



Spatial aspects of trait homogenization within the German flora

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ABSTRACT

Aim Biotic homogenization, the replacement of local biota by non-indigenous and locally expanding species, is among the major effects of species invasions. Almost all studies related to this topic are focused on the species level, on taxonomic homogenization. Homogenization effects on trait diversity (functional homogenization) may be very important for ecosystem functioning, but they are rarely analysed, especially not at different spatial scales within a single study. This paper aims to examine how the presence of alien species (species introduced since 1500 AD) affects the distribution of ploidy levels in the German flora at different spatial scales.

Location Germany.

Methods We used a resampling method and the Morisita–Horn dissimilarity index to calculate dissimilarities of ploidy level within and between alien and indigenous plants at three different spatial scales in Germany: (1) the entire country as one location, (2) between grid cells, and (3) within grid cells of a lattice covering Germany.

Results We found a significant differentiation effect within grid cells of c. 130 km², with alien plants increasing the variability of ploidy levels. The differentiation effect varies according to the scale used. At the coarsest scale (entire Germany), ploidy levels of alien plants tend to be more homogeneous in composition compared with those of native plants. At the intermediate scale (between grid cells), and even more pronounced at a small scale (within grid cells), ploidy levels are more heterogeneously distributed across Germany than those of native plant species.

Main conclusions Homogenization of ploidy levels at a large scale (entire Germany) and differentiation at a small scale (within grid cells) is comparable with the patterns found in taxonomic homogenization analyses. This analysis is a first step towards understanding the impacts of plant invasions on a trait level. Differentiation and homogenization of ploidy levels might mirror the distribution of related ecological traits and therefore might have an impact on ecosystem functioning.

Keywords

Alien plants, biotic homogenization, functional homogenization, Germany, multiple spatial scales, plant invasions, ploidy level.

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INTRODUCTION

The loss and introduction of species are important and widely discussed topics in biodiversity research. Biotic homogenization, the increasing similarity of different regions due to the

replacement of local biotas by non-indigenous species, is considered one of the most important reasons for biotic impoverishment worldwide (Meffe & Carroll, 1997). Biotic homogenization increases with human influence and is facilitated by, for example, homogenization of the landscape,

urbanization, increasing global transport, and nitrogen input into ecosystems (Hobbs & Mooney, 1998; McKinney & Lockwood, 1999; Olden, 2006).

There are two distinct processes resulting in biotic homogenization: species gains, for example through invasions or range expansions (winning species); and species losses, through extinctions or range contractions (losing species) (McKinney & Lockwood, 1999). The interplay of both processes can result in increasing, decreasing or unchanged taxonomic similarity (Olden & Poff, 2003). Specifically, communities can become more similar through the loss of rare species, leading to biotic homogenization, especially when they are replaced by widespread species. In contrast, species invasion can also lead to biotic differentiation due to different species colonizing different regions.

Effects of scale dependencies are well known for biodiversity patterns in general (e.g. Levin, 1992; Whittaker *et al.*, 2001) and invasion processes in particular (e.g. Rouget & Richardson, 2003; Pauchard & Shea, 2006; Kühn & Klotz, 2007). Homogenization can also be scale-dependent (Olden & Poff, 2003). Usually the number of introduced species will exceed the loss of natives (Sax *et al.*, 2007), but disproportionately high so at a small scale. At a fine spatial resolution, it is less likely that the same alien species will be introduced and the same native species will go extinct in all locations (McKinney & Lockwood, 2005; Olden, 2006). This results in biotic differentiation across regions over time. Conversely, at coarser scales, homogenizing effects are implicitly favoured due to a greater number of sampled habitats and communities and hence an increasing probability of finding any given species (Olden, 2006). However, using geographical distance to explain scale-dependent homogenization patterns has resulted in conflicting conclusions (Rejmánek, 2000; McKinney, 2005b; Qian & Ricklefs, 2006). McKinney (2005b) found that species introduced from less distant sources (within the USA) have a greater homogenizing effect on community composition than species from more distant sources (outside the USA). In contrast, Rejmánek (2000) and Qian & Ricklefs (2006) found a differentiation effect of alien plant species among the floras of neighbouring North American regions, but a homogenization effect among floras at greater distance. Our analysis focused on different geographic scales with the same extent but changing resolution.

