

Differences in the trait compositions of non-indigenous and native plants across Germany

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Received: 23 February 2009 / Accepted: 2 October 2009 / Published online: 16 October 2009
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Abstract This paper explores the differences in the trait compositions of non-indigenous (neophytic) and native plant species for selected traits in Germany. Our set of functional traits addresses species' reproductive biology, life history, morphology and ecophysiology. To take account of broad-scale heterogeneity across the country we compared the relative frequencies of neophytes and natives with particular trait attributes at the scale of grid cells (c. 130 km² each). Subsequently, we compared the differences at the grid cell scale to the differences in the corresponding comparisons at the scale of the entire country. Finally, we explored how variation in the trait compositions of the non-indigenous species across the country relates to variation in the trait compositions of the natives. We found remarkable differences in the trait compositions of neophytes and natives at the grid cell scale.

Neophytes were over-represented in insect- and self-pollinated species and in species with a later and longer flowering season. Furthermore, the proportions of species with mesomorphic or hygromorphic leaf anatomy, of annual herbs and of trees as well as of non-clonals and polyploids were significantly higher in neophytes than in natives. These differences at the grid cell scale could vary distinctly from the corresponding differences observed at the country scale. This result highlights the complexity of the invasion process and suggests an importance of spatial scale for the comparisons. Correlation analysis indicated, that for traits relating to plant morphology and ecophysiology, the relative frequencies of the non-indigenous species increased with those of the natives. This suggests that favourable environments for natives with particular attributes constitute an increased suitability for neophytes with these attributes as well. Our study provides a step forward towards an integrated understanding of traits in plant invasions across spatial scales and broad-scale heterogeneity and underlines the necessity to understand the role of functional traits in plant invasions with reference to spatial scale and in the context of the environment.

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Keywords Biological invasions ·
Broad-scale heterogeneity · Spatial scale ·
Invasion ecology · Functional traits ·
Environment

Introduction

Ecologists have long been interested in the role of plant species characteristics in favouring successful invasion. Despite considerable efforts little progress has been made in this area (Williamson 1999; Küster et al. 2008; Lambdon et al. 2008; Moles et al. 2008). To reproduce and flourish a plant species needs to be well adapted to the conditions at a given locality. One approach in the search for characteristics that allow successful invasion has therefore been to compare the relative frequencies of selected traits between non-indigenous and native plant species. This indicates which traits allow non-indigenous species to increase over native species (see review in Pyšek and Richardson 2007).

Traditionally, these comparisons have been undertaken based on species inventories at extremely coarse spatial grains such as entire countries (see e.g. Crawley et al. 1996; Williamson and Fitter 1996; Cadotte and Lovett-Doust 2001). To improve our knowledge of plant invasions it is critical, however, to integrate our understanding of invasion processes across a range of spatial scales (see also Pauchard and Shea 2006; Theoharides and Dukes 2007). Biological invasions are inherently spatial processes, which coarse resolution maps of species presence and absence fail to describe adequately (Hulme 2003). In fact, relative trait frequencies at the country scale lack information about the actual distribution of species with particular traits. Furthermore, these analyses do not account for differences in the environment across the country. Consequently, such analyses neglect variation in the occurrences of species with particular attributes that has been shown to relate to variation in environmental factors (see e.g. Cabido et al. 1993; Ellenberg 1996; Wright et al. 2005; Kühn et al. 2006). Although the importance of the environment in assessing the characteristics of successful invaders has long been recognized (e.g. Noble 1989), empirical multispecies studies of traits in plant invasion success have so far largely ignored that invaders do not encounter a homogenous environment (but see Lake and Leishman 2004; Thuiller et al. 2006; Leishman et al. 2007).

