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COMMENT

Ecology should take credit for its accomplishments: a reply

Michael L. Rosenzweig*

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Methinks that Collins, Vázquez and Sanders (CVS) doth protest too much (*Evol. Ecol. Res.*, **4**: 457–464). Camouflaged among the thorns of its criticisms is its agreement with almost all of my paper (Rosenzweig, 2001a, *Evol. Ecol. Res.*, **3**: 361–367). It agrees implicitly that the influence of homogenization is a complex set of questions. It agrees that four of them address species diversity:

- What will homogenization do to the steady state of global species diversity?
- What will it do to local steady states?
- What will happen to global diversity in the interim (before it reaches a new steady state)?
- What will happen to local diversity in the interim?

Not only does CVS agree with the questions (more than half the battle), it also agrees with my answers to all but the first. In fact, regarding even steady-state global diversity (that first question), it does agree that the answer previously contained in the literature (and which I have often heard repeated by fine global ecologists in seminars) is an unjustified extrapolation from one scale to another (Vitousek *et al.*, 1996, *Am. Sci.*, **84**: 468–478).

I suspect that the authors would also agree with me that the threat of homogenization to global steady states at taxonomic levels above the species level is likely to be quite real. But they did not mention that, so I cannot be sure.

I agree with CVS that only a small fraction of exotics cause changes that are ever likely to be interpreted as serious or threatening. I also agree that this small fraction should not be ignored. Nor should we ignore the academic questions associated with understanding why this fraction is small and why some exotic species do cause so much change.

In addition to my remarks in 'The Four Questions', I have expressed my concern elsewhere (Rosenzweig, 2001b, *Proc. Natl. Acad. Sci. USA*, **98**: 5404–5410). And I successfully argued (not without some forceful and respectable opposition) for an index of environmental quality that, in essence, gives localities demerits for harbouring exotic species at the expense of natives (National Research Council, 2000, *Ecological Indicators for the*

* e-mail: scarab@u.arizona.edu

Nation. Washington, DC: National Academy Press). Towards the end of a forthcoming book (Rosenzweig, in press, *Embracing Nature: Redesigning Our World can Save Earth's Species*. Oxford: Oxford University Press), I even characterize the threat as 'the exotic dagger'. Unable to disguise my feelings, I therein call house sparrows and European starlings 'avian cockroaches' and opine that 'Perhaps Tom Lehrer was slightly wrong when he chanted, "It's not against any religion to want to dispose of a pigeon". But only slightly'.

So, exotic species are a hot-button public issue likely to attract attention and support for ecology and conservation biology. But that is all the more reason to make sure that any dire warnings about exotics emanate solely from scientific logic, and that we never substitute our own aesthetic sensibilities, moral judgements or theology for such logic. In the long run, we maximize public support of science if, when we are wearing our (virtual) white coats, the public can trust us to restrict what we say to our scientific opinions, and not cloak our value judgements with the mantle of those white coats.

Keeping the need for disinterest in mind, I tried scrupulously to do nothing but report the results of my research on the exotic threat. I therefore do not apologize for the fact that my conclusions seem to diminish that threat (if only slightly). I contend that those conclusions are scientifically valid. In the same spirit of disinterest, I welcomed CVS's scientific views to the pages of *Evolutionary Ecology Research*.

Nevertheless, I do find unsatisfactory much of what CVS has to say about the effect of homogenization on global species diversity. In what follows, I organize my objections under five headings.

Is area a minor influence on species diversity? CVS says so. A judgement call, perhaps, but I cannot agree that a variable which they themselves claim accounts for an average of 45.3% of the variance can be characterized as explaining a 'small amount of variation'. If a group of medical researchers found a treatment that proved useful in extending the lifespans of 20% of patients afflicted with a single type of cancer, they would rightly trumpet their success in all the media and carry it into the halls of NIH to argue for more financial support. We ecologists must be prepared to take credit for our achievements too. And discovering the regularities of species–area relationships is among the most praiseworthy. It has taken a small army of investigators working diligently for two centuries. As CVS insists, other variables besides area do influence species diversity. But none is as well understood or as strong as area.