Biotic homogenization is important at both taxonomic and functional levels. Although the threat of functional homogenization was described by McKinney & Lockwood (1999: as 'ecological homogenization'), and Olden *et al.* (2004) stressed it as a potentially important issue, previous studies on homogenization have focused on taxonomic effects. The term functional homogenization refers to the increasing similarity of ecological 'roles' filled within different species assemblages (species sharing similar traits) (Olden & Rooney, 2006), for example due to the loss of species with rare traits. Shifts in the trait composition of a species assemblage could potentially have strong impacts on ecosystem processes (Sankaran & McNaughton, 1999; Díaz & Cabido, 2001; Petchey & Gaston, 2002).

While some studies discussed theoretical functional homogenization (e.g. for plants: Wiegmann & Waller, 2006; for ants: Holway & Suarez, 2006), only the recently published work of Smart *et al.* (2006) has calculated functional homogenization at two spatial scales. That study focused on species richness patterns within and between 1-km² grid cells in the UK, and found that plant communities became functionally more similar when local plant species richness declined, while increasing species richness led to greater variance in trait syndromes between habitats.

In the present study we focused on homogenization of a genetic trait, namely ploidy level. An important correlate of invasion success is the adaptability of species (Daehler, 2003; Richardson & Pyšek, 2006). In turn, adaptive potential is promoted by genetic variability providing opportunities for selection. Genetic diversity could be measured by a number of characteristics, for example allelic composition of a particular set of loci, abundances of genotypes or mean heterozygosity (Olden *et al.*, 2004). We worked with ploidy-level data, where different ploidy levels represent genetic entities below the species level. A high ploidy level (polyploidy) seems to be a common trait of invasive plants (Baker, 1965; Barrett & Richardson, 1986; Amsellem *et al.*, 2001). Polyploidization increases the DNA content (Soltis & Soltis, 1999) and often leads to increased genetic variability such as increased heterozygosity. So it is commonly accepted that polyploid species should have a greater ability to colonize or invade new habitats (Ehrendorfer, 1980; Stebbins, 1985; Thompson & Lumaret, 1992; Schierenbeck & Ainouche, 2006).

Our aim was to determine specifically whether alien plant species contribute to the homogenization of ploidy levels, and if this contribution varies across three different spatial scales in Germany: (1) across the entire country (large scale), (2) among 130-km² grid cells in Germany (medium scale), and (3) within grid cells (small scale). Therefore we calculated dissimilarities within and between ploidy levels of native and alien plant species. Considering ongoing discussions about scale-dependent effects of taxonomic homogenization, we hypothesize that patterns of ploidy homogenization would follow these established patterns: homogenization of ploidy levels at a large scale, and differentiation of ploidy levels at a small scale of analysis.

METHODS

Data sources

Plant distribution data were taken from the data base FLORKART, provided by the German Federal Agency for Nature Conservation on behalf of the Network for Phytodiversity in Germany (NetPhyD). The almost square grid cells are based on the German ordnance survey grid, each cell covering 10' longitude × 6' latitude (*c.* 130 km²). Due to heterogeneous mapping intensity in Germany, we analysed only sufficiently well mapped cells (*n* = 1928), following Kühn *et al.* (2003). Data on ploidy levels were taken from the data base BIOLFLORE on biological and ecological traits of the Flora

of Germany (Klotz *et al.*, 2002; Kühn *et al.*, 2004b). Many species ($n = 246$) are listed with more than one ploidy level (Durka, 2002). In order to calculate dissimilarities, ploidy levels need to be treated as a categorical variable and cannot be averaged to obtain a species' specific value. Therefore, ploidy levels were weighted by $1/(\text{number of ploidy levels})$: for species with more than one ploidy level, we allocated for each species the same total weight, and assumed that all ploidy levels occur with equal frequency. This is unlikely to be the case in the field, but information at this level of detail is not available.