This is particularly surprising because the relationship between the diversity of non-indigenous and native species has already received much attention in

relation to environmental factors. Several broad-scale studies, for instance, observed the dimension of human activities to correlate specifically with non-indigenous species richness (see e.g. Kühn et al. 2003; Richardson et al. 2005). Furthermore, the numbers and proportions of non-natives have been shown to vary distinctly between habitats, with disturbed habitats often showing the largest proportions (e.g. Crawley et al. 1996; Maskell et al. 2006; Chytrý et al. 2008). Nevertheless, at scales of landscapes and larger generally a positive relationship between the diversity of native and non-indigenous species has been observed (e.g. Shea and Chesson 2002; Davies et al. 2005; Fridley et al. 2007; Kühn and Klotz 2007). It appears that increased habitat diversity due to spatial heterogeneity in environmental conditions or management and/or resource availability provides increased niche opportunities for both, native and non-indigenous species (see Fridley et al. 2007 for a recent review). So far, however, very little is known about the relationship between the relative trait frequencies of non-indigenous and native species. It dates back to Darwin (1859) that ecologists have wondered whether the suitability for establishment should be greater for non-indigenous species similar to natives because of a potential pre-adaptation to the new environment (Mitchell et al. 2006; Procheş et al. 2008; Diez et al. 2008). While a fairly large number of studies has analysed taxonomic relatedness as a proxy for species similarity (e.g. Daehler 2001; Diez et al. 2008), to the best of our knowledge hardly any study has addressed this question at the functional level of traits.

In order to understand better the role of species characteristics in the success of non-native plant species, we compared the relative frequencies (proportions) of neophytic and native species with particular trait attributes (trait values) across Germany. We focused on seven traits that together cover a broad range of species' life-history, reproductive biology, morphology and ecophysiology and have frequently been explored in previous studies, either in the context of plant invasions (see e.g. Pyšek and Richardson 2007; Küster et al. 2008 and references therein), and/or in research on trait value shifts between plant species assemblages of contrasting environments (see e.g. Ellenberg 1996; Lavorel and Garnier 2002; Levin 2002; Wright et al. 2005; Kühn

et al. 2006; Kühner and Kleyer 2008). Specifically, we asked the following three questions:

1. Are there differences in the trait compositions of natives and neophytes when we take account of broad-scale heterogeneity across the country? The differences were explored by comparing the proportion of a particular trait value between the pool of neophytes and the pool of natives at the scale of grid cells (c. 130 km² each). Reducing the spatial grain to the grid cell scale is a simple albeit straightforward way to account implicitly for broad-scale heterogeneity in environmental factors across the country, such as environmental conditions, management and resource availability.
2. How do the differences in the trait compositions of neophytes and natives vary between the grid cell scale and the country scale?
3. How does variation in the trait compositions of neophytes relate to variation in the trait compositions of natives across the country at the scale of grid cells?

Methods

Data

We compared the relative frequencies of trait values between naturalized neophytes and native plant species in Germany. Neophytes are plant species introduced after 1500. We considered them as naturalized if they were able to maintain self-sustaining populations without direct human intervention (Richardson et al. 2000).

We investigated the compositions of the following traits: pollen vector, end and length of flowering season, growth form, clonal growth, leaf anatomy and ploidy. For definition of trait values see [Appendix I](#). Information on traits was derived from the database BIOLFLOR (Klotz et al. 2002). From genera that have a high number of apomictic microspecies, such as *Rubus*, *Ranunculus* and *Hieracium*, we retained only the major well-defined taxa. For species occurring with variable trait values we used the predominant one. If a species was reported to occur with variable predominant trait values the species was counted for each predominant trait value. For the number of species and the effective number of

species counts that was used in the calculations see [Appendix I](#). Species occurrences were derived as presence/absence information per grid cell with 10' longitude × 6' latitude (c.12 km × 11 km) from FLORKART, a database of the German Network for Phytodiversity, maintained at the Federal Agency for Nature Conservation (<http://www.floraweb.de>). The total area of Germany is covered by 2,995 grid cells. As mapping was organized at a regional level compilation of data and recorder intensity differed between grid cells. In the database the time of recording is referred to as: before 1950, from 1950 to 1979 and after 1979. To reduce heterogeneity in mapping intensity we considered all records from 1950 onwards and used only well-recorded cells. A grid cell was considered well-recorded if at least 45 out of 50 'control' species were present. The control species were composed of the 45 most frequent species according to Krause (1998) and five additional species that were known to be easily overlooked in mapping surveys or regarded as difficult to identify. All of these control species could reasonably be assumed to occur in every grid cell in Germany (Kühn et al. 2006). Grid cells at the border of Germany were considered if >50% of their area lies within Germany (Kühn et al. 2006). This resulted in valid information of species occurrences for 2,733 grid cells. Of these grid cells we used only those with occurrences of more than 20 neophytes to avoid arbitrary proportions in trait attributes due to small sample size. The resulting dataset consisted of 2,375 grid cells.

