LINKING GLOBAL PATTERNS IN BIODIVERSITY TO EVOLUTIONARY DYNAMICS USING METABOLIC THEORY

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INTRODUCTION

Starting in 2002, with a paper entitled "Global biodiversity, biochemical kinetics and the energetic-equivalence rule," we have been developing a theoretical framework to understand the mechanisms underlying broadscale biodiversity gradients, particularly the latitudinal gradient. This work is part of a broader Metabolic Theory of Ecology (MTE) being developed to predict various aspects of the structure and function of ecological systems (Brown et al. 2004). Although MTE has been criticized (see Hawkins et al. 2007), support for its predictions continues to grow (Anderson et al. 2006, Anfodillo et al. 2006, Lopez-Urrutia et al. 2006, Meehan 2006, Robinson 2006). In the preceding paper, Hawkins et al. (2007) criticize the original work of Allen et al. (2002) based on their analyses of a large number of empirical data sets. Here we respond to their major criticisms and discuss important issues raised by their paper.

WHAT IS THE THEORY AS FIRST PROPOSED BY ALLEN ET AL. (2002)?

Hawkins et al. (2007) characterize our theory as based only on "the effects of temperature on enzyme kinetics." This oversimplification stems from an incomplete reading of Allen et al. (2002) and subsequent publications. Since Allen et al. (2002), we have published several papers that clarify our position (Allen et al. 2003, Brown et al. 2003), test model assumptions (Savage et al. 2004, Gillooly et al. 2005b), and expand on the theory by presenting new derivations and data (Allen and Gillooly 2006, Allen et al. 2006; Allen and Savage, *in press*). Yet, Hawkins et al. (2007) evaluate only a single prediction from Allen et al. (2002). They consider the more "detailed theoretical aspects" of this work, while potentially critical, they admit, as beyond the scope of their paper.

So what is the theory? Our theory aims to uncover the mechanisms controlling the origin and maintenance of biodiversity gradients based on the constraints of energetics on speciation–extinction dynamics. The theory specifies that the process of speciation is influenced by the effects of individual-level variables (i.e., body size, temperature) on rates of genetic divergence among populations, and by the effects of ecosystem-level variables (e.g., net primary production) on the numbers of genetically diverging populations maintained in communities. The process of extinction, as with Hubbell's Neutral Biodiversity Theory, NTB (Hubbell 2001), is assumed to be a function of both the speciation rate and population abundance (Allen et al. 2007; Allen and Savage, *in press*).

Unlike most recent work on species–energy theory, we have proposed that two forms of energy, kinetic energy and chemical potential energy, both help to regulate biodiversity through their effects on rates of speciation and extinction, but in different ways (Fig. 1). Specifically, we have proposed that kinetic energy influences biodiversity through its effects on individual metabolic rate, because metabolic rate constrains evolutionary rates through its effects on rates of individual turnover (1/generation time) and mutation (Allen et al. 2002, 2007). This assumption is now supported by data showing that (1) rates of individual turnover and rates of mutation show the same temperature dependence as metabolic rate (Savage et al. 2004, Gillooly et al. 2005b, Allen et al. 2006); (2) rates of speciation in one group of oceanic plankton also show this same temperature dependence (Allen et al. 2006); and finally, that (3) species richness is positively correlated with speciation rates (Emerson and Colm 2005, Allen and Gillooly 2006). These findings are consistent with the "evolutionary speed" hypothesis of Rohde (1978, 1992).

With respect to chemical potential energy, we have proposed that NPP and the factors that control its availability (i.e., water, nutrients, temperature) influence speciation rates through their effects on total community abundance, and therefore the total numbers of genetically diverging populations (Allen et al. 2002, 2006, 2007). This is consistent with the "more individuals hypothesis" (Wright 1983), as well as with NBT (Hubbell 2001).

