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Trait interactions help explain plant invasion success in the German flora

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Summary

1. The search for characteristics that promote invasion success constitutes one of the most challenging tasks in invasion ecology. So far the main focus in multispecies studies of plant invasion success has been on single traits. Only few generalizations have emerged from this work and single traits yielded very limited explanatory power for invasion success. Here we hypothesize that the consideration of ecological strategies, determined by different combinations of traits, will improve explanatory power.

2. To test this hypothesis we analysed the relative importance of 40 traits for species' invasion success in the German neophytic flora. Success was expressed as map grid cell frequency. After quantifying the relevance of single traits, we quantified the importance of different trait combinations for invasion success by calculating a multiple trait model, with explicit consideration of trait interactions. In all analyses we considered the effects of phylogeny.

3. In general, neither single traits nor phylogenetic relatedness held much explanatory power. In contrast, the amount of variation explained in the multiple trait model was distinctly higher, mainly due to the incorporation of trait interactions. Thus, particular combinations of trait attributes rather than distinctive attributes *per se* appear to be associated with invasion success.

4. In single trait analysis, traits associated with flowering and reproductive biology, and with ecological tolerance and the residence time of the species were significantly associated with invasion success. Multiple trait analysis revealed that the relationship between the length of flowering season and invasion success was contingent upon pollination modes. Moreover, the success of polyploids and of species with certain vegetative reproductive trait attributes depended on the species' flowering phenology.

5. *Synthesis*. Our results indicate that different ecological strategies, determined by particular combinations of traits, can facilitate plant invasion success. Our findings highlight the importance of incorporating trait interactions when testing for characteristics that promote plant invasion success. Improved explanatory power of traits suggests that our new approach can provide an important step forward in the risk assessment and management of new arrivals in regional floras.

Key-words: life-history traits, macroecology, non-indigenous plant species, phylogenetic effects, plant ecological strategies, single traits, trait combinations

Introduction

Biotic invasions are recognized as a major component of global change. Non-indigenous species can have profound effects on ecosystem functioning, biodiversity and evolutionary processes (Lodge 1993; Vitousek *et al.* 1996; Mack *et al.* 2000; Mooney & Cleland 2001). From an ecologist's point of view, biotic invasions can also provide opportunities by serving as natural experiments that advance our understanding of basic ecological processes (Darwin 1859; Sakai *et al.* 2001; Sax *et al.* 2005).

Whether certain traits of species are generally associated with invasion success and can therefore be used to predict and, ultimately, prevent biological invasions, is one of the most challenging questions in invasion ecology (see also Kolar & Lodge 2001; Rejmánek *et al.* 2005b; Pyšek & Richardson 2007). Many previous studies have addressed this question, yet their results have often been ambiguous,

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*Correspondence author. E-mail: eva.kuester@ufz.de and only few traits have consistently been found to correlate with invasion success (Williamson 1999; Mack *et al.* 2000; Kolar & Lodge 2001; Lloret *et al.* 2004; Cadotte *et al.* 2006a; Herron *et al.* 2007; Pyšek & Richardson 2007).

It is likely that some of the inconsistencies are caused by the use of different conceptual and methodological approaches. The conceptual approaches applied to study plant invasion success are based on different species comparison groups (non-indigenous with natives, within the non-indigenous in the target region and within the non-indigenous from a particular source region). Hence, they focus on different stages of the invasion process and answer slightly different questions (see Hamilton *et al.* 2005; Pyšek & Richardson 2007 for details). Furthermore, there is clearly a need for more standardized trait correlation analyses that use full species lists and account for a potential bias due to phylogenetic relationships (Cadotte *et al.* 2006a). However, a few recent studies have addressed these issues (see e.g. Hamilton *et al.* 2005; Lloret *et al.* 2005; Cadotte *et al.* 2006a and references therein; Cadotte *et al.* 2006b), with some also taking account of other covariates such as residence time or habitat. Although statistically significant relationships emerged, low explanatory power of traits seems to be quite characteristic.