We excluded casual species (species unable to maintain self-sustaining populations; see also Richardson *et al.*, 2000; Pyšek *et al.*, 2004), as their unstable populations have no permanent impact on the flora, nor are they currently considered a threat to native species. All analyses at all spatial scales were done for two status groups, defined as alien and native plant species. Natives are indigenous to Germany and alien species were introduced after 1500 AD. We deliberately excluded archaeophytes (pre-1500 aliens), which differ markedly in ecology, as they occupy mainly arable fields, which are in themselves a most homogeneous habitat and therefore not representative (Pyšek *et al.*, 2002; Kühn *et al.*, 2004a). After grouping and combining FLORKART and BIOLFLOR data, the resulting data base comprised 2358 species, including 1988 natives and 370 aliens.

Data analysis

Biotic homogenization is generally measured by the similarity or dissimilarity of a specific set of characteristics (functional attributes, species inventories, etc.) between either different regions and/or different time spans. Of the variety of similarity (or dissimilarity) indices, only a few are able to handle abundance or frequency data (Krebs, 1999). We used the Morisita–Horn dissimilarity index (MH) (Wolda, 1981; Smith, 1986). It is computed as:

$$D_{\text{MH}} = \frac{2 \sum (x_{ij}x_{ik})}{(\lambda_j + \lambda_k) \sum x_{ij} \sum x_{ik}}, \text{ with} \quad (1)$$

$$\lambda_j = \frac{\sum x_{ij}^2}{(\sum x_{ij})^2} \text{ and } \lambda_k = \frac{\sum x_{ik}^2}{(\sum x_{ik})^2},$$

where x_{ij} and x_{ik} are the frequencies of ploidy level i in sample j and k . The Morisita–Horn index is less sensitive to species richness and sample size than most other indices (Wolda, 1981). Dissimilarity is a measure of heterogeneity, where the variability of traits between and within plant assemblages increases with dissimilarity. The index ranges from zero (total identity between two samples) to one (absolute dissimilarity of these samples). We measured distances based on ploidy levels and corresponding frequencies for each set of randomly drawn grid cells.

We tested homogenization effects at three different spatial scales. Starting with the coarsest spatial resolution (focusing on the national level), we used only a German species list of alien and native plant species. At the next scale, we measured

dissimilarities between grid cells. Calculations within single grid cells formed the finest resolution.

As sample sizes differed a lot, we used a resampling technique. We calculated MH (1) within status groups (alien and native plant species) to compare mean distribution of dissimilarities, and (2) between status groups to compare the groups' dissimilarities directly. To avoid comparisons of huge matrices that are not computable and are not spatially independent, we sampled 1000 times a set of 30 (arbitrarily chosen, following Kühn *et al.*, 2003) randomly chosen grid cells or ploidy levels. This has the advantage of producing many small matrices, which are easier to handle but still represent the attributes of the whole data set (Kühn *et al.*, 2003).

In our first analysis at the coarsest spatial scale, we only used a checklist of all species from our data set and their corresponding weighted ploidy level values. We ended up with a list of 2777 entries for the entire country (2350 ploidy level \times species combinations for native plants, 427 for alien plants). At this scale we ignored spatial distribution information. First, we estimated the mean dissimilarity per matrix-pair within each status group separately. Second, we compared the ploidy-level data between natives and aliens using a resampling technique to control for the bias of different sample sizes. We resampled 1000 times 427 ploidy levels (see above) from the native ploidy level distribution. We built 1000 resampled ploidy level by species matrices and calculated the MH dissimilarity between the species based on the ploidy levels within each of these matrices. Then we compared the mean observed MH distance of alien species with the distribution of 1000 mean MH distances of natives based on the resampling.

At the second spatial scale (between grid cells), we resampled sets of 30 out of all 1928 cells and calculated mean MH within natives and alien plants for all species among the sampled cells, as described above. Due to the large size of our data set and the resulting high number of different combinations, we decided not to calculate dissimilarities between status groups (natives and aliens).

At the finest spatial scale, within grid cells, we did not use a resampling procedure but calculated dissimilarities based on ploidy level \times species matrix of all species per grid cell between and within status groups. Furthermore, we correlated the dissimilarity of grid cells with the mean ploidy level per grid cell and the percentage of aliens to explore the relationship between the homogenization effect of alien ploidy level and the overall pattern within grid cells.

All analyses were performed in R (R Development Core Team, 2005).

