ronments, such as marine systems, and to smaller organisms such as plankton and bacteria.

Literature Cited

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2003. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548.

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.

Gelman, A., J. B. Carlin, and D. B. Rubin. 1995. Bayesian data analysis. Chapman and Hall, New York, New York, USA.

Hawkins, B. A., et al. 2007. A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. Ecology 88:1877–1888.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Kluge, J., M. Kessler, and R. R. Dunn. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Global Ecology and Biogeography 15:358–371.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Sterner, R. W. 2004. A one-resource "stoichiometry"? Ecology 85:1813–1816.

Thomas, A., B. O'Hara, U. Ligges, and S. Sturtz. 2006. Making BUGS Open. R News 6:12–17.

SUPPLEMENT

OpenBUGS code for statistical models (*Ecological Archives* E088-113-S1).

METABOLIC THEORY AND DIVERSITY GRADIENTS: WHERE DO WE GO FROM HERE?

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Introduction

Evaluating the Metabolic Theory of Ecology (MTE) of Brown et al. (2004) with respect to broadscale diversity gradients (see Allen et al. 2002, 2006) was the motivation of Hawkins et al. (2007). We used 46 data sets to test predictions for the slope(s) describing the relationship between species richness and temperature. The predicted slopes were found in very few data sets, leading us to question MTE as a general framework for understanding terrestrial diversity gradients. Latimer

(2007) reanalyzes some of our data sets using a Bayesian approach and supports our conclusions, whereas Gillooly and Allen (2007) [hereafter G&A] disagree with our approach and raise a number of epistemological issues regarding our evaluation of MTE. Here, we address these issues, focusing on the structure of theories and how a change in epistemological framework undermines the relative strengths of MTE.

Theories, Hypotheses, and Models

We view MTE as a general *theory*, defined as "a logical construction comprising propositions, some of which contain established information (axioms) while others define questions (postulates). The working part of

a theory provides the information and logical basis for making generalizations" (Ford 2002:43).

From a body of knowledge encompassed by a theory, *postulates* are derived that must be investigated to support the theory's generality (Ford 2002). Allen et al. (2002:1545) established one postulate, stating unambiguously that their extension of MTE "quantitatively predicts how species diversity increases with environmental temperature." Such clarity is rare among theories purporting to explain broadscale diversity gradients (but see Field et al. [2005]). Allen et al. (2002) and subsequently Brown et al. (2004) also presented their *hypothesis* for diversity gradients as a formal *model*, proposing that the relationship between ln-transformed richness and $1/kT$ (where k is Boltzman's constant and T is temperature in kelvins) has a negative relationship with a slope between −0.6 and −0.7 (in the 2004 version of the model). They also made numerous *data statements*, which define the scientific procedure for investigating a postulate by specifying the measurements to be taken, the data requirements, and the statistical tests to be applied (Ford 2002).

Allen et al. (2002) tested their model using seven data sets comprising both altitudinal and latitudinal gradients. Hawkins et al. (2007) simply expanded this test to a large number of broadscale data sets selected solely on the basis of data availability. The results were inconsistent with MTE predictions in most cases (see also Algar et al. 2007). In response, G&A claim that we oversimplified the theory and used the wrong methodology. However, we used the methods developed by Allen et al. (2002), and the model that we tested was exactly as described by Allen et al. (2002) and Brown et al. (2004).

G&A also argue that we misunderstand Allen et al. (2002), because we ignored later developments in MTE that provide an evolutionary and mechanistic basis for the theory (e.g., Allen et al. 2006). We strongly support evolutionary approaches to understanding diversity gradients (see, e.g., Hawkins et al. 2005, 2006, *in press*), but the newer models must be the subject of future tests. For now, we cannot find where in Allen et al. (2006) or G&A these new developments are said to invalidate Allen et al. (2002) and Brown et al. (2004), so we have to assume that slopes between −0.6 and −0.7 still constitute a valid prediction of their models. Adding a mechanism to a model based on the same theory should not change the basic patterns predicted by the model, unless one or the other is intrinsically wrong or incorrectly developed. As the more recent papers provide no new prediction for the relationship between richness and temperature, it is unclear how the new developments invalidate the conclusions of Hawkins et al. (2007). Alternatively, if the new work shows that the original prediction was not correct, then we agree that the MTE model presented in Allen et al. (2002) and Brown et al. (2004) is not an unequivocal explanation for diversity gradients. This leads us to the next issue: what assumptions must be met and what data statements are necessary to test a theory?

