

Species–area curves, homogenization and the loss of global diversity

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ABSTRACT

Species–area relationships have been widely used to examine the latitudinal gradient in species diversity, the effect of habitat loss on species diversity and the impact of exotic species on species diversity. Using species–area curves, Rosenzweig concluded that the spread of exotic species will not affect long-term global diversity much. We disagree with this conclusion on several grounds. First, total terrestrial area is larger than any of the provinces that make it up. This makes extrapolation necessary to predict global diversity using species–area curves, and extrapolation is statistically unjustifiable. Second, z , the slope of the species–area relationship, does not necessarily equal 1, as Rosenzweig assumes. Third, the amount of variation in species diversity explained by area is small and the prediction intervals around the estimated global diversity are likely to be too large to be used for prediction. Fourth, complete homogenization of the world's biota is unlikely to occur, which makes the prediction of global diversity in the steady state even more difficult. This also makes the predicted transitional regional diversity lower than under complete homogenization. Finally, and perhaps most importantly, we believe that focusing on species diversity is not the best way to think about the impact of homogenization. Instead, we need to focus on the impact of invaders on the abundance and distribution of native species and on the functioning of ecosystems.

Keywords: exotic species, global and regional species diversity, homogenization, species–area curves.

INTRODUCTION

One of the few laws in ecology is that there is a relationship between the size of an area and the number of species that reside in it (Schoener, 1976). This relationship can be described by a species–area curve, which plots the number of species, S , as a function of area, A . The function that best describes this relationship varies (Connor and McCoy, 1979), but one commonly used form of this relationship is $S = cA^z$, where c and z are constants (but see Connor and McCoy, 1979; Crawley and Harral, 2001). Species–area curves have been used to examine the latitudinal gradient in species diversity (Rosenzweig, 1995), the effect of

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habitat loss on species diversity (Pimm *et al.*, 1995) and the impact of exotic species on species diversity (Brown, 1995; Vitousek *et al.*, 1996; McKinney, 1998; Rosenzweig, 2001). Rosenzweig (2001) uses species–area curves to determine how the introduction of exotic species by humans will affect regional and global species diversity. He concludes that the spread of exotic species will: (1) increase regional diversity in both the short and long term; (2) decrease short-term global diversity; and (3) not affect long-term global species diversity much. The last conclusion, if true, suggests that invasion ecologists and the general public who are interested in preserving global biodiversity have little to fear. However, we do not think that some of Rosenzweig’s conclusions are necessarily true and, even if they were, we believe that he is not addressing the relevant questions in invasion biology. In this paper, we outline several methodological and conceptual problems in Rosenzweig’s paper and remind ecologists that exotic species present a real threat to native biotas.

One important feature of species–area curves is that the slope, z , depends on the overlap in the species composition of the localities used to draw the curve. When localities share many species, there is a ‘slow’ increase in the number of species with area, and z will be relatively small. Alternatively, when localities share just a few species, there is a ‘faster’ increase in the number of species with area, and z will be relatively high. Examples of the former are species–area curves constructed using localities belonging to a single biogeographic province (usually termed ‘intra-provincial’ curves). Examples of the latter case are curves constructed using localities belonging to different biogeographic provinces (usually termed ‘inter-provincial’ curves). Figure 1 shows two intra-provincial curves and one inter-provincial curve and highlights their major differences.

EXTRAPOLATING INTER-PROVINCIAL CURVES

Previous studies (e.g. Vitousek *et al.*, 1996) have used intra-provincial species–area curves to examine the impact of homogenization (i.e. creation of the ‘New Pangaea’) on global

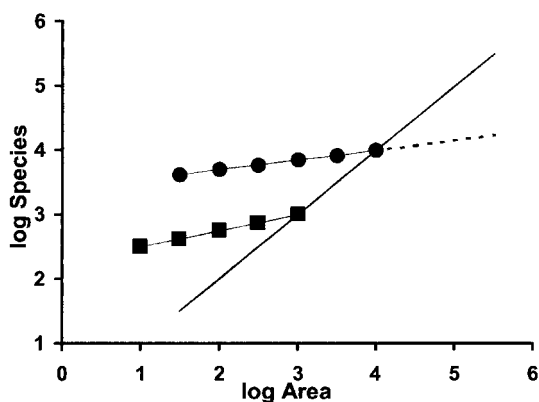


Fig. 1. A schematic plot showing an inter-provincial curve and two intra-provincial curves. The inter-provincial curve (solid line) plots the number of species in different biogeographical provinces. The island (■) and mainland (●) intra-provincial curves show the number of species on isolated islands and on portions of a mainland (or nearby islands), respectively. The dashed line represents an inappropriate extrapolation of the mainland intra-provincial curve to areas larger than the size of the province. The slope of each line is the z -value and is obtained by linear regression when both axes are log-transformed.