RESULTS

Ploidy levels of native plants ranged from haploid to 24-ploid. Alien plant species did not show this wide range of diverse ploidy levels (diploid, 12-ploid). Only about 6.5% of all ploidy levels are odd numbered, and about 94% of all ploidy levels are equal to or smaller than hexaploid. Both groups differed, with

80% of native ploidy levels and 83% of alien ploidy levels being di- and tetraploid, respectively ($\chi^2 = 130.5$, $P < 0.01$).

The counts of different ploidy levels per species ranged from 1 to 7 for native plants and from 1 to 5 for alien species. For 97% of native as well as alien species, only one or two ploidy levels are known. Both distributions show a log-linear decrease. The number of ploidy levels per species did not differ significantly between native and alien species ($\chi^2 = 28$, $P = 0.11$).

The geographical variation of the mean ploidy level per grid cell and the mean MH are given in Appendix S1 in Supplementary Material. A visual comparison of alien and native mean ploidy level and MH values shows very similar patterns, although alien ploidy levels were more heterogeneously distributed. Mean ploidy levels and MH values per grid cell were generally higher in native plants than in alien plants. High values of both parameters were more frequent in the north-western and south-eastern parts of Germany.

At the coarsest spatial scale, ploidy levels between native and alien were very similar (Fig. 1a). However, the mean dissimilarity of ploidy level was significantly higher among native plants than among alien plants (Fig. 1b; z -test, $z = -7.49$, $P < 0.001$).

In contrast, between grid cells alien ploidy levels showed a higher dissimilarity than native ploidy levels (Fig. 2; paired

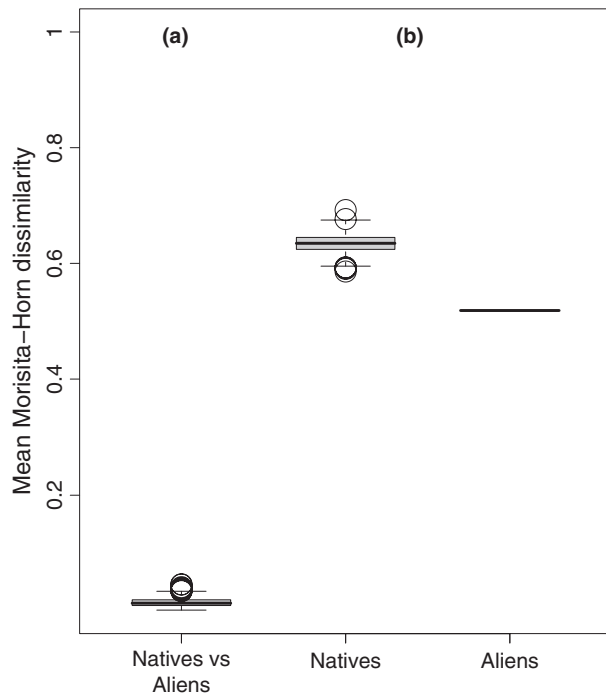


Figure 1 Large-scale dissimilarities (mean Morisita-Horn index) of native and alien ploidy levels of the German flora ($n = 2777$ entries of species and their ploidy-level information), calculated for 1000 subsets of 427 randomly sampled native ploidy-level and whole 427 alien ploidy-level data. (a) Dissimilarity between ploidy levels of natives and alien plants. (b) Dissimilarity within ploidy levels of natives and aliens, respectively. The figure shows Morisita-Horn dissimilarity (lines), 25% to 75% quartiles (grey boxes) and ranges (whiskers). Open circles are shown if extreme values are more than 1.5 times the interquartile range of the box.