Another reason for the lack of generalities and explanatory power of previous trait correlation studies may be that they too narrowly focused on the role of single traits. Plant traits are not independent from each other, but are known to vary, correlate and trade-off, due to environmental conditions, evolutionary history and biophysical constraints (Westoby *et al.* 2002; Reich *et al.* 2003; Westoby & Wright 2006). Recurrent patterns of trait combinations can be observed and different sets of trait combinations have already been conceptualized to different plant ecological strategies (see e.g. Westoby 1998; Grime 2002). If different ecological strategies can support invasion success, then we should thus expect particular trait combinations – rather than single traits – to correlate with invasion success. In statistical terms, we expect that trait interactions explain a substantial amount of variation in invasion success.

To test this hypothesis we analysed the relationships between 40 traits and plant invasion success in Germany. We focused on naturalized species to determine trait correlates influencing the invasion stage from establishment to spread. The traits investigated covered a wide range of plant morphology, life-history and biogeography. After quantifying the relevance of single traits we determined the importance of particular trait combinations by performing a multiple trait analysis with explicit consideration of trait interactions. In all analyses we disentangled the effects of phylogeny and determined their relative importance for invasion success.

Methods

DATA

The study was based on a species inventory covering a sample of up to 90% (388 species) of the naturalized neophytes in Germany. Neophytes are defined as plant species introduced after 1500 (see Richardson *et al.* 2000; Kühn & Klotz 2002). We considered species as naturalized if they were able to maintain self-sustaining populations without direct human intervention (Richardson *et al.* 2000). As a measure of invasion success we used the species' geographical distribution in Germany, as given by the number of occupied grid cells. Presence/absence information per grid cell with 10′ longitude × 6′ latitude (*c.* 130 km^2) was available from FLORKART, a data base of the German Network for Phytodiversity, maintained at the Federal Agency for Nature Conservation (http://www.floraweb.de). The records in the data base were derived from regional mapping schemes and range from the 19th century up to 2001. In the data base three periods refer to the time of recording: before 1950, from 1950 up to 1979 and after 1979. In some regions a considerable amount of data was compiled before 1980 and sufficient data since 1980 is lacking. To have the most comprehensive coverage for Germany we therefore used all records from 1950 onwards to count the grid cell frequency of species. The whole area of Germany is covered by a total of 2995 cells.

Explanatory variables (see Table S1 in Supplementary Material) covered genetics, morphology, flowering phenology, floral and reproductive biology, life strategy, geographic range, introduction history and habitat range in Germany. Data were derived from the BIOLFLOR data base (Klotz *et al.* 2002). In addition to the traits available in BIOLFLOR we constructed a composite trait, which indicates the potential of single individuals to reproduce with seeds. The trait follows the idea that in colonizing species the likelihood of establishment should be greater for self-compatible than for self-incompatible or dioecious species (Baker 1955, 1967) and was derived from dicliny, self-incompatibility, type of apomixis and pollen vector. It comprises values from 1 to 4 with increasing potential for independent reproduction with seeds.

The set of explanatory variables was subclassified into (1) morpho–physio–phenological (morphological, physiological and phenological) traits, henceforth referred to as 'primary' biological traits, (2) ecological performances, resulting from an interplay of distinct primary traits and external (here environmental) variables, henceforth referred to as 'secondary' traits, and (3) variables describing the introduction history of the species (Supplementary Table S1; see also Violle *et al.* 2007). Moreover, the group of primary and secondary traits was divided according to their applicability for risk-assessment. The values of the variables on the habitat range in Germany can only be known after the plant species has already invaded: these variables are therefore considered as non-predictive.

Data on explanatory variables were not complete: the number of species within traits ranged from 72 to 388 (see Supplementary Table S1). Group sample sizes for the categorical traits were unbalanced. We did not analyse very rare attributes (trait values), that is, those with < 10 species in the group.

ANALYSES

We used general linear models to analyse the effect of traits on the grid cell frequency of species. To approximate a normal distribution we used the base-10 logarithm of the number of occupied grid cells. If necessary, continuous explanatory variables were $\log_{10}$-transformed to correct for heteroscedastic residuals, to reduce the influence of outliers or to improve linearity in the regression analysis.

