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BIODIVERSITY RESEARCH

Linking biotic homogenization to habitat type, invasiveness and growth form of naturalized alien plants in North America

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ABSTRACT

Aim Biotic homogenization is a growing phenomenon and has recently attracted much attention. Here, we analyse a large dataset of native and alien plants in North America to examine whether biotic homogenization is related to several ecological and biological attributes.

Location North America (north of Mexico).

Methods We assembled species lists of native and alien vascular plants for each of the 64 state- and province-level geographical units in North America. Each alien species was characterized with respect to habitat (wetland versus upland), invasiveness (invasive versus non-invasive), life cycle (annual/biennial versus perennial) and habit (herbaceous versus woody). We calculated a Jaccard similarity index separately for native, for alien, and for native and alien species. We used the average of Jaccard dissimilarity index (1 – Jaccard index) of all paired localities as a measure of the mean beta diversity of alien species for each set of localities examined in an analysis. We used a homogenization index to quantify the effect of homogenization or differentiation.

Results We found that (1) wetland, invasive, annual/biennial and herbaceous alien plants markedly homogenized the state-level floras whereas non-invasive and woody alien plants tended to differentiate the floras; (2) beta diversity was significantly lower for wetland, invasive, annual/biennial and herbaceous alien plants than their counterparts (i.e. upland, non-invasive, perennial and woody alien plants, respectively); and (3) upland and perennial alien plants each played an equal role in homogenizing and differentiating the state-level floras.

Main conclusions Our study shows that biotic homogenization is clearly related to habitat type (e.g. wetland versus uplands), species invasiveness and life-history traits such as life cycle (e.g. annual/biennial and herbaceous versus woody species) at the spatial scale examined. These observations help to understand the process of biotic homogenization resulting from alien vascular plants in North America.

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Keywords

Biological invasions, exotic species, floristic differentiation, life history, non-native species, species traits, taxonomic homogenization.

INTRODUCTION

The introduction of alien species, which are also called exotic or non-native species, can cause a decrease in biotic similarity among areas when different species are introduced to each area and remain localized, a process called biotic differentiation (Olden & Poff, 2003; Qian *et al.*, 2008). However, over time, alien species often spread widely and cause an increase in biotic similarity among different areas, a process called biotic homogenization (Olden & Poff, 2003; McKinney, 2004; Rooney *et al.*, 2004). Furthermore, the introduction of the same species to different areas and the extinction or extirpation of localized native species can also cause biotic homogenization. By definition, biotic homogenization will lead to a

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decrease in beta diversity, i.e. spatial turnover of species between areas, whereas biotic differentiation will lead to an increase in beta diversity.

Biotic homogenization, which may be divided into subcategories such as genetic homogenization, taxonomic homogenization and functional homogenization (Olden, 2006), is one of the key processes leading to the global change of biological communities (Lockwood & McKinney, 2001). It has become an important research agenda because it represents processes of species invasion and extirpation, which are among the key components of the current biodiversity crisis (Olden, 2006; Leprieur *et al.*, 2008). However, like many other ecological processes, biotic homogenization is not uniformly taking place across and within regions or landscapes; and a great number of ecological and biological attributes may influence biotic homogenization (Pyšek & Richardson, 2007). For example, studies to date have shown that the level of homogenization may depend on habitat conditions (Lambdon *et al.*, 2008; Qian *et al.*, 2008), species involved (Rahel, 2000; Qian & Ricklefs, 2006), time after introduction and human interventions (Olden *et al.*, 2005; Smart *et al.*, 2006). Specifically, factors influencing biotic homogenization include, but are not limited to, (1) differences or similarities in human-selected introduced species and propagule pressure, (2) dispersal abilities, life-history traits and environmental tolerances of the introduced species, and (3) the environmental and biological attributes of the recipient region (Blackburn & Duncan, 2001; Kennard *et al.*, 2005; Moyle & Marchetti, 2006; Leprieur *et al.*, 2008).

