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# The four questions: What does the introduction of exotic species do to diversity?

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## ABSTRACT

The breakdown of isolating barriers between biogeographical provinces will not have much effect on species diversity. In the short term, it will reduce global diversity, but increase local diversity. At steady state, the effects on global diversity disappear, but local increases remain. The real damage to diversity will come from shrinking the areas of the Earth that harbour wild species. The considerable damage exotic species have been known to do comes primarily from direct effects of particular introductions.

*Keywords*: alien species, extinction, Homogocene, New Pangaea.

## INTRODUCTION

Slobodkin (2001) reasonably and thoughtfully calls for ecologists to distinguish science from cant. Among the topics he treats is the exotic species 'problem'. He doubts that the influx of exotic species can be characterized as 'bad'. One exotic species that he believes may not be either bad or particularly damaging, however, is that ubiquitous treasure of avifaunas all over the world, *Passer domesticus*, the house sparrow. We have become used to them, he claims. And, he implies, well we might because they are damned successful. He concludes (after Sagoff, 1999), 'if a species is not clearly a medical or agricultural pest, let's learn to love it!'

The literature that frets about exotic species is rich and fearful, otherwise Slobodkin would not have included the matter in his essay. Introduced species have exterminated some natives (e.g. Pimm, 1987) or at least reduced their abundances by orders of magnitude (e.g. Roane *et al*., 1986). In fact, *Passer domesticus* is one such exotic, as contemporary witnesses have attested (e.g. Eaton, 1914).

Nevertheless, Slobodkin is perfectly correct. The words 'good' and 'bad' constitute value judgements and so lie beyond the bounds of science. If what we do were to turn the whole Earth into a cinder, no science could judge that a bad outcome. Were exotic species to reduce diversity by 30%, no ecologist could test whether that loss of species would be a bad thing. And the latter remains true even if we could prove that the loss of one of those species would deprive us of some wonder-drug or some ecosystem service crucial to our

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water supply. The belief that what people want is good is just that – a belief. So is the belief that what we need is good. So are our moral convictions, in particular that we are stewards of the planet.

Yet, I suspect most ecologists – perhaps even most people – share the conviction that loss of diversity is bad (Wilson, 1984; Kellert and Wilson, 1993). Interest in the consequences of species' introductions goes beyond the academic. So, in this paper, I turn away from considering individual exotic species – a hard problem, at least for now, which may turn out to be like trying to predict which molecules of water will boil off as we heat our coffee – and look instead at species diversity itself. Species diversity is a system property, and so we can make predictions about it by studying it as the product of a dynamical system.

I shall focus on those predictions I believe we can already rely on. They all concern what Gordon Orians terms 'The Homogocene' – a time – and what Hal Mooney calls 'The New Pangaea' – a place. That is, they consider the effects of our breaking down the geographical barriers that have long separated the Earth's biogeographical provinces, breaking them down by introducing species to provinces outside those in which they evolved, and doing it so rapidly that we blur or even obliterate all provincial differences.

In the spirit of Slobodkin's call for ecologists to behave like the scientists they are – most especially when addressing the public – this paper points out three value-free things that we may expect from the Homogocene. First, the question of how introductions affect species diversity is really four questions. Second, it has four answers. Third, compared to the influence of area, the exotic species effect is small.

## THE FOUR QUESTIONS

What will happen to species diversity as a result of the breakdown of biogeographical barriers? To develop answers to this question, we need to specify its spatial and temporal scales. There are two very dissimilar temporal and spatial scales. Hence, there are four questions:

- How will the steady-state global diversity differ in the New Pangaea?
- How will the steady-state diversity differ in a portion of the New Pangaea?
- What will happen to global diversity in the New Pangaea before it reaches its new steady state?
- What will happen to diversity in pieces of the New Pangaea before it reaches its new steady state?

### The steady-state questions

Creating a New Pangaea is essentially equivalent to making the area of the world's largest province equal to that of all its previous provinces combined, while simultaneously shrinking the others to zero. Thus, the steady-state effects of the Homogocene are area effects. We can answer them from species–area relationships.

