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Perspectives in Plant Ecology, Evolution and Systematics 10 (2008) 241–250

Perspectives in Plant Ecology, Evolution and Systematics

www.elsevier.de/ppees

Correlates of naturalization and occupancy of introduced ornamentals in Germany

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Received 18 October 2007; received in revised form 14 May 2008; accepted 30 May 2008

Abstract

Invasions are multistage processes and the performance of a species at different stages depends on socio-economic, biogeographical, ecological and evolutionary factors. Most studies addressing the factors that determine invasion success focus on one particular stage, usually by examining data on introduced species that have successfully naturalized, whereas species that fail to naturalize are often not considered. In this study, we examined naturalization success (whether a species escaped from cultivation and became naturalized in the wild) and occupancy (the number of grid cells of 6′ longitude × 10′ latitude in which it is recorded) of up to 8018 ornamental plant species introduced into botanical gardens in Germany. Data on these introductions were extracted from the SYSTAX database (Information System of German Botanical Gardens), information on successful naturalization in Germany from the BiolFlor database and data on species traits from SYSTAX and the European Garden Flora. The effect of propagule pressure, biogeography, winter hardiness, life strategy, morphology and genetic variability on the probability of naturalization and the number of grid cells occupied was tested using regression models. The influence of phylogenetic dependence was considered within simple single variable models as a nested random effect. All traits that appeared significant in these simple models were combined in a multivariable model. The simplified multivariable model revealed an increasing probability of naturalization for species with a higher winter hardiness, a wider native range and a higher planting frequency in botanical gardens (Nagelkerke-R^2 of 0.196). Moreover, interactions between plant height and planting frequency and between growth form and winter hardiness also affected the probability of naturalization. The number of grid cells occupied was best explained by the winter hardiness (pseudo-R^2 of 0.61). The stratified pre-selection of ornamental plants by gardeners may hold the key to their successful escape from cultivation and subsequent naturalization.

Keywords: Alien plants; Genetic variability; Invasion process; Planting frequency; Traits; Winter hardiness

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doi:10.1016/j.ppees.2008.05.001

Introduction

The process of biological invasions can be divided into different stages (Williamson and Brown, 1986; Richardson et al., 2000). The human-mediated transport of a species outside its natural distribution range is the first step of this process. Subsequently, the species is released or escapes into the wild and occurs as a casual (depending on repeated input of propagules therefore not persisting for a longer period of time; Pyšek et al., 2004). Some species become naturalized (also termed 'established' in the literature; Williamson, 1996); the stage of naturalization is characterised by developing self-sustaining populations which persist without direct intervention by humans (Richardson et al., 2000; Pyšek et al., 2004). Further on, the species may become invasive, i.e. reproducing in large numbers and rapidly spreading over a large area (Pyšek et al., 2004). Frequent failures within this chain of processes results in only a fraction of the species passing from one stage to the next (Williamson and Brown, 1986; Williamson, 1996; Richardson and Pyšek, 2006).

Recently, an increasing number of studies have examined traits that are related to invasion success (see Pyšek and Richardson, 2007 for a review). Many studies compared traits of naturalized alien species with natives (Pyšek et al., 1995; Thompson et al., 1995; Crawley et al., 1996; Williamson and Fitter, 1996) or widespread (invasive) with less abundant (non-invasive) alien plant species (Scott and Panetta, 1993; Pyšek et al., 1995; Starfinger, 1998; Prinzing et al., 2002; Lloret et al., 2005; Herron et al., 2007). Early stages of the invasion process – namely escape from cultivation and naturalization – are, however, less often examined (Reichard and Hamilton, 1997; Goodwin et al., 1999; Pyšek et al., 2003; Dehnen-Schmutz et al., 2007b; Essl, 2007; Milbau and Stout, 2008). This shortcoming is mainly due to the lack of data regarding introduced species that failed to naturalize. Thus, little is known about the traits associated with different stages of invasion.

Initial stages of the invasion process such as import, release and escape are mainly influenced by socio-economic factors, whereas later on, biogeographical, ecological and evolutionary factors gain a more important role (Williamson, 2006). Socio-economic factors include all activities related to the amount and frequency of import (such as quantity of exchanged goods, travel frequency, transportation routes) and planting, which strongly influences propagule pressure (Williamson and Fitter, 1996), one of the potentially most important factors of invasions (Williamson, 1999; Lockwood et al., 2005). Besides propagule pressure, invasion success depends on biogeographical parameters such as native range size (Rejmánek, 1996, 2000): a large native range often reflects a wide ecological niche of the species (Goodwin et al., 1999; Prinzing et al., 2002) and consequently increases the probability of finding suitable growing conditions in the invaded range. Traits concerning life-history strategies like growth form and life span revealed more complex patterns. Both short-lived (Thompson et al., 1995; Williamson and Fitter, 1996) and long-lived species (Pyšek et al., 1995; Cadotte and Lovett-Doust, 2001) have been found to be more abundant compared with natives; a pattern that depends partly on the invaded habitat (Pyšek et al., 1995). Plant height is generally regarded to reflect competitive ability and to be positively correlated with invasion success (Crawley, 1987). However, contradictory results have been found in different studies: no relationship was found by Hamilton et al. (2005), Lloret et al. (2005) and Cadotte et al. (2006), whereas other studies showed a positive association with invasiveness (Crawley et al., 1996; Goodwin et al., 1999), which is supported by congeneric studies (Pyšek and Richardson, 2007). Genetic factors play a very important role in invasions (Sakai et al., 2001). A high genetic variability makes it more likely that a species is pre-adapted or can adapt by evolution to the new environment (Müller-Schärer et al., 2004). This may even be more important since introduced species are generally constrained by founder effects and inbreeding depressions that reduce genetic diversity and fitness (Allendorf and Lundquist, 2003). It has to be noted, however, that these limitations can be mitigated by multiple introductions and in some cases genetic diversity is not connected to invasion success (Roman and Darling, 2007). Recently, the importance of interactions among traits affecting invasiveness has been discussed (Lloret et al., 2005; Herron et al., 2007; Küster et al., 2008).