Phylogenetic relatedness between species can confound comparative studies. As closely related species tend to be more alike than more distantly related species, the independence of data cannot simply be assumed (Felsenstein 1985; Harvey & Pagel 1991; Rohlf 2001;

Freckleton *et al.* 2002). An over-estimation of the statistical degrees of freedom due to non-independence in data results in pseudoreplication (Hurlbert 1984). Furthermore, phylogenetic effects may promote bias in the parameter estimates (see Peres-Neto 2006). However, there has been substantial debate in literature concerning phylogenetic correction and its application (see Garland *et al.* 2005; Carvalho *et al.* 2006; Sol *et al.* 2008 and references therein for recent commentaries and for summaries on methods). We accounted for the phylogenetic relationships between the species following Desdevises *et al.* (2003; see also Diniz-Filho *et al.* 1998). We expressed the phylogeny in the form of principal coordinates via a principal coordinate analysis (PCoA) (see Supplementary Appendix S1). Principal coordinates (PCos) significantly explaining variation in grid cell frequency ($P < 0.05$) were included as covariates in the phylogenetic informed (PI) models to correct for phylogenetic relationships. We also conducted cross-species (CS) analyses to partition the variation explained into the portion of variation explained strictly by traits, strictly by phylogeny and by that part correlating with both (see Supplementary Appendix S1 and Westoby *et al.* 1995; Desdevises *et al.* 2003).

First, we analyzed all traits separately in single trait models. In the models with start and end of flowering season we allowed for curvilinear relationships by including second and third order polynomials, as the assumption of linear trends for these traits is not self-evident. We used an *F*-test based on sequential sums of squares (Type I SS) to test for the significance of traits, and for factors with more than two levels we completed our analyses by performing *a posteriori* comparisons. We used general multiple comparisons, type Tukey, allowing for covariates and imbalance (Bretz *et al.* 2002, 2004). The procedure accounts for correlations between the test statistics by using the exact multivariate *t*-distribution (see Westfall 1997; Bretz *et al.* 2001 for details).

Secondly, we performed a multiple trait analysis. The high number of potential explanatory variables, each containing a different set of missing values, required data reduction methods prior to model development. We excluded all variables not (marginally) significant in PI single trait analysis from the modelling procedure. An exception was growth form, since we hypothesized that different traits might be relevant for the different growth forms. Furthermore, we did not consider non-predictive variables, variables with more than 30% of missing values, and variables, only available for, and applicable to, specific plant species groups. We assessed the collinearity and redundancy in the resulting set of variables by performing hierarchical variable clustering, agglomeration method complete linkage, with squared Spearman's rank correlation coefficients as similarity measures (Harrell 2001). We picked one variable from each cluster, with clusters of correlated variables defined by a similarity level of squared Spearman's rank correlation coefficient ≥ 0.49. In selecting variables from clusters, a decision was taken in favour of primary biological traits. As secondary measures of ecological performance result from the interplay of multiple distinct biological, ecological and physiological traits (Pyšek & Richardson 2007; Violle *et al.* 2007) their inclusion only seems to be reasonable when primary biological traits covering these aspects are not available. Eight variables were derived from this exploratory process of data reduction (see Supplementary Table S1) and considered in the subsequent multivariable modelling. The sample design was non-orthogonal, including missing cells, so that not all interactions were estimable. We regarded all sensible twofold interactions (Quinn & Keough 2002) and we pre-selected those interactions with sufficient combinations (see Table S2 for full model). To avoid correlation between main effects and their interactions we standardized all continuous explanatory variables. We simplified the model by performing a backward selection procedure using the Akaike information criterion. Pre-selected phylogenetic PCos were kept in the model as covariates. *F*-ratio statistics for the effects in the final model were based on Type III sums of squares. We calculated the amount of variation explained strictly due to interactions by subtracting the amount of variation explained in the final model excluding interactions from the final model including interactions.

All statistical analyses were performed within R (R Development Core Team 2005, Version 2.2.1) using the packages MASS (Venables & Ripley 2002), multcomp (Bretz *et al.* 2004), effects (Fox 2005), Hmisc (Harrell 2006) and car (Fox 2007).

Results

SINGLE TRAIT ANALYSES

We found distinctive traits significantly associated with grid cell frequency of neophytes in single trait analyses (Table 1). However, the explanatory power of most of the single trait models was quite poor, even when phylogenetic information was incorporated (range R^2 all PI models: 0.053–0.191). In general, neither phylogenetic effects nor traits explained a considerable amount of variation (see Table 1). The measures of ecological performance in Germany were the best explanatory variables. Variation explained strictly due to the trait was highest for the number of vegetation units inhabited (14.9%). However, the group of habitat range variables (Table 1) entirely comprises non-predictive variables, that is, those without relevance for risk assessment. The year of first occurrence in the wild was also a comparably good predictor (9.5%). The highest proportion of variation explained by primary and predictive traits was, however, only 3.3% (see Table 1). Depending on the trait and the species subset, phylogeny and traits jointly explained up to 3.9% (Table 1) and strictly phylogenetic effects from 1.2% to 8.4%.

