IDEA AND PERSPECTIVE

Advancing the metabolic theory of biodiversity

James C. Stegen,***Brian J. Enquist and Regis Ferriere**
Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
*Correspondence and present address:
E-mail: stegen@email.unc.edu
Department of Biology, University of North Carolina, CB# 3280, Coker Hall, Chapel Hill, NC 27599 3280, USA

Abstract

A component of metabolic scaling theory has worked towards understanding the influence of metabolism over the generation and maintenance of biodiversity. Specific models within this 'metabolic theory of biodiversity' (MTB) have addressed temperature gradients in speciation rate and species richness, but the scope of MTB has been questioned because of empirical departures from model predictions. In this study, we first show that a generalized MTB is not inconsistent with empirical patterns and subsequently implement an eco-evolutionary MTB which has thus far only been discussed qualitatively. More specifically, we combine a functional trait (body mass) approach and an environmental gradient (temperature) with a dynamic eco-evolutionary model that builds on the current MTB. Our approach uniquely accounts for feedbacks between ecological interactions (size-dependent competition and predation) and evolutionary rates (speciation and extinction). We investigate a simple example in which temperature influences mutation rate, and show that this single effect leads to dynamic temperature gradients in macroevolutionary rates and community structure. Early in community evolution, temperature strongly influences speciation and both speciation and extinction strongly influence species richness. Through time, niche structure evolves, speciation and extinction rates fall, and species richness becomes increasingly independent of temperature. However, significant temperature-richness gradients may persist within emergent functional (trophic) groups, especially when niche breadths are wide. Thus, there is a strong signal of both history and ecological interactions on patterns of species richness across temperature gradients. More generally, the successful implementation of an eco-evolutionary MTB opens the perspective that a process-based MTB can continue to emerge through further development of metabolic models that are explicit in terms of functional traits and environmental gradients.

INTRODUCTION

The metabolic theory of ecology addresses how the relationship between organismal metabolism, body size and temperature scales up to population, community and ecosystem properties (Brown *et al.* 2004). Understanding the processes responsible for gradients in biodiversity is a central goal of ecological research (Brown 1981; May 1986) and may be the ultimate frontier for metabolic theory. To tackle this grand challenge, a first generation of metabolic models have linked temperature to mutation rate (Gillooly *et al.* 2005, 2007; Allen *et al.* 2006), speciation rate (Allen *et al.* 2006) and species richness (Allen *et al.* 2002). We refer to this body of work as the 'metabolic theory of biodiversity'

(MTB). A central prediction of MTB is that the natural log of speciation rate or species richness plotted against $1/kT$ will reveal a linear slope of $c. -0.65$, where k is Boltzmann's constant $(8.62 \times 10^{-5}$ eV/K$)$ and T is environmental temperature in Kelvin (Allen *et al.* 2007).

The predicted influence of temperature on species richness has received detailed empirical evaluation (e.g. Hawkins *et al.* 2007a). Across a broad range of taxonomic groups a great deal of variation exists in the relationship between temperature and species richness, and only a few datasets appear to support the −0.65 slope prediction (Fig. 1) (Algar *et al.* 2007; Hawkins *et al.* 2007a,b; Latimer 2007; but see Gillooly & Allen 2007). As a result, MTB is tasked with the challenge of mechanistically explaining this variation.

The aim of this study is to show how MTB can be extended to deepen our understanding of the metabolic basis of speciation, extinction and species richness along environmental gradients. We first show that the scope of the MTB models developed in Allen *et al.* (2002, 2006) can be broadened to provide a more realistic and flexible framework for linking individual metabolism to ecology and evolution. We do this by relaxing several key assumptions related to temperature-dependent metabolism. Secondly, we propose a theoretical extension of MTB that implements the dynamical MTB discussed by Allen *et al.* (2007). This dynamical MTB combines feedbacks among temperature- and/or resource-dependent mutation rate, speciation rate, extinction rate and community structure (see also Gillooly & Allen 2007). We implement this framework by merging trait-based community ecology (McGill *et al.* 2006) with the theory of adaptive dynamics and its extensions (Champagnat *et al.* 2006). As an example of this approach we evaluate the influence of temperature-dependent mutation rate on speciation rate, extinction rate and species richness within an evolving ecological interaction network. Our approach thus offers a novel perspective on how organismal metabolism influences macroevolutionary rates and patterns.