Within this study we analysed the influence of various traits on the success at two different stages of the invasion process, namely on the probability of naturalization and the occupancy, measured as the number of grid cells from which the species is recorded in Germany; the latter is the measure of invasion success as successful invasive species are widely distributed. We used data on ornamental species from various botanical gardens, since horticulture is one of the most important pathways for the introduction of invasive species (Weber, 2003). In Germany, almost 30% of all alien species listed in the BiolFlor database (Klotz et al., 2002) are ornamentals (Kühn and Klotz, 2003). Within this study, we tested the effect of parameters that are related to propagule pressure, biogeography, winter hardiness, life strategy, morphology and genetic variability and their two-way interactions on the naturalization and occupancy of ornamental species in Germany. We therefore asked: which factors and traits determine invasion success or failure of alien plant species introduced as garden ornamentals?

Methods

Data sources

Analyses were performed on up to 8018 introduced ornamental vascular plant that are included in the European Garden Flora (hereafter referred to as EGF; Walters et al., 1986–2000) and were introduced into at least one of 30 German botanical gardens according to the SYSTAX database (http://www.biologie.uni-ulm.de/systax/), the Information System of German Botanical Gardens (Hoppe et al., 1999). Of these, 219 neophytes (plant species introduced after 1500 AD, see Pyšek et al., 2004 for definition) escaped from cultivation and naturalized in Germany, according to the BiolFlor database (Klotz et al., 2002). We compared their traits with those species that have not become naturalized in Germany. Native species and archaeophytes (aliens introduced before 1500 AD; see Pyšek et al., 2004) were not considered in the analyses. Casual aliens (sensu Richardson et al., 2000; termed ephemerophytes in the BiolFlor database) were treated as not naturalized. We refrained from analysing the characteristics of casual aliens since our knowledge on their occurrence in Germany is incomplete. The BiolFlor database only contains frequently occurring casuals (119 species in our dataset, representing maybe a tenth of the casual species of Germany). To account for different climatic requirements of cultivated species, we excluded all species which require any kind of glasshouse storage during winter according to the EGF, thus omitting all species obviously unable to grow without human support. Horticultural varieties and cultivars were not considered, apart from in the calculations of genetic variability (see below). We limited the analysis to species that are intentionally introduced by gardeners, and derived a dataset that is generally not confounded by the influence of multiple pathways of introduction. A few introduced species might also have entered accidentally.

Species characteristics (Table 1) were derived from the SYSTAX database and EGF. Traits obtained from EGF were number of continents comprising native range, region of origin, winter hardiness, growth form, life span, maximum plant height, storage organ and mode of propagation (Table 1). If not given in EGF, information on individual species was taken from Mabberley (1997) and Brickell (1989). The number of continents (Africa, Asia, Australia, Europe, North America and South America) on which the species has its native distribution range was recorded; this served as a proxy for the size of the native range. The region of origin separates species originating from the Old and the New World. A finer resolution of the region of origin would result in an unmanageable number of combinations between categories. Old world species are potentially better pre-adapted to human influenced environments due to a longer co-evolutionary history than New World species (di Castri, 1989). Furthermore, distance to travel within the Old World is shorter, on average. Winter hardiness gives an indication of the lowest temperatures a species can withstand and is based on horticulturists' knowledge. Hardiness is not derived from range characteristics but climatic tolerance and thus the correlation with occupancy is not circular. Winter hardiness is given in the EGF on an ordinal scale: 1 – withstands temperatures of −20 °C and below, 2 – withstands −20 to −15 °C, 3 – withstands −15 to −10 °C, 4 – withstands −10 to −5 °C and 5 – withstands −5 to 0 °C. Due to its quasi-metric character (temperature steps of 5 °C each), we assumed a metric scale during modelling. From the SYSTAX database we calculated two values: (1) the number of subspecific taxa per species (including varieties and cultivars), serving as a proxy for genetic variability and (2) the number of botanical gardens in Germany growing the species, which represented the frequency of introduction as a proxy for propagule pressure and was related to socio-economic prevalence.

Due to the lack of data or attributes (e.g. not all species have storage organs), we performed the analyses of most characteristics with less than 8018 species (see Table 1 for details).

The data on species distribution originated from the FLORKART database (http://www.floraweb.de) of the German Network for Phytodiversity (NetPhyD), maintained at the German Federal Agency for Nature Conservation.