However, despite the fact that knowing what factors influence biotic homogenization is important to predicting and controlling the invasion of alien species, there have been nearly no detailed studies relating biotic homogenization to the factors that are thought to influence this process, especially at the continental scale. For example, what habitats are more homogenized than others, and if (and what) life-history traits of the involved species and habitat features might be most responsible? These are critical questions that need immediate answers, especially given the fact that the patterns and responsible factors are most likely to vary across space and to be scale-dependent. Here, as the first attempt to address the above issues or relationships at a continental extent, we use a large dataset of native and alien plants in North America to analyse biotic (taxonomic) homogenization process in North America according to ecological and biological attributes. We use habitat types (wetland versus upland), species invasiveness (invasive versus non-invasive), life cycles (annual/biennial versus perennial) and habit types (herbaceous versus woody) in this study partly because most of these attributes have been considered in other studies of alien plants in North America (e.g. Ricklefs *et al.*, 2008) and partly because other attributes for alien plants in North America are not available for the continental flora. Based on a subset of alien plant species in North America, Ricklefs *et al.* (2008) found that wetland, annual/biennial and herbaceous plants spread more widely than their counterparts (upland, perennial and woody plants, respectively). Furthermore, recent studies show that invasive species promote biotic homogenization (Houlahan & Findlay, 2004; Fleishman *et al.*, 2005). Accordingly, we predict that biotic homogenization is stronger for wetland, invasive, annual/biennial and herbaceous plants than for their counterparts.

METHODS

North America in this study is defined as a region including the states of the continental United States, the provinces (or equivalent units) of Canada, and Greenland. The study area comprises 16,226 native species (including hybrids) and 3427 naturalized alien species of vascular plants (Qian & Ricklefs, 2006; Qian, 2008). We assembled species lists of vascular plants (ferns, gymnosperms and angiosperms) for each of the 64 state- and province-level geographical units (Fig. 1) from Kartesz's (1999) North American plant database, including six species reported subsequently (e.g. Al-Shehbaz, 1999). Species were treated as aliens to the study area if they are not native to America north of Mexico. We determined the native versus alien status of each species in America north of Mexico based on a large body of the botanical literature and reliable Internet sources (e.g. A Global Compendium of Weeds located at http://www.hear.org/gcw).

Each alien species was characterized with respect to habitat (wetland versus upland), invasiveness (invasive versus non-invasive), life cycle (annual/biennial versus perennial) and habit (herbaceous versus woody). Plants included in the category of wetland habitat are those classified as aquatic, floating, submerged, or wetland plants in Kartesz (1999); all other plants were included in the category of upland habitat. A species was considered as 'invasive' if it was included in Swearingen (2008) or USDA (2008); all other plants were

Figure 1 Geographical distribution of the 64 state and provincial floras included in this study. The dots represent the 64 geographical units used in this study.

considered as non-invasive. Numerous sources (e.g. Flora of North America Editorial Committee, 1993–2007; Kartesz, 1999; many state and provincial floras) were used to document the status of habitat, life cycle and habit of the vascular plants in North America.

Each of the 64 floras was compared with each of the remaining floras. For each pairwise comparison, we calculated a Jaccard similarity index (J) separately for native (J_{native}), for alien (J_{alien}), and for native and alien (J_{total}) species: $J = a/(a + b + c)$, where J ranges from 0 to 1, a is the number of species shared between two localities and b and c are the numbers of species unique to either locality (Legendre & Legendre, 1998). J_{alien} and J_{total} were calculated for each category of habitat, invasiveness, life cycle and habit. We used the average of Jaccard dissimilarity index (1 − Jaccard index) of all paired localities as a measure of the mean beta diversity (β_{Jacc}) of alien species for each set of localities examined in an analysis. Because observations resulting from paired localities are not completely independent of one another and using degree of freedom based the number of observations ($N = 2016$ in our case) will inflate the rate of type I error in a significance test (i.e. t-test comparing pairwise attributes), we conservatively took the number of geographical unties ($N = 64$) as degree of freedom. A similar method was used in previous studies (e.g. Harrison *et al.*, 1992).

