BIODIVERSITY RESEARCH

Why do alien plant species that reproduce in natural habitats occur more frequently?

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ABSTRACT

The invasion process can be divided into several phases. We consider invasion patterns related to two aspects of the invasion process: the spread of a species in Germany as counted by the number of occupied grid cells, and the degree of naturalization in Germany (i.e. whether a plant species is exclusively naturalized in human-made habitats or also in (semi-)natural habitats). Although in Germany the area of natural habitats is smaller than that of human-made habitats, the area of occupancy of the respective alien plant species is the opposite. We tested whether both patterns could be explained by niche-breadth variables, namely the number of inhabited habitat types, and vegetation formations, the range of human impact levels, the number of inhabited continents, the number of inhabited floristic zones (climatic zones), and the amplitude of oceanity. Tests were conducted across species and across phylogenetically-independent contrasts, using generalized linear models, in particular, hierarchical partitioning. The number of occupied grid cells could be explained by niche-breadth variables, especially by number of habitats, number of formations, and amplitude of oceanity. Contrary to our expectations, none of these variables could explain the degree of naturalization in cross-species analyses, and amplitude of oceanity is the only stably significant variable that explains the degree of naturalization when analysing phylogenetically-independent contrasts. We conclude that the degree of naturalization is probably independent from niche breadth, and that properties of a larger area of occupancy, i.e. sample size (or propagule pressure), could be responsible for this pattern.

Keywords

Area of occupancy, biological invasions, degree of naturalization, Germany, niche breadth.

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INTRODUCTION

Although the complete process of biological invasions is a continuum, it can be divided into several phases or stages (Williamson, 1996). Recently, different phases of the invasion process have been given particular attention (Williamson, 1999; Richardson *et al.*, 2000b; Kolar & Lodge, 2001; Heger & Trepl, 2003; Cassey *et al.*, 2004; Colautti & MacIsaac, 2004). Although terminology and concepts might differ, all these treatments recognize (though not always explicitly) some common phases: (i) transport of a particular species to a new biogeographical region; (ii) establishment in that new region; (iii) spread; and (iv) invasion. From one phase to the next, several filters play a role (Richardson *et al.*, 2000b; Colautti & MacIsaac, 2004) so that, generally speaking, about 10% of species progress from one phase to the next (ten's rule) (Williamson, 1993; Williamson & Fitter, 1996). At each phase, different factors influence the species; thus the recognition of these phases and of the relevant factors at each phase and between one phase and the next are crucial in developing successful tools

for predicting invasions (Richardson *et al.*, 2000b; Kolar & Lodge, 2001; Heger & Trepl, 2003; Cassey *et al.*, 2004). Traits that are likely to be associated with the first phase (transport to new region) are probably those of the dispersal unit (e.g. longevity, adherent capacity). Traits that are likely to be associated with the latter phases are more related to competitive ability and the matching of habitat and climate (Crawley *et al.*, 1996; Pyšek, 1998). These variables are related to the ecological niche of a species.

One problem in invasion ecology is the definition of the final phase: what is an invader? Several concepts are discussed in the literature (e.g. Davis & Thompson, 2000; Richardson *et al.*, 2000b; Daehler, 2001; Davis & Thompson, 2001). For Germany, first there is no unambiguous agreement on how to classify species according to impact (*sensu* Davis & Thompson, 2000). Second, we do not have data for the speed of spread for most of the alien species to classify them as invaders according to the strong criteria of Richardson *et al.* (2000b). Data that are available for distinguishing successful invaders from less successful ones are:

(i) the area of occupancy in Germany, using the number of grid cells in which a particular (here: alien) species is found (see Gaston, 2003); and (ii) the degree of naturalization in Germany, i.e. whether a species occurs exclusively in human-made habitats or also in (semi-)natural habitats. Williamson (1996) noted that the distinction between plants naturalized in human-made vegetation and those naturalized in (semi-)natural vegetation is not considered within his conceptual framework and thus are not covered by the 'tens rule'. However, the area of occupancy is more related to the 'spread' phase of the invasion process which might be independent of the last one ('invasion').

