Metabolic Theory and Patterns of Species Richness[1]

Identifying and explaining biogeographic gradients in species richness is a long-standing preoccupation of ecologists. By and large, terrestrial species richness increases toward the equator and decreases with elevation, but most explanations of these patterns are phenomenological; they originate from statistical correlations whose significance is based on a trivial test of the null hypothesis that there is no relationship between richness and the hypothesized "causal" variable. The recent axiomatic derivation of the Metabolic Theory of Ecology (MTE) provides a notable exception: based on biochemical kinetics of metabolism, MTE presents a precise, quantitative prediction of how species richness should vary with (appropriately scaled) environmental temperature: linearly, with slope ≈ -0.65 (J. P. Allen, J. H. Brown, and J. F. Gillooly. 2002. "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule." Science 297:1545–1548).

In the focal Concepts and Synthesis paper for this Forum, Hawkins et al. test the predictions of MTE with 46 different data sets compiled for a variety of terrestrial plants, invertebrates, and ectothermic vertebrates; the geographic extents of these data sets range from a small region in Spain to continents and hemispheres. How might this confrontation between theory and data have come out? First, richness–temperature relationships all could be linear with slopes whose confidence intervals include –0.65. Such a result would be a powerful confirmation of MTE. Second, a few of the data sets might not fit the predictions. Such a result would support MTE and would highlight interesting situations in which ecological or evolutionary constraints might alter fundamental scaling relationships. For example, water availability or nutrient limitation may interact strongly with temperature in water-limited systems, leading to unexpected relationships between temperature and richness (Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a metabolic theory of ecology." Ecology 85:1771–1789). Last, most data sets could fail to support MTE. This is the result that Hawkins et al. find, and they conclude that MTE is a poor predictor of observed biogeographic patterns of species richness. Whether this result is due to shortcomings of MTE, inappropriate data, or different methods of statistical analyses is explored in further detail by Latimer and by Gillooly and Allen in their commentaries on Hawkins et al.'s paper.

My goal in assembling this Forum was first and foremost to provide a jumping-off point for future studies of MTE and species richness. Progress in this field will be most rapid when a theory whose structure is agreed upon is tested with standard methods and suitable data sets. These include: the correct scaling of temperature; a fixed and clearly defined activation energy of metabolism; whether to use ordinary least-squares (OLS) or reduced-major-axis (RMA) regression, and even whether a linear relationship ought to be assumed; and the appropriate taxonomic ranges and geographic scales of the data. It is critically important that all participants in this debate agree on core axioms and assumptions.

How we test theories depends on their structure and presentation. Brown et al. (2004: 1787) asserted that "[a] strength of [MTE] is that it makes explicit quantitative predictions based on first principles." Allen et al. (2002), Brown et al. (2004), and now Hawkins et al. use a strong, deductive approach to test MTE: Is the observed relationship between temperature and richness the same as that predicted by the theory? An inductive approach, in which theory is continually refined as more observations accumulate, provides opportunities for synthesis from which general theories may eventually emerge. Such an approach is cautiously advocated by Gillooly and Allen. Bayesian inference allows one to formalize induction. There is thus a certain irony that the hierarchical Bayesian reanalysis of Hawkins et al.'s data by Latimer fails to provide additional support for MTE as a mechanism underlying latitudinal gradients in species richness, *given the data at hand.*

A new theory generates much excitement, but this initial excitement can be tempered as the theory is scrutinized carefully and challenged by data. Synthesis emerges from the ongoing confrontation of theory and data, but its rate of emergence depends on the flexibility and open-mindedness of the participants. By sharing data and offering constructive critiques, the participants in this Forum not only have established the benchmark for future studies of processes underlying biogeographic patterns of species richness; they also have provided an example of how scientific theories evolve and develop.

—AARON M. ELLISON
Associate Editor-in-Chief

Key words: Bayesian inference; deduction; induction; latitudinal gradient; metabolic theory of ecology; species richness.

---

[1] Reprints of this 26-page Forum (including the Hawkins et al. Concepts and Synthesis paper) are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006, USA.