2005, 2006; Wilson et al. 2007; Bucharová and van Kleunen 2009; Pyšek et al. 2009a; Castro-Díez et al. 2011). Here we follow this approach.

We ask what is the relative role of distribution characteristics of temperate trees and shrubs in their native range, compared to their biological traits, in affecting whether or not they become invasive in other parts of the world?

Methods

Species data

Native woody plants of the Czech Republic (Kubát et al. 2002; Danihelka et al. 2012) were taken as a source species pool to obtain a sample of shrubs and trees that are native to central Europe. This yielded 94 species, which were screened for their occurrence as invasive (following the definition in Richardson et al. 2000) in other parts of the world using the global database of Richardson and Rejmánek (2011).

Information on distributional characteristics and species biological traits was, unless specified otherwise, derived from CzechFlor, a working database of the Czech flora held at the Institute of Botany, Průhonice (see Pyšek et al. 2012a, b for details). The distribution in the native range was inferred from data for the Czech Republic and included: (1) *Number of grid cells from which the species is reported* (range 1–590, $n = 679$), a measure of a species' regional frequency; this system uses a grid of $10'$ (longitude) \times $6'$ (latitude), which at 50°N is approximately $12.0 \times 11.1 \text{ km}$ or 133.2 km^2 (Schönfelder 1999). The data were taken from the Database of the Flora of the Czech Republic (www.florabase.cz, accessed in June 2012), with permission of the original data providers (Institute of Botany AS CR, Masaryk University Brno and Czech Botanical Society). As shown previously, species frequencies in the Czech Republic are closely correlated with those in temperate Europe (Pyšek et al. 2009a). (2) *Number of habitats in which the species occurs* (1–26) out of 88 habitats defined in Sádlo et al. (2007), see also Chytrý (2012) for overview. Here as well, 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* (258–1,450 m a.s.l.) and (4) *Altitudinal range* (170–1,335 m), derived from the range of altitudinal belts over which a species is reported to occur. (5) *Number of global floristic zones* (1–5) in which the species occurs in the whole of its native range; floristic zones (taken from Klotz et al. 2002) are characteristic sequences of plant assemblages reflecting the climate zones from the poles to the equator.

Biological traits included: (1) *Life history*: tree or shrub; (2) *Height*, calculated as the mean from minimum and maximum height reported in the

national flora (0.1–40 m); (3) *Timing of first flowering*, defined as the month in which a plant starts to flower in the native range (2–7); (4) *Flowering period*, defined as the number of months over which a plant flowers in the native range (1–4); (5) *Propagule size* is the size of the dispersal unit (seed or fruit; 0.6–45 mm); (6) *Ploidy level* refers to the number of homologous copies of chromosomes: diploid or polyploid; (7) *Type of reproduction*: only by seed, or both by seed and vegetatively; (8) *Self-compatibility*, defined as the ability to produce viable zygotes after selfing: yes/no; (9) *Number of plants needed for reproduction*: one or two (derived from self-compatibility and type of reproduction; one coded if self-compatible and/or reproducing vegetatively); (10) *Pollen vector*: insects, wind, self; (11) *Dispersal mode* describes the vectors which disperse generative propagules (seeds or fruits): wind, animals.

The phylogenetic information was taken from DaPhnE (Durka and Michalski 2012), which is a dated phylogeny covering the vascular plants of the British Isles, Germany, The Netherlands, and Switzerland. The topology of the tree for the families is based on that of the Angiosperm Phylogeny Group (AGP) III. Following 518 recent molecular studies, partial phylogenetic subtrees were pruned to the backbone tree. 1,103 internal nodes were dated based on 261 recent studies and an ultrametric tree was calculated. The resulting tree thus has branch lengths providing a proxy for evolutionary time. Phylogenetic information was available for 93 of the 94 species; because *Crataegus × subsphaericea* was missing from DaPhnE, we used the phylogenetic information of *Crataegus praemonticola* instead.