Analysis

Separately for natives and neophytes, we calculated the proportion of species with a particular trait value in a trait for (a) each grid cell and (b) the entire country (2,375 grid cells). We compared the proportions of natives with a particular trait value against the proportion of neophytes with this trait value for each grid cell. We used Fisher's paired comparison randomization test (Manly 1998) to explore whether the differences between the proportions of neophytes and natives were more often positive (higher proportion of neophytes than natives with this trait value) or negative (lower proportion of neophytes with this trait value) than expected by chance. To assess the strength of evidence for the existence of scale effects we also

calculated the difference between the proportion of neophytes and natives with a particular attribute at the country scale. For each trait value we then compared the differences from the grid cell scale with the difference from the country scale to determine the fraction of grid cell scale comparisons with a higher and lower, respectively, proportion of neophytes relative to natives than in the corresponding comparison at the country scale. It is crucial to note that all these results have to be seen relative to all other trait values of a particular trait in the analysis. The proportions of species in trait values of a particular trait are compositional data, because they add up to 1. Hence, the proportions are not independent from each other and confer only relative information.

We examined the association between relative trait value frequencies of natives and neophytes with correlation analyses. To meet the assumptions of correlation analysis we first transformed the proportions to logarithms of ratios of proportions, henceforth referred to as log-ratios. This is a generally suitable method to ‘break’ the unit sum constraint (Kühn et al. 2006; Aitchison 1986). Additionally, random variation in log-ratios can often be assumed to be normally distributed. The observed n number proportions, here proportions of species with a particular trait value in a trait, is replaced by $(n-1)$ logarithms of ratios of proportions (Aitchison 1986). One of the proportions in the trait is used in the denominator—the choice of the denominator in forming the log-ratios, however, is unimportant (for further details see Kühn et al. 2006 or Aitchison 1986). Because neither division by zero is admissible nor taking the logarithm of zero we replaced zero values in the compositions by a number, smaller than any of the values observed (Aitchison 1982), namely 0.001, and reduced the non-zero values from the other respective trait values by a corresponding amount. We then analysed corresponding trait value log-ratios of neophytes and natives using Dutilleul’s modified t -test for correlation. The procedure accounts for potential spatial autocorrelation in the relative frequencies of species with particular trait values between grid cells when calculating the degrees of freedom (see Dutilleul 1993; Legendre et al. 2002 for further details). Finally, we checked the sensitivity of the results to different zero-replacements and performed the calculations with other replacement values, namely 0.00015 and 0.0001. Because these

led to the very same conclusions we only report the results from the zero-replacement with 0.001.

Calculations were performed within R (R Development Core Team 2008), versions 2.6.0–2.8.0.

Results

Comparing the trait compositions of neophytes and natives at the scale of grid cells

We found distinct differences between the trait compositions of neophytes and natives at the scale of grid cells (see Fig. 1). Compared to natives, a higher proportion of neophytes was insect- or self-pollinated, had a delayed end of the flowering season and a flowering season of 4 months or longer. Furthermore, the proportions of species with mesomorphic or hygromorphic leaf anatomy, of annual herbs and of trees as well as of non-clonals and polyploids were significantly higher in neophytes than in natives (Fig. 1). Neophytes were significantly underrepresented by the following attributes: wind-pollination, an earlier end of flowering and a length of flowering of up to 2 months, the growth forms shrub and perennial herb, helomorphic, hydromorphic and scleromorphic leaf anatomies, clonality and diploidy. No significant difference was observed for species with a flowering season of 3 months.