Modelling of naturalization

The probability of naturalization was first modelled separately for every trait with a generalized linear mixed effects model using penalized quasi-likelihood (GLMMPQL) (Venables and Ripley, 2002) assuming a binomial error distribution (naturalized yes/no). A phylogenetic correction of the analysis is crucial when assessing the effect of species traits (Harvey and Pagel, 1991; Tremlová and Münzbergová, 2007), since adaptation of two closely related species is most likely a result of their phylogenetic relatedness. Different methods are suggested to overcome this problem, such as the calculation of phylogenetically independent contrasts (Felsenstein, 1985) or variation partitioning (Desdevises et al., 2003). However, applying these techniques requires the knowledge of phylogenies of the species studied, which was not available in our study. We therefore implemented taxonomical information as a proxy for phylogenetic relationships as a random factor in mixed effects models (see e.g. Prinzing et al., 2001; Cassey et al., 2004; Duncan and Blackburn, 2004; Sol et al., 2008). Taxonomical data on order, family and

Table 1. Overview of the parameters used to model the probability of naturalization and occupancy (number of grid cells occupied); parameters were derived from European Garden Flora (EGF; Walters et al., 1986–2000) except for number of gardens and number of subspecific taxa, which originate from the SYSTAX database

Parameter	Description	Naturalization			Occupancy		
		N	Estimate(s)	*p*-Value	*N*	Estimate(s)	*p*-Value
Growth form	Herb, shrub, tree	7375	-3.89^{a}; -4.88^{b}; -3.98^{a}	<0.01	207	3.59; 3.25; 3.9	n.s.
Plant height	Maximum height measured in meter	6883	0.44	<0.001	193	0.34	<0.05
Life span	Annual, biennial, perennial	7885	−3.72; −3.84; −4.23	n.s.	218	4.73; 2.53; 3.49	n.s.
Winter hardiness	1 (<−20 °C minimum temperature), 2 (−20 to −15 °C), 3 (−15 to −10 °C), 4 (−10 to −5 °C), 5 (−5 to 0 °C)	7957	−0.56	<0.001	214	−0.378	<0.001
Region of origin	New World, Old World	7670	−4.29; −4.13	n.s.	219	4.04^{a}; 3.31^{b}	<0.05
Number of continents	Number of continents comprising native range	8014	0.77	<0.001	219	−0.33	n.s.
Mode of propagation	Vegetative, generative	1862	−4.33; −4.04	n.s.	63	3.61; 4.5	n.s.
Type of storage organ	Bulb, corm, rhizome, Stolon, sucker, tuber	1970	−4.27; −5.37; -3.69; −2.9; −3.57; −5.86	n.s.	81	2.48; 2; 3.2; 3.96; 3.79; 1.95	n.s.
Number of gardens	Number of gardens cultivating a species	8002	0.27	<0.001	219	0.06	<0.05
Number of subspecific taxa	Number of subspecific taxa per species	8018	1.16	<0.001	219	0.244	n.s.

The encoding of winter hardiness was taken from the EGF (notice that 1 is the hardest and 5 the least hardy category). Number of species *N* with available information. Estimates for categorical data are labelled with superscript letters, which are different if the respective post-hoc test was significant. Error probabilities for naturalization were derived directly from the model output for continuous data and from the post-hoc tests for categorical data. *p*-Values for occupancy were derived from model comparisons with the null model (*F*-test). *p*-Values greater than 0.05 were considered as not significant and marked with n.s.

genus of a species was included as a nested random effect in the single predictor models.

All traits significantly influencing the probability of naturalization in the single variable models were included in a multivariable model (6338 species) allowing for interactions between traits. Continuous variables were standardized to zero mean and unit variance. The multivariable model was a standard generalized linear model (GLM) instead of GLMMPQL, which means that we were unable to consider the phylogenetic relationships in this multivariable model. Since GLMMPQL operates with pseudo-likelihood, neither AIC values (Akaike information criterion, Akaike, 1978) nor deviance would have been calculable and consequently no model comparisons and simplification could be performed. Simplification of the GLM was done by backward elimination using error probabilities from model comparisons. The significance of a chosen model in comparison with the null model or the more complex model was tested by a χ^2 test (Crawley, 2002). The null model was built using only the overall mean of the response variable as the parameter. Post-hoc tests were performed for the categorical variables using a sequential Bonferroni procedure to control Type I error rates. As a coefficient of determination, we used Nagelkerkes R^2 (Nagelkerke, 1991), which calculates the amount of information gained by the model when including factors in comparison to the null model.

Modelling of occupancy

The relationship between species attributes and occupancy of naturalized neophytes in Germany (up to 219 species, see Table 1) was analysed as follows: occupancy was measured as the number of grid cells (6′ longitude × 10′ latitude of the national grid; each ca. 130 km^2) occupied by a given species. The values were logarithmically transformed to the base e to normalize the data. Single and multivariable modelling was performed with linear mixed effects models including taxonomy as a random effect. All traits that were significant in single variable models were included in the multivariable model (177 species) thus allowing for us to test for interactions. Simplification of the multivariable model for occupancy was performed by backward elimination using error probabilities from model comparisons using F tests. To assess the proportion of explained variation in the mixed effect model, we employed a pseudo-R^2 approach by calculating the squared Pearson correlation coefficient between observed and predicted values (Kissling and Carl, 2008).