Statistical analysis

Invasiveness (yes/no) of 94 central-European tree and shrub species in other parts of the world was a binary response variable. Explanatory variables were five distributional characteristics in the native range and 11 biological species traits, treated as fixed effects. Before analyses, altitudinal range of occurrence, plant height and propagule size were log-, and number of grid cells and number of habitats in native range square root-transformed to normalize the data (e.g. Sokal and Rohlf 1995), and all variables were checked for collinearity by calculating tolerance values (Quinn and Keough 2002). All calculations were done in R

2.14.0 (R Development Core Team 2011). The data were first analysed (1) by generalized linear models without taking into account species relatedness using the function *glm* (e.g. Zuur et al. 2009 pp. 245–259), then (2) on taxonomic hierarchy used as a surrogate for phylogeny with classes, subclasses, orders, families and genera nested as random effects (e.g. Blackburn and Duncan 2001; Pyšek et al. 2011), using generalized linear mixed effect models with the function *lmer* (e.g. Zuur et al. 2009 pp. 323–341), and finally (3) with a phylogenetic correlation structure based on Brownian motion (Freckleton et al. 2011), using the functions *corBrownian* and *compar.gee* from R-package ‘ape’ (Paradis et al. 2004). The phylogenetic correlation structure was based on the updated phylogeny DaPhnE (Durka and Michalski 2012).

To find optimal fixed structure of the models, the modelling followed Quinn and Keough (2002, pp. 111–125), because due to the high number of explanatory variables, it was impossible to fit full models containing all fixed explanatory variables and their possible interactions. The procedures yielded minimum adequate models containing only significant factors (i.e., significantly different from zero and from one another) and, at the same time, minimizing Akaike Information Criterion (AIC; e.g. Crawley 2002), based on the maximum likelihood method. The analyses were first separately conducted for the distributional characteristics and species traits, by backward simplifications of additive multiple linear models using an automatic step-wise process of model simplification using deviance tables, and then all two-way interactions of significant distributional characteristics with all species traits were examined by the same way. This enabled to keep the number of explanatory variables 10 times smaller than the number of observations (e.g. Neter et al. 1996), following the previous finding that the probability of a central European species becoming alien is directly dependent only on its distributional characteristics in the native range while its ability to become invasive directly depends also on their traits (Pyšek et al. 2009a).

To reveal the best model of random components in the models based on taxonomic hierarchy, the modeling started with a beyond-optimal model (Diggle et al. 2002) containing all random explanatory variables and all fixed explanatory variables and their two-way interactions. Using this beyond optimal model the optimal structure of the random

component was found based on AIC, evaluated by restricted maximum likelihood method. The nested models included (1) a model without taxonomy (i.e., with no random effect), (2) with only classes included, (3) with subclasses within classes, (4) with orders nested within subclasses and classes, (5) families nested within all higher taxonomic levels, and (6) genera nested within all higher taxonomic levels.

Because the analyses with phylogenetic correlation structures were first fitted to get initial regression estimates consistent with logistic regressions on logit transformed data of phylogenetically non-informed analyses and then refitted using generalized estimation equations (gee; Liang and Zeger 1986), both approaches differed only due to inclusion of phylogeny in gee, as gee is an extension of glm that allows for correlated responses (Carl and Kühn 2007). However, the analyses on taxonomic hierarchy differed from the previous ones in estimation approach, and differences between analyses of taxonomic hierarchy and phylogenetically informed and uninformed analyses thus can be also attributed to differences in model estimation. Moreover, the phylogenetic gee models converged only for the individual distributional and biological traits, but not for their interactions. The gee models, unlike the glm models on phylogenetically non-informed analyses, thus did not enable to test the interactions between distributional and biological traits.

Results

Of the 94 species forming the source area species pool, 25 (26.6 %) are reported as invasive in at least one region of the world (as defined in Richardson and Rejmánek 2011) (Fig. 1).

In phylogenetically non-informed analyses the probability that a central-European tree or shrub becomes invasive in other parts of the world directly increases with increasing number of grid cells occupied in its native range, its mean height and early start of flowering (Fig. 2a–c and Table S1 in Supplementary Material). However, the probability of a species being invasive also depends on the interaction of several of its traits with the number of grid cells occupied. These interactions are significant in spite of the fact that the interacting biological traits, number of

plants needed for reproduction, mode of pollination and mode of seed dispersal, have no direct effect, i.e. without taking the interaction with native distribution into account they do not affect invasiveness. The probability of invasiveness depends significantly less on increasing number of grid cells for species not depending on another plant for reproduction (Fig. 2d and Table S1), for those that are wind- rather than insect-pollinated (Fig. 2e and Table S1), and those that have fruits dispersed by animals rather than by other means (Fig. 2f and Table S1).