We used a homogenization index (H), which is J_{total} minus J_{native} (Rahel, 2000), to quantify the effect of homogenization or differentiation. A positive H indicates a homogenization effect, whereas a negative H indicates a differentiation effect. Because the same set of native floras were used in both groups of each pair of attributes and because all comparisons were conducted at the continental extent, there appeared no systematic bias with regard to species richness of native floras. We divided H-values into seven classes (1–7; see Results) to compare the distributions of frequencies of H-values among H-classes between paired categories of the four attributes (i.e. habitat, invasiveness, life cycle and habit). We used the G-statistic (Sokal & Rohlf, 1981), which has a chi-square distribution, to test how well the distribution of H-values among H-classes for one group of alien plants matches that for its counterpart (e.g. wetland versus upland plants). We added one to the number of H-values of each H-class for each of two plant groups in a comparison to make all values transformable by logarithm in G-statistic analyses.

RESULTS

Of the 3427 naturalized alien species of vascular plants in North America (north of Mexico), 935 were classified as invasive species. Wetland, annual/biennial and woody species made up 21.1%, 32.9% and 24.5%, respectively, of the entirety of the alien flora of North America (Table 1). Each alien species occupied on average 16.1% of the 64 geographical units included in this study. Wetland, invasive, annual/biennial and herbaceous plants occupied a 2.44-, 3.25-, 1.94- and 1.35-fold, respectively, larger proportion of the 64 geographical units than their counterparts (i.e. upland, non-invasive, perennial and woody plants, respectively) (Table 1). Beta diversity was significantly ($P < 0.05$) lower for wetland, invasive, annual/biennial and herbaceous plants than their counterparts (Table 1).

Table 1 Numbers of alien species, geographical extent measured as proportion (means ± SD) of geographical units occupied, and beta diversity (β_{Jacc}, mean ± SD) for each subcategory of habitat, invasiveness, life cycle and habit of alien vascular plant species in North America. The number of cases for distribution extent and β_{Jacc} is 2016 for each subcategory. The differences were significant in all comparisons between paired subcategories within a category ($P < 0.05$).

Category	Subcategory	No. species	Geographical extent	β_{Jacc}
Habitat	Wetland	722	0.303 ± 0.304	0.574 ± 0.186
	Upland	2705	0.124 ± 0.187	0.756 ± 0.130
Invasiveness	Invasive	935	0.325 ± 0.302	0.583 ± 0.185
	Non-invasive	2492	0.100 ± 0.156	0.802 ± 0.112
Life cycle	Annual/ biennial	1127	0.239 ± 0.276	0.629 ± 0.157
	Perennial	2300	0.123 ± 0.192	0.741 ± 0.144
Habit	Herbaceous	2587	0.183 ± 0.246	0.667 ± 0.150
	Woody	840	0.094 ± 0.148	0.818 ± 0.147

Homogenization indices ranged from −0.082 to 0.064 (Table 2), indicating that homogenization and differentiation effects both had played a role. When the range of homogenization indices was divided into seven classes (Class 1, $H < -0.06$; Class 2, $-0.06 \le H < -0.04$; Class 3, $-0.04 \le H < -0.02$; Class 4, $-0.02 \le H < 0$; Class 5, $0 \le H < 0.02$; Class 6, $0.02 \le H < 0.04$; Class 7; $H \ge 0.04$) and the frequency of distributions of paired categories of the four attributes were compared, wetland, invasive, annual/biennial and herbaceous plants markedly homogenized the state-level floras whereas non-invasive and woody plants tended to differentiate the floras (Fig. 2). It appears that homogenization and differentiation had an even effect for upland and perennial plants (Fig. 2). For each of the four comparisons (Fig. 2), the

Table 2 The lowest and highest values of homogenization index (H) for each subcategory of habitat, invasiveness, life cycle and habit of alien vascular plant species in North America. The number of cases for distribution extent and β_{Jacc} is 2016 for each subcategory.