diversity. Rosenzweig (2001) claims these studies are flawed. To determine the effect of homogenization of the earth's biota on global and regional diversity, Rosenzweig argues that an inter-provincial curve should be used. Although Rosenzweig correctly argues that intra-provincial z -values cannot be used to examine the impact of homogenization, we are not convinced that inter-provincial curves are a correct approach for two reasons. First, the total global terrestrial area (the size of the New Pangaea) is larger than that of any of the provinces that make it up. This means that Rosenzweig must extrapolate the results of his regression analysis beyond the range over which the data were collected. However, Zar (1999) points out that extrapolation is statistically unjustifiable. Second, even if it were statistically justifiable to extrapolate from the set of provincial points to determine diversity for the New Pangaea, it is not empirically justifiable. Crawley and Hurrall (2001) convincingly showed that z -values vary with spatial scale. If Crawley and Hurrall are correct, then the z -value of the New Pangaea might differ from the z -value of the inter-provincial curves. Thus, there is no basis, either statistical or empirical, to support the assumption that inter-provincial curves can predict the effect of homogenization on global diversity.

Although we think it is unwise to do so, if one does use inter-provincial curves to predict global diversity in a homogenized world, there is no *a priori* reason to support Rosenzweig's assumption that the slope of the species–area curve, z , should equal 1. Instead of assuming any particular slope, we examined empirically derived inter-provincial curves for 13 taxa (Table 1). The mean slope for these taxa is 0.70, with a range of 0.38–1.15 and a 95% confidence interval of 0.56–0.84. If we set $z = 0.70$ and use Rosenzweig's approach, we find that complete loss of the world's isolating barriers will result in a 44.5% decrease in global species diversity, a value substantially higher than the 0% reduction Rosenzweig obtained by setting $z = 1$. Figure 2 shows how the impact of complete homogenization on global diversity varies with z .

Table 1. Inter-provincial curves for 13 taxa

Taxon	z -value	R^2	Reference
Higher plants	0.78	0.22	Gaston and Hudson (1994)
Amphibians	0.72	0.49	Gaston and Hudson (1994)
Birds	0.52	0.61	Gaston and Hudson (1994)
Mammals	0.90	0.77	Gaston and Hudson (1994)
Dragonflies	0.66	0.63	Gaston and Hudson (1994)
Tiger beetles	0.38	0.42	Gaston and Hudson (1994)
Dynastine beetles	0.42	0.22	Gaston and Hudson (1994)
Swallowtails	0.43	0.28	Gaston and Hudson (1994)
Arthropods on bracken fern	0.61		Rosenzweig (1995, p. 266)
Terrestrial cave-dwelling species	0.72		Rosenzweig (1995, p. 267)
Angiosperms	0.97		Rosenzweig (1995, p. 265)
Vertebrate frugivores	1.15		Rosenzweig (1995, p. 265)
Insects on British trees	0.89		Rosenzweig (1995, p. 267)
Mean \pm standard deviation	0.70 \pm 0.23		

Note: The z -value is the slope of the species–area curve and R^2 is the amount of variation in species diversity explained by area.

HIGH VARIATION IN SPECIES DIVERSITY

A more general criticism of the use of regression models to predict the effects of homogenization on global diversity is also statistical. Regression models usually explain only a small amount of the variation in species diversity. For example, we examined species–area curves for eight taxa that had R^2 -values associated with them (Table 1). We found that only 45.3% of the variation (range of 21.6–77.3%) in species diversity is explained by area. Four of the eight slopes are not statistically significant ($P > 0.05$). The small amount of variation explained might result from having a small number of provinces (maximum $n = 9$). However, the mean amount of variation explained for intra-provincial curves is not much higher, even though they tend to have more points. For the 100 species–area curves examined by Connor and McCoy (1979), the mean number of points is 22.1 (median = 18) and the mean amount of variation explained is 53.2% (median = 56.7%). Furthermore, the amount of variation explained does not depend on the number of points ($R^2 = 0.013$, $P > 0.25$). Perhaps we should not be surprised that area, by itself, does not explain more of the variation in species diversity among provinces. Although area is clearly important, many other factors (e.g. climatic or habitat diversity, evolutionary history, productivity) can strongly influence provincial species diversity (Ricklefs and Schluter, 1993). Selecting data sets that do not confound the area effect with other explanatory variables can be difficult. The best data sets are likely to come from provinces with climatically similar biomes (M.L. Rosenzweig, personal communication). But, because we want to predict global diversity, we *must* include areas with different climates.

