

## Response to Comment on "Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule"

Contrary to the critique by Storch (1), the model that we presented (2) was not intended to be a comprehensive theory that could account for all patterns and processes of species diversity. It was intended to show that species richness in many groups of plants and animals has the same relationship to environmental temperature that metabolic rate has to body temperature. We offered a model based on the direct effect of metabolic rate on resource use, and thereby on population density, to illustrate one class of mechanistic process that could, by itself or in interaction with other processes, account for this pattern. We were well aware that this model could apply only to ectothermic organisms and not to endothermic birds and mammals.

We suggested that species richness of endotherms varies directly with abundance, which tends to be higher in warmer, more productive places, and that this might account for the pronounced decrease in species richness of birds and mammals from equator to poles. Storch (1) claims that this explanation cannot be correct because population densities of birds are lower in tropical than high-latitude environments. Few good comparative data exist on avian population densities; the data cited by Storch were collected from one tropical forest site in Peru (3) and one temperate forest site in New Hampshire (4). Differences in sample area and census meth-

ods complicate the comparison, but we agree that there were certainly many more species and lower average population densities per species—but not necessarily lower total densities of birds—in Peru.

A major problem, however, is that the data were collected only for breeding bird populations. Most of the breeding individuals at the temperate forest site, but not the tropical site, were migratory species that occur in New Hampshire only during the warm, productive summer. Some of these migrants travel as far south as South America, winter in tropical forests, and add to the densities and species richness of birds in low-latitude habitats. So, averaged over a year, a given area of tropical forest may well support about an order of magnitude more individuals and species of birds than a high-latitude temperate forest. Clearly, additional data on bird and mammal populations across the latitudinal gradient would be useful in understanding the patterns of species diversity.

In addition, Storch claims that we "did not provide any clue to a reliable causal understanding of the phenomena described." Applying metabolic scaling theory to ecology allowed us to give much more than "a quantitative description of several interrelated phenomena." It allowed us to make and validate precise quantitative predictions about how species diversity varies with tempera-

ture. The fact that the temperature dependence of species richness in several kinds of ectotherms is quantitatively almost identical to the temperature dependence of metabolic rate implies that (i) species diversity is powerfully influenced by metabolic processes—the uptake, transformation, and allocation of energetic and material resources in organisms—and (ii) much of the variation in species diversity is due to temperature, as a consequence of its effect on the kinetics of biochemical reactions and ecological interactions. Except for Rohde (5), ecologists trying to account for patterns of abundance, distribution, and diversity have generally not emphasized the pervasive influence of temperature and biological kinetics. We agree with Storch that we have not presented a complete and comprehensive theory of biodiversity, but we have shown that any such theory must include the fundamental influence of temperature on biological metabolism and ecological relationships.

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### References

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