Category	Subcategory	Lowest H	Highest H
Habitat	Wetland	−0.035	0.037
	Upland	−0.080	0.037
Invasiveness	Invasive	−0.048	0.053
	Non-invasive	−0.082	0.024
Life cycle	Annual/biennial	−0.043	0.045
	Perennial	−0.055	0.031
Habit	Herbaceous	−0.074	0.064
	Woody	−0.031	0.006

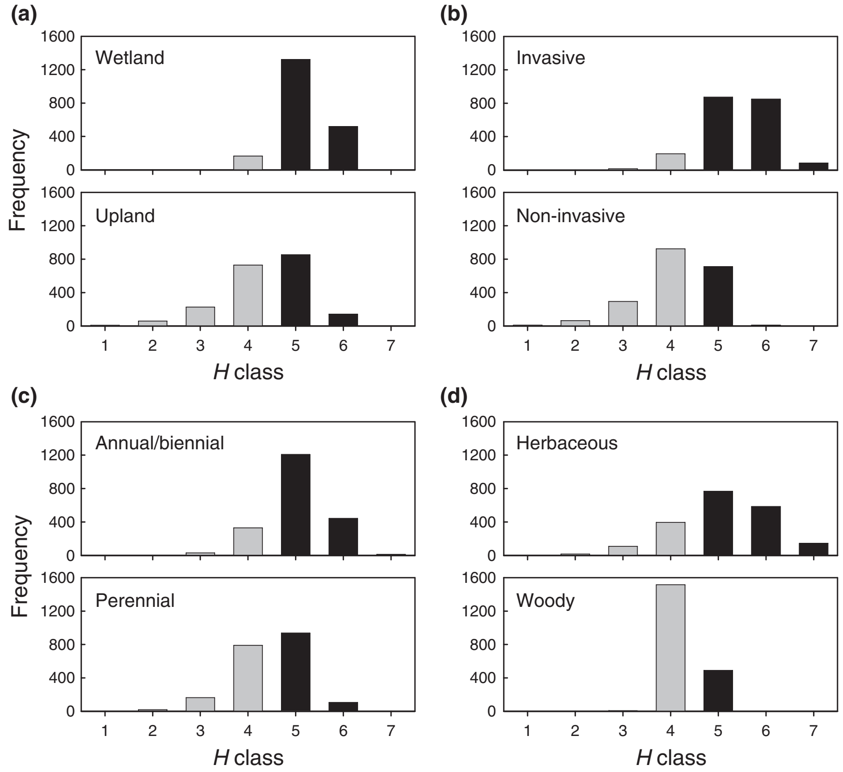

Figure 2 Frequency of homogenization indices (*H*) in each of the seven *H*-classes according to habitat (a), invasiveness (b), life cycle (c) and habit (d) of alien vascular plants in North America. Black bars indicate homogenization effect, and grey bars indicate differentiation effect. (See Results, for details of the *H*-classes.)

distribution mode for wetland, invasive, annual/biennial and herbaceous plants tended to shift towards larger *H*-values, compared with their counterparts (Fig. 2); and distributions of *H*-values among the seven *H*-classes differed significantly between paired groups of vascular plants, with heterogeneity *G* being 1059, 2087, 584 and 1866, respectively, for habitat, invasiveness, life cycle and habit ($P < 0.001$).