Comparing the trait compositions of neophytes and natives across spatial scales

The differences in the trait compositions of neophytes and natives varied distinctly between the grid cell and the country scale (see Table 1). The most remarkable deviations were found for the compositions of pollen vector, end and length of flowering season, growth form and leaf anatomy. In more than 90% of the grid cell comparisons the proportion of neophytes was, relative to natives, higher than in the corresponding comparison at the country scale for self-pollinated neophytes, for neophytes with an end of flowering season between October and December, a flowering season longer than 4 months and hygromorphic leaf anatomy. In other words: neophytes with these attributes that established in Germany (presence at the country scale) tend to be over-represented compared to the natives with these attributes at the grid

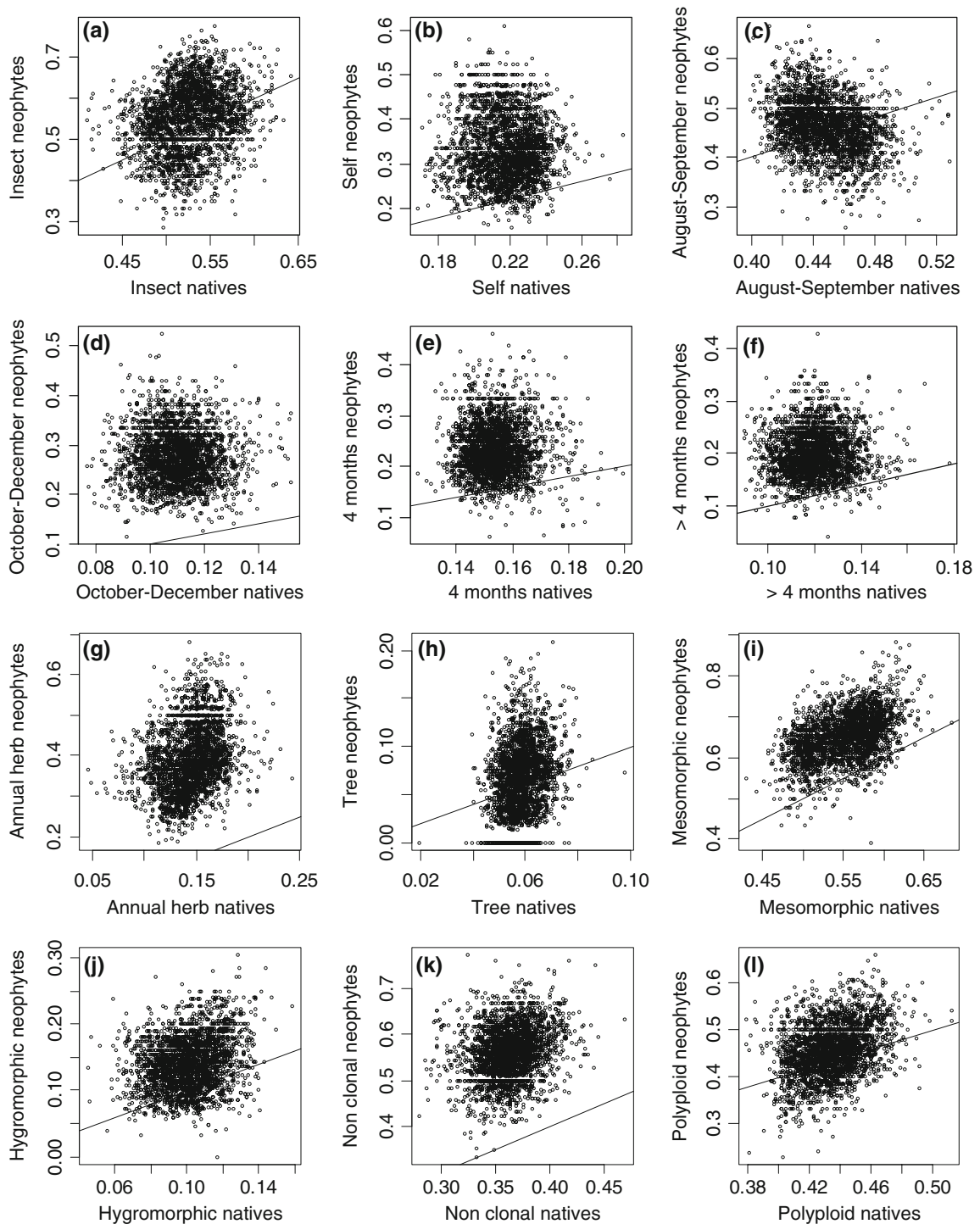


Fig. 1 Differences in the proportions of neophytes and natives in a trait value at the scale of grid cells. The line marks equal proportions. When the proportions of neophytes in a trait value are higher than the proportions of natives the resulting marks scatter above the line. Depicted are only those attributes where

proportions are significantly higher in neophytes ($P < 0.001$ for all attributes). Pollen vector (a–b), end of flowering season (c–d), length of flowering season (e–f), growth form (g–h), leaf anatomy (i–j), clonal growth (k), ploidy (l)