As provincial area grows, species diversity increases almost linearly (Rosenzweig, 1999). Assuming precise linearity, homogenizing the world into a single province will have no impact on its global steady-state species diversity. The proof is trivial. Let

$$S_i = CA_i^z$$

where $S_i$ is the number of species in an area $i$, $A_i$ and $z$ is the traditional symbol for the curvature of the power equation for SPARs (Rosenzweig, 1995). Linearity means $z = 1$ and $S_i = CA_i$.

Recalling that the very definition of separate provinces declares their species to be non-overlapping, we obtain:

$$\Sigma S_i = C \Sigma A_i$$

So, the diversity of a large province whose area is the sum of several small ones is equal to the sum of the diversities of the several smaller provinces. Creating a New Pangaea does not change the steady-state species diversity of the world. That conclusion is not strictly true if $z \neq 1$. But it deviates little unless $z$ is far from 1.

Samples of areas within a province, however, conform to a much smaller $z$-value. Their SPARs tend toward $z$'s between 0.1 and 0.2 (Rosenzweig, 1999). Combining several intra-provincial SPARs with the inter-provincial one, we obtain a pattern somewhat like the rail spurs of a freightyard (Fig. 1). From it, we determine that any area contained within a province will echo the diversity of its province as a whole (Rosenzweig and Ziv, 1999). In other words, if aggregating provinces were all we humans were doing, the species diversities of sub-areas within the New Pangaea would exceed (!) those of any current province. One can easily calculate the equation of the echo pattern to obtain the prediction of diversity increase compared to each of today's provinces (Rosenzweig and Ziv, 1999).

Of course, the Earth will take quite some time to attain its new steady state. Thus, we cannot expect to obtain data to validate our prediction. Moreover, in the discussion, I note

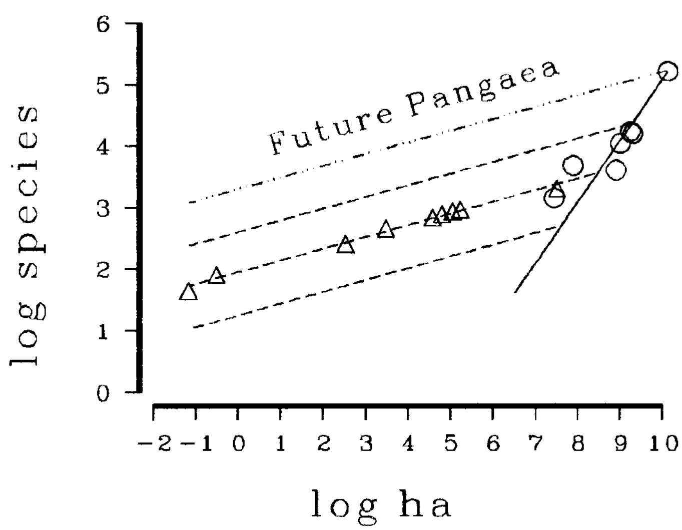


**Fig. 1.** Species–area curves at two scales. The inter-provincial scale is the steep, solid line. It is drawn with a slope of 1.00 to emanate from the world's terrestrial plant species diversity (circle at upper right). The other circles come from entire provinces or large portions of them, but have not been used to draw the line. The shallower-sloped, dashed lines follow the results of Dony (1963) for Britain. They all have a slope of 0.19 but emanate from various province sizes. Dony's actual data appear as triangles. The predicted curve for a New Pangaea (all other things being ignored) is the highest line paralleling Dony's (dots and dashes).

that we never will reach the steady state predicted solely from considering provincial homogenization; other processes more consequential than homogenization will drive diversity away from that state. Nevertheless, this prediction is so at odds with the literature that I have to digress and compare it to what many others have come to accept.

Frank Preston was one of the first to notice that $z$ changes with geographical scale. He published a figure tracing bird diversity from a house lot to the entire world (Preston, 1960). To predict that homogenization will deplete species diversity, you take the quasi-linear middle segment of his figure and extrapolate along a straight line to a point over the area of the entire Earth (Fig. 2). This indeed predicts disaster, but the prediction is totally unwarranted.