None of the factors affecting plant invasiveness either directly or indirectly by interaction, i.e. number of grid cells occupied in the native range, plant mean height, start of flowering, number of plants needed for reproduction, and pollination and seed dispersal mode, significantly depended on plant taxonomy (Table S2 in Supplementary Material). That plant taxonomy did not affect the relationship between the number of grid cells occupied and invasiveness is also apparent from only slight clustering of the number of grid cells occupied on the phylogenetic tree (Fig. 3, right panel). Large-scale phylogenetic trends described by taxonomy thus appeared unimportant, as is also apparent from the virtually random distribution of invasive species on the phylogenetic tree (Fig. 3, left panel).

However, relationships between species' invasiveness and their traits were affected by small-scale phylogenetic autocorrelations examined by the phylogenetic correlation structure. Due to the strong phylogenetic clustering for closely related species, namely those in the genera *Rubus* and *Rosa*, the effects of mean height (Fig. A1 in Supplementary Material) and start of flowering (Fig. A2 in Supplementary Material) were no longer significant when phylogenetic autocorrelation was taken into account (plant height: $F = 0.260$; phylogenetic degrees of freedom $dfP = 1, 12.9$; NS; start of flowering: $F < 0.0001$, $dfP = 1, 12.9$; NS). On the other hand, due to a strong phylogenetic clustering of the ability of the plants to reproduce vegetatively (Fig. A3 in Supplementary Material), the probability of invasiveness was significantly affected by this mode of reproduction in phylogenetically informed analysis (Fig. 4 and Table S3), but not in phylogenetically non-informed analyses (Fig. 2). The only factor that was significant in phylogenetically non-informed analyses and remained so in phylogenetically informed, was the number of grid cells in the native range ($F = 27.155$; $dfP = 1$,