DISCUSSION

Biotic homogenization is an emerging ecological phenomenon worldwide (e.g. Spear & Chown (2008) for the globe and South Africa; Rahel (2000), McKinney (2004), and Qian & Ricklefs (2006) for North America; Smart *et al.* (2006), Kühn & Klotz (2006), Lambdon *et al.* (2008), and Leprieur *et al.* (2008) for Europe; and Castro *et al.* (2007) for South America). Knowing where rapid homogenization is occurring and what kind of species are most responsible for the homogenization is critical to understanding basic invasion biology and to developing conservation and management priorities. This study is the first attempt to examine the relationship between biotic homogenization and environmental and biological traits at a continental extent. The results of this study support our hypotheses on the strength of biotic homogenization, i.e. wetland plants > upland plants, invasive plants > non-invasive plants, annual/biennial plants > perennial plants, and herbaceous plants > woody plants. These results are robust to the effect of difference between species richness of compared floras. For example, when we used the Simpson index (which was not affected by the difference in species richness between sample areas; Simpson, 1960), to conduct a set of supplementary analyses (see Appendix S1 in Supporting Information), the pattern of differences in biotic homogenization between paired traits did not change and the differences in the strength of biotic homogenization even substantially increased: the ratios of beta diversity for upland versus wetland plants, non-invasive versus invasive plants, perennial versus annual/biennial plants and woody versus herbaceous plants were 1.32, 1.37, 1.18 and 1.22, respectively, when Jaccard index was used (Table 1) and were 1.95, 2.37, 1.55 and 1.52, respectively, when Simpson index was used (Appendix S1).

Aquatic and wetland vascular plants usually show broader distributional ranges than terrestrial and upland vascular plants (Santamaría, 2002; Ricklefs *et al.*, 2008). Santamaría (2002) considered the generality of wide distributions of aquatic and wetland vascular plants as a result of a combination of the following features of this group of plants: (1) broad tolerance ranges, (2) clonal growth and multiplication, (3) long-distance dispersal of sexual propagules and high local dispersal of asexual clones, and (4) broad plastic response. Other explanations for wide distributional ranges of aquatic and wetland plants include the uniformity of the aquatic environment (Sculthorpe, 1967; Barrett *et al.*, 1993).

We believe that the uniformity of some key components of aquatic and wetland environment across a broad geographical extent and long-distance dispersal of propagules are among the key factors leading to the generality of wide distributions of aquatic and wetland plants. Broad-scale distributions of terrestrial plants are largely determined by climatic factors such as temperature and precipitation. Although climatic factors also influence distributions of wetland plants, their effects are generally weaker on wetland plants than on upland plants because water availability is not an issue for most aquatic and wetland sites and water buffers aquatic plants against rapid fluctuations in air temperature. Thus, the geographical extent with suitable sites for a wetland plant species is generally wider, compared with that for a terrestrial plant species. High long-distance dispersal rate has been considered as one of the key factors contributing to wide distributional ranges of wetland plants. Broad-scale dispersal of sexual and asexual propagules of wetland plants, largely due to passive transportation by water-birds (Darwin, 1859; Green *et al.*, 2002), is common. Birds disperse plant seeds, either internally via the digestive tract or externally by adhering to their feathers, feet and bill (Green *et al.*, 2002). Experiments have shown that the seeds of many plant species survive gut passage (De Vlaming & Proctor, 1968; Charalambidou & Santamaría, 2002); in some cases gut passage has enhanced seed germination (Smits *et al.*, 1989). Furthermore, dispersal of wetland plants may be facilitated by water transportation (Duarte *et al.*, 1994; Ricklefs *et al.*, 2008). The seeds of many plant species have structures that allow them to float at the water surface and to travel long distance with the aid of wind or water currents (Santamaría, 2002). In addition, compared to terrestrial habitats as a group, wetlands generally include fewer types of habitats and thus have a higher chance of sharing the same species among different wetlands. There is a large body of literatures on homogenization of freshwater and marine fishes and several of these literatures (e.g. Scott, 2006; Gardiner *et al.*, 2009) infer that aquatic homogenization is actively promoted by physical homogenization of the watersheds and water bodies (such as building dams and similar kinds of water pollution) that are widespread. This physical homogenization of wetlands may also play a role in creating similar habitats for wetland plants.