Some relationships could be hypothesized between the two groups mentioned (i.e. species naturalized in human-made habitats and species naturalized in (semi-)natural habitats): (i) The number of occupied grid cells of plant species of (semi-)natural habitats might be lower than those of human-made habitats because the availability of (semi-)natural habitats is likely to be lower. (ii) The number of occupied grid cells of plant species of (semi-)natural habitats might be higher for two reasons: (a) abundant species have a wider niche breadth and might therefore invade human-made as well as (semi-)natural habitats more easily or (b) invasion into (semi-)natural habitats might have other reasons, e.g. a function of stochasticity or of propagule pressure.

Our aim is to test the relationship between the number of occupied grid cells and the degree of naturalization and relate this to factors that are associated with realized niche breadth, namely variables that are related to the species' habitats in Germany (number of inhabited habitat types, the number of inhabited vegetation formations, the range of human impact on the habitats), and variables related to a species range in the world (number of inhabited continents, the number of inhabited floristic zones, and the amplitude of oceanity). We do so by exploring the properties of a large number of elements (here species) in the two groups under investigation (see Brown, 1999), and not using case studies of particular species.

METHODS

Concepts and definitions

The niche of a species can be defined as a species distribution along various niche axis (Schoener, 1989); this reflects all the environmental conditions and resources that a species utilizes or requires. Hutchinson (1957) distinguished between the 'fundamental niche' and the 'realized niche'. The former describes the overall potential of a species that can only be found in monocultures under laboratory conditions. The latter is the reduced niche due to predators or competitors. In our study, we used measures of the realized niche. We define niche breadth as the extent (minimum to maximum) of a species distribution along such a niche axis.

Neophytes are alien plant species that reached Germany after 1500, whereas archaeophytes arrived earlier, since the Neolithic (Holub & Jirásek, 1967; Schroeder, 1969). Recently, this terminology was also used in the English and international literature (e.g. Schroeder, 1969; Preston *et al.*, 2002; Pyšek *et al.*, 2004a).

Archaeophytes and neophytes differ markedly (Pyšek *et al.*, 2002; Kühn *et al.*, 2003), e.g. in their ecology, mode of introduction or evolutionary history. Therefore they should not be pooled in an analysis. For this analysis, we only used neophytes.

We distinguish between three different degrees of naturalization (Richardson *et al.*, 2000b; Pyšek *et al.*, 2004a): casuals and two levels of naturalized. 'Casuals' are alien plant species which rely on repeated introductions for their persistence. Information on casuals in BiolFlor (Klotz *et al.*, 2002) is biased towards frequent casuals and lacks rare casuals ('occasionals'). We therefore excluded them from the analysis. In this analysis, we only considered naturalized species, i.e. 'alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention from humans' (Richardson *et al.*, 2000b: 98). These naturalized species could be divided further into those that are naturalized exclusively in human-made habitats and those that are naturalized in (semi-)natural habitats (Pyšek *et al.*, 2004a). Individuals of the latter group may also grow in human made habitats but not necessarily have to do so (e.g. *Impatiens parviflora*). Human-made vegetation is found, for example, in urbanized areas, on arable fields, in agricultural grasslands, or in most of the coniferous forests of the German lowlands. Semi-natural vegetation occurs, e.g. in river floodplains, scree and boulder vegetation or due to a natural fire regime, but includes also planted old forests where the species composition is similar to that of natural forests.

The naturalization process is a continuum from species that exclusively reproduce in human-made habitats via species that predominantly reproduce in human-made habitats and only rarely reproduce in (semi-)natural habitats to species that predominantly reproduce in (semi-)natural habitats. Although being a continuum process, a distinction of this naturalization continuum into the phases 'naturalization in human-made habitats' and 'naturalization in (semi-)natural habitats' is widely accepted (e.g. Richardson *et al.*, 2000b; Pyšek *et al.*, 2004a). This distinction is also well established in Central Europe (e.g. Holub & Jirásek, 1967; Schroeder, 1969; Lohmeyer & Sukopp, 1992; Pyšek *et al.*, 2004a; also referred to by Williamson, 1996). According to Schroeder (1969), species that are naturalized in human-made habitats are also called 'epecophytes' and those that are able to reproduce in native or (semi-)natural vegetation are called 'agriophytes'. Throughout this paper, we call the first group 'plant species naturalized in human-made vegetation' and the second one 'plant species naturalized in (semi-)natural vegetation', keeping in mind that the latter group most often is also naturalized in human-made vegetation. Though these two species groups are not necessarily exclusive regarding their habitat preferences, they are distinct as the second group is more advanced in the invasion process (Richardson *et al.*, 2000b).