All statistical analyses were performed using the R-package (R Development Core Team, 2006). The following additional packages were used: calculation of GLMMPQL with the MASS package (Venables and Ripley, 2002), multiple comparisons with the multcomp package (Bretz et al., 2004) and the linear mixed effects models with the nlme package (Pinheiro and Bates, 2000; Pinheiro et al., 2007).

Results

The 8018 species analysed belong to 1711 genera and 222 families. The most frequent families were Liliaceae (676 species), Rosaceae (623) and Asteraceae (533), the most frequent genera were Rhododendron (197), Saxifraga (114) and Iris (107). The most prevailing growth form was herbaceous (63%) and the dominating life span perennial (95%).

Ornamental plants from Rosaceae and Asteraceae are more often naturalized than introduced ornamentals from other families, in particular, the Liliaceae is underrepresented (Fig. 1a). Compared with all neophytes in Germany, ornamental species from the Rosaceae are more frequently naturalized, whereas Onagraceae, Poaceae and Brassicaceae naturalize more rarely (Fig. 1b).

In the single parameter models, naturalization was significantly affected by the number of gardens, number of continents comprising native range, winter hardiness, growth form, height and number of subspecific taxa

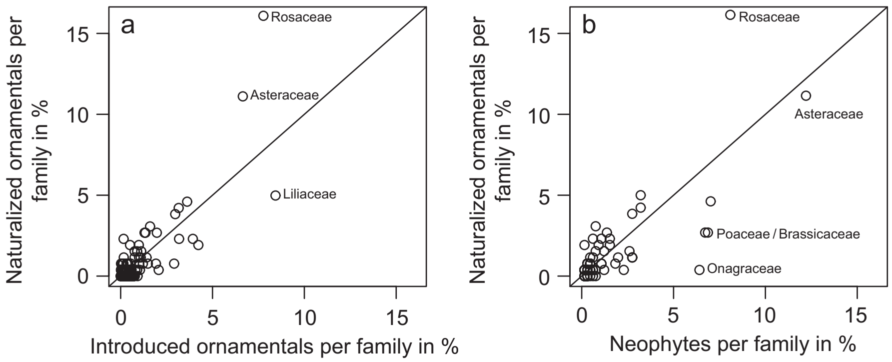

Fig. 1. Percentage of naturalized ornamentals per family versus (a) the percentage of introduced ornamentals in Germany and (b) the percentage of all neophytic species in the German flora. The bisecting lines mark equal proportions.

Table 2. Results of the log-ratio test of the minimal adequate generalized linear model explaining the probability of naturalization of introduced ornamentals in Germany (6338 species)

Explaining variable	χ^2	Df	*p*-Value
Hardiness	10.002	1	<0.001
Growth form	24.204	2	<0.001
Plant height	4.381	1	<0.05
Number of continents	12.343	1	<0.001
Number of gardens	193.682	1	<0.001
Hardiness × growth form	8.346	2	<0.05
Plant height × number of gardens	5.153	1	<0.05

The model does not include taxonomy. Nagelkerke-$R^2 = 0.193$.

(Table 1). The probability of naturalization is high when a species is planted in many botanical gardens, originates from many continents, has a high winter hardiness, is tall or a shrub. Region of origin, mode of propagation, type of storage organ and life span did not have a significant effect on the probability of naturalization. The simplified multivariable model (Nagelkerke-R^2 of 0.19) included winter hardiness, growth form, plant height, number of continents comprising native range and number of gardens, as well as the two interactions hardiness × growth form and plant height × number of gardens (Table 2). The post-hoc test of the interaction hardiness × growth form revealed that the probability of naturalization of shrubs and trees decreases more strongly with decreasing hardiness compared with herbs. The interaction between plant height and number of gardens shows that tall species are more likely to naturalize if planted in a few gardens and short species if they are planted in many gardens.

The species' occupancy in Germany was explained by winter hardiness, plant height, region of origin and the number of gardens in single parameter mixed effect models (Table 1). Species occupancy increases when a species is tall, can withstand low minimum temperatures, originates from the New World and is planted in many botanical gardens. In the simplified multivariable model accounting for taxonomy, only winter hardiness remained as a single parameter ($F = 10.491$, $p<0.01$, Fig. 2) with a pseudo-R^2 of 0.61.

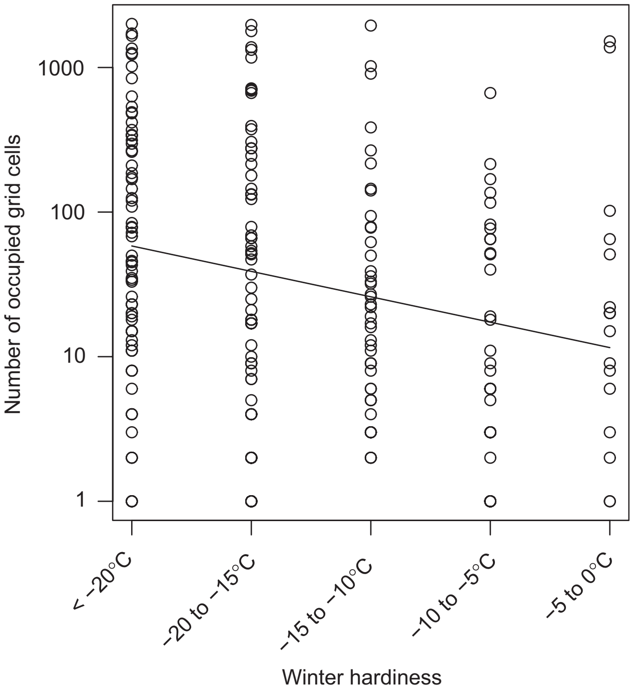

Fig. 2. Occupancy of naturalized ornamentals in Germany on a logarithmic scale versus winter hardiness. Regression line results from the minimum adequate model of the multivariable mixed effect model (including taxonomy as random effect). Categories of winter hardiness are taken from the European Garden Flora (notice that hardiness decreases from left to right).