ASSUMPTIONS AND DATA STATEMENTS

To test a theory we first need to know when and where it applies. Clearly, MTE applies to ectotherms, but G&A say that we should exclude many groups of ectotherm organisms that are able to "maintain relatively constant body temperatures in different thermal environments," and thus the model only applies to "true ectotherms." Also, it is "not expected for groups that are narrowly defined" (G&A). Further, Allen et al. (2002:1547) say, "…we do not mean to imply that temperature is the only variable that affects biodiversity," which G&A reiterate. They recognize that other factors are important (see also Whittaker et al. 2001, Willig et al. 2003), and their stated purpose was to "only predict the slope of the diversity–temperature plots" (Allen et al. 2002:1547). This was also the purpose of Hawkins et al. (2007). Additional restrictive conditions with respect to MTE's applicability are also advanced by G&A: we should avoid areas with extreme water deficits and regions without a broad range of temperatures, although Latimer (2007) reports that the latter condition does not explain poor model fits. Taken together, the restrictive conditions lead to a revised claim that MTE explains richness gradients when it is not too hot, too dry, the wrong region, the wrong scale, or the wrong group. At this point, it is legitimate to question the scope and generality of the theory.

If a model is built on unrealistic assumptions, empirical data should rarely agree with it. The model of Allen et al. (2002:1546), stating that "the natural logarithm of species richness should be a linear function of $1000/T$" (or $1/kT$ in Brown [2004]), is based on several key assumptions (e.g., communities follow the energetic equivalence rule, and abundance and average body size are spatially invariant). Testing these assumptions thus requires detailed data on variation in body size and abundance at broad spatial scales. It is also difficult to know whether the assumptions are realistic, or how violating them affects the model's predictions (see Currie et al. 2004). G&A question our analysis because the data were not selected carefully to meet all of the assumptions, but it is clear that neither Allen et al. (2002) nor any of the subsequent papers were able to check the assumptions for the data that they used. Our data are at least equivalent to the broadscale data that they and others have used to support MTE. Therefore, if our data are questionable then all published analyses cited by G&A using broadscale data are equally questionable. Proponents should not dismiss nonconfirmatory results based on data quality, unless they subject results claimed to support their model to an equally rigorous evaluation of the data and consideration of underlying assumptions.

G&A's criticisms of our use of some data sets highlight that proponents must be much more explicit about data statements than they have been. We welcome the clarifications that they provide, but additional data statements are still needed. How do ecologists obtain the "correct" data? How should we test MTE predictions in

a given situation? It is obvious that data should lie in the model's domain, but these must be clearly defined: which taxonomic groups are appropriate; in what environmental conditions does it apply (e.g., what temperature range and water deficit); which measure of temperature should be used? These issues are critical if they want to generate a formal, testable theory for diversity gradients.

Another key issue regarding data statements concerns statistical methods. For example, should we use model I or model II regression? Proponents' claims are inconsistent on this: compare Allen et al. (2002) and Brown et al. (2004) and note that G&A introduce yet another method. Should we use spatially explicit regression models rather than nonspatial methods, or do these only increase uncertainty when correcting Type I errors due to spatial autocorrelation? Further, because multiple factors interact to affect biodiversity, should we generate models with many variables and use partial regression coefficients for temperature? If so, what variables must be included? Shifting to a multiple regression approach will also mean that multicollinearity will be a potentially serious problem (Graham 2003). Finally, and most importantly, the potential overlap of predictions of MTE and those of alternative models must be considered. This leads to our final point about confronting models with data.

Hypothesis Testing and Model Selection

We agree that MTE initially had an advantage over theories based on purely correlative methods. The attractive feature of the model of Allen et al. (2002) was that it provides a theoretical prediction that can be compared with observed slopes. Testing such predictions is usually done in a Fisherian-Popperian framework. However, G&A argue that this results in "unreasonably casting aside this young theory." Although this epistemological framework may indeed be questioned and alternative frameworks do exist (see Hilborne and Mangel 1997), it is widely accepted that the Fisherian-Popperian framework permits "strong" tests in ecology, as opposed to weak tests based on inductive curve fitting (see McGill 2003).

Hawkins et al. (2007) compared observed and predicted slopes using 46 data sets, further dividing nonlinear data into pieces to increase the chances of finding supportive slopes in regions where energy is expected to influence diversity strongly (Hawkins et al. 2003, Whittaker et al. 2007). Although many 95% CI intervals encompassed the predicted slopes, they also encompassed zero, giving the null hypothesis of no relationship between richness and temperature equal standing from a hypothesis-testing perspective. Further, the distribution of slopes was extremely broad and centered nowhere near −0.65. Ultimately, using OLS regression, only one of the 46 data sets was consistent with the coupled predictions of Allen et al. (2002) and Brown et al. (2004) that the relationship between

rescaled temperature and ln-transformed richness is both linear and has a slope near −0.65 (none were consistent using RMA regression). G&A accuse us of being too Popperian, but an acceptance rate of 0–2% offers minimal support for a hypothesis under any framework and casts serious doubt about the validity of the postulate. To sidestep this, G&A recommend a shift from a falsificatory to a confirmatory testing procedure. This is in part what Latimer (2007) did using a Bayesian approach, by finding a "consensus" slope for 23 of our data sets instead of testing individual slopes against the predicted value of −0.65. It is important to note that Hawkins et al. (2007) also used a similar approach by performing a meta-analysis for the same purpose, with results that were largely confirmed by Latimer's (2007) reanalysis. Even so, switching tests of MTE from a falsificatory to a confirmatory procedure also creates new problems, to which we now turn.