For Germany, lists of plant species naturalized in (semi-)natural habitats based on extensive vegetation surveys are available from Lohmeyer & Sukopp (1992, 2001) and are incorporated in BiolFlor (Klotz *et al.*, 2002). Unfortunately, a comprehensive database on vegetation data is not yet available (unlike, e.g. for the Netherlands, http://www.synbiosys.alterra.nl, or the Czech Republic, http://www.sci.muni.cz/botany/database.htm). Therefore it is not yet possible to calculate the proportion of (records

naturalized in (semi-)natural vegetation) / (records naturalized in human-made vegetation).

We therefore used the maximum degree of naturalization that a plant species has reached in Germany. This means that if a species occurs in natural vegetation only once it is classified as a species of (semi-)natural habitats. However, less than 5% of the species mentioned by Lohmeyer & Sukopp (1992, 2001) were mentioned only once as naturalized in (semi-)natural habitats. Most of them were recorded repeatedly from (semi-)natural vegetation.

Data sources

Data on plant traits were obtained from BiolFlor, a database on biological and ecological traits of the flora of Germany (Klotz *et al.*, 2002). This database contains information on more than 60 traits for all German native plant species and naturalized aliens as well as regularly occurring casual aliens (Kühn *et al.*, 2004b). Data from BiolFlor are species specific and are not spatially explicit. We thus consider habitat preferences to be a species trait in this analysis. BiolFlor also includes data on degree of naturalization (Kühn & Klotz, 2002) incorporated from Lohmeyer & Sukopp (1992, 2001). Data on degree of naturalization and data of niche-breadth variables are completely independent from each other.

The following variables were used as proxies for niche breadth (Prinzing *et al.*, 2002; Brändle *et al.*, 2003) from BiolFlor (Klotz *et al.*, 2002):

1 Variables related to species' habitats in Germany

• *Number of habitat type*: this counts in how many of the 21 main habitat according to the system of Haeupler & Muer (2000) types a plant species could be found; information on this was collated by Haeupler (2002);

• *Number of formations* in which a plant occurs are counted from the 10 main vegetation formations that aggregate phytosociological classes in which a plant species could be found according to the system of Schubert *et al.* (2001);

• *Range of 'hemerobic levels'* a species can colonize (Hemeroby describes the human impact on vegetation; Jalas (1955), Sukopp (1972)). Plants can occur in one or several of the six levels that classify this human impact on a habitat, ranging from 'no influence' and 'little influence' (e.g. moderate logging of only single trees) to 'complete alteration' due to, e.g. landfills, spoil piles, railway tracks, etc. (for details see Klotz & Kühn, 2002).

2 Variables deduced from the global distribution of species

• *Number of continents* in which a plant naturally occurs according to Schubert & Vent (1990);

• *Number of inhabited floristic zones* are counted from latitudinal zonation according to the system of Schubert & Vent (1990); they are more or less parallel to the latitudinal climatic zones of the earth; detailed information on the methods that where used to define the zones and how the species were assigned can be found in Meusel *et al.* (1965, 1978), Meusel & Jäger (1992);

• *Amplitude of oceanity* is a measure of the extent of a species' range from the coasts to centres of a continent according to the system of Jäger in Schubert & Vent (1990); detailed information on the methods that where used to define oceanity and how the species were assigned can be found in Meusel *et al.* (1965, 1978),

Meusel & Jäger (1992). The amplitude of oceanity is high when a species covers a wide range from the sea towards the inland and is low if a species is either restricted to the coasts or to the centres of the continents.

It must be noted that not all data mentioned above are available for all species in BiolFlor. Our species pool for analysis thus contains 113 species naturalized in human-made habitats and 74 species naturalized in (semi-)natural habitats while BiolFlor notes 314 neophytes that are naturalized in human-made vegetation and 156 neophytes that are naturalized in (semi-)natural vegetation (Kühn & Klotz, 2002).