Single trait analysis indicated that polyploid species on average occupied a higher number of grid cells than diploid species. Annuals were more widely distributed than perennials. Species developing runners were more widespread than those generating rhizomes. Species occupied more grid cells the longer their flowering period, the later the end of their flowering season and the higher their potential for independent reproduction with seeds. Furthermore, the single trait models indicated that neophytes were more common the higher the number of floristic zones occupied and the earlier their time of occurrence in Germany. Finally, all variables relating to the habitat range in Germany were significantly associated with invasion success (Table 1). Classification of species with respect to their occurrence in urban areas showed that urbanoneutral species were the most frequent. The number of hemerobic levels, habitat types, vegetation formations and vegetation units were positively correlated with map grid cell frequency.

MULTIPLE TRAIT ANALYSES

Of the eight variables considered for multivariable modelling five were important for model development. The minimum

Table 1. Cross-species (CS) and phylogenetic informed (PI) single trait models with invasion success ($\log_{10}$-transformed number of occupied grid cells) as dependent variable

	CS			PI			Variation explained (%)	
Variable	d.f.	*F*	*P*	d.f.	*F*	*P*	Phylogeny and trait	Trait only
Genetics								
Ploidy	1,344	6.15	**0.01***	1,343	8.15	**0.005***	**–0.5**	**2.2**
Morphology								
Life span	1,350	4.48	**0.04**	1,348	4.9	**0.03**	**0**	**1.3**
Vegetative propagation and dispersal	4,329	3.47	**0.009***	4,328	1.75	0.14	2.0	2.0
Existence of storage organs	1,380	3.03	0.08	1,378	1.33	0.25	–	–
Storage organs	4,288	4.11	**0.003***	4,287	2.51	**0.04**	**2.1**	**3.3**
Shoot metamorphoses	4,323	4.46	**0.002***	4,320	2.51	**0.04**	**2.4**	**2.8**
Flowering phenology								
Length of flowering season	1,377	15.74	**< 0.001***	1,376	12.9	**< 0.001***	**0.8**	**3.2**
End of flowering season	1,377	11.82	**< 0.001***	1,376	7.48	**0.007***	**1.2**	**1.9**
Floral and reproductive biology								
Independence in reproduction with seeds	1,273	6.19	**0.01***	1,270	6.63	**0.01***	**0**	**2.2**
Pollen vector	2,326	4.77	**0.009***	2,324	2.88	0.06	1.2	1.6
Life strategy								
Ecological strategy types	5,347	3.12	**0.009***	5,345	1.91	0.09	1.7	2.6
Ruderal life strategy	1,357	3.23	0.07	1,355	3.19	0.08	–	–
Native geographic range								
Number of floristic zones	1,322	3.25	0.07	1,319	5.29	**0.02**	**–0.5**	**1.5**
Old world vs. new world only	1,333	2.96	0.09	1,331	2.42	0.12	–	–
Introduction history								
Year of first occurrence in the wild	1,134	20.75	**< 0.001***	1,133	14.88	**< 0.001***	**3.9**	**9.5**
Habitat range in Germany								
Urbanity	2,331	12.93	**< 0.001***	2,329	12.32	**< 0.001***	**0.7**	**6.6**
Number of hemerobic levels	1,338	6.25	**0.01***	1,335	6.63	**0.01***	**0**	**1.8**
Number of habitat types	1,351	49.63	**< 0.001***	1,348	38.71	**< 0.001***	**3.1**	**9.3**
Number of vegetation formations	1,305	22.98	**< 0.001***	1,303	19.31	**< 0.001***	**1.3**	**5.7**
Number of vegetation units	1,305	59.84	**< 0.001***	1,303	55.63	**< 0.001***	**1.5**	**14.9**