Thus, Allen et al. (2002) and subsequent papers are developing a quantitative theoretical framework that links ecological and evolutionary dynamics of individ-

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Thermal kinetic energy
Temperature, T

Chemical potential energy
Net primary production (NPP)

Evolutionary rate per population
Function of T and body size

Total number of populations
Function of metabolic rate and NPP

Overall speciation rate
Function of evolutionary rate per population and
total number of populations

Overall extinction rate
Function of average abundance per species

Biological diversity
Function of overall speciation rate
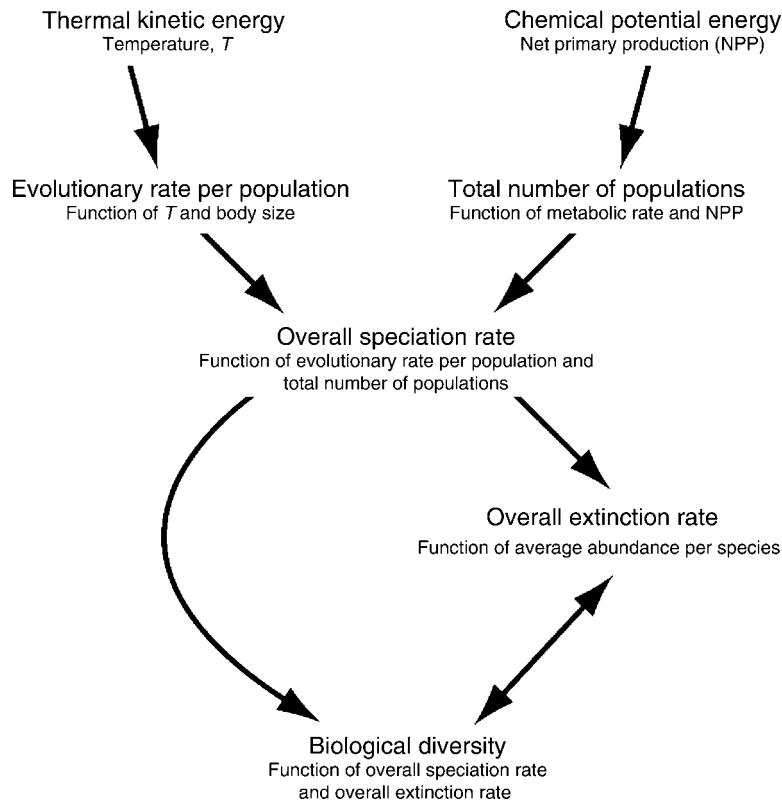and overall extinction rate

FIG. 1. The theoretical framework proposed by Allen et al. (2007) for the relationship of biological diversity to kinetic and potential forms of energy in the environment (modified from Allen et al. [2007]).

uals and populations to patterns of biodiversity in communities.

WHAT DOES THE THEORY PREDICT?

Contrary to the assertion by Hawkins et al. (2007), Allen et al. (2002) clearly state that "we do not mean to imply that temperature is the only variable that affects biodiversity." We have specifically mentioned that nutrient and water availability are important to consider, and that they may interact strongly in water-limited systems (Brown et al. 2003, 2004, Allen et al. 2005, 2007). Thus, we agree with the central conclusion of Hawkins et al. (2007) that "based on an overwhelming amount of evidence ... any explanation that depends solely on temperature will likely be incomplete." Indeed, our theory predicts that water limitation should constrain biodiversity through its effects on community abundance.