We calculated the frequency of occupied grid cells as a proxy for the area of occupancy of species from FLORKART (http:// www.floraweb.de), a database on the flora of Germany, maintained by the German Centre for Phytodiversity at the Federal Agency for Nature Conservation. FLORKART originally contains over 14 Mio. records and was compiled from several regional mapping schemes and local floras usually having a resolution of $3' \times 5'$ (*c.* 32 km^2) or finer. Unfortunately, data at this resolution has considerable gaps, so the data that we used had to be aggregated to a resolution of $6' \times 10'$ (*c.* 130 km^2) resulting in 2.6 Mio. unique records (i.e. a species in a given time period). Records date from the 19th century until 2001 with an increased sampling effort after the 1960s. In our version of FLORKART, the time of recording is referenced as three time periods: before 1950, 1950 until 1979 and since 1980 (for more details see Kühn *et al.*, 2004a). As data in FLORKART was derived from regional mapping schemes at different times there are some regions which have most of their data previous to 1980 and lack sufficient data since 1980 while most of the regions have sufficient data available since 1980. To have the most sufficient coverage of Germany, we used all records from 1950 onwards to simply count the number of occupied grid cells.

Data on land cover in Germany were derived from the Corine Land Cover maps provided by the 'Federal Statistical Office of Germany' (Statistisches Bundesamt, 1997). The Federal Agency for Nature Conservation provided the respective data in grid cell format which was transformed from the digital maps mentioned above. This information was not used to classify the species to the two degrees of naturalization.

Data analysis

To account for phylogenetic relationships between species we used phylogenetically-independent contrasts (PICs) (Felsenstein, 1985; Harvey & Pagel, 1991). This is necessary because the traits of different species are not independent of each other but linked by phylogeny. We calculated PICs using the program CAIC (Comparative Analysis of Independent Contrasts, Purvis & Rambaut 1995). This program provides two algorithms for calculation, the options 'brunch' for categorical or binary variables and 'crunch' for continuous variables. However 'degree of naturalization' is an ordinal variable and CAIC provides no options for ordinal variables. To test the stability of the results we calculated the contrasts with both options. Results that were comparable using both methods ('brunch' and 'crunch') are considered to be stable. All PICs were calculated using the phylogeny

of Durka (2002). Because we have no information about branch lengths we set all branch lengths to the same arbitrary value. PICs were analysed with ordinary least square regressions through the origin (data from the option 'crunch') (Garland *et al.*, 1992) and sign tests (data from the option 'brunch') (Burt, 1989). The use of phylogenetically-independent contrasts allows us to remove an effect of phylogeny. Comparing results from cross-species analysis with analysis across phylogenetically-independent contrasts we can see whether a pattern is linked through phylogeny or independent of it. When the two analyses show comparable results we consider the resulting pattern to be stable.

Relationships between the degrees of naturalization or the number of occupied grid cells and several traits related to niche breadth were analysed using Generalized Linear Models (GLM). As the degree of naturalization has two states, we used a logistic regression. For the number of occupied grid cells (count data) we used a GLM with Poisson error distribution (e.g. Crawley, 2002). Contrasts of the number of occupied grid cells were double square root (i.e. $y^{1/4}$) transformed to approximate normal distribution. For multiple explanatory variables we used backward selection to get a minimum adequate model (Crawley, 2002). Only the results of the minimum adequate models are presented here.

Multicollinearity in the data (i.e. that many of the independent variables are correlated) may lead to several minimum adequate models that could theoretically be expected in the model selection process of multiple regressions (Dalgaard, 2002). We therefore used also 'hierarchical partitioning' (MacNally, 1996; MacNally & Walsh, 2004). In this method the explained variance is calculated for generalized linear models using all possible combinations of independent variables. From this, the proportions of the variance are calculated that could exclusively be explained by a particular variable and the proportion of the variance that could jointly be explained by that particular variable and other independent variables. Hence, we were able to retrieve variables that are likely to have the greatest influence in explaining variance. Hierarchical partitioning may lead to negative results for joint effects if one variable is acting as a suppressor variable (Chevan & Sutherland, 1991). The significance of the variables was tested by 1000 randomizations of the explanatory variables using the 95% confidence limit of the *z*-scores (z = [observed value − mean(randomizations)]/sd(randomizations)). We used 'log likelihood' as a goodness-of-fit measure. As the signs of the regression coefficients (slopes) may not be the same for a particular variable in all possible combinations, it is not possible to state the direction of a relationship for the results of variation partitioning. The relationship could be assessed, however, by using only the significant variables in a single model afterwards.

All statistical analyses were carried out using the program R (http://www.r-project.org).

RESULTS

The area of anthropogenic land cover in Germany is much higher than of (semi-)natural land cover (Fig. 1). An overview on the 10 most frequent species that are naturalized in human-made habitats or in (semi-)natural habitats and their numbers of occupied grid cells is presented in Table 1.

