

## LETTER

# The role of exotic species in homogenizing the North American flora

## Abstract

Exotic species have begun to homogenize the global biota, yet few data are available to assess the extent of this process or factors that constrain its advance at global or continental scales. We evaluate homogenization of vascular plants across America north of Mexico by comparing similarity in the complete native and exotic floras between states and provinces of the USA and Canada. Compared with native species, exotic plants are distributed haphazardly among areas but spread more widely, producing differentiation of floras among neighbouring areas but homogenization at greater distance. The number of exotic species is more closely associated with the size of the human population than with ecological conditions, as in the case of native species, and their distributions are less influenced by climate than those of native species.

## Keywords

Beta diversity, climate, exotic species, geographical distribution, homogenization, Jaccard index, North America.

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## INTRODUCTION

Introduced species that spread widely through agricultural, urban, and other disturbed habitats (Mack *et al.* 2000) tend to increase the similarity of the biotas of different regions (Vitousek *et al.* 1996; Lockwood & McKinney 2001). This tendency towards biotic homogenization has been reported on various geographical scales for several types of organisms (Olden & Poff 2004). However, because few studies have addressed homogenization at continental scales, the general nature of this phenomenon is poorly understood. Exotic species can result in biotic differentiation between two areas when different species are introduced to each area and remain localized (Olden & Poff 2003). However, over time, many exotic species spread and might hasten the extirpation of localized native species. These processes eventually increase biotic similarity, although idiosyncratic loss of native species could also increase differentiation of floras. For aquatic biota at a semi-continental scale, Rahel (2000) determined that introduced species of freshwater fish have increased the similarity of faunas in 90% of 1128 paired comparisons between the 48 conterminous states in the USA. However, no terrestrial biotas have been subjected to such an analysis at a similar scale. Nor have the responses of native and exotic distributions to climate and other

environmental factors been compared to determine whether exotic species are constrained by different factors. Our continent-wide analysis includes all state- and province-level vascular floras in America north of Mexico. Specifically, we wished to determine whether exotic species increased or decreased floristic similarity between regions, and whether turnover of exotic and native species between regions responded to the same environmental variables.

## MATERIALS AND METHODS

North America in this study is defined as a region including states and provinces (areas) of the continental USA and Canada. We assembled vascular plant (fern, gymnosperm and flowering plant) species lists for each of the 64 state- and province-level geographical units from Kartesz's (1999) North American plant data base, including several species reported subsequently. Species were treated as exotics to an area if they are not native to America north of Mexico. Our designation of exotic differs from that of Kartesz (1999), and from studies based on his designations (e.g. Rejmánek 2003; Stohlgren *et al.* 2003). The geographical range of Kartesz's database includes Canada, Greenland and the entire USA, including Hawaii, Puerto Rico, and all US Virgin Islands, which are located in the Caribbean. In

Kartesz's database, a plant is considered to be native if it occurs naturally anywhere within this geographical range (Kartesz 1999). As a result, many species that are exotic to America north of Mexico are considered as native in Kartesz's database because they occur naturally in Hawaii, Puerto Rico or the US Virgin Islands. We determined the native vs. exotic 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>). We excluded four geographical units that are located in the former Northwest Territories and Greenland from data analyses because current data of exotic plants in these high latitude areas are not available. We distinguished Labrador and the island of Newfoundland.

Climate data were extracted from the International Institute of Applied System Analysis climatic database (Leemans & Cramer 1991): (i) mean annual temperature (an indicator of ambient energy, Rahbek & Graves 2001); (ii) mean coldest month (January) temperature (related to frost and freezing tolerance); (iii) difference between mean January temperature and mean July temperature (temperature seasonality); (iv) annual precipitation (water availability); and (v) summer precipitation (water availability during the north temperate growing season – May to August). In addition: (vi) actual evapotranspiration and (vii) potential evapotranspiration were calculated following the approach developed by Cramer and Prentice (Cramer & Prentice 1988; Prentice *et al.* 1992, 1993). To account for collinearity between the climate variables and to reduce the number of variables in data analyses, we subjected the seven climate variables to a principal component analysis (PCA) based on their correlation matrix (see Table S1).