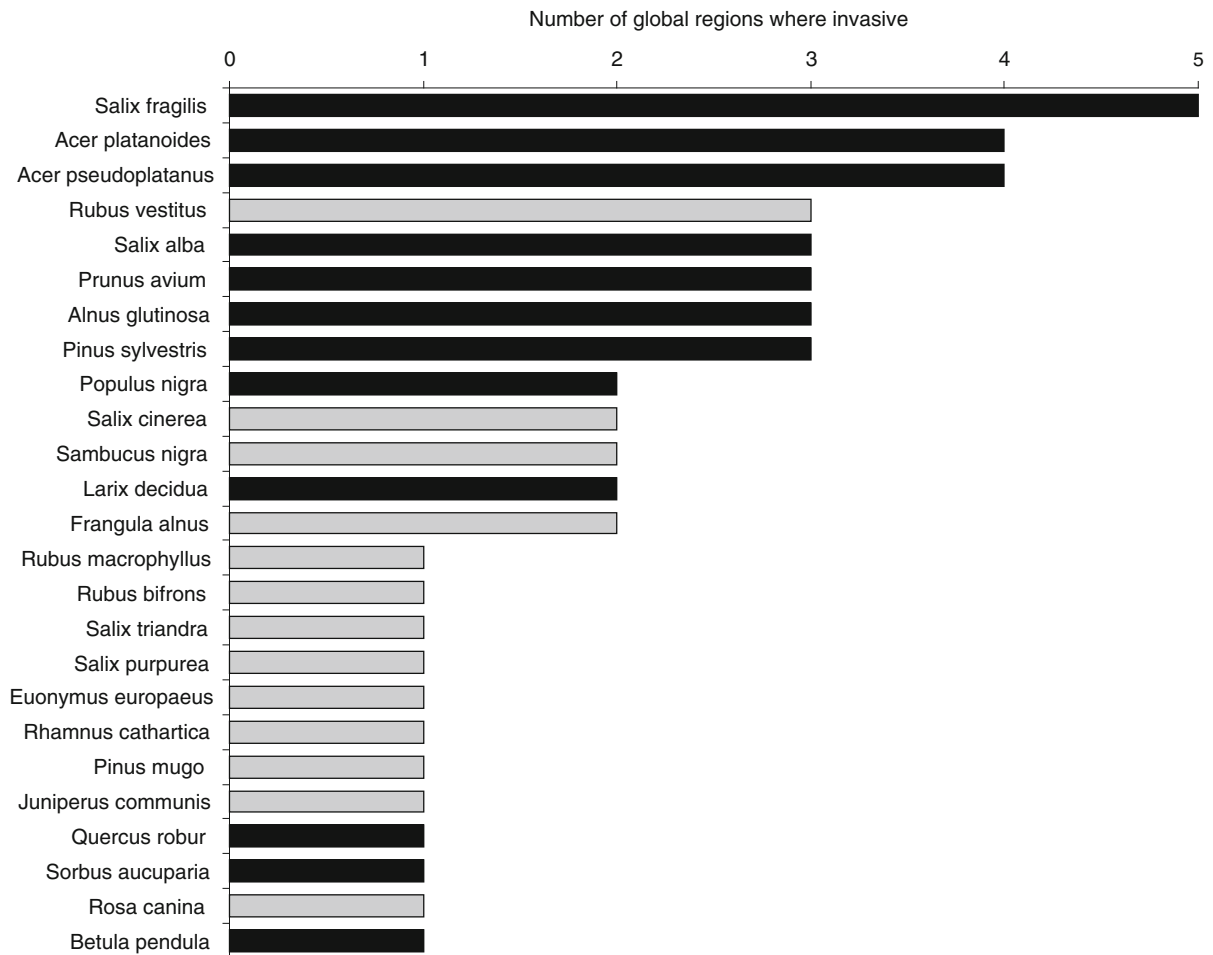


Fig. 1 Overview of 25 of the 94 species from the central-European pool that are reported as invasive in at least one of the 15 broadly defined geographical regions of the world (Richardson and Rejmánek 2011). Trees are in *black*, shrubs in *grey*

12.9; $P < 0.001$ in the model with phylogenetic correlation structure; see Table S3 for parameter estimates).

Discussion

Native distribution and biological traits interact in determining the invasiveness of woody plant species

Our results indicate that tall woody plant species flowering early in the season and occurring with a high regional frequency in their native range are significantly more likely to become successful invaders

outside their native range (central Europe in our case) than species not possessing these traits. This confirms the generally high predictive value of the native range size, a reasonably good proxy for propagule pressure (Rejmánek 1996; Rejmánek et al. 2005; Goodwin et al. 1999; Pyšek et al. 2009a), introduction effort (Bucharová and van Kleunen 2009) or ecological versatility (e.g., Kühn et al. 2004), expressed as ability to tolerate a range of climates and/or occupy many habitats, all of which are difficult to measure directly in macroecological studies (Richardson and Pyšek 2006). Among woody plants, size and other characteristics of the native range were found to be good predictors of invasiveness in the genus *Acacia* (Hui et al. 2011; Gallagher et al. 2011). Also plant size has