We found that the number of occupied grid cells of species naturalized only in human-made habitats is significantly lower than the number of occupied grid cells of species naturalized in (semi-)natural habitats (Fig. 2). In other words, the wider the distribution of a species, the higher the probability that the species is naturalized in (semi-)natural vegetation.

We tested whether the number of occupied grid cells could be explained by several variables related to niche breadth with backward selection of generalized linear models. All niche-breadth variables were significant in the cross-species analysis (Table 2). All variables were positively correlated with degree of naturalization, except for the number of continents (which are negatively correlated). Removing the influence of phylogeny by analysing phylogenetically-independent contrasts (Table 2), we found that this result is stable for the number of habitat types, number of formations, range of hemerobic levels and amplitude of oceanity, retaining the same relationship as in the cross-species analysis. The results show that number of occupied grid cells could be explained by niche-breadth variables.

When testing whether the probability of naturalization in (semi-)natural habitats is also related to niche breadth (Table 3), we found that in cross-species analyses, none of the niche-breadth variables were significantly related to the degree of naturalization. Using phylogenetically-independent contrasts, the amplitude of oceanity was found to be significant in a univariate analysis (using the two states of 'degree of naturalization'). The amplitude of oceanity and the number of formations were significantly positively related to the degree of naturalization in multivariate regression (having degree of naturalization coded as 'continuous' variables, i.e. 1 and 2).
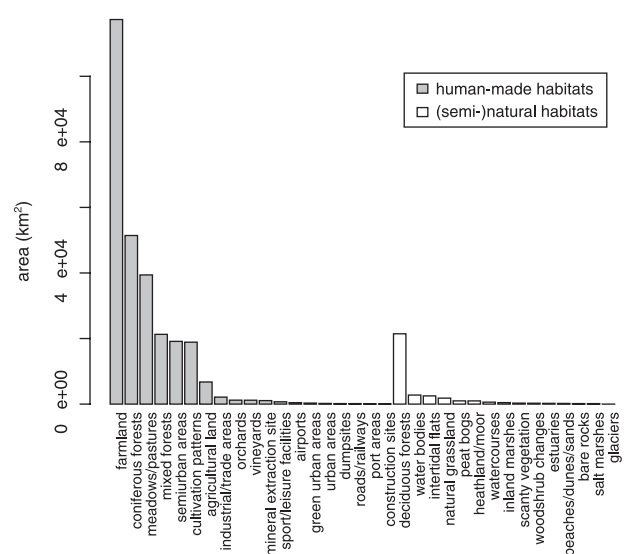
Figure 1 Area of human-made land cover (grey bars) and (semi-)natural land cover (open bars) in Germany, calculated according to Corine Land Cover Map (Statistisches Bundesamt, 1997).

Table 1 The ten most frequent species naturalized in human-made vegetation and in (semi-)natural vegetation (see 'Concepts and definitions') in Germany according to FLORKART and BiolFlor (Kühn & Klotz, 2002), nomenclature follows Jäger & Werner (2002). The total number of grid cells in Germany is 2995

Species naturalized in human-made vegetation	No. of occupied grid cells	Species naturalized in (semi-)natural vegetation	No. of occupied grid cells
Matricaria discoidea	2960	*Conyza canadensis*	2864
Veronica persica	2805	*Galinsoga ciliata*	2713
Juncus tenuis	2519	*Impatiens parviflora*	2584
Lupinus polyphyllus	1750	*Solidago canadensis*	2571
Berteroa incana	1701	*Galinsoga parviflora*	2543
Lolium multiflorum	1695	*Armoracia rusticana*	2488
Geranium pyrenaicum	1592	*Solidago gigantea*	2248
Sisymbrium altissimum	1529	*Robinia pseudoacacia*	2233
Veronica filiformis	1347	*Epilobium ciliatum*	2205
Oxalis corniculata	1100	*Elodea canadensis*	2203
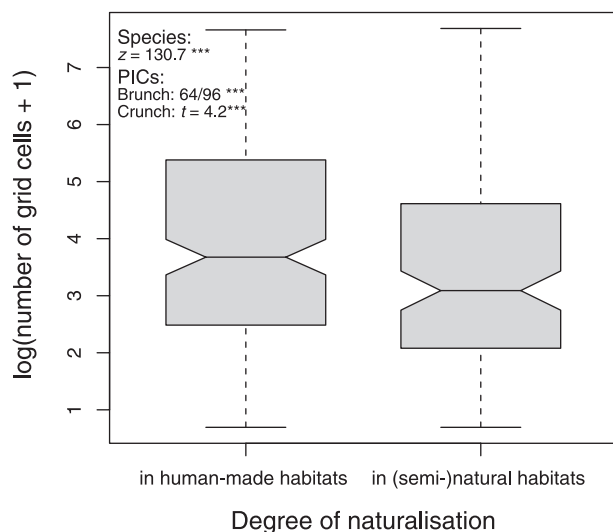
Figure 2 The number of grid cells occupied by neophytic plant species naturalized in (semi-)natural vegetation and neophytic plant species naturalized in human-made vegetation in Germany. The test statistics for the cross-species analysis ('Species') is the *z*-value of the logistic regression. Option Brunch in phylogeticall-independent contrasts presents the numbers of positives/numbers of all observations (using sign test), and option 'crunch' presents the *t*-statistic of an ordinary least-square regression.