Human population data used in this study were obtained from <http://factfinder.census.gov> for the USA (for the year 2005) and from <http://www40.statcan.ca/101/cst01/demo02.htm> for Canada (for the year 2005) except for Labrador and the island Newfoundland, for which we used <http://en.wikipedia.org/wiki/>.

For each pairwise comparison, we calculated a Jaccard index of similarity ( $J$ ) separately for native and non-native 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). The exponential rate of decrease in the Jaccard index with respect to distance is a measure of beta diversity (Nekola & White 1999). Distances used in this analysis included geographical distance ( $10^3$  km), and differences in latitude, longitude and climate (represented by PC1, PC2 and PC3 scores). Because pairwise comparisons create non-independent observations, we followed the suggestion of Harrison *et al.* (1992) to base statistical inference on  $n - 2$  d.f., where  $n$  is the number of floras (i.e. 60).

We quantified homogenization ( $H$ ) resulting from exotic species by the increase in similarity between two areas resulting from species exotic to North America, i.e.  $H = \text{similarity}(\text{native} + \text{exotic}) - \text{similarity}(\text{native})$  (Rahel 2000), based on the Jaccard index of similarity (Faith 1983; Legendre & Legendre 1998).

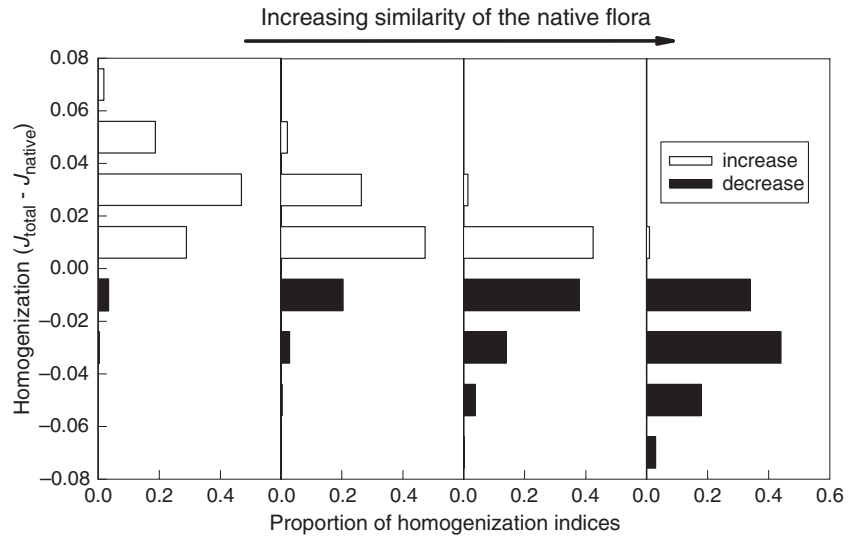
## RESULTS

The entirety of North America, including arctic latitudes, has 19 653 species of vascular plants, 3427 of which are exotics. Our study is based on the floras of 60 states and provinces, which on average have  $2231 \pm 813$  SD native species and  $593 \pm 254$  SD exotic species. Conversely, native species are distributed across an average of  $8.2 \pm 11.2$  SD, and exotic species,  $10.3 \pm 14.5$  SD, states and provinces. Exotic species comprise a relatively large proportion of the floras of the northeastern USA, Florida, Louisiana, and the Pacific Northwest and are under-represented in the inter-mountain west (see Fig. S1).