Table 1 Comparing the trait compositions of neophytes and natives across spatial scales

Trait	Trait value	Lower	Higher
Pollen vector	Wind	96.2	
	Insect	67.4	
	Self		98.3
End of flowering season	March–May	98.7	
	June–July	84.8	
	August–September		88.8
	October–December		92.5
Length of flowering season	Up to 2 months	99.3	
	3 months		81.7
	4 months		83.7
	>4 months		95.3
Clonal growth	Yes	66.2	
	No		66.2
Growth form	Shrub	90.7	
	Tree	82.0	
	Perennial herb		61.3
Leaf anatomy	Annual herb		83.4
	Mesomorphic	96.4	
	Helomorphic		53.5
	Hydromorphic		56.8
	Scleromorphic		66.4
Ploidy	Hygromorphic		96.4
	Diploid	87.1	
	Polyploid		87.1

Fraction of grid cells (in %) with a lower and higher, respectively, proportion of neophytes in the trait value relative to natives than in the corresponding comparison at the country scale. Trait values where differences towards the country scale comparison concern >90% of the grid cell scale comparisons are in bold. Depicted is the predominant fraction only

cell scale. In contrast, the proportions of wind-pollinated neophytes, of neophytes with an end of flowering season in March to May, a length of the flowering season of up to 2 months, with the growth form shrub and mesomorphic leaves were lower in more than 90% of the grid cell comparisons than in the corresponding comparison at the country scale.

Relationships between variation in the trait compositions of neophytes and natives across the country

Correlation analyses between the trait compositions of neophytes and natives at the grid cell scale revealed significant relationships for clonal growth, growth form, leaf anatomy and ploidy (see Table 2). The proportion of neophytic clonals increased with the proportion of native clonals and, accordingly, the proportion of neophytic non-clonals with the proportion native non-clonals. Additionally, the proportions of shrubs and trees, in relation to the proportions of

perennial herbs, were positively correlated between neophytes and natives. No significant correlation was observed for annual herbs. Furthermore, the proportions of species with scleromorphic, hygromorphic, helomorphic and hydromorphic leaves, in relation to the proportion of species with mesomorphic leaves, were positively correlated between neophytes and natives. Finally, the proportion of neophytic polyploids increased with the proportion of native polyploids and, correspondingly, the proportion of neophytic diploids with the proportion of native diploids. The trait compositions of pollen vector, end of flowering season and length of flowering season were not significantly correlated between neophytes and natives.

Discussion

The analysis of the trait compositions at the scale of grid cells allowed us to take account of broad-scale

Table 2 Correlation analysis between corresponding trait value log-ratios of neophytes and natives using Dutilleul's modified *t*-test for correlation

Trait	Trait value ratio	Pearson's <i>r</i>	d.f.	<i>F</i>	<i>P</i>
Pollen vector	Insect/wind	0.15	85.7	2.05	0.16
	Self/wind	-0.06	212.0	0.63	0.43
End of flowering season	March–May/June–July	-0.06	217.7	0.72	0.40
	August–September/June–July	-0.22	35.6	1.88	0.18
	October–December/June–July	-0.04	180.0	0.34	0.56
Length of flowering season	Up to 2 months/3 months	-0.12	156.8	2.45	0.12
	4 months/3 months	0.04	292.6	0.49	0.48
	>4 months/3 months	0.05	352.1	0.97	0.33
Clonal growth	No/yes	0.22	200.1	10.58	0.001
Growth form	Shrub/perennial herb	0.13	371.7	6.20	0.01
	Tree/perennial herb	0.24	261.0	16.05	<0.001
	Annual herb/perennial herb	0.42	15.5	3.25	0.09
Leaf anatomy	Scleromorphic/mesomorphic	0.11	500.5	6.19	0.01
	Hygromorphic/mesomorphic	0.26	184.5	13.27	<0.001
	Helomorphic/mesomorphic	0.43	36.1	8.15	0.007
	Hydromorphic/mesomorphic	0.50	104.0	35.28	<0.001
Ploidy	Diploid/polyploid	0.34	61.5	7.91	0.007