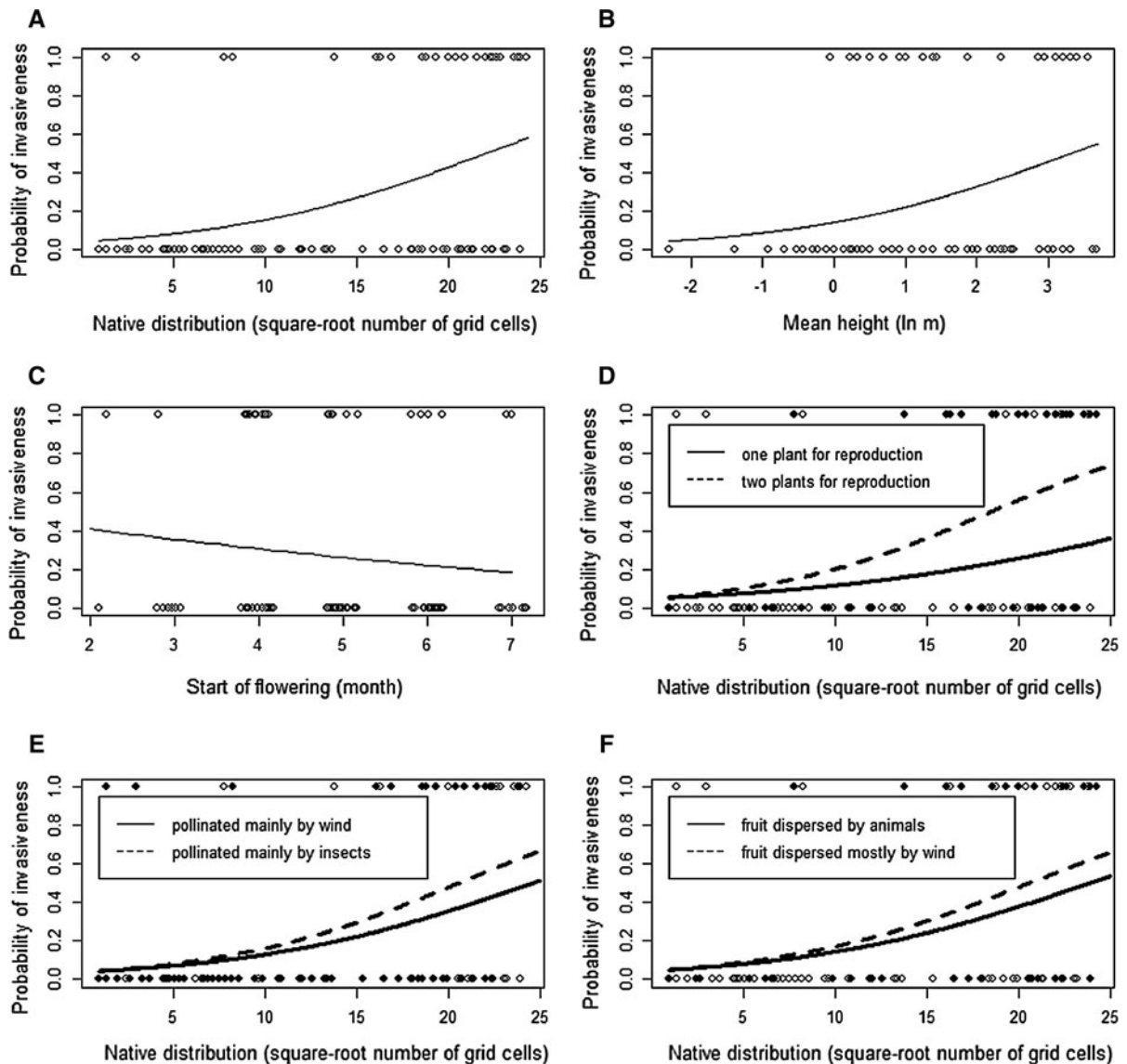


Fig. 2 Factors with significant direct (a–c) and indirect (by interaction with native distribution; d–f) effects on invasiveness of central-European trees and shrubs in other parts of the world in phylogenetically non-informed analyses. **a** Probability of invasiveness as a function of the number of grid cells occupied in the native range: $\chi^2 = 16.949$; $df = 1$, $P < 0.0001$. **b** probability of invasiveness as a function of average plant height: $\chi^2 = 5.509$; $df = 1$, $P < 0.05$. **c** Probability of invasiveness on the start of flowering: $\chi^2 = 5.206$; $df = 1$, $P < 0.05$. **d** Difference in the probability of invasiveness with increasing number of grid cells in the native range compared for plants independent on another individual for reproduction (white points) and plants depending on other plant (black points): $\chi^2 = 12.135$; $df = 1$, $P < 0.001$. **e** difference in probability of invasiveness with

increasing number of grid cells in the native range for plants pollinated mainly by wind (white points) and mainly by insects (black points): $\chi^2 = 6.052$; $df = 1$, $P < 0.05$. **f** Difference in probability of invasiveness with increasing number of grid cells in the native range for plants with animal dispersed fruits (white points) and plants with fruits dispersed by other means (black points): $\chi^2 = 5.891$; $df = 1$, $P < 0.05$. Figures are visualized as single (a–c) or double (d–f) variable models back-transformed to probabilities from logistic regressions. χ^2 -values are given for the minimal adequate model (MAM) containing all significant variables in a single model. Parameter values of the MAM are given in Table S1 of Supplementary Material. Points on x-axis in (c) are randomly jittered to visualize the individual observations