Discussion

The examination of the number of naturalized species per family revealed a disproportionately high occurrence of naturalization in the rose family (Rosaceae) with most naturalized species belonging to the genera *Cotoneaster*, *Prunus* and *Spirea.* Similar overrepresentation of Rosaceae has not been detected on neither a global (Pyšek, 1998) nor continental scale (Weber, 1997). We assume that naturalization in this family in Germany might be related to horticultural activities. However, we lack the data to test this hypothesis.

The influence of species traits and other parameters on the invasion process has been discussed with ambiguous conclusions (see Cadotte et al., 2006; Pyšek and Richardson, 2007). Invasions are idiosyncratic processes and general rules are difficult to apply (Williamson, 1999). Indeed, it is evident that a large proportion of variation in our study (80% of the multivariable model for naturalization) and in comparable studies (e.g. Dehnen-Schmutz et al., 2007b) remain unexplained.

First, we focus on parameters of general importance, acting on more than one stage in the invasion process. A recent review (Pyšek and Richardson, 2007) summarized multispecies studies and identified robust parameters acting throughout the invasion process, such as plant height, vigorous vegetative growth, extended flowering and attractiveness to humans. However, most of these parameters had only indirect influence within our study or were not tested due to the lack of data, save the attractiveness to humans which is probably mirrored by planting frequency and plant height, which only influenced the probability of naturalization. Within our study, species' tolerances to low temperatures improved their chances of becoming naturalized and increased their area of occupancy. Frosts may limit survival of seedlings and saplings so that the probability of naturalization directly correlates with the hardiness of species. The potential range of a species with enhanced hardiness increases towards the more continental east of Germany and thus increases the occupancy of a species. This contrasts with the study of Herron et al. (2007) who found no association between winter hardiness and success of introduced woody plants in New England at the stage of spread. The positive association of plant height with the probability of naturalization (single- and multivariable model) and occupancy (single variable model) agrees with the results of other studies (Crawley et al., 1996; Williamson and Fitter, 1996; Goodwin et al., 1999; van Kleunen et al., 2007). We consider the interaction between plant height and number of gardens of minor ecological importance since the standardized regression estimate was low and significance was not stable when building a model only with the two variables and their interaction in a separate model.

Second, certain parameters are stage specific (Kolar and Lodge, 2001; Pyšek et al., 2003; Dehnen-Schmutz et al., 2007b). Most studies focus on one stage of the invasion process, and comparability between studies is restricted due to different types of comparison and approaches (e.g. comparing successful and unsuccessful species in the native range or in the introduced range or natives and aliens; see Pyšek and Richardson, 2007 for discussion). Thus it seems preferable to analyse different stages of the invasions process using the same data. We found parameters that were specific to the stage of naturalization. Range size often is a very influential parameter that, in our study, was only correlated with naturalization (Rejmánek, 1996; Goodwin et al., 1999; but see Kühn et al., 2004). Our analysis did not reveal a relationship between the number of continents in the native range and the occupancy of ornamentals in Germany. This contrasts other studies, which found that the size of the native range is positively correlated with species' area of occupancy (Scott and Panetta, 1993; Starfinger, 1998; Prinzing et al., 2002). Due to the lack of data, we could only approximate native range size by using the number of continents which comprise the native range. Thus, more detailed information on range sizes might influence the results.

We revealed a higher probability of naturalization in the wild for plant species which are more frequently cultivated, which concurs with results from Great Britain (Dehnen-Schmutz et al., 2007a, b) and south-eastern Australian cities (Mulvaney, 2001). We used the number of botanical gardens in which a species is cultivated as a proxy for propagule pressure. Propagule pressure has frequently been recognized as an important determinant of the probability of naturalization (see e.g. Williamson, 1999; see e.g. Lockwood et al., 2005; Daehler, 2006; Křivánek et al., 2006). The influence of the planting frequency in gardens on occupancy was only revealed in the single variable models, indicating that increased propagule pressure through frequent planting and human-mediated dispersal has some influence on species' invasion (e.g. Kowarik, 2003; Křivánek et al., 2006). We assume, however, that winter hardiness is more important than planting frequency. The latter may be correlated with hardiness, since plant species more resistant to frost are more frequently planted. Winter hardiness generally increased the probability of naturalization in our study but its influence differed among growth forms and affected herbs less than shrubs or trees. We hypothesize that trees may be more sensitive to frost, since they have a longer life span and thus a longer juvenile period, during which they are exposed to the detrimental effects of frost. We did not find a correlation between the number of subspecific taxa, as a proxy for genetic variability, and invasion success. We expected that a high genetic variability would enable a species either to find appropriate sites or adapt to a wide range of environmental conditions (Sakai et al., 2001; Maron et al., 2004). We argue that genetic variability and thus invasion success may be more strongly influenced by the number of introductions (Roman and Darling, 2007) than by the number of subspecific taxa, which in botanic gardens often result from plant breeding. Therefore, the number of subspecific taxa is a very coarse measure for genetic diversity and may be biased by plant breeders' preferences for specific groups. However, plant breeders may have attempted to breed new cultivars in a variety of taxonomic groups. We point out that our measure of genetic variability is collinear with planting frequency (Kendalls $\tau = 0.35$, $p < 0.001$; see also van Kleunen et al., 2007). This can be explained by mutual facilitation: ambitious planting and breeding give rise to a high number of cultivars and a high number of subspecific varieties encourage frequent planting.