Beyond that, CVS makes the mistake of applying tests of significance to these regression studies. Statistical tests of hypotheses do require tests of significance. Statistical estimation of a parameter value does not. I used regression solely for the purpose of estimation. And nothing in CVS suggests that this was an error. Its complaint is that my estimate is premature, that we do not yet know enough to say that the inter-provincial z-value is approximately unity.

Is there a single z-value for inter-provincial species–area curves? What is it? I agree that we do not yet know the answers to either of these questions. But we do know quite a bit more than CVS suggests. Certainly, the theory of provincial diversity does not predict that inter-provincial species–area curves should have slopes of unity. In fact, it makes no absolute prediction of z whatsoever. But it does predict relative z (Rosenzweig, 1999, in *Advanced Theoretical Ecology: Principles and Applications*, edited by J. McGlade, pp. 249–281. Oxford:

Blackwell Science). It predicts that inter-provincial species–area curves should have slopes steeper than those of islands in distant archipelagos. The latter appear to be in the range 0.5–0.6 (Rosenzweig, 1995, *Species Diversity in Space & Time*. Cambridge: Cambridge University Press). For 10 years, I have worked to find inter-provincial data sets adequate for the estimation of z and I have yet to find one that falls below this threshold.

Make no mistake about the difficulty of obtaining adequate data sets. It is severe – much more so than CVS realizes:

- Good scientific practice demands that the influence of a variable be determined by varying it while others are held constant. When this is impossible, partial regression can compensate, but only if the data set contains enough points for a second signal to penetrate the noise – and this is almost never the case for a multi-province study. Hence, even though provincial diversity is influenced by more than area alone, we need data sets whose points come from provinces where those other influences are kept as close to constant as practical. That desideratum disqualifies most of the studies in the literature.
- Data should also come from complete provinces, or the estimate of slope will suffer. In theory, data could come from fractions of provinces, fractions adjusted so that their points lie on a line that exactly parallels the true inter-provincial SPAR. But of course doing that means already knowing what we are trying to discover – that is, the true slope of the inter-provincial SPAR. If we should guess wrong and use fractions of smaller provinces that tend to lie farther from the true SPAR than those of larger provinces, the slope will seem gentler than it really is. Conversely, if we use fractions of smaller provinces that are closer, the slope will seem steeper. Finally, if the distances of the fractions have no tendency to vary with province size, the mean estimate will not suffer, but unexplained variance will be high. Lawton's data on bracken-eating insects provide a good and relevant example (Lawton, 1999, *Oikos*, **84**: 177–192). No province contributes its entire area of bracken, except for New Zealand and Hawaii. (And Hawaii contributes no information about the slope because it has zero bracken-eating species.) I have examined these data and the variance about the regression is so very high that the estimate of z depends upon the method of regression. Excluding Hawaii, linear regression on the log-transformed values yields an estimated z of 0.59 ($R^2 = 0.78$); non-linear regression on the arithmetic values yields an estimated z of 1.17 ($R^2 = 0.72$).
- Nevertheless, we have found a few more useful data sets than CVS cites. A fossil plant set yields $z = 1.00$ ($R^2 = 0.94$; Rosenzweig, 2001b). Cerapachyine and ponerine ants of New Zealand, Oceania and Southeast Asia yields $z = 0.94$ ($R^2 = 1.0$; Rosenzweig, 2001b). Tropical freshwater fishes yields $z = 1.5$ ($R^2 = 0.99$; Rosenzweig and Sandlin, 1997, *Oikos*, **80**: 172–176).

In summary, one must admit that we do not know the precise value of inter-provincial z. However, it is not too speculative to say that it exists and most probably lies between 0.85 and 1.15. I stand by what I wrote (Rosenzweig, 2001a, p. 362): 'as provincial area grows, species diversity increases almost linearly'.

What is the effect of incomplete homogenization? The question I chose to answer in my work is 'What would be the impact of complete homogenization?' This is, after all, the question posed in the literature and in all the seminars I have heard on the issue. It seemed counterproductive to try to answer a different question. But – as the mathematical argument in my original paper shows – given an inter-provincial z of exactly unity, incomplete homogenization makes absolutely no difference.

On the other hand, to the extent that true inter-provincial z lies below unity, incomplete homogenization will reduce the damage done by breaking down barriers between provinces. That ought to be straightforward: if homogenization is disruptive, the less there is, the less disruption.