Allen et al. (2002) make several predictions about global-scale gradients in biodiversity and the underlying mechanisms. First, they predict that evolutionary rates should show the same body size and temperature dependence as mass-specific metabolic rate, B, defined as

$$B = b_o M^{-1/4} e^{-E/kT} \qquad (1)$$

where b_o is a normalization constant that varies by

taxonomic group, M is body mass, E is the average activation energy of metabolic rate ($\sim$0.6–0.7 eV, where 1 electronvolt = 1.602×10^{-19} J), k is Boltzmann's constant (8.62×10^{-5} eV/K, where K is degrees kelvin), and T is average body temperature in degrees kelvin. Second, using Eq. 1, Allen et al. (2002) extend the energetic-equivalence rule (EER) of Damuth (1987) to predict the combined effects of size and temperature on community abundance. Extensive population abundance data for endotherms and ectotherms were presented in support of this prediction. These data indicated that the total energy flux per population per unit area, B_T, was independent of body size and body temperature.

Based on this EER, Allen et al. (2002) then predict that species richness, S, in plots of fixed area, A, should be described by the following function for both endotherms and ectotherms:

$$S = (J/A)(B_o/B_T)e^{-E/kT}. \qquad (2)$$

In this expression, B_o (the normalization constant for metabolic rate) is a function of organism size and b_o, B_T varies by taxonomic group and with plot area A, and J/A is the total density of individuals per unit area (see Allen et al. 2002). Note that because Eq. 2 includes temperature and community abundance, it encompasses both the "evolutionary speed" hypothesis and the "more individuals" hypothesis. In other words, this expression

attempts to unify ecological and evolutionary explanations for species richness.

As a result, Eq. 2 yields different predictions for endotherms vs. ectotherms. For endotherms, Eq. 2 predicts that species richness, S, should increase linearly with total abundance per unit area, J/A, irrespective of environmental temperature, provided that the size distribution of organisms is held constant. This prediction is consistent with a recent global-scale analysis of bird community data (Pautasso and Gaston 2005). Conversely for ectotherms, species richness should vary as a function of abundance, body size, and environmental temperature. So, when abundance and size are both held constant, Eq. 2 predicts that plots of $\ln(S)$ vs. $1/kT$ (inverse temperature) should yield a straight line with a slope of $\sim{-}0.6$ to -0.7 eV. Hawkins et al. (2007) focus on evaluating only this latter prediction.

Do Data Support the Theory?

Allen et al. (2002) evaluated the predicted temperature dependence of species richness using global scale data on richness for both aquatic and terrestrial taxonomic groups (trees, amphibians, fish, fish ectoparasites, and gastropods). In doing so, they were careful to point out that the assumptions of size and abundance invariance with respect to temperature gradients must be viewed as "working hypotheses." Given this caveat, data from Allen et al. (2002) and other researchers (e.g., Kaspari et al. 2004), are broadly supportive of this model prediction.

In contrast, Hawkins et al. (2007) test the theory and conclude that there is virtually no support for this particular prediction of Allen et al. (2002) based on data from terrestrial ecosystems. However, their conclusion depends strongly on their choice of data and methodology, as well as on their interpretation of the data. The following are a few examples.

First, nearly half of the data sets presented by Hawkins et al. (2007) are for restricted groups of insects (e.g., Eupelmidae wasps). Allen et al. (2002:1546) are careful to point out that model assumptions are "not expected to hold true for groups that are narrowly defined...." Total insect diversity clearly peaks in the warm tropics, but restricted taxa can show markedly different patterns (e.g., Ichneumonid wasps; Janzen 1981). Furthermore, and importantly, many of these insect groups maintain relatively constant body temperatures in different thermal environments, including the bumble bees, sphinx moths, dung beetles, and butterflies (Heinrich 1981; see also Bartholomew and Heinrich [1978] for dung beetles, Heinrich and Vogt [1993] for bumble bees, Heinrich and Casey [1973] for moths). Thus, these groups would not be predicted to show the same exponential temperature dependence for species richness as shown by true ectotherms.