The logarithm of exotic species richness is strongly and positively correlated with the logarithm of native species richness at the state and province scale ( $r = 0.64$ ,  $n = 60$ ,  $P < 0.0001$ ), a pattern also found by Sax *et al.* (2002), Rejmanek (2003) and Stohlgren *et al.* (2003). Regardless of this correlation, native and exotic floras respond to different factors. Native plant species richness was strongly related (total  $R^2 = 0.88$ ) to pervasive climate variables and the range of elevation within a region, representing ecological heterogeneity (see Table S4), whereas exotic species richness was related primarily to the size of the human population within each region (partial  $r^2 = 0.74$ ) (Rejmanek 2003; Taylor & Irwin 2004) and did not respond uniquely to ecological variables. In contrast, number of native species was less closely associated with human populations (partial  $r^2 = 0.25$ ). Thus, the intensity of human activity is a strong predictor of exotic species richness (Taylor & Irwin 2004).

Patterns of distribution of native and exotic species differ in such a way that exotic species tend to homogenize floras whose native plant species differ greatly, but differentiate more closely related floras. Over all 1770 paired comparisons between state and provincial floras,  $H$  averaged close to 0 ( $0.012 \pm 0.022$  SD; range  $-0.080$  to  $0.067$ ), as one would expect from the similar geographical spread of native and exotic species. However, distant areas with low Jaccard similarities ( $J < 0.40$ ) tend to be homogenized by exotic species whereas closer areas ( $J > 0.40$ ) tend to be differentiated (Fig. 1) (Rejmánek 2000; McKinney 2004).

From the perspective of entire floras or faunas, patterns of distribution can be represented by the turnover of species between areas within a region, or beta diversity (Whittaker 1972; Cody 1975; Wilson & Shmida 1984; Harrison *et al.* 1992; Rahbek 1997; Nekola & White 1999). We quantify



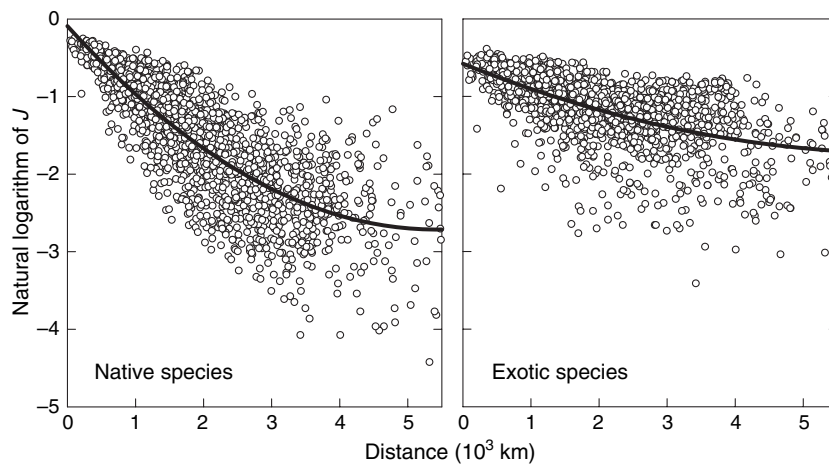
**Figure 1** Distribution of homogenization indices ( $H$ ) among pairs of state- and province-level floras. The pairs of floras are grouped by degree of native plant similarity ( $J_{\text{native}}$ ). Native floras portrayed in the left-hand side panel are more distant ( $J_{\text{native}} = 0.00\text{--}0.20$ ) than those in the middle ( $J_{\text{native}} = 0.20\text{--}0.40$  and  $0.40\text{--}0.60$ ) and right-hand side ( $J_{\text{native}} > 0.60$ ) panels. Numbers of pairwise comparisons, from left to right, were 797, 538, 335 and 100.

beta diversity as the exponential rate of decrease in similarity with distance ( $x$ ), i.e.  $\beta = d \ln J / dx$  (Nekola & White 1999; Vellend 2001).  $\beta$  allows one to compare species turnover between groups of taxa (e.g. native vs. exotic), among areas within regions, with respect to a common distance metric (Qian *et al.* 2005). In our analysis, we consider distance in terms of geography (km), degrees of latitude or longitude and environment based on climate variables.

