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References and Notes

1. H. S. Lenihan, C. H. Peterson, *Ecol. Appl.* **8**, 128 (1998).
2. H. S. Lenihan *et al.*, *Limnol. Oceanogr.* **44**, 910 (1999).
3. R. Zimmerman *et al.*, *NOAA Tech. Memo. NMFS-SE-FC-249* (1989).
4. M. A. Luckenbach, R. Mann, J. E. Wesson, Eds., *Oyster Reef Restoration: A Symposium and Synthesis of Approaches* (Virginia Institute of Marine Sciences Press, Gloucester Point, VA, 1998).

People and Biodiversity in Africa

GROWING HUMAN PRESSURE ON EARTH'S biodiversity demands rapid development of a sound scientific and economic foundation for conservation. Andrew Balmford and coauthors, in their report "Conservation conflicts across Africa" (30 Mar., p. 2616), say that their analysis of African diversity patterns contradicts my earlier analysis and proposal for reconciling some of the conflicts between biodiversity conservation and human needs (*1*). Their claim of contradiction, however, is based on a misrepresentation of my analysis and conclusions.

In their analysis, they aggregate mammals, birds, snakes, and amphibians into a single group and compare the total number of species to human population density, whereas I focused specifically on plant diversity in relation to soil fertility and net primary productivity (NPP). I explicitly stated that many vertebrates, particularly large birds and mammals, have a diversity pattern very different from that of plants, and reach their highest diversity in areas with high NPP. This brings their conservation into direct conflict with agriculture, a point I have elaborated elsewhere (*2*).

This conflict is most acute in the developing world, where human population density is strongly correlated with soil fertility and NPP. Infrastructure for food storage and transport has reduced this correlation in most developed countries, where high-production agriculture and urban-based economies have shifted populations out of rural areas. Although the most productive lands will continue to be used intensively, lower human population densities may allow conservation of certain types of species, such as predatory birds, in these agricultural landscapes.

Balmford *et al.*'s analysis does provide a good example of the ubiquitous pattern of maximum diversity at intermediate levels of NPP, which is found in many types of organisms over a range of spatial scales (*2, 3*). However, their use of model estimates rather than measurements of NPP, and the low spatial resolution at which they evaluated diversity, raise questions about the relevance of their analysis to real conservation decisions.

"...more species will be saved if we use our understanding of ecology to minimize the human and economic costs associated with each species that we do save."

The most serious deficiency in Balmford *et al.*'s analysis is the failure to recognize that the diversity of different types of organisms reaches a maximum at different levels of NPP (*2, 3*), with the plant maximum typically at relatively low levels and the diversity of animal predators maximized at high levels. By combining all types of vertebrates, from salamanders and sparrows to eagles and elephants, into a single group, they ignore the fundamental differences among contrasting types of organisms and thus obscure the opportunities for a strategic approach to conservation that could maximize conservation of specific types of organisms while minimizing negative impacts on human welfare and economics.

There is no doubt that conservation will be more difficult and expensive in areas with high human population densities. There will be tradeoffs between human economies and natural ecosystems, and species will continue to become extinct. Nonetheless, more species will be saved if we use our understanding of ecology to minimize the human and economic costs associated with each species that we do save.

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References and Notes

1. M. A. Huston, *Science* **262**, 1676 (1993).
2. ———, *Biological Diversity: The Coexistence of Species on Changing Landscapes* (Cambridge Univ. Press, Cambridge, 1994).
3. S. I. Dodson *et al.*, *Ecology* **81**, 2662 (2000); D. J. Currie, *Am. Nat.* **137**, 27 (1991).

Response

HUSTON RAISES THREE ISSUES CONCERNING our evidence that across Africa, vertebrate species richness covaries with human population density, and that both variables exhibit a similar hump-shaped relation with NPP. First, regarding our modeled estimates of NPP, we used these because field measurements of NPP in Africa are scarce. They are also usually measured over periods that are too short, given the marked interannual variability in Africa's climate, to provide reliable estimates of average NPP levels over time scales that are relevant to biodiversity distribution patterns. Crucially, the modeled NPP values we used compare closely with observations for a range of test sites (*1*).