The problem is that SPARs, mathematically speaking, have a non-Abelian property. They are determined hierarchically, in one direction, from the large to the small scale. At the large scale, processes of speciation and extinction set provincial diversity. From these, the province achieves its steady state. Smaller areas simply echo the results at the larger scale (Rosenzweig and Ziv, 1999).

If one were to begin with small pieces of a province and then try to extrapolate beyond the province-size from which the small pieces come, one must assume that the extrapolated larger province shares the rate curves that characterize the smaller province. But it does not share these curves. The larger province will have a higher speciation rate curve or a lower extinction rate curve, or both (Rosenzweig, 1995). Hence, the extrapolated segments are simply unreal. To build from a smaller province to a larger one, one must follow the interprovincial SPAR, not the intra-provincial one.

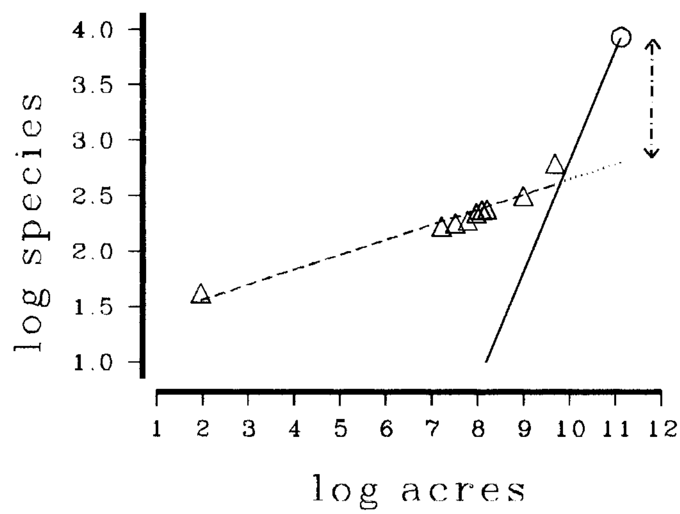


**Fig. 2.** False extrapolation of intra-provincial SPAR leads to the prediction that the Homogocene will be a time of depressed species diversity. The SPAR (dashes) depicts bird diversities in the Nearctic (Preston, 1960), beginning from the area on which the Preston Laboratory sat. The inter-provincial SPAR is drawn southwestward from the area and bird diversity of the entire terrestrial world (circle) with a slope of 1. The extrapolation (tiny dashes) appears as an extension to Preston's SPAR. It leads out to the underestimate of the world's bird diversity during the Homogocene, an underestimate whose magnitude is the vertical distance between the extrapolation and the inter-provincial SPAR.

### The transitional questions

Before global diversity reaches its new steady state in the New Pangaea, many new interactions will need to sort themselves out. Many will cause extinctions. We know this because many already have. So this is not a prediction in the strictest sense; it is merely an extrapolation.

While these extinctions are going on, nothing is happening to advance the rate of speciation. Thus, the extinctions bring us a net loss of species in the world (Rosenzweig, in press a).

We cannot say the same thing at the local scale. Here, even before diversity reaches its new steady state, we may expect increases. Operationally, these increases come about because we are introducing new species to areas faster than those new species exterminate natives. If that sounds like the language of island biogeography, it should. It involves precisely the same kind of thinking. During the Homogocene, each area within an old biogeographical province receives its species from a much larger pool. That raises its 'immigration' rate curve, in turn leading to an increase in diversity.

Meanwhile, the newly introduced species may cause extinctions of the natives. Shouldn't that counterbalance the increase in the immigration rate? No. The extinctions happen following an increase in diversity. This is entirely consistent with a single extinction rate curve having a positive slope (as in island biogeography). I know of no evidence, theoretical or empirical, to suggest that the position of this extinction rate curve should change.