Native and exotic floras differed in the rate at which  $\ln J$  decreased with geographical distance (interaction of native vs. exotic and distance:  $F = 630$ , d.f. = 1,56,  $P < 0.0001$ ). The separate  $\ln J$ -distance relationship for exotic species

had a lower intercept at zero distance ( $\exp[\ln J] = J = 0.56$ ) and lower beta diversity ( $\beta = -0.35$ ) compared with native species ( $J = 0.91$ ,  $\beta = -0.97$ ) (Fig. 2). Thus, compared with native plants exotic floras differ more among close areas (lower intercept) but are more broadly and uniformly distributed (less steep decline in  $J$  with distance).

North-south and east-west components of distance differ with respect to ecological change, temperature predominating over latitude and precipitation over longitude. The separate regressions for native and exotic species had similar intercepts ( $J = 0.51$ ,  $0.50$ ), and beta diversity with respect to latitude ( $-0.045$  and  $-0.039$  per degree). However, as in



**Figure 2** Relationship between the Jaccard index of similarity and geographical distance. Native species (left) and exotic species (right) are shown in all paired comparisons between state- and province-level areas within North America. Lines are least-squares quadratic fits to the data. For native species, the relationship had an intercept of  $-0.092 \pm 0.037$ , an initial slope of  $-0.967 \pm 0.034$ , and a quadratic coefficient of  $0.089 \pm 0.007$  ( $F = 1630$ , d.f. = 2,57,  $P < 0.0001$ ,  $R^2 = 0.649$ ). The relationship for exotic species had an intercept of  $-0.579 \pm 0.028$ , an initial slope of  $-0.351 \pm 0.026$ , and a quadratic coefficient of  $0.027 \pm 0.005$  ( $F = 481$ , d.f. = 2,57,  $P < 0.0001$ ,  $R^2 = 0.353$ ).

the case of beta diversity over geographical distance, exotic species exhibited lower beta diversity ( $-0.006$ ) than native species ( $-0.024$ ) with respect to longitude (see Table S2).

To examine the role of climate difference in determining species turnover,  $\beta$  for native and exotic species was related to scores of the first three principal components of a PCA based on climatic variables. PC1 (accounting for 77.5% of variance) represented a north-south gradient of temperature and precipitation, PC2 (14.5%) represented an east-west gradient contrasting the wetter east and the drier west, and PC3 (5.0%) represented an east-west gradient contrasting the more seasonal continental climates of the Midwest with those of the east and west coasts. The separate regressions of  $\ln J$  on the differences in component scores for native and exotic species produced a higher intercept for native species ( $J = 0.77$  vs.  $0.56$ ), but higher beta diversity for native species with respect to PC1, i.e. latitude ( $-0.30$  vs.  $-0.16$ ), PC2 ( $-0.43$  vs.  $-0.09$ ) and PC3 ( $-0.26$  vs.  $-0.16$ ) (see Table S3).

Because the environmental and geographical distances used in this analysis are intercorrelated, we developed a comprehensive model to examine the decrease in  $\ln J$  for native and exotic species, retaining only effects that contributed uniquely to at least 1% of the explained sum of squares (see Table S5). These models were developed by elimination of non-significant terms from complete models; interactions were generally small and were not included. The results reinforce the conclusion that the distributions of exotic species are more idiosyncratic than those of native species ( $J_{\text{native}} = 0.87$ ,  $J_{\text{exotic}} = 0.58$ ;  $R^2_{\text{native}} = 0.79$ ,  $R^2_{\text{exotic}} = 0.55$ ) and less sensitive to both latitudinal and longitudinal variation.