Results with $P < 0.05$ are in bold

heterogeneity across the country. We detected remarkable differences between the trait compositions of neophytes and natives (see Fig. 1). Depending on the trait attribute these differences at the grid cell scale could vary distinctly from the corresponding differences observed at the country scale (see Table 1). Correlation analyses highlighted, that for some trait attributes, the establishment of the non-indigenous species follows the pattern of native species with these characteristics at broad spatial scales (see Table 2).

All in all, the analysis at the scale of grid cells underpins the relevance of several attributes for successful invasion, some of which became already apparent in previous analyses that focused on larger scales. For instance, we also found the proportions of longer and later flowering species to be distinctly over-represented in neophytes—a finding that has also been reported by Cadotte and Lovett-Doust (2001) and Lake and Leishman (2004) (but see Thompson et al. 1995; Williamson and Fitter 1996). An extended flowering period is likely to be beneficial in association with colonization and disturbance (Lake and Leishman 2004; Cadotte et al. 2006). Furthermore, our results corroborate the importance

of polyploidy for successful invasion (see also Pandit 2006; Küster et al. 2008). Many characteristics of polyploids have already been hypothesized to be beneficial in colonization (see Soltis and Soltis 2000; Levin 2002). Interestingly, we found the proportions of annuals and also of trees to be over-represented in neophytes. At first sight a seemingly contradictory finding, which, however, provides further evidence for the hypothesis that there exist two contrasting groups of successful invaders: tall competitors and small, rapidly maturing, long-flowering species with high reproductive outputs (see Crawley et al. 1996; Pyšek and Richardson 2007). Additionally, neophytes were over-represented in non-clonals. While studies of clonality so far reported ambiguous trends (see Pyšek and Richardson 2007), we speculate that our finding could simply reflect the differential success of growth forms. Indeed, it needs to be acknowledged that plant traits tend to be cross-correlated and that correlation does not necessarily imply causation (Westoby and Wright 2006). One of the most intriguing results was the distinct over-representation of insect- and especially self-pollinated neophytes. Albeit reproductive traits and pollen vector in particular have gained substantial interest in invasion

ecology their importance has been largely neglected in the absence of empirical evidence (see Pyšek and Richardson 2007 and references therein; but see van Kleunen and Johnson 2007; Küster et al. 2008; van Kleunen et al. 2008). When pollinators and/or mates are scarce selfing provides reproductive assurance (Darwin 1876), a feature of particular importance in colonizing plants (Baker 1955, 1967). Additionally, Aarssen (2000) set forth the time-limitation hypothesis which emphasises the benefit of selfing for annuals as a concurrent product of strong r-selection in ephemeral habitats (see also Snell and Aarssen 2005). The overrepresentation of insect-pollinated neophytes may also be a by product of their attractiveness to humans. A large fraction of them has been introduced deliberately for ornamental purpose. Frequency of introductions and plantations could have resulted in increased propagule pressure (see also Hanspach et al. 2008). Finally, we observed pronounced differences between neophytes and natives in leaf anatomical adaptations that relate to the supportive tissues, the water storage and the regulation of aeration. While by far the largest fraction of the natives had no particular adaptation, that is, a mesomorphic leaf structure, the proportions of neophytes with this leaf type were even higher. Additionally, neophytes with hygromorphic leaves, that is, soft leaves with thin cuticles and epidermis, were distinctly over-represented (see also Lake and Leishman 2004). Because leaf structure is associated with disturbance regime, climate and soil type (see e.g. Wright et al. 2002; Wright et al. 2005; Kühner and Kleyer 2008), the differences could reflect differences in habitats occupied by neophytes and natives. However, in a recent study Leishman et al. (2007) showed that, at least in disturbed habitats, non-natives in general tend to have leaf traits that support faster growth strategies.