TOWARDS A MORE GENERAL MTB

Allen *et al.* (2002, 2006) predicted the temperature dependence of species richness and per-capita speciation rate to
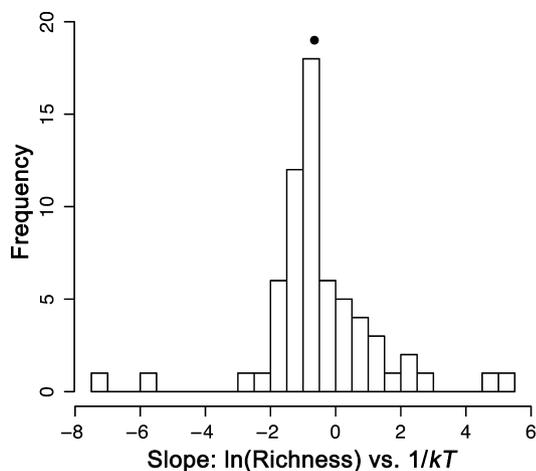

Figure 1 Slopes of temperature-richness gradients reported in the empirical literature. Slopes are from significant regressions of log-transformed species richness as a function of inverse temperature, T, multiplied by Boltzmann's constant, k. Non-significant regressions are not presented and represent 38% of empirical analyses. Solid circle indicates a slope of −0.65. *Source*: Allen *et al.* (2002), Kaspari *et al.* (2004), Hunt *et al.* (2005), Algar *et al.* (2007), Hawkins *et al.* (2007a), Kreft *et al.* (2007). Some analyses regressed ln(richness) against $1000/T$ and the slopes from these regressions were converted to their values for an independent variable of $1/kT$.

follow the same exponential 'Boltzmann' form, $e^{-E/kT}$, as individual metabolic rate, where $E = 0.65$ eV is the mean activation energy of metabolic reactions (Gillooly *et al.* 2001, 2006; Brown *et al.* 2004). These predictions are derived from a number of assumed temperature (in)dependencies. To generalize the predicted temperature dependence of speciation and species richness we introduce activation energy 'scalars'. These scalars characterize how individual metabolism 'scales up' to higher levels of biological organization. For example, Enquist *et al.* (2003) show that temperature has no influence over the rate of energy flux *across* plant communities, consistent with a scalar of zero, but that *within*-community energy flux scales with temperature in the same way individual metabolism scales with temperature, consistent with a scalar of one.

Generalized model of temperature-dependent speciation rate

To scale up from individual processes to the macroevolutionary rate of speciation in communities, Allen *et al.* (2006) combined metabolic theory with population genetics (e.g. Kimura 1983). Here 'community' refers to the collection of populations evolving at a given temperature, and the community speciation rate V_m (species per time) is given by

$$V_m \propto f_+ s J_s J_m \alpha / D_s^+ \qquad (1)$$

where f_+ is the fraction of mutations that are beneficial; s is the coefficient of selection; J_s is effective population size (the number of reproducing individuals in a population) of incipient taxa, which influences the per-individual probability of fixation of beneficial mutations; J_m is *effective* community abundance (the total number of reproducing individuals in a multi-species community), which scales the per-individual mutation rate to the whole community; α is mutations per nucleotide per unit time; and D_s^+ is the genetic divergence (substitutions per nucleotide) from beneficial mutations between incipient taxa and serves as a proxy for the total genetic divergence required for speciation (see also Wright *et al.* 2009). Note that Allen *et al.* (2006) defined J_m as total community abundance and here we redefine this variable as effective community abundance because only individuals that reproduce influence the community speciation rate.

By considering the influence of temperature on each term in eqn 1, we derive a generalized form of the temperature dependence of community speciation rate. Temperature dependence is assumed only for those variables that are (or appear to be) influenced by individual metabolism. Specifically, as in Allen *et al.* (2006), we assume that D_s^+, f_+ and s are independent of temperature. Including exponential temperature dependencies on all other variables yields

$$V_m(T) \propto J_s(T) J_m(T) \alpha(T) \propto e^{(\delta + \varphi + \omega)E/kT} \quad (2)$$

Here, δ, φ and ω are activation energy scalars, respectively, for J_s, J_m and α. It is therefore the value of E multiplied by the sum of δ, φ and ω that determines the temperature dependence of community speciation rate. While metabolic theory predicts that temperature positively influences the rate of mutations so that $\omega = -1$ (Gillooly *et al.* 2005, 2007) it has yet to make an explicit prediction for δ and φ. Allen *et al.* (2002) do, however, predict the temperature dependence of *total* population size (see also Savage *et al.* 2004).