In CS analyses each trait served as independent variable and in PI analysis each trait plus pre-selected phylogenetic principal coordinates were tested as independent variables. Results for variables with $P < 0.1$ in CS and/or PI analysis are depicted in the table. Variables with $P \geq 0.1$ were DNA content, life form, growth form, existence of vegetative propagation and dispersal, root metamorphoses, leaf anatomy, leaf persistence, start of flowering season, strategy types of reproduction, floral UV-pattern, floral UV-reflection, blossom type, types of generative diaspores, weight generative diaspores, weight germinules, zonal distribution, continents, oceanity, amplitude in continentality–oceanity gradient, mode of immigration. Results for phylogenetic covariates and variation explained by strictly phylogenetic effects are not presented. Variation partitioning was applied for variables significant in CS and/or PI analyses. Results with $P < 0.05$ and variables with consistent findings in both analyses are in bold. Asterisks indicate results with $P < 0.05$ after controlling the false discovery rate (Benjamini & Hochberg 1995), column by column.

adequate model contained ploidy, pollen vector, shoot metamorphoses and length and end of flowering season (Table 2). Growth form, life span and number of floristic zones occupied were not relevant. Three interactions remained in the model (Table 2). The minimum adequate model explained 23.3% of variation in grid cell frequency (multiple R^2). 3.4% of variation explained was strictly attributed to phylogenetic effects and 4.3% to joint effects (Fig. 1). The main portion of variation explained resulted solely from effects of traits (15.6%). Nearly two-thirds of this portion was attributed exclusively to trait interactions (Fig. 1).

The effect of the length of flowering season on invasion success differed among pollination types (Fig. 2). In contrast to insect- and self-pollinated species, grid cell frequency of wind-pollinated species was negatively correlated with the length of flowering season. Frequencies for insect- and self-pollinated species showed a somewhat positive trend, but for insect-pollinated species this relationship was very weak. Furthermore, the effect of the end of flowering varied between diploid and polyploid neophytes (Fig. 3). In particular, polyploid species tended to be more widespread the later the end of flowering. The effect of the end of flowering season also differed among shoot morphologies (Fig. 3). For species with pleiocorms, without shoot metamorphosis and, in particular, for species with rhizomes, grid cell frequency was more or less positively associated with a later end of flowering season. For species with runners the opposite trend was observed.

Discussion

As expected, single traits held little explanatory value for plant invasion success. The conspicuous increase of variation

Table 2. ANOVA table on the effect of traits and phylogenetic covariates on invasion success ($\log_{10}$-transformed number of occupied grid cells) for the final model

Source	d.f.	SS	*F*	*P*
Principal coordinate 1	1	1.415	2.33	0.13
Principal coordinate 3	1	2.883	4.76	0.03
Pollen vector	2	1.889	1.56	0.21
Ploidy	1	0.0003	0.0005	0.98
Shoot metamorphoses	3	2.865	1.58	0.20
Length of flowering season	1	0.019	0.03	0.86
End of flowering season	1	1.754	2.89	0.09
Pollen vector × Length of flowering season	2	4.304	3.55	0.03
Ploidy × End of flowering season	1	2.140	3.53	0.06
Shoot metamorphoses × End of flowering season	3	5.732	3.15	0.03
Residual	164	99.431		

Akaike information criterion served for determining the variables in the final model. Phylogenetic principal coordinates were kept in the model as covariates. R^2 adjusted = 0.158, R^2 multiple = 0.233.

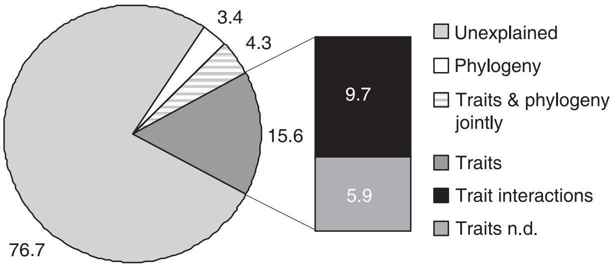

Fig. 1. Variation partitioning in the simplified final model (in percent). Variation in invasion success explained by the simplified final model 23.3%. Left-hand pie chart: variation partitioning among traits and phylogeny. Right-hand cut out: variation explained exclusively by traits (15.6%). Trait interactions: amount of variation strictly due to interactions; Traits n.d.: Allocation of variation explained between main effects of traits only, and main effects of traits and interactions jointly. Variation explained by main effects and interactions jointly was not determined, because variation explained by main effects only could not be determined as it is not permissible to calculate a model with higher order terms only.