Although we analysed more than 8000 imported species, the species selection is not random, since ornamentals are stratified by the preferences of the custodians of botanical gardens. Crawley et al. (1996) detected a higher proportion of woody plants and geophytes compared with native flora in Great Britain. Large, showy plants (Williamson and Fitter, 1996), vigorous growers, plants that are easy to propagate, climatically suitable and resistant to pests and diseases (Dehnen-Schmutz et al., 2007b) are preferred. Van Kleunen et al. (2007) showed that those species from the Iridaceae family that have a wide range, a high number of subspecific taxa and a big maximum height are favoured for cultivation. Dehnen-Schmutz et al. (2007b) raised the question whether the characteristics of valuable garden plants and capable invaders are widely overlapping or even equal; therefore this human pre-selection promotes the invasion process (Kitajima et al., 2006). Milbau and Stout (2008) have shown that species introduced in Ireland for ornamental reasons were more likely to become invasive. The invasion success of ornamental plant species, though, does not necessarily depend on human pre-selection for two reasons: Firstly, species may also have been pre-adapted to environmental conditions in the new range (Mayr, 1965; Sax and Brown, 2000; Sol, 2007) and thus survive and reproduce successfully. However, those pre-adaptations may make them also preferential to gardeners. Secondly, it was demonstrated that repeated introductions and secondary releases through cultivation encourage plant naturalization and invasion (Mack, 2000; Kowarik, 2003; Richardson, 2006). Repeated introductions increase the probability that a species will encounter suitable environmental conditions in space and time. While cultivation protects from unfavourable conditions (e.g. drought, parasites), it also facilitates continuous propagule pressure and thus increases the probability of naturalization and invasion.

We found an influence of planting frequency, biogeography and morphology on the probability of naturalization of introduced ornamentals in Germany. However, species occupancy, reflecting how widespread a species is, was only associated with winter hardiness. Since our analysis covers two stages of the invasion process, direct comparisons between the important factors can be made. These results highlight that naturalization is a key stage in the invasion process, determined by complex action of number of factors, including species traits (Pyšek and Richardson, 2006; Richardson and Pyšek, 2006); more attention should be paid to this stage in studies of the invasion process if we want to understand its principles better (Pyšek et al., 2008). Nonetheless, we acknowledge constraints due to unequal statistical power between the stages that result from the unequal numbers of species. With our study, we highlight the importance of horticultural activities regarding both pre-selection and planting frequency on the invasion success plants. Further studies are required to gain a better understanding of the underlying mechanisms.

Acknowledgements

We thank Ivan Ostrý, Zuzana Sixtová and Ulrike Eichhorn for technical assistance and thousands of volunteers that collected floristic data for the FLORKART database, hosted by the Federal Agency for Nature Conservation, which we were kindly allowed to use. We are grateful to Katharina Dehnen-Schmutz (University of York), Henrik von Wehrden (University of Halle), two anonymous reviewers and our colleagues from the Department of Community Ecology (UFZ), especially Gudrun Carl, Susan Ebeling, Eva Küster, Oliver Schweiger and Marten Winter for their valuable comments. We thank Jane Stout (Trinity College Dublin) for linguistic improvements.

JH was funded by the Federal Ministry for Education and Research as part of the project INVASIONS (research Grant 01LM0206). PP was supported by institutional long-term research plans no. AV0Z60050516 from the Academy of Sciences of the Czech Republic, and no. 0021620828 from MSMT CR and Centre for Biodiversity no. LC06073 (MSMT CR). We acknowledge additional support by the Integrated Project ALARM: Assessing LArge scale environmental Risks with tested Methods (GOCE-CT-2003-506675) (Settele et al., 2005) from the European Commission within Framework Programme 6.

References

Akaike, H., 1978. A Bayesian analysis of the minimum AIC procedure. Ann. Inst. Stat. Math. 30, 9–14.

Allendorf, F.W., Lundquist, L.L., 2003. Introduction: population biology, evolution, and control of invasive species. Conserv. Biol. 17, 24–30.

Bretz, F., Hothorn, T., Westfall, P., 2004. The multcomp Package: Multiple Tests and Simultaneous Confidence Intervals, version 0.4-8.

Brickell, C. (Ed.), 1989. The Royal Horticultural Society Gardeners' Encyclopaedia of Plants and Flowers. Dorling Kindersley, London.

Cadotte, M.W., Lovett-Doust, J., 2001. Ecological and taxonomic differences between native and introduced plants of Southwestern Ontario. Ecoscience 8, 230–238.