Comparing the differences from the grid cell scale to the country scale highlighted the complexity of the invasion process. Some attributes in neophytes appeared to be particularly over-represented in the grid cells. Among these were again self-pollination, a delayed end of the flowering season and a long flowering season as well as a hygromorphic leaf anatomy. Not all attributes, however, which were over-represented at the grid cell scale, were also over-represented at the grid cell scale compared to the country scale. For species with mesomorphic leaves,

for instance, even the opposite was observed. At the country scale the proportion of neophytes with mesomorphic leaves was larger relative to natives than in most of the grid cell comparisons. What do these trends tell us? Let us assume a species with a particular attribute becomes introduced to Germany. Considering the extreme cases, it may establish only locally or it may disperse across the whole country. The comparisons at the grid cell scale take into account this variation, which may relate to, for instance, broad-scale environmental variation, species' dispersal capabilities or the spatial bias of introductions. These comparisons therefore spot attributes that generally favour a non-native plant species to establish in Germany. Taken alone, however, the findings hardly carry any information about processes. The proportions of neophytes in a certain attribute could prevail because these attributes support a more effective reproduction and dispersal, but not necessarily. Such a pattern could clearly also be observed if more species with this attribute were introduced in frequent numbers all over the country. Single comparisons at the country scale cannot inform on processes either, they are, however, valuable to record the differences between the overall species pools of neophytes and natives with particular attributes. The non-indigenous species pool is likely to be biased towards species with attributes that are valuable to humans or towards species with attributes that constitute particular adaptations to the environment of the donor region (see also Prinzing et al. 2002). In the integration of results across scales a bigger picture can emerge. Attributes, that are distinctly over-represented towards the country scale, such as self-pollination, a later and longer flowering season and a hygromorphic leaf anatomy, indicate a functional significance for effective dispersal and spread for the non-native species. Species with mesomorphic leaves, in contrast, may have been introduced very frequently and a large fraction of them may also have established due to generally favourable environmental conditions in Germany for species with this leaf type, but not all of them may have dispersed effectively. A comparison across spatial scales can thus be a valuable tool to detect relevant processes that are obscured when looking at a single spatial scale. Overall, the present findings once more underpin that success of non-indigenous species is influenced by a series of processes, which

interact throughout the different invasion stages (see also Theoharides and Dukes 2007; Catford et al. 2009).

Our third question asked how variation in the trait compositions of neophytes relates to variation in the trait compositions of natives across the country. For a considerable number of traits we observed the relative frequencies of neophytes to increase with those of the natives, indicating that favourable environments for natives with particular attributes constitute an increased suitability for neophytes with these attributes as well. This concerned functional traits relating to plant morphology and ecophysiology which exhibit well-known shifts in plant species assemblages along environmental gradients of, for instance, disturbance, geology or climate (see e.g. Ellenberg 1996; Lavorel and Garnier 2002; Levin 2002; Wright et al. 2005; Kühner and Kleyer 2008). It appears that the relative frequencies of attributes addressing the reproduction of species are uncorrelated between neophytes and natives. Several reasons may explain this pattern. First, the discrepancies could arise from introduction bias and/or different dispersal abilities of neophytes with particular attributes. Distributions of neophytes in Germany have been shown to increase with residence time (see Küster et al. 2008) and are therefore likely to be far from their maximum (see also Williamson et al. 2009). If some species suffer from a distinct spatial introduction bias due to attractiveness to humans, e.g. insect-pollinated species, and others from a different introduction bias or still considerably lag behind their potential distribution, e.g. wind-pollinated species, and yet others are extremely over-represented, e.g. selfers, this is likely to cause discrepancies. Second, it is possible that these traits are associated with a shift in species composition across the gradients that our study covered only to a limited amount. In this context it is probably important to note, that our models did not incorporate trait value shifts within species. Trait value shifts of plant species assemblages in contrasting environments that relate to variation in pollen vector or flowering phenology of different species have, however, rarely been explored (but see Kühn et al. 2006). Interestingly, Kühn et al. identified altitude as an important correlate of shifts in pollination type. The fact that neophytes are well

known to decrease with increasing altitude (e.g. Becker et al. 2005; Pyšek et al. 2005; Chytrý et al. 2008) may indicate that the lack of correlation results from an under-representation of neophytes along this gradient. It is, however, also possible that these traits generally do not constitute important adaptations to the environmental gradients covered. Flowering phenological and reproductive traits tend to be strongly linked to phylogeny (Kochmer and Handel 1986; Chazdon et al. 2003; Levin 2006; Lososová et al. 2006). Particularly in long-resident species, shifts in the relative frequencies of particular attributes between contrasting environments could therefore be the result of cross-correlations to other traits—as a result from species biogeographic and evolutionary history—that strongly relate to environmental gradients (see also Kühn et al. 2006).