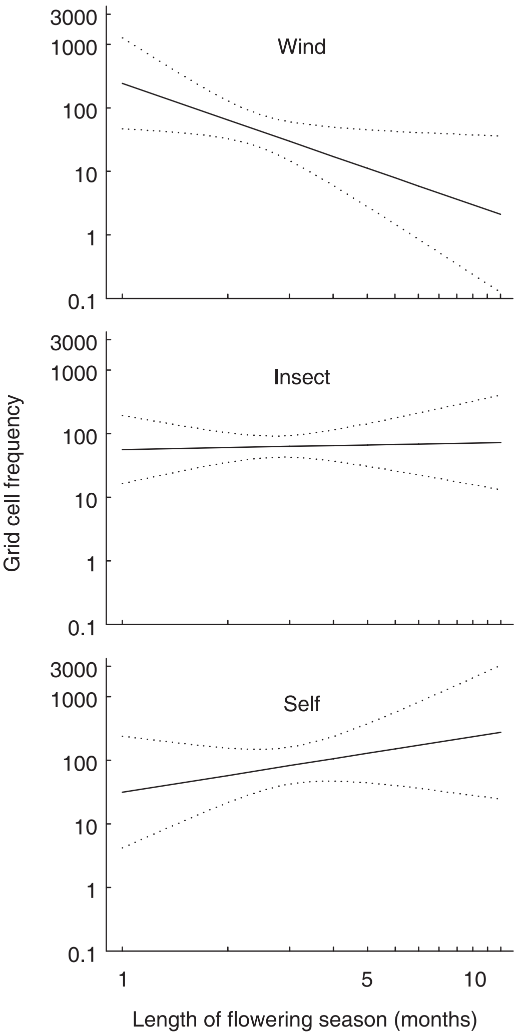

Fig. 2. Interaction between pollen vector and length of flowering season. Relationship between $\log_{10}$ (number of occupied grid cells) and $\log_{10}$ (length of flowering season) for wind, insect and self-pollinated plant species; fitted values with 95% confidence intervals. Distribution of data is presented in Supplementary Table S3.

explained in the multiple trait analysis resulted mostly from trait interactions (Fig. 1). This suggests that coarse-scale patterns detected in the single trait analyses are underlain by some much more detailed fine-scale patterns of major importance (see Figs 2–3).

INFLUENCE OF TRAITS ON INVASION SUCCESS

Single trait analysis indicated that traits significantly associated with plant invasion success in Germany are linked to flowering and reproductive biology, ecological tolerance and the residence time of the species. The relevance of the potential for independent reproduction with seeds suggests that Baker's law applies to invasion success as well (see also Rambuda & Johnson 2004; van Kleunen & Johnson 2007). Consistent with previous studies the single trait analysis also suggested that a longer flowering period was positively correlated with invasion success (see e.g. Lloret *et al.* 2005; Cadotte *et al.* 2006b). Other studies, however, failed to detect a significant effect of flowering phenology (Thompson *et al.* 1995; Williamson & Fitter 1996; Celesti-Grapow *et al.* 2003) and pollen vector has already performed badly in a series of studies (see summary in Pyšek & Richardson 2007). The results from the multiple trait analysis may provide an explanation for the lack of clarity. The influence of the length of flowering season on invasion success depended on the pollen vector (Fig. 2). In contrast to insect- or self-pollinated neophytes, wind-pollinated species were less frequent the longer the flowering season. It is likely that wind-pollinated plants simply do not gain from a longer flowering season. A longer flowering season either means that the individuals flower longer, thus investing in