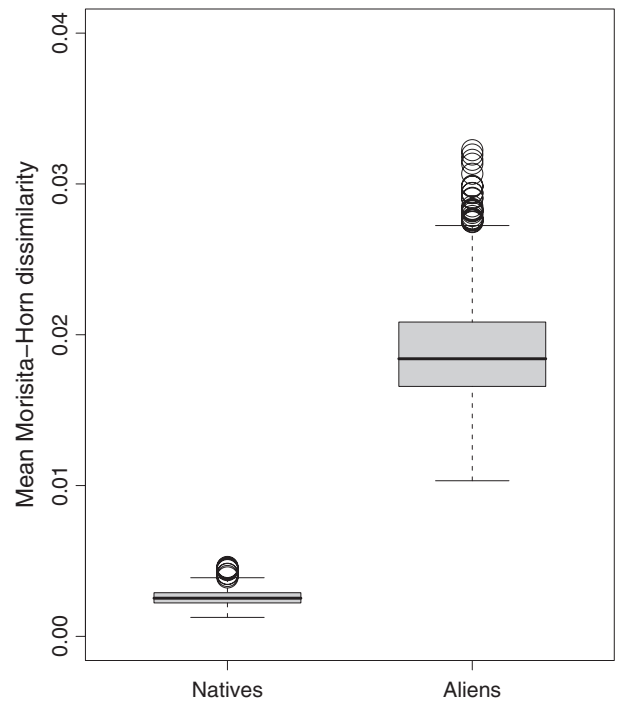


Figure 2 Spatial dissimilarities (mean Morisita-Horn index) of native and alien ploidy levels, calculated for 1000 subsets of 30 randomly sampled grid cells. Cells were sampled from a list of all 1928 analysed grid cells, including species with their different ploidy level and corresponding frequencies.

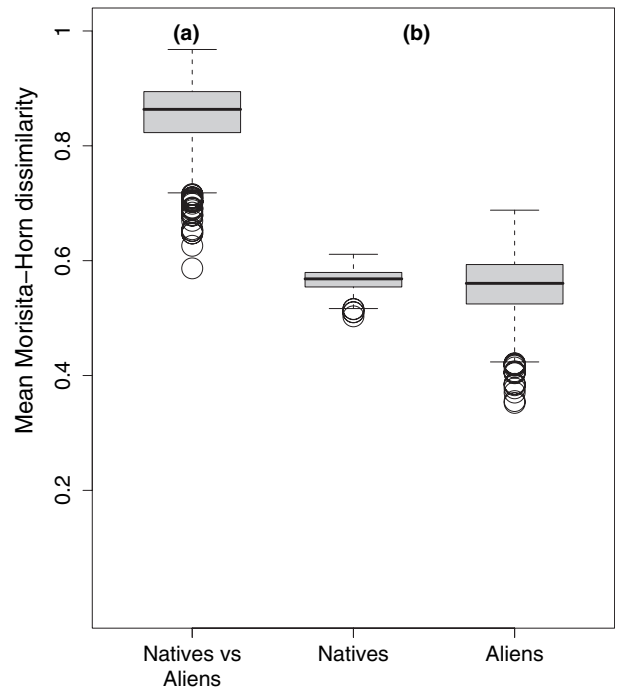


Figure 3 Small-scale dissimilarities (mean Morisita-Horn index) of native and alien ploidy levels. Per grid cell ($n = 1928$), all ploidy levels with corresponding frequencies of all species were included. (a) Dissimilarity between ploidy levels of natives and aliens. (b) Dissimilarity within ploidy levels of natives and aliens, respectively.

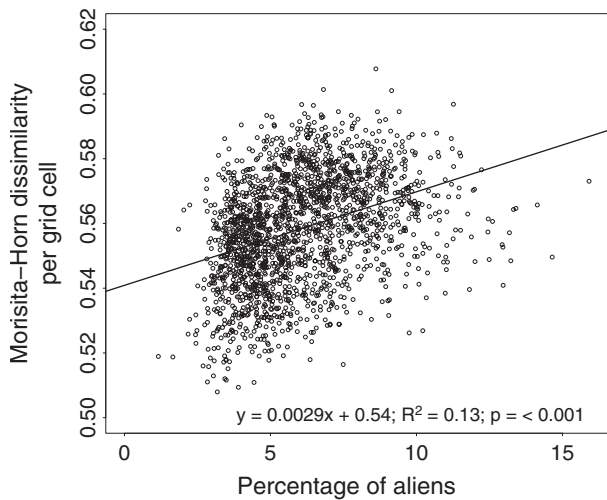


Figure 4 Dissimilarities of all ploidy-level information per grid cell ($n = 1928$) vs. percentage of aliens per grid cell.

t -test, d.f. = 999, $t = -150.8$, $P < 0.001$). However, the dissimilarity values were, in general, very small.