## DISCUSSION

The lower beta diversity of exotic plants is consistent with the homogenizing effect of introduced species, particularly among areas that are distant from one another. Because many exotic species are closely associated with disturbed environments and may be excluded from intact habitats (e.g. Naeem *et al.* 2000; Hector *et al.* 2001), homogenization might reflect the generation by human activities of a modified, relatively uniform environment through which exotic species have spread. The Jaccard indices of exotic and native plant floras are equivalent at a geographical distance of  $0.863 \times 10^3$  km and a value of  $J = 0.422$ . Various distance measures explain less of the variation in Jaccard indices in exotic compared with native plant floras. Turnover of exotic plants is more susceptible to geographical distance and latitude distance than it is to climate variables, as in the case of native plants. This likely reflects recent introduction of exotics and the role of human activity in their spread (e.g. Taylor & Irwin 2004). Native floras

provide more evidence of being in equilibrium with their environments in the sense that species turnover occurs along strong environmental gradients, including both the climate axes of PC1 (strongly correlated with latitude) and PC2 (strongly correlated with longitude). Native plants also are more localized in the sense that they exhibit greater species turnover (lower Jaccard index with distance) than introduced floras (Fig. 2).

Because few native species have yet been extirpated from state and provincial floras, the pattern of homogenization and differentiation reflects the sporadic occurrence of exotic species with respect to suitable habitats, on the one hand, and both natural and human-assisted spread of exotics with less regard to the ecological constraints acting on native species, on the other (e.g. Seabloom *et al.* 2003). We presume that over time, irregularities in the distribution of exotics resulting from haphazard colonization or introduction will diminish with further spread, and their homogenizing influence will extend to progressively more similar floras.

Plant diversity is decreasing at a global scale but has increased at continental and regional scales (Sax *et al.* 2002) because new species have been introduced more rapidly than native species have disappeared (Hobbs & Mooney 1998; Rahel 2000), and there has been insufficient time for extinction processes to catch up with introductions (Rahel 2002). However, at local scales, such as on Staten Island, New York, introductions of several hundreds of exotic plant species through 1930 were accompanied by the disappearance of a similar number of native species, partly owing to habitat loss from urbanization (Robinson *et al.* 1994; Rahel 2002). Introduction of exotic species, extirpation of native species and environmental changes that facilitate these processes ultimately result in homogenization (Rahel 2002), although haphazard extirpation of native species (Rooney *et al.* 2004) could also increase differentiation between areas. Because these processes are likely to continue (Vitousek *et al.* 1997; Rahel 2002), the idiosyncratic initial distributions of exotic species resulting from haphazard colonization and introduction will eventually be evened out, and this will tend to increase homogenization between progressively closer areas, leading to a greater degree of biotic homogenization at the continental scale.

The absence of a strong ecological signal in the distribution of exotic species suggests either that these species have not reached ecological equilibrium, in spite of occupying somewhat more states and provinces than native species on average or that exotics occupy habitats defined more closely by human activities (i.e. urban, agricultural and disturbed environments) than by climate (cf. Stohlgren *et al.* 1999; Naeem *et al.* 2000). The weak effect of distance on the Jaccard index for exotic species reflects the tendency of introduced species to spread widely, possibly reflecting

predominately dispersal by human transportation systems and a weak influence of climate. Although it is not possible to predict the consequences of global climate change, it is not unreasonable to speculate that native species, whose distributions follow more closely upon physical conditions of the environment, might experience strong pressure upon their populations, potentially leading to local extirpation and range restriction. In contrast, there is less evidence that many exotic species will be similarly affected. Thus, we face the prospect of local floras becoming increasingly dominated by established exotics whose present distributions are determined more by human activity than by environmental limitations.