Many authors fail to report the confidence or prediction intervals surrounding the estimate of species diversity as a function of area. Both intervals are likely to be large and flare near the endpoints of the curve (Haas, 1975). Thus, predictive ability decreases for very large or very small areas.

Furthermore, what we really want to predict is how many species will occur in a given area, not the mean number of species in all areas of a given size. This distinction is the difference between prediction intervals and confidence intervals. To predict the number of

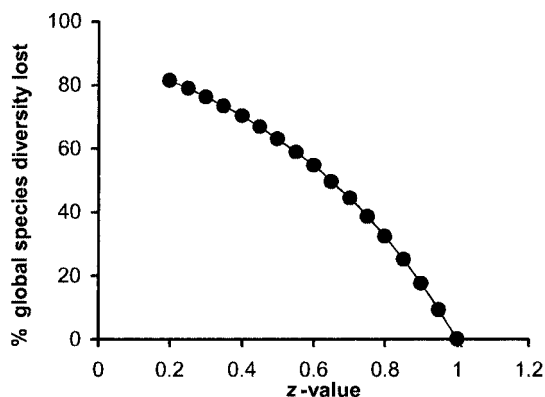


Fig. 2. The effect of varying z -values on the percentage of global diversity lost. If $z = 1$, as Rosenzweig (2001) suggests, then there would be no loss of diversity due to homogenization of the world's biota. But as z -values decrease, the amount of global biodiversity lost increases.

species on a single island of a given size, prediction intervals ought to be used, and they are even wider than confidence intervals (Myers, 1990).

We are not arguing that ecologists should abandon the use of species–area curves to predict changes in diversity. We are simply pointing out some important problems with their use. These problems are not trivial and have often been ignored. Thus, although we think area is among the most important influences on species diversity, we think that it is important to note that our ability to predict changes in species diversity is limited and that reporting point estimates without confidence limits can be misleading.

INCOMPLETE HOMOGENIZATION

Aside from the theoretical and statistical issues, we agree with Rosenzweig that increased transport among biogeographic provinces could be the same as removing geographic barriers and will increase biotic interchange. However, complete homogenization of biotas is unlikely to occur. Opportunities for homogenization have occurred in the past, but biotas have not been completely homogenized. Several authors have summarized past episodes of biotic interchange between land masses and bodies of water and found less than complete homogenization (Vermeij, 1991; McKinney, 1998; Mooney and Cleland, 2001). For example, during the Great American Interchange, which resulted from the isthmian land bridge that formed between North and South America during the Pleistocene, 11% of North American mammal genera invaded South America, whereas only 2% of South American genera invaded North America (Vermeij, 1991).

Current invasion episodes show a similar pattern. Some taxa are more likely to be transported and to establish populations outside their native ranges than others (Daehler, 1998; Pyšek, 1998; Lockwood, 1999; Vázquez and Simberloff, 2001). In addition, invasion rates between pairs of regions that interchange species seem to be asymmetric. For example, plant invaders in many parts of the world are mostly of European origin, but European ecosystems do not seem to be equally invaded by exotic plants (Crosby, 1986; Söyrinki, 1991; Pyšek, 1998; Arroyo *et al.*, 2000; Scherer-Lorenzen *et al.*, 2000).

Furthermore, empirical evidence shows that most species do not establish populations in their introduced ranges. The empirically derived ‘tens rule’ suggests that only about 10% of imported species are found in the wild, and 10% of those found in the wild establish populations (Williamson, 1996). Thus, only about 1% of the species transported across barriers would establish populations. The outcome of these processes will probably affect both global and regional steady-state diversity. But there is no way of knowing exactly what this effect will be because the world can no longer be characterized as either separate provinces or as a unified New Pangaea. In other words, species–area curves are useful in the black and white scenario in which the world’s land masses are divided into provinces or united in the new Pangaea. But in the grey world that is likely to emerge as a result of incomplete homogenization, species–area curves cannot accurately predict diversity.