Conclusions and future directions

Our analysis is a first step towards an integrated understanding of traits in plant invasions across spatial scales and broad-scale variation in environmental factors. The considerable variation in the compositions across the country (Fig. 1) underlines the necessity to understand plant invasions in the context of the environment. Distinct trends in the differences between grid cell and country scale suggest that spatial scale is important for the comparison of relative trait value frequencies between natives and neophytes. Correlations in the trait compositions between neophytes and natives highlight the influence of the environment on species establishment: for certain traits it appears that the relative suitability indeed increases for non-natives with functional similarity to the natives at broad spatial scales. This probably deserves further attention as it could be of importance in the prediction of future invasions, also in the context of climate and land-use change. In conclusion our study suggests that the traits of a species influence successful invasion via establishment opportunities in the environment and via colonization opportunities, where the colonization potential appears to reflect a species' intrinsic dispersal capacities as well as human-aided dissemination (see also Lockwood et al. 2005; Thuiller et al. 2006; Bucharova and van Kleunen 2009).

Broad-scale analyses of inventories provide preliminary models (see also Fridley et al. 2007)—several aspects deserve yet further exploration. First, our approach worked only with trait value shifts of species assemblages that relate to differences in species composition. A more realistic model would also consider trait value shifts within species. Second, we used species presence/absence data. A further advance would be an investigation of the effect of species abundances. Third, it may be very valuable to explore the importance of differences in trait combinations between non-indigenous and native species (see also Küster et al. 2008). Fourth, finally, it remains to be investigated how the broad-scale patterns compose from finer spatial grain. At fine spatial scales biotic interactions become important (Huston 1999; Fridley et al. 2007; Melbourne et al. 2007) and negative interactions, such as competition,

shared predators or pathogens may impede the invasion of similar species (see Webb et al. 2006; Mwangi et al. 2007; Diez et al. 2008). Hence, invaders with functional differences from the resident species may be more successful. Future approaches could therefore address functional trait analyses between resident and non-indigenous species within habitats or at local scales.

Acknowledgments We thank all volunteers who contributed to the FLORKART plant inventory for their effort. Many thanks to Helge Bruelheide, Adam Butler and Stijn Bierman for helpful comments and discussion and to two anonymous reviewers for valuable comments and suggestions.

Appendix I

See Table 3.

Table 3 Number of species and number of species counts (2,375 grid cells)

	Number of species		Number of species counts			
	Trait	Natives	Neophytes	Trait value	Natives	Neophytes
	Pollen vector ^a	1,818	344	Insect	1,088	224
				Self	397	68
				Wind	487	70
	End of flowering season	2,066	375	March–May	200	44
				June–July	732	114
				August–September	944	148
				October–December	190	69
	Length of flowering season	2,066	375	Up to 2 months	900	165
				3 months	742	117
				4 months	243	56
				>4 months	181	37
	Clonal growth	1,973	376	Clonal	1,185	160
				Non-clonal	788	216
	Growth form ^a	2,052	373	Annual herb	272	118
				Perennial herb ^b	1,606	195
				Shrub	203	57
				Tree	81	30
	Leaf anatomy	1,747	312	Scleromorphic	302	40
				Mesomorphic	939	228
				Hygromorphic	131	15
				Helomorphic	282	17
	Ploidy ^a	1,935	371	Hydromorphic	93	12
				Diploid	1,231	249
				Polyploid	862	149

The number of species counts was used in the calculations. Note that the effective number of species counts in trait values does not necessarily sum to the original number of species

^a If species were reported to occur with variable prevalent trait values, species were counted several times—one time for each predominant trait value. Data were taken from Klotz et al. (2002)

^b Includes biennials

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