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## REFERENCES

- Cody, M.L. (1975). Towards a theory of continental species diversities. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge, MA, pp. 214–257.
- Cramer, W.P. & Prentice, I.C. (1988). Simulation of regional soil moisture on a European scale. *Nor. Geogr. Tidsskr.*, 42, 149–151.
- Faith, D.P. (1983). Asymmetric binary similarity measures. *Oecologia*, 57, 287–290.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992). Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.*, 61, 151–158.
- Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Lawton, J.H. (2001). Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies [review]. *Ecol. Res.*, 16, 819–831.
- Hobbs, R.J. & Mooney, H.A. (1998). Broadening the extinction debate: population deletions and additions in California and Western Australia. *Conserv. Biol.*, 12, 271–283.
- Kartesz, J.T. (1999). A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. In: *Synthesis of the North American Flora. Version 1.0* (eds Kartesz, J.T. & Meacham, C.A.). North Carolina Botanical Garden, Chapel Hill, NC.
- Leemans, R. & Cramer, W.P. (1991). *The ILASA Database for Mean Monthly Values of Temperature, Precipitation and Cloudiness on a Global Terrestrial Grid. Research Report RR-91-18*. International Institute for Applied Systems Analysis, Laxenburg, Austria.
- Legendre, P. & Legendre, L. (1998). *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.
- Lockwood, J.L. & McKinney, M.L. (2001). *Biotic Homogenization*. Kluwer Academic Publishers, New York, NY.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.*, 10, 689–710.
- McKinney, M.L. (2004). Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biol. Invasions*, 6, 495–504.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, 91, 97–108.
- Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. *J. Biogeogr.*, 26, 867–878.
- Olden, J.D. & Poff, N.L. (2003). Toward a mechanistic understanding and prediction of biotic homogenization. *Am. Nat.*, 162, 442–460.
- Olden, J.D. & Poff, N.L. (2004). Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology*, 85, 1867–1875.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.*, 19, 117–134.
- Prentice, I.C., Sykes, M.T. & Cramer, W. (1993). A simulation model for the transient effects of climate change on forest landscapes. *Ecol. Modell.*, 65, 51–70.
- Qian, H., Ricklefs, R.E. & White, P.S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecol. Lett.*, 8, 15–22.
- Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in neotropical birds. *Am. Nat.*, 149, 715–730.
- Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. USA*, 98, 4534–4539.
- Rahel, F.J. (2000). Homogenization of fish faunas across the United States. *Science*, 288, 854–856.
- Rahel, F.J. (2002). Homogenization of freshwater faunas. *Annu. Rev. Ecol. Syst.*, 33, 291–315.
- Rejmánek, M. (2000). Invasive plants: approaches and predictions. *Austral Ecol.*, 25, 497–506.
- Rejmánek, M. (2003). The rich get richer – responses. *Front. Ecol. Environ.*, 1, 122–123.
- Robinson, G.R., Yurlina, M.E. & Handel, S.N. (1994). A century of change in the Staten-Island flora: ecological correlates of species losses and invasions. *Bull. Torrey Bot. Club*, 121, 119–129.
- Rooney, T.P., Wiegmann, S.M., Rogers, D.A. & Waller, D.M. (2004). Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conserv. Biol.*, 18, 787–798.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.*, 160, 766–783.
- Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl Acad. Sci. USA*, 100, 13384–13389.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A. *et al.* (1999). Exotic plant species invade hot spots of native plant diversity [review]. *Ecol. Monogr.*, 69, 25–46.
- Stohlgren, T.J., Barnett, D.T. & Kartesz, J. (2003). The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.*, 1, 11–14.
- Taylor, B.W. & Irwin, R.E. (2004). Linking economic activities to the distribution of exotic plants. *Proc. Natl Acad. Sci. USA*, 101, 17725–17730.

- Vellend, M. (2001). Do commonly used indices of beta-diversity measure species turnover? *J. Veg. Sci.*, 12, 545–552.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996). Biological invasions as global environmental change. *Am. Sci.*, 84, 468–478.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494–499.
- Whittaker, R.H. (1972). Evolution and measurement of diversity. *Taxon*, 21, 213–251.
- Wilson, J.A. & Shmida, A. (1984). Measuring beta diversity with presence-absence data. *J. Ecol.*, 72, 1055–1064.

#### SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Sample area and principal component analysis of climate variables.

**Appendix S2** The relationship of  $J$  to latitude, longitude and climate distances.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.00982.x>

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