Cadotte, M.W., Murray, B.R., Lovett-Doust, J., 2006. Ecological patterns and biological invasions: using regional species inventories in macroecology. Biol. Invas. 8, 809–821.

Cassey, P., Blackburn, T.M., Sol, S., Duncan, R.P., Lockwood, J.L., 2004. Global patterns of introduction effort and establishment success in birds. Proc. R. Soc. Lond. B Biol. Sci. 271, 405–408.

Crawley, M.J., 1987. What makes a community invasible? In: Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.), Colonization, Succession, and Stability. Blackwell, Oxford, pp. 429–451.

Crawley, M.J., 2002. Statistical Computing: An Introduction to Data Analysis Using S-Plus. Wiley, Chichester.

Crawley, M.J., Harvey, P.H., Purvis, A., 1996. Comparative ecology of the native and alien floras of the British Isles. Philos. Trans. R. Soc. Lond. B Biol. Sci. 351, 1251–1259.

Daehler, C.C., 2006. Invasibility of tropical islands by introduced plants: partitioning the influence of isolation and propagule pressure. Preslia 78, 389–404.

Dehnen-Schmutz, K., Touza, J., Perrings, C., Williamson, M., 2007a. A century of the ornamental plant trade and its impact on invasion success. Divers. Distrib. 13, 527–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C., Williamson, M., 2007b. The horticultural trade and ornamental plant invasions in Britain. Conserv. Biol. 21, 224–231.

Desdevises, Y., Legendre, P., Azouzi, L., Morand, S., 2003. Quantifying phylogenetically structured environmental variation. Evolution 57, 2647–2652.

di Castri, F., 1989. History of biological invasions with special emphasis on the Old World. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson M. (Eds.), Wiley, Chichester, UK, pp. 1–30.

Duncan, R.P., Blackburn, T.M., 2004. Extinction and endemism in the New Zealand avifauna. Glob. Ecol. Biogeogr. 13, 509–517.

Essl, F., 2007. From ornamental to detrimental? The incipient invasion of Central Europe by *Paulownia tomentosa*. Preslia 79, 377–389.

Felsenstein, J., 1985. Phylogenies and the comparative method. Am. Nat. 125, 1–15.

Goodwin, B.J., McAllister, A.J., Fahrig, L., 1999. Predicting invasiveness of plant species based on biological information. Conserv. Biol. 13, 422–426.

Hamilton, M.A., Murray, B.R., Cadotte, M.W., Hose, G.C., Baker, A.C., Harris, C.J., Licari, D., 2005. Life-history correlates of plant invasiveness at regional and continental scales. Ecol. Lett. 8, 1066–1074.

Harvey, P.H., Pagel, M.D., 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Herron, P.M., Martine, C.T., Latimer, A.M., Leicht-Young, S.A., 2007. Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. Divers. Distrib. 13, 633–644.

Hoppe, J., Boos, E., Stützel, T., 1999. SysTax – ein Datenbanksystem für Systematik und Taxonomie. In: Begeman, F., Harrer, S., Jiménez-Krause, D. (Eds.), Dokumentationen und Informationssysteme im Bereich pflanzengenetischer Ressourcen in Deutschland. Zentralstelle für Agrardokumentation und -information (ZADI), Bonn, pp. 64–79.

Kissling, D., Carl, G., 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. Glob. Ecol. Biogeogr. 17, 59–71.

Kitajima, K., Fox, A.M., Sato, T., Nagamatsu, D., 2006. Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. Biol. Invas. 8, 1471–1482.

Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Bundesamt für Naturschutz, Bonn.

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16, 199–204.

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

Křivánek, M., Pyšek, P., Jarošík, V., 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv. Biol. 20, 1487–1498.

Kühn, I., Klotz, S., 2003. The alien flora of Germany – basics from a new German database. In: Child, L.E., Brock, J.H., Brundu, G., Prach, K., Pyšek, P., Wade, P.M., Williamson, M. (Eds.), Plant Invasions: Ecological Threats and Management Solutions. Backhuys, Leiden, pp. 89–100.

Kühn, I., Brandenburg, M., Klotz, S., 2004. Why do alien plant species that reproduce in natural habitats occur more frequently? Divers. Distrib. 10, 417–425.

Küster, E.C., Kühn, I., Bruelheide, H., Klotz, S., 2008. Trait interactions help explain plant invasion success in the German flora. J. Ecol., in press, doi:10.1111/j.1365-2745.2008.01406.x.

Lloret, F., Medail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P., Hulme, P.E., 2005. Species attributes and invasion success by alien plants on Mediterranean islands. J. Ecol. 93, 512–520.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20, 223–228.

Mabberley, D.J., 1997. The Plant Book, second ed. Cambridge University Press, Cambridge.

Mack, R.N., 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. Biol. Invas. 2, 111–122.

Maron, J.L., Vilà, M., Bommarco, R., Elmendorf, S., Beardsley, P., 2004. Rapid evolution of an invasive plant. Ecol. Monogr. 74, 261–280.

Mayr, E., 1965. The nature of colonising birds. In: Baker, H.G., Stebbins, G.L. (Eds.), The Genetics of Colonizing Species. Academic Press, New York, pp. 29–43.

Milbau, A., Stout, J.C., 2008. Factors associated with alien plants transitioning from casual, to naturalized, to invasive. Conserv. Biol. 22, 308–317.