Hierarchical partitioning revealed only slightly different results (Fig. 3). Variation in the cross-species analysis for the number of occupied grid cells could significantly be explained by the number of formations, amplitude of oceanity, and the number of habitat types, all of them having a positive relationship. Variation in the analysis of phylogenetically-independent contrasts (option 'crunch') can be explained by the number of continents, the number of formations, and the amplitude of oceanity (all with a positive relationship). Although the amplitude of oceanity seems to be the most important factor explaining the variance for the degree of naturalization and although the proportion of explained variance of additional niche-breadth variables are also quite high, none of them was significant in the randomization test. The partitioning of the variance of phylogenetically-

Table 2 Relationship between the number of occupied grid cells in Germany and niche-breadth variables. Data points were either species or phylogenetically-independent contrasts (PICs). PICs are of the 'crunch' type for continuous variables calculated in CAIC. Analysis of species and of 'crunch' data was done using generalized linear models with stepwise backward selection. Significant results are shown in bold

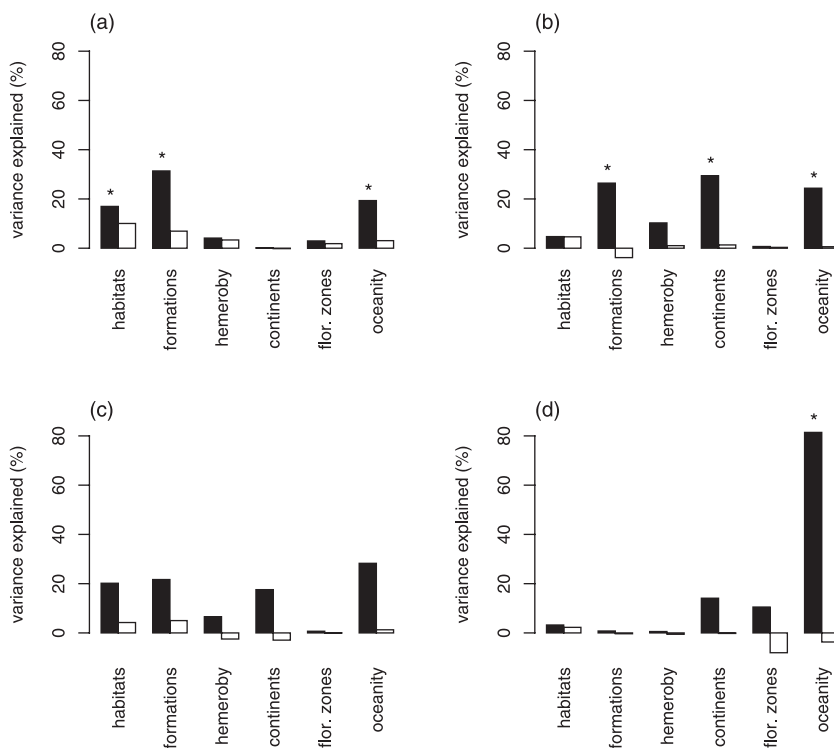|	Species		PICs 'crunch'	
	Slope	P	Slope	P
Number of habitat types	**0.2**	**< 0.001**	**1.9**	**0.009**
Number of formations	**0.46**	**< 0.001**	**2.9**	**0.003**
Range of hemerobic levels	**0.13**	**< 0.001**	**2.1**	**0.02**
Number of continents	**−0.05**	**< 0.001**	n.s.	
Number of floristic zones	**0.06**	**< 0.001**	n.s.	
Amplitude of oceanity	**0.37**	**< 0.001**	**2.3**	**0.002**

independent contrasts in the degree of naturalization showed that the overwhelming and only significant variable with a positive influence on contrasts of degree of naturalization is the amplitude of oceanity.