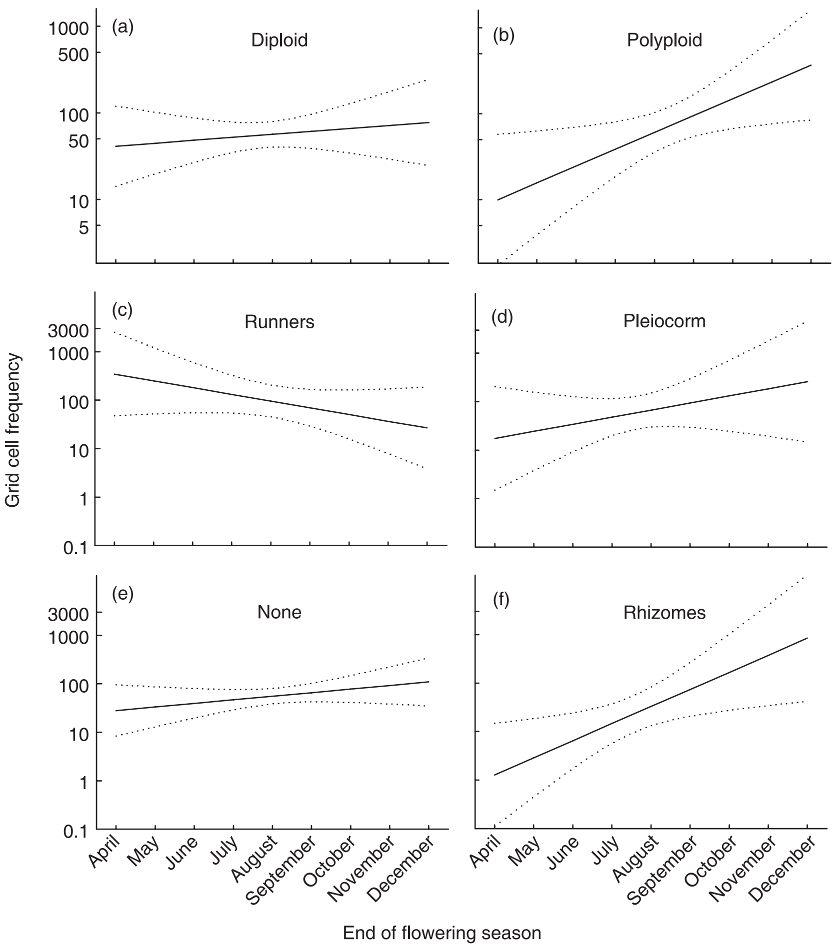

Fig. 3. Interaction of ploidy (a, b) and shoot metamorphoses (c–f) with end of flowering season. Relationship between $\log_{10}$ (number of occupied grid cells) and end of flowering for diploid and polyploid plant species and for species with different shoot metamorphoses (Runners: Usually lateral shoots with long thin internodes and adventitious roots. Severance from the mother plant causes the formation of individual ramets. Pleiocorm: System of compact, perennial shoots occurring at the proximal end of the persistent primary root. The connections between the shoots and the primary root are persistent. Rhizom: Transformed shoot growing subterraneously or close to the soil surface, mostly thickened with short internodes, with adventitious roots and (mostly) scale-like leaves.). Fitted values with 95% confidence intervals. Distribution of data is presented in Supplementary Table S3.

flower production for a longer time, and/or that the time frame for reproduction of the species is longer, thus reducing synchrony in the flowering of the individuals. Wind-pollinated species, however, are known to have very well-defined flowering seasons. Moreover, because of its passive nature, the efficiency of wind-pollination is expected to be enhanced by intra-population synchronization, like a mass release of pollen occurring upon specific environmental cues, and therefore shorter durations of flowering (Whitehead 1969; Rabinowitz *et al.* 1981; Whitehead 1983; Proctor *et al.* 1996; but see Bolmgren *et al.* 2003). The multiple trait analysis also suggested a more complex pattern for the correlation between the end of flowering season and invasion success (Fig. 3). The relationship depended on the shoot morphology of species. In contrast to the generation of runners, the nature of vegetative reproduction in rhizomes and pleiocorms does not notably support dispersal or spread. Potentially, the positive effect of a later flowering end points to the importance of seed production for spread in these species. Moreover, a later flowering end could confer an advantage by avoiding competition in the local community (see also Celesti-Grapow *et al.* 2003). Furthermore, the advantage of polyploidy in invasion success seemed to be constrained by the end of flowering season. Various characteristics of polyploids have been suggested to confer an advantage in colonization or to entail a wider ecological tolerance (see e.g. Soltis & Soltis 2000; Soltis *et al.* 2003 for details) and lately polyploidy has also been proven important for invasion success (see Verlaque *et al.* 2002; Pandit 2006). The particular relevance of a late end of the flowering season for the polyploids may reflect the influence of a longer flowering season with a later flowering end (correlation between end and length of flowering: Pearson's r: 0.66, $N = 181$, $P < 0.001$). As polyploids had a later start of the flowering season than diploids (CS analysis, ANOVA: $F_{1,179} = 5.919$, $P = 0.02$; PI analysis, ANCOVA: $F_{1,174} = 9.072$, $P = 0.003$) a particularly early end may be disadvantageous.