Second, the authors include data sets in which extreme gradients in water availability occur in the opposite direction of temperature (e.g., the African data sets, which include the Sahara), and they exclude data sets for which water availability is not an issue (i.e., aquatic ecosystems), on the basis that such data are beyond the scope of their paper. In cases of extreme water limitation, they show that richness often decreases with increasing temperature and consider this to be evidence that temperature is not operating in the same way across systems. This is not necessarily the case. For example, Hawkins et al. (2007) show that plant richness in Catalonia decreases with increasing temperature. Yet, the original publication by these authors concludes that, after correcting for the effects of water availability and other variables, richness actually increases exponentially with temperature (Pausas et al. 2003: Fig. 2). In other words, these results are consistent with the prediction of Allen et al. (2002).

Third, Hawkins et al. (2007) do not consider the quality and extent of the data sets that they have assembled, and how these differences might affect their results. A review of the original publications shows that many of the data sets in Hawkins et al. (2007) measure richness, and especially temperature, in different ways. For example, in their measure of richness, the study of Amazonian amphibians did not include any species that could not be identified or that were part of a "species group" (Diniz-Filho et al. 2006; data from Diniz-Filho et al. [2004]). In the case of the Australian tiger beetles, the very limited data consist of only 1–3 species in many areas, which led the original authors to conclude "the small sample sizes make *any* interpretation questionable" (Pearson and Juliano 1993:201). In measuring temperature, the authors point to the methods of the original publications, but many of these studies did not measure temperature (e.g., Field et al. 2005), or used measures of temperatures that were quite different (e.g., highest temperature of the decade in Hawkins and Porter [2003]). In short, the haphazard compilation of data by Hawkins et al. (2007) raises serious questions about the applicability of their analyses and the conclusions that they have reached.

Still, in spite of these problems, Hawkins et al. (2007) raise some important and interesting questions about how the theory of Allen et al. (2002) should be confronted with data. Hawkins et al. (2007) use a strict Popperian approach that aims to falsify the theory based on best-fit statistical criteria of a single-model prediction. In doing so, they find that 42% of the data sets that show linear relationships with temperature reject the "null" prediction (i.e., 0.6–0.7 eV activation energy) of Allen et al. (2002), based on the 95% confidence intervals. But, they also argue that data sets exhibiting "significant" nonlinearity can be viewed as showing no support for the prediction of Allen et al. (2002). Based on these criteria, they break nonlinear data sets in two and report many weaker relationships for lines fit through only a portion of the data.

From our perspective, this approach by Hawkins et al. (2007) results in unreasonably casting aside this
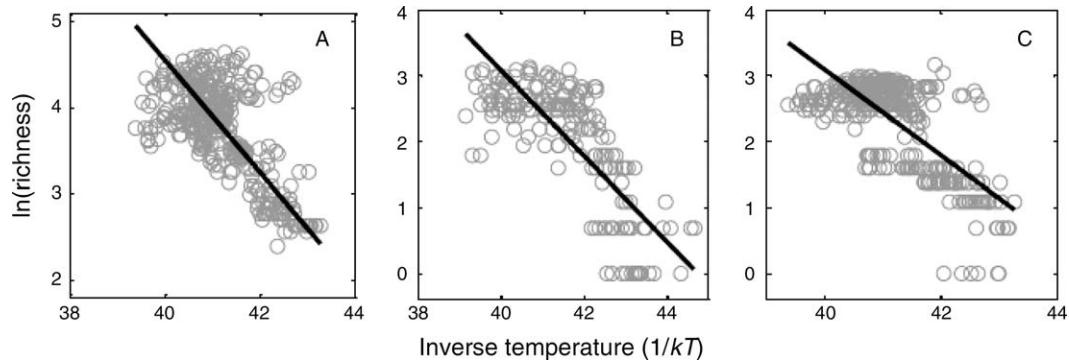
Fig. 2. Species richness–temperature relationships that Hawkins et al. (2007) conclude are not supportive of the Allen et al. (2002) model. Here, k is Boltzmann's constant (8.62×10^{-5} eV/K, where K is degree kelvin), and T is average body temperature in degrees kelvin. The straight lines in the figure, with a slope of −0.65, represent the relationship predicted by Allen et al. (2002). Results are for: (A) European trees ($r^2 = 0.37$), (B) North American tiger beetles ($r^2 = 0.54$), and (C) European amphibians ($r^2 = 0.50$). Lines are fit using best-fit criteria, where the slope is fixed at −0.65 (r^2 values are based on these fits). Note that we have not plotted the two best examples of this result to avoid reusing the data sets from Allen et al. (2002), but the same result holds even more strongly for these data (North American amphibians, $r^2 = 0.74$; North American trees, $r^2 = 0.58$).