Invasive species are often locally abundant. While it is stated that invasive species promote biotic homogenization (e.g. Houlahan & Findlay, 2004; Fleishman *et al.*, 2005), there has been little evidence to support this hypothesis (McKinney & La Sorte, 2007), particularly at a broad geographical extent. Our finding that invasive species have played a greater role than non-invasive species in homogenizing the flora of North America at the state/province level is consistent with the finding of McKinney & La Sorte's (2007) study at smaller scales (counties, cities and preserved areas). Explanations for a greater role of invasive plants (versus non-invasive plants) in biotic homogenization include that invasive species have been generally characterized by their greater genetic and phenotypic elasticity, diverse reproductive modes, high growth rate, greater dispersal ability and greater ability to tolerate broader habitat conditions, which ultimately contribute to the faster spread and thus greater distribution (e.g. Rejmánek & Richardson, 1996; Goodwin *et al.*, 1999; Devin & Beisel, 2007; Gosper & Vivian-Smith, 2009). The larger and thus more overlapped distribution ranges of the invasives and their close association with human activities together reorganize and homogenize the overall floras or faunas over larger regions and the globe.

Perennial and woody plants usually have larger sizes but smaller numbers of seeds than annual/biennial herbaceous plants; these characteristics of perennial and woody plants may have hampered their spread (Salisbury, 1942; Leishman *et al.*, 1995; Ricklefs *et al.*, 2008). Relative to woody species, herbaceous species and short-lived plants such as annual/biennials usually produce more and small seeds, show greater genetic flexibility and evolutionary rates due to their shorter life cycles (Rejmánek & Richardson, 1996; Cox, 2004). All the above-mentioned characteristics enable short-lived species to spread more broadly and, over time, eventually occupy larger geographical ranges than long-lived woody species and dominate habitats. Of course, the invasive characteristics mentioned above would work better when species are released from their natural enemies or introduced to more suitable environments. We do not believe, however, that the observed differences in distribution range among habitat or species types are caused by the time factor as there is no evidence that species in the groups with greater homogenization were introduced earlier. However, because woody plants tend to have longer life cycles and more limited dispersal, they might have not yet spread as wide as they would eventually do whereas herbaceous plants are spreading faster and are less influenced by this time-lag.

How ongoing biotic homogenization will exactly reshape the structure of biomes in specific regions and across the globe remains largely unknown. Our study includes only a small number of many ecological and biological attributes that may affect biotic homogenization. In the future, the possible effect of other attributes on biotic homogenization should be investigated and comparisons of biotic homogenization effects among continents or regions and detailed analyses at smaller scales (i.e. within each continent or landscape; e.g. McKinney & La Sorte, 2007; Qian *et al.*, 2008) should be conducted. Such comparisons could help identify and predict the specific locations (versus habitat types) where intense biotic homogenization is now occurring and/or likely to occur in the future. More importantly, there is a need to study the impacts of biotic homogenization caused by alien species on native biotas, the related processes (e.g. time-scales) and resistance from native communities, especially when possible extinctions of rare and endangered species are at stake.

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SUPPORTING INFORMATION

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

Appendix S1 Beta diversity measured as one minus Simpson index.

BIOSKETCHES

Hong Qian's research is multidisciplinary and particularly lies at the interface of ecology and biogeography. His research involves a wide range of spatial scales (from local to global) and a variety of taxa (e.g. bryophytes, vascular plants, vertebrates, and invertebrates). In particular, he is interested in understanding the relative roles of historical and contemporary factors in determining the patterns in biodiversity.

Qinfeng Guo has broad interests in community ecology and biogeography. He is currently working on biodiversity patterns at various scales that may affect the process and patterns of biotic invasions and ecosystem functions. He also studies how life-history traits and genetics may influence species invasiveness and how history and habitat characteristics may affect invasibility.

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