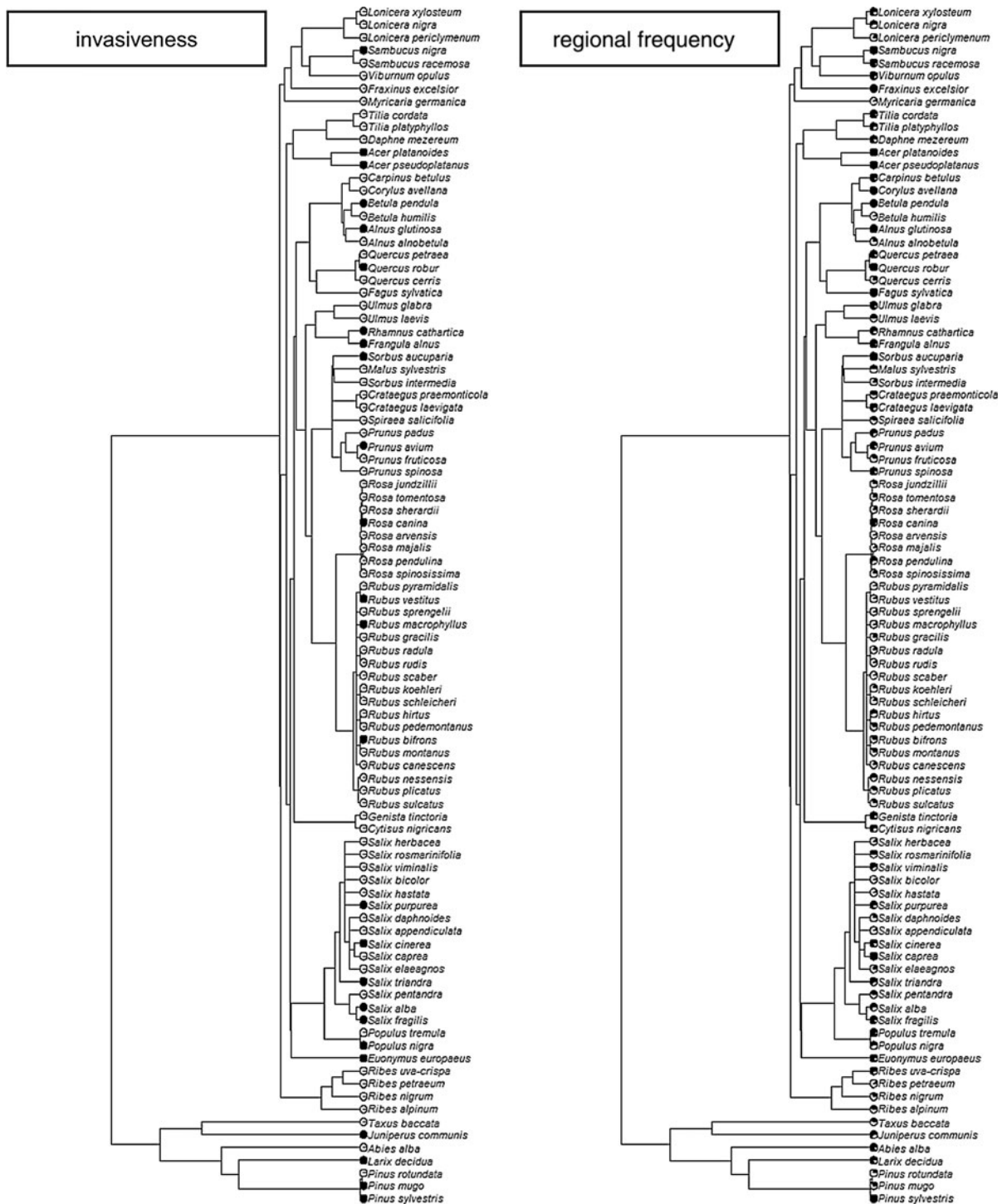


Fig. 3 Comparison of distribution of central-European trees and shrubs on phylogenetic tree following Durka and Michalski (2012) based on their invasiveness (left; species invasive outside central Europe marked by black circles, those not reported as

invasive with empty circles) with that based on their regional frequency in the native range (right; the more black the circle the more broadly distributed the species)

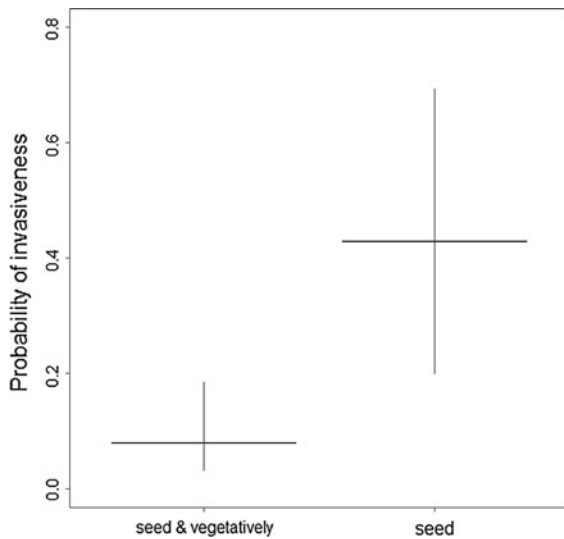


Fig. 4 Probability of invasiveness (with 95 % confidence intervals back-transformed from logits) for plants reproducing both by seed and vegetatively and plants reproducing only by seed on phylogenetically informed analysis. $F = 14.714$; $df = 1, 12.9$; $P < 0.01$. Parameter values are given in Table S3 of Supplementary Material

