TECHNICAL COMMENTS

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

Allen *et al.* (*1*) attempted to extend the energetic-equivalence rule (*2*): According to their theory, the total energy flux of populations is independent not only of body size but also of temperature. Because temperature positively affects metabolic rate (that is, the energy flux of an individual), population abundances of ectotherm species must be lower in areas with higher environmental temperature to satisfy the energy equivalence. If the total number of individuals in a community is also roughly independent of temperature, under the model of Allen *et al*., the species richness of a community must consequently be higher. Although the data presented in the study fit the quantitative predictions of the theory well, at least two problems prevent the theory from being entirely convincing.

First, because metabolic rate is related to external temperature only in ectotherms, the theory predicts that only these organisms will decrease their population abundances and increase species richness with temperature. But there is good evidence that the species richness of some endothermic animals—birds—is also positively related to temperature (*3*) and, moreover, that their population densities are lower in the tropics as well (*4*). There is also some evidence that low bird population abundance in the tropics compensates for their high species richness, exactly as the theory based on biochemical kinetics predicts for ectotherms. For instance, the total number of breeding birds in an Amazonian community is approximately equal to the number of birds in a temperate community of the same area, but the species richness is 10 times higher, and the mean abundance of individual species is consequently 10 times lower (*5*). Therefore, the relationship between temperature and species richness is more general than suggested by the theory of Allen *et al*. (*1*) and is not fully explicable by biochemical kinetics (*3*). The good quantitative fit could be due to some deeper relationship between energy flux and species richness that is not confined to ectotherms.

A second, even more important problem is that the authors did not provide any clue to a reliable causal understanding of the phenomena described. It is not clear why the population energy flux should be temperature independent (although the data seem to be consistent with that claim) or why individual populations in tropical areas or other places with higher energy input should not appropriate relatively larger amounts of energy. The only mechanistic explanation of higher species richness in warmer areas that Allen *et al*. mention is that based on a relationship between metabolic rate and mutation rate or generation time, but there is no reason that these rates should be quantitatively related to the resulting species richness such that energy equivalence emerges. (Note that the relationship between an increase in speciation rate and resulting increase in species richness is not linear.) Allen *et al*. therefore present a quantitative description of several interrelated phenomena, rather than any comprehensive theory based on first principles.

Any causal understanding of the documented quantitative relationships should include an explanation of why the higher energy input into an ecosystem is not followed by an increase of population abundances of resident species, and why it is instead followed by the increase of species richness. Such an explanation should explicitly account for the mechanisms of population regulation involved. One can imagine, for instance, that the amount of energy that can be appropriated by individual species populations is temperature independent because of peculiarities of density dependence (*6*) or that it is limited by constraints not directly related to metabolic rate. In that case, the extra energy could be appropriated by other species, and all the quantitative relationships would follow. However, the species richness would then be determined not by speciation and extinction rates but by intraspecific and interspecific competition controlling populations of coexisting species.

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