The results could be summarized as follows: Widespread species are predominantly characterized by a wider range of habitats, formations and oceanic amplitude. Degree of naturalization is not related to most of the niche-breadth variables we used, except for a positive relationship with amplitude of oceanity in the PIC analysis.

DISCUSSION

We found that alien plants occurring in (semi-)natural habitats are more widespread in Germany than those found in human-made habitats. (Semi-)natural habitats are less abundant in Germany than human-made ones but alien plant species reproducing in (semi-)natural habitats also occur in human-made habitats. Although we could verify that widespread species have a wider habitat niche, we were unable to verify this for the degree of naturalization. A higher degree of naturalization therefore does not seem to be related with a wider habitat niche.

	Species		PICs			
			Brunch		Crunch	
	Slope	*P*	Proportion	*P*	Slope	*P*
Number of habitat types	n.s.		24/42	0.4408		n.s.
Number of formations	n.s.		15/31	1	**0.13**	**0.01**
Range of hemerobic levels	n.s.		15/34	0.6076		n.s.
Number of continents	n.s.		12/29	0.4583		n.s.
Number of floristic zones	n.s.		25/47	0.7709		n.s.
Amplitude of oceanity	n.s.		**24/35**	**0.04096**	**0.04**	**0.002**

Table 3 Relationship between the degree of naturalization in Germany and niche-breadth variables. Data points were either species or phylogenetically-independent contrasts (PICs). PICs are of the 'crunch' type for continuous variables calculated in CAIC or of 'brunch' type for binary variables as calculated by the method of Burt (1989). Analysis of species and of 'crunch' data was done using generalized linear models with stepwise backward selection, 'brunch' data was tested by the sign test, proportions are positive/all observations. Significant results are shown in bold.

Figure 3 Hierarchical partitioning of the proportions of explained variance in the number of occupied grid cells (number of occupied grid cells) in Germany using species (a) and phylogenetically-independent contrasts (option 'crunch'; b) as data points, and in degree of naturalization (naturalized in human-made habitats vs. (semi-)natural habitats) in Germany using species (c) and phylogenetically-independent contrasts (option 'crunch'; d) as data points. Explanatory variables are number of habitat types ('habitat'), number of formations ('formations'), range of hemerobic levels ('hemeroby'), number of continents ('continents'), number of floristic zones ('flor. zones'), amplitude of oceanity ('oceanity'). Black bars show the variance exclusively explained by the particular variable, open bars show the variance explained jointly by the respective variable and others. Asterisks indicate significant results (being outside the 0.95 confidence range) after 1000 randomizations.

The relationship between the area of occupancy and niche breadth is very well known (e.g. Gaston *et al.*, 2000) and has been repeatedly verified for plants (e.g. Thompson *et al.*, 1998, 1999; Brändle *et al.*, 2003). Unfortunately, relationships between niche breadth and range size (e.g. the area of occupancy) are often confounded with sample-size effects (Gaston, 1994; Thompson *et al.*, 1999). Since we consider almost the entire German distribution regarding habitat variables and the world distribution regarding range variables as species specific traits from BiolFlor (Klotz *et al.*, 2002), we argue that the relationship between degree of naturalization and number of occupied grid cells is probably not just an artefact but reflects the real situation.

An obvious interpretation of our data is that species that are naturalized in (semi-)natural habitats naturalize there after having naturalized in human-made habitats as a consequence of the invasion process (Richardson *et al.*, 2000b). This would mean that species of (semi-)natural habitats should inhabit a higher number of habitats or vegetation units. We furthermore assumed that plant species that occur in both classes of habitats should occur in a wider range of hemerobic levels. We did not find any support for either of these statements in our analysis. One reason for this could be that there are some (semi-)natural habitats which are ecologically very similar to anthropogenic habitats, e.g. open forests and old city parks or natural rocks and castle walls (Dehnen-Schmutz, 2004). In these cases, the hemerobic level of human-made habitats might be on the less impacted side of the range, not adding much to niche breadth regarding hemeroby. Whether a plant species naturalizes in human-made habitats or in (semi-)natural habitats might also be a species-specific characteristic. Species that are typical woodland species in their native range might only be able to establish in woodlands in their new range. An example of this would be *Impatiens parviflora* that

grows in moist forests in Europe (e.g. Coombe, 1956; Trepl, 1984). When such plants are also capable of establishing in human-made vegetation such as city parks, it is very likely that they will have a larger area of occupancy due to a higher area of potentially suitable habitats.