been repeatedly identified as a trait conferring invasiveness both in vascular plants in general (see Pyšek and Richardson 2007 for review) and in woody plants (Bucharová and van Kleunen 2009). Early flowering, or ability to flower over extended period of time, is another trait frequently found to support invasiveness in vascular plants (Pyšek and Richardson 2007; Küster et al. 2008; Godoy et al. 2009).

However, our analysis also indicates that there are other traits that can strengthen the relationship between a species' invasiveness and its regional frequency in the native range; species reproduced by selfing, or in a wider sense those that do not depend for reproduction on another individual, those pollinated by wind and dispersed by animals are more likely to become invasive even if not supported by high occurrence frequency in the native range. The dispersal by animals, vertebrates in particular, is a key factor in favouring invasiveness of woody plants; overall, birds are the most important agent of dispersal, involved in dispersal of 43 % of globally invasive trees and 61 % of shrubs (Richardson and Rejmánek 2011). The dispersal by vertebrates can compensate for the absence of other features generally associated with invasiveness, such as wind dispersal (Rejmánek et al. 2005). Therefore, traits that have no

direct effect on invasiveness but interact with the distributional characteristics in native range may represent so far neglected mechanisms of a subtle interplay of factors and can improve our ability to predict the invasiveness of woody plant species (see also Küster et al. 2008).

In a previous study using central-European herbaceous species as a source pool (Pyšek et al. 2009a), the probability of a species becoming alien outside its native distribution range was determined not only by its regional frequency in the native range, but also by its tolerance of a wide range of climates acquired in the region of origin, measured as the number of floristic zones in which the species occurs in the native range. Biological traits only had a direct effect in the more advanced stage of the invasion process, i.e. the ability of becoming a “weed”, which is comparable to invasiveness, i.e. the stage addressed here. Due to the lack of rigorous global data on distribution of alien plants and their performance (see Stohlgren et al. 2011), it was necessary to base the previous study on a source with less standardly classified data on performance of central-European vascular plant species in other parts of the world (Randall 2002). In the present paper, the classification of global invasion success is based on rigorous criteria adopted for defining invasive species, following those commonly used in the literature (Richardson et al. 2000, 2011; Pyšek et al. 2004a). The global classification, summarized in Richardson and Rejmánek (2011), represents substantial progress in providing a rigorous scientific basis for analysing patterns of invasiveness among the world's woody plant species. Its great advantage is the assessment of invasiveness made or scrutinized based on primary information, by the same authors. This makes this data more reliable than studies simply adopting the classifications from primary sources.

Life form and life strategy, early flowering, tall stature, generative reproduction, number of ploidy levels and opportunistic dispersal by a number of vectors were found as contributing to “weediness” of central-European herbaceous species introduced to other continents (Pyšek et al. 2009a). These traits identified for herbs therefore reasonably well overlap with those reported here for woody plants, with one major exception that is the non-significant role of the floristic zones in the latter. Interestingly, this proxy for ability to tolerate a range of climatic conditions, acquired in the native area throughout the species

evolutionary history, did not have any effect in our analysis of woody plants. One possible explanation could be that the vast majority of woody plant species were introduced for horticultural or forestry purposes, therefore into regions that were a priori selected as climatically suitable, and provided with enough time and human care to adapt to local conditions in cultivation (e.g. hardening; Mack 2000; Hanspach et al. 2008). The non-significant effect of floristic zones also suggests that, unlike in herbs, the role of native distribution in woody plants relates purely to the opportunities for introduction from the native region.

The role of species relatedness in determining invasiveness

When species relatedness was approximated by taxonomy, none of the factors directly or indirectly affecting plant invasiveness was associated with any of the examined taxonomic levels, i.e. classes, subclasses, orders, families or genera. This confirms our previous finding that pest risk assessment should be performed at the level of species, while generalizations based on higher taxonomic levels can be misleading (Pyšek et al. 2009a).