If predictions of MTE become vague and not subject to falsification, how does MTE differ from other theories (see Lavers and Field 2006)? G&A optimistically interpret our results as promising, despite the extreme range of slopes found. They note that, after controlling for the effects of other variables, one data set shows an "exponential increase of richness with temperature," arguing that this is consistent with the model of Allen et al. (2002). But it may also be consistent with most theories for geographical diversity gradients, highlighting the limitation of the confirmatory approach when multiple models make qualitatively similar predictions. We also consider a defense of MTE based on the "youth" of the theory to be an a posteriori attempt to salvage it after its central predictions fail. Proponents should abandon the "baby in the bathwater" argument in either a falsificatory or a confirmatory epistemological context.

Using a confirmatory approach, G&A nonrandomly select three of our 46 data sets for reanalysis, but instead of fitting the best model under least squares, they force a slope of −0.65 and interpret the explanatory power of their model based on coefficients of determination. Notably, one of the groups that they selected (tiger beetles) is inconsistent with two of their restrictive conditions, being a narrowly defined taxonomic group and comprising species that thermoregulate (Pearson and Vogler 2001, Dajoz 2002). They also select amphibians, but many of these also thermoregulate (Hutchinson and Dupré 1992). This illustrates the difficulty in understanding when the theory applies. Irrespectively, we repeated their approach for all 46 data sets, ignoring any nonlinearity following G&A but violating the postulate of linearity by Allen et al. (2002). The coefficients of determination of these tests were very low, with 27 being zero, and eight others being less than 0.30 (Table 1). Across all data sets, the r^2 values were substantially lower than the r^2 values from OLS fits (paired t test = −5.39; $P < 0.001$), despite low overall fits of temperature using either method (average $r^2_{G\&A}$ =

TABLE 1. Coefficients of determination (r^2) for linear regressions of ln-transformed richness against rescaled temperature using ordinary least squares [OLS] vs. the "forced slope" method of Gillooly and Allen (2007) [G&A].

Group	Region	OLS	G&A
Amphibians	Afrotropics	0.216	0
Amphibians	Australia	0.003	0
Amphibians	Brazil	0.590	0
Amphibians	China	0.404	0.384
Amphibians	Europe	0.502	0.499
Amphibians	Iberia	0.010	0
Amphibians	North America	0.767	0.739
Angiosperms	China	0.353	0.059
Ants	Colorado/Nevada	0.053	0
Ants	New World	0.582	0.545
Blister beetles	North America	0.347	0.312
Bumble bees	global	0.165	0
Butterflies	Australia	0.030	0
Butterflies	California	0.306	0
Butterflies	western Palearctic	0.136	0
Butterflies (summer)	North America	0.606	0.261
Butterflies (winter)	North America	0.499	0
Dung beetles	Iberia/France	0.008	0
Dung beetles	western Palearctic	0.111	0
Eupelmid wasps	Palearctic	0.084	0
Grasshoppers	North America	0.284	0.016
Hawk moths	Mexico	0.221	0.209
Hawk moths	southeastern Asia	0.025	0
Orthoptera	Catalonia	0.101	0
Plants	California	0.192	0
Plants	Catalonia	0.044	0
Plants (exotic)	Great Britain	0.656	0.190
Plants (native)	Great Britain	0.519	0.490
Pteridophytes	Europe	0.208	0
Pteridophytes	Iberia	0.055	0
Reptiles	Brazil	0.014	0
Reptiles	China	0.383	0.381
Reptiles	Europe	0.607	0.588
Reptiles	Iberia	0.002	0
Reptiles	North America	0.838	0.620
Reptiles	southern Africa	0	0
Seed plants	Iberia	0.082	0
Snakes	Afrotropics	0.278	0
Tiger beetles	Australia	0.113	0.099
Tiger beetles	India	0	0
Tiger beetles	North America	0.560	0.544
Tiger beetles	northwestern South America	0.156	0.153
Trees	Europe	0.458	0.372
Trees	North America	0.588	0.584
Woody plants	Kenya	0.338	0
Woody plants	southern Africa	0.019	0.012

Note: Regressions were done across all values within each of the 46 data sets ignoring any nonlinearity in the data.