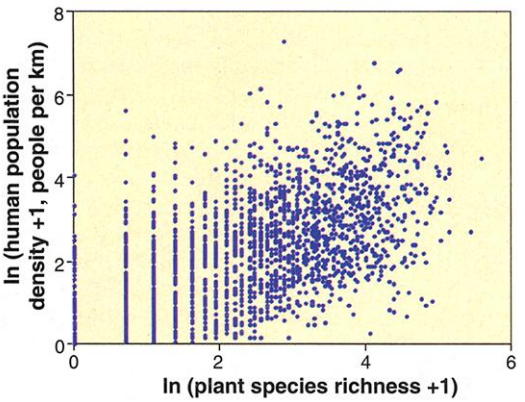
Second, Huston says that by combining data for all terrestrial vertebrates we "ignore the fundamental differences among contrasting types of organisms." Yet, functioning ecosystems require many functional groups, and hence, as conservationists, we are concerned with all biodiversity, rather than particular subsets of it. That said, in our original analyses we did test explicitly for between-taxon variation, but found little: Each of the four main groups of terrestrial vertebrates exhibited positive correlations across 1° grids between species richness and human density (*2*). Our results also hold when reexamined separately for 10 functional groups ranging from nectarivores to large carnivores: Species richness consistently covaries with the density of human settlement (*3*). As predicted by Huston, the relation between NPP and species richness of functional groups is variable. However, regardless of the exact form of the relation, species richness peaks at intermediate or high (and, critically, never at low) NPP (*3*).

Huston's third criticism is that although these patterns might be true for some heterotrophs, plants are different. However, preliminary analyses suggest that this is not the case. For the 2661 African plant species mapped to date by botanists at the University of York [(*4*); ~7% of the continent's total], the number of species in 1° grids correlates positively with human density (see the figure; Spearman rank correlation $r_s = 0.56$, $N = 1957$ grid cells; compare with $r_s = 0.54$ for terrestrial vertebrates). This continent-wide pattern is also confirmed within Kenya and South

Africa, where national human census data are most reliable (*5*).

Finally, although Huston says the plant richness–NPP relation should peak at low productivity [for which (*6*) provides no evidence], we found that the continent-wide pattern is weakly hump-shaped [regression using (ln + 1) transformed data: overall r^2 = 0.42, with r^2 values for NPP and NNP[2] of 0.36 and 0.06, respectively], with the peak at higher NPP values than was true for terrestrial vertebrates (10.7 compared with 9.3 tons of carbon per hectare per year).

Although we agree that continental-scale analyses need to be supplemented by detailed, landscape-level planning (*7*), we maintain that our findings reveal a fundamentally important and taxonomically consistent problem. Conservationists, development agencies, and policymakers must address this if their efforts to maintain Africa's biodiversity are to succeed.



Positive correlation. Human population density versus species richness for 2661 African plants (*4*). Variables were (ln + 1) transformed. The relation is similar to that for terrestrial vertebrates.

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References and Notes

1. F. I. Woodward, T. M. Smith, W. R. Emmanuel, *Glob. Biogeochem. Cycles* **9**, 471 (1995).
2. A. Balmford *et al.*, *Science* **291**, 2616 (2001).
3. See the supplementary table available at http://www.sciencemag.org/cgi/content/full/293/5535/1591/DC1; for all statistical methods, see (*2*).
4. J. C. Lovett, S. Rudd, J. Taplin, C. Frimodt-Moller, *Biodiv. Conserv.* **9**, 37 (2000).
5. S. Tokumine, dissertation, University of York (2000).
6. D. J. Currie, *Am. Nat.* **137**, 27 (1991).
7. G. Fonseca *et al.*, *Nature* **405**, 393 (2000).

CORRECTIONS AND CLARIFICATIONS

NEWS FOCUS: "Max Planck's meeting of the anthropological minds" by M. Balter (17 Aug., p. 1246). A description of genetic and linguistic studies of the peoples of the Caucasus, by Mark Stoneking and coworkers in Leipzig, was inaccurate. The study compared Armenians (who speak an Indo-European language) with other Cau-