Müller-Schärer, H., Schaffner, U., Steinger, T., 2004. Evolution in invasive plants: implications for biological control. Trends Ecol. Evol. 19, 417–422.

Mulvaney, M., 2001. The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. In: Groves, R.H., Panetta, F.D., Virtue, J.G. (Eds.), Weed Risk Assessment. CSIRO Publishing, Collingwood, Victoria, Australia, pp. 186–193.

Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effect Models in S and S-PLUS. Springer, New York, Berlin.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., 2007. The nlme Package, version 3.1–83.

Prinzing, A., Durka, W., Klotz, S., Brandl, R., 2001. The niche of higher plants: evidence for phylogenetic conservatism. Proc. R. Soc. Lond. B Biol. Sci. 268, 2383–2389.

Prinzing, A., Durka, W., Klotz, S., Brandl, R., 2002. Which species become aliens? Evol. Ecol. Res. 4, 385–405.

Pyšek, P., 1998. Is there a taxonomic pattern to plant invasions? Oikos 82, 282–294.

Pyšek, P., Richardson, D.M., 2006. The biogeography of naturalization in alien plants. J. Biogeogr. 33, 2040–2050.

Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), Biological Invasions. Springer, Berlin, Heidelberg, pp. 97–125.

Pyšek, P., Prach, K., Smilauer, P., 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. In: Pyšek, P., Prach, K., Rejmánek, M., Wade, M. (Eds.), Plant Invasions: General Aspects and Special Problems. SPB Academic Publishing, Amsterdam, pp. 39–60.

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

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

Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z., Weber, E., 2008. Geographical and taxonomic biases in invasion ecology. Trends Ecol. Evol. 23, 237–244.

R Development Core Team, 2006. R: A language and environment for statistical computing.

Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced into North America. Conserv. Biol. 11, 193–203.

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

Rejmánek, M., 2000. Invasive plants: approaches and predictions. Aust. Ecol. 25, 497–506.

Richardson, D.M., 2006. Pinus: a model group for unlocking the secrets of alien plant invasions? Preslia 78, 375–388.

Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. 30, 409–431.

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

Roman, J., Darling, J.A., 2007. Paradox lost: genetic diversity and the success of aquatic invasions. Trends Ecol. Evol. 22, 454–464.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32, 305–332.

Sax, D.F., Brown, J.H., 2000. The paradox of invasion. Glob. Ecol. Biogeogr. 9, 363–371.

Scott, J.K., Panetta, F.D., 1993. Predicting Australian weed status of southern African plants. J. Biogeogr. 20, 87–93.

Settele, J., Hammen, V., Hulme, P.E., Karlson, U., Klotz, S., Kotarac, M., Kunin, W.E., Marion, G., O'Connor, M., Petanidou, T., Peterseon, K., Potts, S., Pritchard, H., Pyšek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M.T., Vighi, M., Zobel, M., Kühn, I., 2005. ALARM: assessing large scale environmental risks for biodiversity with tested methods. GAIA – Ecological Perspectives in Science, Humanities, and Economics 14, 69–72.

Sol, D., 2007. Do successful invaders exist? Pre-adaptations to novel environments in terrestrial vertebrates. In: Nentwig, W. (Ed.), Biological Invasions. Springer, Berlin, pp. 127–141.

Sol, D., Vilà, M., Kühn, I., 2008. The comparative analysis of historical alien introductions. Biol. Invas., in press, doi:10.1007/s10530-007-9189-7.

Starfinger, U., 1998. On success in plant invasions. In: Starfinger, U., Edwards, G.R., Kowarik, I., Williamson, M. (Eds.), Plant Invasions: Ecological Mechanisms and Human Responses. Backhuys, Leiden, pp. 33–42.

Thompson, K., Hodgson, J.G., Rich, T.C.G., 1995. Native and alien invasive plants: more of the same? Ecography 18, 390–402.

Tremlová, K., Münzbergová, Z., 2007. Importance of species traits for species distribution in fragmented landscapes. Ecology 88, 965–977.

van Kleunen, M., Johnson, S.D., Fischer, M., 2007. Predicting naturalization of southern African Iridaceae in other regions. J. Appl. Ecol. 44, 594–603.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York.

Walters, S.M., Brady, A., Brickell, C.D., Cullen, J., Green, P.S., Lewis, J., Matthews, V.A., Webb, D.A., Yeo, P.F., Alexander, J.C.M., 1986–2000. European Garden Flora. Cambridge University Press, Cambridge.

Weber, E.F., 1997. The alien flora of Europe: a taxonomic and biogeographic review. J. Veg. Sci. 8, 565–572.

Weber, E., 2003. Invasive Plant Species of The World. CABI Publishing, Wallingford, UK.

Williamson, M., 1996. Biological Invasions. Chapman & Hall, London.

Williamson, M., 1999. Invasions. Ecography 22, 5–12.

Williamson, M., 2006. Explaining and predicting the success of invading species at different stages of invasion. Biol. Invas. 8, 1561–1568.

Williamson, M.H., Brown, K.C., 1986. The analysis and modelling of British invasions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 314, 505–522.

Williamson, M.H., Fitter, A., 1996. The characters of successful invaders. Biol. Conserv. 78, 163–170.