Explaining Latitudinal Diversity Gradients

DIFFERENCES IN MEASURED RATES OF SPECIation and extinction among living species are commonly used to explain latitudinal diversity gradients. The logic is straightforward: the higher the net diversification rate (the difference between the speciation and extinction rate), the greater the number of species. In this vein, J. T. Weir and D. Schluter conclude from their recent study of birds and mammals that decreased extinction rates rather than increased speciation rates account for the higher net diversification rates posited to drive latitudinal diversity gradients ("The latitudinal gradient in recent speciation and extinction rates of birds and mammals," Reports, 16 March, p. 1574).

However, speciation and extinction rates may have little bearing on the cause of latitudinal diversity gradients. Although we have only a poor understanding of what controls species numbers, it is clear that resource availability is of critical importance, and in particular, that the harshness (and reduced area) of the poles limits population numbers. That is, the polar carrying capacity—the number of species that can be supported—is less than that of equatorial regions, and thus we should expect a latitudinal biodiversity gradient. Critically, rates of speciation and extinction do not control carrying capacities, but only reflect rates of species turnover, and the rate at which biotas reapproach their carrying capacities in response to perturbation, or as their carrying capacities shift in response to changing biotic and abiotic influences.

Under this framework, Weir and Schluter's exciting discovery that origination and extinction rates for birds and mammals increase with latitude may have little bearing on the reason that there are latitudinal diversity gradients. Instead, their data suggest that the frequency of extinction and replacement for these animals has been higher at high latitudes than at lower latitudes. This observation implies that ecological disturbance is more frequent, or has greater impact, at higher latitudes, consistent with the greater effects of the Plio-Pleistocene glacial cycles at high latitudes, as Weir and Schluter note.

If we are to explain latitudinal diversity gradients, we need to focus more on the determinants of carrying capacities, and less on the rates at which species turn over, or on how quickly species numbers adjust to

perturbation or to changing carrying capacities.

CHARLES R. MARSHALL

Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA. E-mail: cmarshal@oeb.harvard.edu

Response

THE STARTING POINT OF OUR STUDY WAS THE previous observation that net diversification rates are higher in the tropics than in the temperate zone (*1*, *2*). This is unexpected if species diversity is at equilibrium, which instead predicts the same average diversification rates everywhere within surviving lineages.

Marshall has not defined "carrying capacity" or its criteria, but his use of the concept suggests an analog to the carrying capacity constant in simple theories of population growth under resource limitation. Yet, although a population carrying capacity might exist on paper, its evidence is typically only that populations are regulated within wide bounds rather than exploding or going extinct (*3*, *4*). Real populations fluctuate according to vagaries of birth and death, and ecologists continue to find clues to the determinants of population size in measurements of these vital rates. Similarly, in the evolutionary process, species diversity is certain to be influenced by the vagaries of past speciation and extinction rates (*5*, *6*). Therefore, measurements of these rates will be useful in understanding present and future species numbers.

The idea has been suggested before that a greater "species carrying capacity" might explain higher species diversity in the tropics compared with the temperate zone (*6*). Unfortunately, the main evidence for a higher species carrying capacity in the tropics is the greater number of species there. At the moment, we are completely unable to explain why, in principle, the numbers of species of birds or plants that can be supported in the temperate zone should not be much greater than the current numbers. Except at the poles, the density of individuals is not much less in the temperate zone than in the tropics (*7*, *8*). What we can record are the frequent disturbances to the temperate zone that have likely knocked back the numbers of species. Our estimates of the impact of these disturbances on species turnover agree with other sources of evidence that point to the influence of extinctions on global patterns of biodiversity (*9*, *10*).

DOLPH SCHLUTER AND JASON WEIR

Biodiversity Research Center and Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

References

1. M. Cardillo, C. D. L. Orme, I. P. F. Owens, *Ecology* **86**, 2278 (2005).
2. R. E. Ricklefs, *Ecology* **87**, 2468 (2006).
3. A. R. E. Sinclair, J. M. Fryxell, G. Caughley, *Wildlife Ecology, Conservation and Management* (Blackwell, Malden, MA, 2006).
4. W. W. Murdoch, *Ecology* **75**, 271 (1994).
5. R. E. Ricklefs, D. Schluter, Eds., *Ecological Communities: Historical and Geographical Perspectives* (Univ. of Chicago Press, Chicago, 1993).

6. G. G. Mittelbach *et al.*, *Ecol. Lett.* **10**, 315 (2007).
7. D. J. Currie *et al.*, *Ecol. Lett.* **7**, 1121 (2004).
8. B. J. Enquist, K. J. Niklas, *Nature* **410**, 655 (2001).
9. B. A. Hawkins, J. A. F. Diniz, C. A. Jaramillo, S. A. Soeller, *J. Biogr.* **33**, 770 (2006).
10. D. Jablonski, K. Roy, J. W. Valentine, *Science* **314**, 102 (2006).