We agree with Rosenzweig that within portions of the New Pangaea – the former biogeographical provinces – complete homogenization could lead to temporary increases in local diversity. The effect of incomplete homogenization on transitional local diversity is qualitatively similar. As with complete homogenization, all portions of the New Pangaea will increase in diversity, but portions with high native diversity will not increase as much as portions with low native diversity. Roughly, we can estimate that the transitional diversity in a given portion of the New Pangaea will be the native species diversity in the former

biological province plus 1% (because of the ‘tens rule’) of the species from all other former provinces. The transitional diversities for provinces assuming incomplete homogenization and no homogenization (present pattern) are shown in Fig. 3. With complete homogenization of the world’s biogeographic provinces, steady-state regional diversity would be high (the squares in Fig. 3). With incomplete homogenization, present diversity (the triangles in Fig. 3) will initially increase because of increasing immigration rates (the circles in Fig. 3). But after the initial increase in diversity, there are likely to be extinctions, and those extinctions will decrease diversity, but not so low as the present level of diversity. Of course, there might be a few new species formed by hybridization (see Mooney and Cleland, 2001, and references therein). With incomplete homogenization, we have no way of knowing what the steady-state diversity will be.

Finally, even if species–area curves predicted that homogenization will have no effect on global diversity, we do not think that focusing on a system property such as species diversity is the best way to think about the ultimate impact of biotic homogenization. Looking only at global or regional diversity misses the point. We need to look at the impact of invaders on the abundance and distribution of native species and on the functioning of ecosystems. Once we understand the impact non-native species have on native biotas, we will undoubtedly decide that some non-native species are worse than others. If Slobodkin (2001) and Rosenzweig (2001) prefer that ecologists avoid using value-laden terminology such as ‘bad’ and ‘good’ to describe some exotic species, then we suggest adopting terminology similar to that proposed by Orwell (1946): ‘All animals are equal, but some are more equal than others’. Some species that are more equal than others include: the Nile Perch, *Lates niloticus*, which has caused the extinction of over 200 species of endemic fish in Lake Victoria (Barel *et al.*, 1985; Kaufman, 1992); the predatory snail, *Euglandina rosea*, a

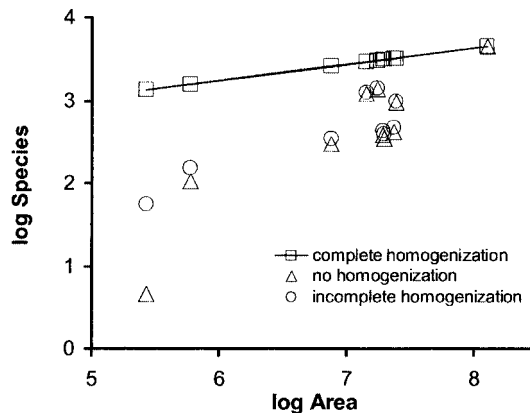


Fig. 3. Effect of incomplete homogenization of the world’s biota on regional (provincial) species diversity of mammals (data from Gaston and Hudson, 1994). The triangle in the upper right-hand corner shows the sum of the diversities for all provinces. The square in the upper right-hand corner is total global diversity assuming an inter-provincial slope of 1.0. The line connecting the squares assumes an intra-provincial z -value of 0.2. The figure shows that all areas will experience increases in species diversity with incomplete homogenization, but the gain in diversity among provinces is not the same. Provinces with fewer native species are predicted to gain a larger number of species, but they will not gain so much that they surpass any province that had more species before homogenization.

biological control agent that has caused many extinctions of native partulid snails on Pacific islands (Civeyrel and Simberloff, 1996; Williamson, 1996), the zebra mussel, *Dreissena polymorpha*, which threatens over 60 species of endemic mussel species in the USA (Ricciardi *et al.*, 1998); and the Argentine ant, *Linepithema humile*, which threatens native invertebrate taxa and potentially even coastal horned lizards in the USA (Ward, 1987; Cole *et al.*, 1992; Human and Gordon, 1997; Holway, 1998; Suarez *et al.*, 1998, 2000) and plants in South Africa (Bond and Slingsby, 1984). These ‘more equal’ species, together with the breaking down of barriers among provinces, are important threats to native communities.

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