Within grid cells, dissimilarities between native and alien ploidy levels were higher than at the other scales (Fig. 3). Ploidy levels of alien plant species were significantly less dissimilar than those of native plants (paired t -test, d.f. = 1927, $t = 7.7$, $P < 0.001$; Fig. 3b). With an increasing percentage of aliens per grid cell, the mean dissimilarity within this grid cell increased significantly although the amount of scatter was considerable ($R^2 = 0.13$, $P < 0.001$; Fig. 4).

DISCUSSION

This study is among the first analysing patterns of trait homogenization at different spatial scales. We were able to show contrasting effects of homogenization based on ploidy levels at different spatial scales. Spatial dependencies of biotic homogenization have been shown in studies of plants (Smart *et al.*, 2006) and fishes (Marchetti *et al.*, 2001), or demonstrated theoretically (Olden & Poff, 2003). We were able to confirm our hypotheses: (1) at the smallest spatial scale, within grid cells, we found differentiation due to more heterogeneous ploidy levels of alien plants compared with those of natives, whereas (2) at the coarsest scale, we found homogenization due to more homogeneous ploidy levels of alien species.

Not only effect direction (whether alien plants lead to the homogenization or differentiation of the overall flora), but also effect size differed among spatial scales. At the coarsest scale, the mean difference in ploidy levels between natives and alien plants was small (but significant). At present, the maximum percentage of alien plants per grid cell is only *c.* 16% and the mean is *c.* 6% per grid cell. This proportion is probably too small to have much impact on the general composition of ploidy levels. Hence, only a considerable increase in the percentage of aliens would lead to a substantial homogeniza-

tion effect in ploidy levels. Olden & Poff (2003) showed that changes in community similarity depend to some degree on the species richness of the recipient community, and on the fraction of new invading species.

At our intermediate scale, we analysed dissimilarities between grid cells to assess the impact of the spatial distribution of alien plant species and natives on the homogenization of ploidy levels in Germany. Although native plants have a wider range of ploidy levels, aliens showed a significantly higher dissimilarity of ploidy level between grid cells. This result suggests that ploidy levels of native plants are more evenly distributed across space than those of alien plants.

The probability of spread is strongly time-dependent (Hamilton *et al.*, 2005; Pyšek & Jarošík, 2005). Native plants have, by definition, had a much longer time period than alien species for establishment, migration and adaptation, often since the last glaciation. All aliens have arrived since 1500 AD. Hence, native plants are distributed more homogeneously over Germany. At a taxonomic level, Kühn *et al.* (2003) showed also a differentiation effect of alien species within the German flora.

The similar geographical distribution of the mean ploidy level and mean dissimilarities suggest that these factors are highly confounded. Areas with a higher mean ploidy level are more likely to be areas that also have high small-scale dissimilarities, i.e. high variability of ploidy levels within grid-cells. This can be explained by the fact that cells with high mean ploidy level values are more likely to include a wider range of different ploidy levels than those with smaller mean ploidy values. These distribution patterns might be correlated with environmental variables, although an analysis of factors determining ploidy distributions is outside the scope of this study.

Olden & Rooney (2006) discuss the limited explanatory power of homogenization analyses with extant species pools, and suggest analysing temporal dynamics of homogenization processes. We nevertheless used a 'space-for-time' approach to analyse homogenization of ploidy level, because we lack floristic data for different time periods. However, spatial patterns also reflect temporal processes (Prinzinger *et al.*, 2004). The main assumption of the space-for-time substitution is that there is a similarity between spatial and temporal patterns (Pickett, 1989). Community changes over long time periods could result in different distribution patterns, as we showed for the distribution of native and alien ploidy levels. The overall trend towards a more homogeneous distribution of ploidy level at the coarsest scale would increase with the establishment of more alien plants (which is likely to happen). This would lead to a higher probability of losing rare ploidy levels among native plants, for example due to competition. Such extinctions result in a loss of genomic information (Petit, 2004). Thus, homogenization of ploidy levels could potentially result in a reduced diversity of related trait characteristics (Naiki & Nagamasu, 2004; Guggisberg *et al.*, 2006). In contrast, differentiation processes observed at smaller spatial scales may lead to a higher local variability of ploidy levels and therefore might result in a higher variability of trait characteristics that are related to ploidy level.