Summarizing our results shows that some of the most obvious or straightforward hypotheses do not account for the observed pattern. Plant species that are more successful in the invasions process because they have reached a higher degree of naturalization are also more successful in respect to range expansion. It seems though that the factors that are related with these two processes are different (Richardson *et al.*, 2000a, 2000b). We therefore will discuss some other hypotheses that might explain the observed pattern. Unfortunately, in most cases we do not have data to test these hypotheses.

It could be argued that the relationship between the number of occupied grid cells and the degree of naturalization is a mere sampling artefact, i.e. that (semi-)natural areas were mapped better than human-made areas. It was argued that the exceptional species richness in cities is an artefact due to the fact that most research institutes and many botanists are there (Barthlott *et al.*, 1999). At least for native species, we were able to show that there is no city effect on the species richness in cities. We have discussed why a sampling artefact for cities is therefore unlikely (Kühn *et al.*, 2004a). Additionally, this would lead to an over-estimation of species naturalized in human-made habitats, as opposed to species naturalized in (semi-)natural habitats. One might also argue that cities (which are the domain of neophytes, e.g. Kühn *et al.*, 2003) may not be better mapped; it could be that rural areas dominated by large agricultural fields (which are the domain of archaeophytes, e.g. Kühn *et al.*, 2003) are less well mapped since they are often regarded as being quite boring from a floristics point of view. However, the proportion of species that are naturalized in (semi-)natural habitats among all naturalized species is similar in neophytes (33.2%) and archaeophytes (35.7%). So we do not assume a sampling bias.

From previous analysis, it is known that the area of occupancy is higher the longer a species has been in its introduced range (e.g. Scott & Panetta, 1993; Rejmánek, 2000; Kolar & Lodge, 2001; Kühn & Klotz, 2003). A similar relationship could be assumed for time since naturalization and degree of naturalization due to the sequential phases of the invasion processes, i.e. most species become naturalized in human-made habitats before they spread into (semi-)natural habitats (e.g. Williamson, 1999; Richardson *et al.*, 2000b; Kolar & Lodge, 2001; Heger & Trepl, 2003; Cassey *et al.*, 2004; Colautti & MacIsaac, 2004). However, using the time of naturalization as provided in BiolFlor (given in years for many species and in centuries for some additional ones, Kühn & Klotz, 2002), the degree of naturalization is neither correlated with time of naturalization in centuries (U-test: W = 4065.5, $p = 0.6$, $N = 184$) nor with time of naturalization in years (logistic regression: z-value = -0.964, $p = 0.3$, $N = 142$).

The reason that species of (semi-)natural habitats are more widely distributed than species of human-made habitats could be an effect of sample or population size. Widespread species tend to be more abundant than rare species (Gaston *et al.*, 2000),

which means that species with larger range size are more likely to have larger population size. This may have several implications. More frequent species tend to have a higher propagule pressure which is considered to be among the most important factors for invasion success (Williamson, 1996; Lonsdale, 1999; Rouget & Richardson, 2003). A larger population could exhibit a higher rate of mutations and consequently it is more likely for microevolution to occur (Sakai *et al.*, 2001; Lee, 2002) which in turn might allow a species to invade (semi-)natural habitats. The reason for larger area of occupancy of species naturalized in (semi-)natural habitats might also be of a statistical nature: since there are more occurrences, there might simply be more chances of coming into contact with and naturalize in a (semi-)natural habitat.

Another aspect related propagule pressure is the 'spatial mass effect' (Shmida & Ellner, 1984). But unlike the process mentioned in the previous paragraph, a plant species might not establish a self-maintaining population (i.e. a sink population) in a (semi-)natural habitat although it may successfully reproduce in it. Due to source populations nearby, which repeatedly recolonize (semi-)natural habitats, it only seems that a species successfully naturalizes in (semi-)natural vegetation when it is in fact a 'pseudo-agriophyte'. It may be argued that the spatial mass effect is the first step of the process of naturalization in (semi-)natural habitats as an effect of propagule pressure.

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