IMPORTANCE OF TRAIT INTERACTIONS FOR INVASION SUCCESS

Our results suggest that particular combinations of trait attributes rather than distinctive attributes *per se* determine invasion success. Clearly, the patterns detected require further effort to explore the underlying processes. However, the majority of traits investigated cannot explain much of the variation in single trait analysis. Only the year of first occurrence in the wild and the habitat range variables for Germany accounted for a sufficient amount of variation, but these variables are no primary biological traits (for the influence of the time since introduction on invasion success of plants in

Germany see also Kühn & Klotz 2003; for details on the influence of habitat range on invasion success see also Kühn *et al.* 2004). The year of first occurrence in the wild, a proxy for residence time, can represent another dimension of propagule pressure (Pyšek & Jarošík 2005; Rejmánek *et al.* 2005b; Richardson & Pyšek 2006). The longer a species is present in a certain region, the more propagules it is able to produce and disperse. Also evolutionary adjustments can take place during this time (see Mack *et al.* 2000; Mooney & Cleland 2001; Sakai *et al.* 2001). The secondary measures of ecological performance presumably pool together species with varying primary biological attributes. Hence, this result may only underline once more the relevance of a distinctive combination of attributes. Specific combinations of attributes have previously been ascribed to invasion success. Newsome & Noble (1986), for instance, clustered successful plant invaders according to their combination of attributes and proposed they could be characterized as 'gap grabbers', 'competitors', 'survivors' and 'swampers'. Plant species variation in traits is not random (Westoby & Leishman 1997). Some combinations of attributes are more common than others and not all combinations are possible. It is therefore likely that trait values which link to invasion success are not universal (see also Mack *et al.* 2000), but vary depending on particular trait combinations. The investigation of interactions in multispecies studies between especially primary biological traits has, however, only recently been considered in the search for traits favouring invasion success. Herron *et al.* (2007) allowed the slope parameters for traits to vary across growth forms of woody species, when developing a predictive model for woody plant species, and found pronounced differences for some relationships. However, they did not take account of phylogenetic relationships in their analysis. Lloret *et al.* (2005) fitted interactions among a variety of primary biological traits, but did not find any importance of the interactions. This may be a direct consequence of a separation between habitats in their study, which revealed that trait attributes favouring invasiveness in plant species vary among different habitats (see also Pyšek *et al.* 1995). Hence, one may argue that the importance of interactions in our analyses reflects some kind of habitat dependency in attributes favouring invasion success. However, the question of whether our results point to different plant strategies associated with invasion success in different habitats, or whether the findings hold for general plant strategies across different habitats, has to be left to future research.

CONCLUDING REMARKS

While the amount of variation explained increased from single to multiple trait analysis, a fairly large part remained unexplained (76.7%). One limitation of our study is that we could not take account of all traits and interactions. Although it seems likely that traits linked to reproduction and ecological tolerance are important for invasion success, it is crucial to note that the evidence is indirect and the patterns detected are of a correlative nature. Anyhow, a growing body of research suggests that success of plant species is influenced by a series of processes or filters within each stage of invasion (Heger 2001; Theoharides & Dukes 2007). Thus, it is likely that other factors beside biological traits are also important for invasion success, for example, the number of introductions of the species, the residence time, and within study site heterogeneity in physical factors (Rejmánek *et al.* 2005a; Theoharides & Dukes 2007). In this context, it also remains to be evaluated to what extent our results depend on filters acting prior to establishment and which thus influenced the species pool analysed, for example, the prevalent environmental conditions in the study area or the traits of the resident community (see Theoharides & Dukes 2007; Moles *et al.* 2008). Nevertheless, our analysis does indicate that to disentangle the link between primary biological traits and invasion success it is necessary to consider that traits potentially interact. Our results therefore support the hypothesis that different ecological strategies can facilitate invasion success and show that particular trait combinations correlate with invasion success. Improved explanatory power of traits with our new approach can provide an important step forward in the risk assessment and management of new arrivals in regional floras.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Incorporation of phylogenetic information.

Table S1. Explanatory variables for modelling invasion success.

Table S2. Full model: Explanatory variables used in the multivariable modelling procedure.

Table S3. Number of species in the trait combinations that appear as interactions in the simplified final model (Figs 2–3).

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