Ploidy levels are rarely studied at a plant community level. However, given the possibility of physiological and ecological changes associated with polyploidization, ecosystem effects may be expected from changes in community ploidy level distribution. Impacts on ecosystem functioning should be higher at small scales than at coarser scales. In fact, it has been shown that polyploidization, creating taxonomic diversity below the level of species, can lead to niche differentiation between different ploidy levels (Petit & Thompson, 1999). A higher diversity of ploidy levels in alien plants and their possible effect on the composition of other ecological traits could lead to a greater degree of niche differentiation among these plants. Consequently, at the smallest scale, differentiation in ploidy levels may have direct consequences for ecosystems. At coarser scales, the results often do not reflect direct interactions, but indicate changes in the potential species pool composition. Further investigations are necessary to determine whether there are direct biotic consequences behind these coarse-scale trends.

Although the relationship between ploidy level and ecological traits is not yet well understood, we consider that our findings are relevant to the diversity and distribution of genomic information. Daehler & Carino (2001) and Olden & Rooney (2006) describe 'genetic homogenization' as an increase in genetic similarity resulting from hybridization processes. We analysed homogenization of ploidy level at an assemblage level rather than a taxonomic level, which provides a particularly novel perspective.

Changes of 'information diversity' need to be considered at all spatial levels of biodiversity research. It is commonly accepted that species diversity is decreasing at the global scale, although at local scales species richness has often increased (Rosenzweig, 2001; Collins *et al.*, 2002; Sax & Gaines, 2003). Sax & Gaines (2003) gave many examples where, at local and regional scales, naturalizations outweigh extirpations and therefore species richness increases. However, proportionately more alien species are widespread than natives, which leads to taxonomic homogenization at a global scale (Weber & Pyšek, 2001; McKinney, 2005a). Our findings show that similar scale-dependent changes also operate for both processes: biotic homogenization acts at coarse scales and differentiation acts at local scales. Marchetti *et al.* (2001) and Taylor (2004) found comparable spatial scale-dependent relationships in homogenization for fish faunas in North America at a taxonomic level. However, Smart *et al.* (2006) found a different pattern. In their paper they stressed the importance of abiotic conditions at small spatial scales. The authors discussed that land-use intensification in the UK tends to lead to a coarse-grained mosaic of species-poor habitats, dominated by a small proportion of the local species pool. As different species were dominant in different ecological situations, they found an overall differentiation of species composition. However, if the 'winning' species share some 'winning' traits, the overall trend may be towards trait homogenization. As Smart *et al.* (2006) suggest, homogenization processes and their spatial-scale dependences are likely to vary between different traits.

CONCLUSIONS

Our finding of a (spatial) scale-dependent ploidy-level homogenization pattern is a first step towards understanding changes in trait composition at broader scales. It is likely that patterns of trait homogenization are also associated with similar patterns of species diversity and trait variability. To investigate the role of ploidy level for a species' ecology, future work may focus on the exploration of patterns in traits showing the ecological amplitude of species, such as the number of occupied habitats, and their relationship with ploidy levels.

We believe that our data provide useful information and allow realistic approximations of the present situation of ploidy-level homogenization in Germany. We could approve our hypotheses: ploidy levels of alien plant species can lead to homogenization, and this effect varies across spatial scales in Germany. At the coarsest scale (the entire country) we found a homogenization effect, and at the small scale (within grid cells) we found a strong differentiation effect of ploidy-level distribution.

ACKNOWLEDGEMENTS

We would like to thank the thousands of volunteers who collected plant distribution data for FLORKART, which was kindly provided by the Federal Agency for Nature Conservation. This work was funded by EU-targeted research project DAISIE (SSPI-CT-2003-511202). Oliver Schweiger and Walter Durka provided valuable comments on earlier drafts. We especially thank Phil Lambdon, Paul Downey and Melanie Josefsson for their very constructive comments and for improving the English.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Distribution of mean ploidy levels and of mean Morisita–Horn dissimilarities of ploidy levels for all German grid cells.

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Editor: Jens-Christian Svenning