0.153; average $r^2_{\mathrm{OLS}} = 0.272$). Although we currently do not have other environmental predictors for all data sets, previous meta-analyses (Hawkins et al. 2003) indicate that r^2 values of other variables (derived from theories related to water–energy balance; e.g., O'Brien [2006]) have much greater statistical explanatory power. Moreover, recent modeling of geographic range overlap explicitly based on MTE generated results with lower explanatory power than those generated using alternative models (Rahbek et al. 2007).

If the confirmatory approach is to be used for testing MTE, and any positive relationship between temperature and diversity is "promising," evaluations will become mainly correlative, as with many competing theories. Therefore, model developers must clearly describe the unique predictions made by their model (Shipley 2000, Currie et al. 2004). This is essential for understanding diversity gradients, because the spatial structure of climatic variation on Earth causes nearly all theories developed to explain broadscale richness gradients to predict a positive correlation between richness and temperature, even when no causal link between them exists, such as in the "pure tropical conservatism" model (Wiens and Donoghue 2004).

Concluding Remarks

MTE can be viewed as the core of a research program. The hypothesis of Allen et al. (2002), together with the model(s) developed to test it, is one facet of the program. Their model(s) can be tested and rejected, but this does not necessarily challenge the core. As pointed out by Hawkins et al. (2007), our evaluation was restricted to the predictions of Allen et al. (2002) and Brown et al. (2004) for richness gradients and cannot be generalized to MTE as a whole (also see Latimer 2007). Even so, we contend that the tests by Hawkins et al. (2007) are as valid as proponents' tests and provide strong evidence against the model as a *general* explanation. Of course, it is difficult to know whether the failure of the model's predictions occurs at the postulate, hypothesis, or theory level. Incorporating additional variables (including spatial variation in average body size and abundance, as well including potential deviations from the energetic equivalence rule) might generate improved models that better fit the empirical data. Perhaps this could support the claim that MTE explains richness gradients, at least in part (see also Latimer 2007). But arguing that it might and showing to what extent it does are very different propositions.

Literature Cited

Algar, A. C., J. T. Kerr, and D. J. Currie. 2007. A test of metabolic theory as the mechanism underlying broad-scale species-richness gradients. Global Ecology and Biogeography 16:170–178 [doi: 10.1111/j.1466-8238.2006.oo275x].

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548.

Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences (USA) 103:9130–9135.

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.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Dajoz, R. 2002. Les coléoptères carabidés et ténébrionidés: écologie et biologie. Tec & Doc, Paris, France.

Field, R., E. M. O'Brien, and R. J. Whittaker. 2005. Global models for predicting woody plant richness from climate: development and evaluation. Ecology 86:2263–2277.

FORUM

Ford, E. D. 2002. Scientific method for ecological research. Cambridge University Press, Cambridge, UK.

Gillooly, J. F., and A. P. Allen. 2007. Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. Ecology 88:1890–1894.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Hawkins, B. A., et al. 2007. A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. Ecology 88:1877–1888.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. Journal of Biogeography 33:770–780.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. In press. Climate, niche conservatism, and the global bird diversity gradient. American Naturalist.

Hawkins, B. A., J. A. F. Diniz-Filho, and S. A. Soeller. 2005. Water links the historical and contemporary components of the Australian bird diversity gradient. Journal of Biogeography 32:1035–1042.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hilborne, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson, V. H., and R. K. Dupré. 1992. Thermoregulation. Pages 206–249 in M. E. Feder and W. W. Burggren, editors. Environmental physiology of the amphibians. University of Chicago Press, Chicago, Illinois, USA.

Latimer, A. M. 2007. Geography and resource limitation complicate metabolism-based predictions of species richness. Ecology 88:1895–1898.

Lavers, C., and R. Field. 2006. A resource-based conceptual model of plant diversity that reassesses causality in the productivity–diversity relationship. Global Ecology and Biogeography 15:213–224.

McGill, B. 2003. Strong and weak tests of macroecological theory. Oikos 102:679–685.

O'Brien, E. M. 2006. Biological relativity to water–energy dynamics. Journal of Biogeography 33:1868–1888.

Pearson, D. L., and A. P. Vogler. 2001. Tiger beetles: the evolution, ecology, and diversity of the cicindelids. Cornell University Press, Ithaca, New York, USA.

Rahbek, C., N. J. Gotelli, R. K. Colwell, G. L. Entsminger, T. F. L. V. B. Rangel, and G. R. Graves. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society B 274:165–174 [doi: 10.1098/rspb.2006.3700].

Shipley, B. 2000. Cause and correlation in biology. Cambridge University Press, Cambridge, UK.

Whittaker, R. J., D. Nogués-Bravo, and M. B. Araújo. 2007. Geographic gradients of species richness: a test of the water–energy conjecture of Hawkins et al. (2003) using European data for five taxa. Global Ecology and Biogeography 16:76–89.

Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28:453–470.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639–644.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annual Review of Ecology, Evolution and Systematics 34:273–309.

FORUM