young theory even though its assumptions and predictions are supported by considerable (but not all) data. This approach risks losing the knowledge that could be gained by pursuing the theory further. For example, in Fig. 2, we have included three data sets from Hawkins et al. (2007), chosen because they are among the most supportive of the predictions of Allen et al. (2002), and thus are not intended to be a representative sample. A straight-line fit to these data, with MTE's predicted slope of −0.65 eV, captures the overall relationship of richness to temperature and explains up to 54% of the variation in these relationships. And yet, each of these data sets is significantly nonlinear. Based on this nonlinearity, Hawkins et al. (2007) argue against the model of Allen et al. (2002). From our perspective, these results are promising, and the nonlinearity points to the need to test whether incorporating other variables in the model will improve predictions. In particular, this is because, as Hawkins et al. (2007) mention, violations of the Allen et al. (2002) model assumptions lead to curvilinear relationships in plots of log-transformed richness vs. inverse temperature. The question of which approach or interpretation is better is a philosophical one.

More generally, however, we would argue that the theory of Allen et al. (2002) is best evaluated not just by testing a single prediction, but rather by using a more holistic approach that evaluates all assumptions and predictions of the theory, as well as the logic behind the theory. Ideally, the performance of the model in predicting patterns of biodiversity should also be compared to that of other predictive models.

Can the Theory Be Improved/Further Developed? Is It Evolving?

Absolutely. Much remains to be done. On the empirical side, testing the predictions of Allen et al. (2002) presents significant challenges. Broadscale data

on body size, community abundance, and species diversity are scarce, but they do exist (e.g., Pautasso and Gaston 2005). Both this theory and NTB point to the need for more and better data in these areas. On the theoretical side, the framework of this theory requires a better understanding of how water limitation and other factors control community abundance, and how abundance in turn affects speciation–extinction dynamics. Recent progress on this issue has been made by Allen and Savage (*in press*) by extending NTB. As further insights emerge, or as modifications are required, the theory will continue to evolve. For example, in Allen et al. (2002), the average activation energy, E, was defined as ~0.78eV, based on analyses of Gillooly et al. (2001). Upon further analyses (e.g., Brown et al. 2004, Gillooly et al. 2005a, b), this value is now consistently defined as 0.6–0.7 eV. Certainly, there is abundant room for additional research on these and other mechanisms.

Closing Thoughts

Allen et al. (2002) and subsequent papers are developing a promising theoretical framework that links short-term species coexistence to long-term speciation–extinction dynamics. As pointed out by Brown et al. (2003), this research indicates that the effect of temperature on rates of biological metabolism must be *an important component* of any theory that attempts to explain broadscale patterns in biodiversity, such as the latitudinal gradient.

To be sure, this approach differs markedly from the approach that describes patterns in biodiversity using statistical models. Statistical models of this sort typically include a few to several variables with the goal of "explaining" as much variance as possible. The choice of variables or models is admittedly relatively straightforward with these models because they are based solely on best-fit criteria. These models can explain substantial variation in patterns of biodiversity and can identify

climatic factors that play an important role. They are less useful in identifying the underlying mechanisms responsible for these patterns, and cannot make a priori predictions.

Both approaches are necessary to build a general theory of biodiversity. We hope that the future will bring more "cross-fertilization" between these and other approaches on this important topic.

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