The only characteristic that had a significant effect on whether or not a species becomes invasive both in phylogenetically non-informed analyses and in models with phylogenetic correlation structure was the regional frequency in the native range. This indicates its overwhelming effect on species' invasiveness, which is fine-tuned by advantageous biological traits shared by a group species and inherited from common ancestors (Harvey and Pagel 1991). It also means that only the effect of the regional frequency is generic and can be used to predict invasiveness of woody plants also beyond our central-European dataset. On the other hand, the species traits that appeared significant in the phylogenetically non-informed analyses but non-significant in informed (plant height and start of flowering), should be considered useful for managers to identify invasive trees and shrubs of central Europe or those of similar kinship structure. For practitioners, unaware or ignorant of phylogenetic relationships, these traits may represent robust predictors of invasive woody species from central Europe. This knowledge can be used for management purposes in other regions where such species can potentially invade.

The mode of reproduction was the only trait that became significant after phylogenetic relatedness was taken into account. This result thus should be considered as generally valid for woody plants. However, that the probability of invasiveness was higher for plants that do not reproduce vegetatively is obviously constrained by the present dataset, in which the majority of plants capable of both vegetative and seed reproduction are clustered in the group of very closely related *Rosa* and *Rubus* species (Fig. A3 in Supplementary Material). When these strongly phylogenetically correlated species are not taken as independent data points and their effect in analysis is thus much weaker than in phylogenetically uninformed analysis, reproduction exclusively by seed supports invasiveness. The interpretation then might be that reproduction by seed as opposed to vegetative dispersal, is associated with invasiveness in woody plant species. Interestingly, Gibson et al. (2011) examined reproductive syndromes in invasive and non-invasive taxa of *Acacia* and found no obvious differences, suggesting that most taxa within this genus are well equipped to become invasive regardless of the mode of reproduction.

However, it needs to be borne in mind that not only variation uncorrelated with phylogeny can be interpreted in terms of present-day ecology (Westoby et al. 1995, Paradis 2012, pp. 238–9). Our method which includes the correlation structure based on the assumption of a Brownian motion model of trait evolution (Freckleton et al. 2011) removes the phylogenetic dependence of the residuals. Therefore results would only change if there is a phylogenetic mismatch in the sense that the phylogenetic correlation structure among being invasive or not is different from the phylogenetic correlation structure of the selected predictor variables (traits) (see Kühn and Dormann 2012 for analogous reasoning in spatial context). Our results showing how factors affecting invasiveness of central European trees and shrubs change when we take into account species relatedness clearly suggest such phylogenetic mismatch. The effect of native distribution can be mostly attributed to a similar phylogenetic correlation structure between invasiveness and distribution, the effect of vegetative reproduction to that describing net phylogenetic effect, and plant height and start of flowering to the mismatch in phylogenetic correlation structure with invasiveness. The results thus show that when interpreting the effect

of species traits on species invasiveness, it is necessary to avoid attributing unrealistically much variance in these traits to plant phylogeny; phylogeny and present-day ecology are not mutually exclusive components of trait variation (Grime and Hodgson 1987; Westoby et al. 1995). Focusing on ecological-evolutionary processes, it is crucial to apply correct statistical approaches to properly disentangle relevant mechanisms. From the viewpoint of management, however, the predictive value of traits that appear to contribute to invasiveness of central-European woody species may be useful despite the fact that these traits are phylogenetically constrained. The difference of these two perspectives is that managers dealing with plant invasions are not interested whether the behaviour of a species results from evolutionary history (i.e., whether it is invasive because it is a *Rosa* or *Rubus*, or whether it is invasive because it shares specific traits), but how they can treat specific cases of invasion. When taking a random sample from the uniformly distributed species pool, choosing a specific *Rosa* or any *Rubus* species is as likely as taking any other species. But, since these genera are more species-rich, it is more likely to choose any *Rosa* or *Rubus* species which share these traits; it is even more likely to choose more *Rosa* or *Rubus* species than other species. Being ignorant of the relationships, the traits of the uninformed analysis would remain diagnostically important simply due to the difference sampling species randomly (i.e., samples are independent when hand-picking them) and analysing them in statistically correct way (i.e. samples are dependent). Therefore, despite of being incorrect and artefacts of closely related clusters of species, the results of phylogenetically uninformed analyses remain helpful from a practitioner's point of view, i.e. when it does not matter whether a species is invasive because it is from a phylogenetic group with many invasive species or whether it shares specific traits with other invasives from that group.

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