On the sin of extrapolation. Is extrapolation really such a boogey man? CVS notes that extrapolation is statistically unjustifiable. Why then did it not previously attack the extrapolation that indicts homogenization as a threat to long-term global species diversity? Why did it wait until my study concluded that it is probably not a threat? Could it be that the sin I have committed is my answer and not my method?

Furthermore, although, statistically speaking, extrapolation may be unjustifiable, scientifically speaking, it may be quite alright. If the detected pattern was predicted by a (deductive) theory, or if its cause can be understood as the outcome of established scientific mechanism, then the scientist may justifiably extrapolate. In fact, scientists often do. CVS itself supplies an example. Calculating that a mere 1% of introduced species have become well-established so far, it extrapolates that 1% into the future as if 1% were an immutable constant.

The case of the species–area curve is perhaps better suited to demonstrate the value of extrapolation in science. Species–area curves are a lot more than mere statistical patterns. We know a great deal about the biological processes that lead to them. These explain why species–area curves should exist in the first place and why they vary in slope with temporal scale (Rosenzweig, 1999). Moreover, the link between area and diversity dynamics was forged by a theory 25 years ago, a theory based on the relationship of area to speciation rates and extinction rates (Rosenzweig, 1975, in *The Ecology and Evolution of Communities*, edited by M. Cody and J. Diamond, pp. 121–140. Cambridge, MA: Harvard University Press). As long as we believe that speciation and extinction will work the same way at the scale of a sixth of the surface of the earth (i.e. its entire terrestrial surface) as they do in today's terrestrial provinces, we have no reason to suspect a change in the patterns they produce.

And we have good reasons to suspect that these processes will not change:

- The inter-provincial species–area curve for northern hemisphere seed plants comes from 11 well-worked time intervals during the past 400 million years (Tiffney and Niklas, 1990, in *Causes of Evolution: A Paleontological Perspective*, edited by R.M. Ross and W.P. Allmon, pp. 76–102. Chicago, IL: University of Chicago Press; Rosenzweig, 2001b). During this period, shallow seas repeatedly advanced and retreated, causing the terrestrial area available in the hemisphere to vary from 33 million to 80 million km^2. The latter extent is about 60% of the entire land surface of the globe (excluding Antarctica). The species–area curve that results from treating these 11 data sets as different provinces separated by time has a z-value almost exactly equal to unity (whether it is taken with a univariate regression or a multiple regression).
- The ubiquity of the dynamics that lead to inter-provincial z-values near unity underlies the echo pattern of species diversity. These are the nearly straight lines that commonly

result when local diversity is plotted against regional diversity (Rosenzweig and Ziv, 1999, *Ecography*, **22**: 614–628).

- The rate at which new species accumulate in the fossil record of marine invertebrates strongly suggests that speciation and extinction have been working at much the same rates for over 500 million years (Rosenzweig, 1998, in *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, edited by M.L. McKinney and J.A. Drake, pp. 311–348. New York: Columbia University Press).

Thus we have a rule that provides a satisfying explanation for modern and ancient patterns and is known to operate at scales ranging from 0.2% (New Zealand) to 60% of what is possible. It would appear rather conservative to extrapolate it less than an additional half-order of magnitude.

But, in fact, it is no extrapolation at all. The true scales here are the temporal scales that characterize rate processes. The areal scales merely correlate with them. So, when I predict that a New Pangaea will have an unchanged steady-state diversity, I am merely saying that I have no reason to suspect that its biological processes will differ from those that now rule life. That is hardly a novel or a bold conjecture.

What is important? My opinion differs substantially from that of CVS. Of course we know that some exotics in some locations dominate abundances and diversity. Therefore, the study of exotic impacts is academically interesting. But recuperation from malignant introductions is an expensive, frustrating undertaking that is rarely successful (e.g. Wilcove and Chen, 1998, *Conserv. Biol.*, **12**: 1405–1407). So I believe the best way to address the practical problem is to redouble efforts to keep the critters out in the first place. Meanwhile the question of how homogenization should affect global steady-state diversity is equally interesting. That we have advanced fairly far along the road to its answer ought not be a reason to diminish the achievement.