Given this sort of reasoning, one can also say that the effects of drawing introductions from a larger pool should be inversely related to the size of the old provincial pool. Thus, local pieces of the most diverse of the old biogeographical provinces ought to get much smaller boosts than those of the least diverse old provinces. Yet both will get boosts.

The literature already documents local diversity increases that exotic species have contributed to (Mooney, in press). Nevertheless, the extinctions that an introduction brings about should take a while. During the transition, both the exotic and the native will turn up in surveys. One might then imagine a caveat: Perhaps, the observed local diversity boosts will turn out to be ephemeral?

I do not think so. First, many introductions have not caused extinctions of natives. Second, we have already noted that local diversities are headed for much higher steady states as a result of the advent of the Homogocene (Fig. 1 shows this). The observed local increases are stepping stones towards that result.

## THE RELATIVE IMPORTANCE OF THE HOMOGOCENE

The answers to the four questions may surprise you. At first, New Pangaea will lose species diversity but, after a while, those losses will be repaired – at least with respect to the number of species. Meanwhile, pieces of New Pangaea will gain species diversity both in the short term (under the influence of island biogeographical dynamics) and in the long term (as speciation repairs the losses to the entire species pool). These answers underscore the importance of Slobodkin's warning: Let the science speak for itself. Do not encumber it with the answers you would prefer it to have.

But make no mistake, our answers do not mean that what we are doing will bring any increases in species diversity. Not in the long term or short term. Not locally or globally. They mean only that the breakdown of isolation between the separate biogeographical provinces does not, *in itself and by itself*, pose a permanent threat to global species diversity. Instead, that loss of isolation, considered as an independent variable, will actually promote increases in local species diversity.

However, such increases will happen on only the tiniest and (previously) most isolated islands. Everywhere else, other influences on species diversity promise to dwarf those caused by the breakdown of biogeographical barriers. Surely the most threatening of those is loss of global area. We are not simply creating a new Pangaea, we are creating a new, greatly shrunken Pangaea (Rosenzweig, in press a).

The New Pangaea's threat to global species diversity disappeared because we looked at the species–area curve among provinces. But the same curve predicts the effect of area-loss itself. The new shrunken natural world of the Homogocene will have a depressed speciation rate curve that will cost it species diversity in direct proportion to its loss of area. That is the root of the mass extinction on which we are now embarked. To stop it, we must learn to reconcile our use of habitat with its use by wild species (Rosenzweig, in press b).

Furthermore, our answers do not deal with diversity at any level other than that of the species. Although the New Pangaea portends no substantial changes in species diversity, it will help to bring about substantial reductions in both generic diversity and other higher diversity levels. There are two ways to understand this.

Mechanically, we can derive it, as before, from a collector's curve. The genus–area curve for separate biogeographical provinces is not linear. It has a $z$-value substantially less than 1 (Flessa, 1975). Hence, a biogeographical province composed of the collection of biogeographical provinces will have fewer genera than did the set of separate provinces (Rosenzweig, 1995).

The mathematical formalism of the latter paragraph is but another way of stating the biologically obvious. Separate provinces may have separate species, but they often share genera and families. That is what keeps $z$-values below 1. On the other hand, when continents lose their independence, entire endemic families may vanish if all their ecological vicars are replaced by those of immigrant families (Simpson, 1950).

Finally, I note that individual exotic species have certainly created problems for ecosystems and for human beings, problems that have nothing to do with diversity at any level. Undeniably, some exotic species have done and are doing substantial, objective ecological damage. Slobodkin himself enumerates many: zebra mussels in North America; red fox, house cat, cane toad and European rabbits in Australia; house mouse, black rat and Norway rat in most of the world; a host of insect pests. Introduced species have clogged waterways and sapped the earth of moisture. Introduced species have damaged our crops. And, of course, introduced species have brought new diseases to *Homo sapiens* – bubonic plague to people in Europe and the Middle East being but the most infamous case, a case lavishly and tragically supplemented by many others, including the HIV virus and the several species of malaria and their mosquito vectors. Exotic species may not threaten overall species diversity, but they have proven again and again that we have other reasons to fear them.

## ACKNOWLEDGEMENTS

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