In developing a prediction for the temperature dependence of total population size, Allen *et al.* (2002) effectively assume that limiting resource supply does not vary with temperature and that population energy flux is 'zero-sum' (e.g. Damuth 1981; Ernest *et al.* 2008). Population energy flux, B_T, is thus predicted to be independent of temperature (Allen *et al.* 2002). In turn, after controlling for mean body size, population size, n, must decline exponentially with temperature because of the exponential increase in individual metabolic rate. Allen *et al.* (2002) provide empirical support for an exponential decline in population size with temperature (see also Savage *et al.* 2004). Furthermore, if resource availability does not vary with temperature among communities, community energy flux is also predicted to be independent of temperature. Recent analyses support the prediction that energy flux compared across communities does not vary with temperature (Enquist *et al.* 2003; Kerkhoff *et al.* 2005; but see Allen *et al.* 2005). If limiting resources do vary with temperature, the temperature dependencies of total population size and total community abundance will be modified (Gillooly & Allen 2007), as will the temperature dependence of community speciation rate. Nonetheless, total population size and total community abundance are expected to have the same temperature dependence as each other, *assuming* that abundance is mechanistically linked to metabolic rate. As discussed below, the link between population and community abundances and their respective relationships to temperature have profound influences on the predicted temperature dependence of speciation.

The predicted temperature dependence of population size and community abundance discussed above is for *total* numbers of individuals. The expected relationship between community speciation rate and temperature is dependent on effective abundance and thus critically depends not only on the temperature dependence of abundance, but also on the relationship between effective and total abundance, at both the population and community levels. Even if total abundances decline with temperature, but there is no relationship between effective and actual abundance so that $\varphi = \delta = 0$, community speciation rate is predicted to increase with temperature: $V_m \propto e^{(0+0-1)E/kT} \propto e^{-E/kT}$.

In contrast, if effective abundance increases tightly with total abundance *and* if total abundances decline with temperature, then one may have $\varphi = \delta = 1$ whereby metacommunity speciation rate is predicted to *decline* with temperature: $V_m \propto e^{(1+1-1)E/kT} \propto e^{E/kT}$. Although empirical relationships between effective and actual abundance are variable, positive relationships have been observed (e.g. Frankham 1996), in which case φ and δ are expected to be positive. As long as $\varphi + \delta \geq 1$, metacommunity speciation rate is predicted to *decrease* with temperature. Thus, the generalized MTB model of speciation rate predicts that temperature can positively *as well as* negatively influence speciation rate, depending critically on the temperature dependencies of 'effective abundance' and resource supply.

Generalized model of temperature-dependent species richness

While the MTB has been developed towards understanding the influence of temperature-dependent metabolism over species richness it has not explicitly detailed the underlying evolutionary processes. This is reasonable considering the uncertainties involved. Nonetheless, given the above arguments we can generalize the Allen *et al.* (2002) model by assuming that mean body size does not vary with temperature and that the area of community, A, is constant. The functional relationship between species richness, S, and temperature can be generalized as

$$S = N_m \bar{B} / A \bar{B}_T \propto e^{\phi E/kT} e^{-E/kT} e^{-\psi E/kT} \propto e^{(\phi - 1 - \psi)E/kT} \quad (3)$$

Here $\bar{B}$ is mean individual metabolic rate; ϕ and ψ are activation energy scalars for *total* community abundance and mean population energy flux, $\bar{B}_T$, respectively. As alluded to in the previous section, zero-sum energetics predict $\phi = 1$ and $\psi = 0$. In this case, species richness is predicted to be *independent* of temperature (i.e. $\phi - 1 - \psi = 0$). However, these assumptions are not consistently supported. For example, tree community abundance per-area does not vary with latitude (Enquist & Niklas 2001), suggesting that N_m may not vary with temperature (i.e. $\phi = 0$). In this case our generalized model predicts $S \propto e^{-0.65/kT}$, similar to Allen *et al.* (2002). Empirical data from Allen *et al.* (2006) provide an intermediate example whereby the temperature dependence of area normalized N_m is consistent with $\phi = 0.69$, which predicts $S \propto e^{-0.2/kT}$. Furthermore, if N_m declines strongly enough with temperature, species richness will also decline with temperature, as observed in some groups (Hawkins *et al.* 2007a).

In sum, by generalizing the Allen *et al.* (2002) model to include other temperature dependencies, we predict that a range of richness-temperature relationships should be observed, among which $S \propto e^{-0.65/kT}$ is a special case.

A link between organismal metabolism and large-scale patterns of species richness may be general, yet specific predictions necessitate a more mechanistic approach whereby some of the key MTB assumptions become MTB predictions. To this end, Allen *et al.* (2007) envisioned MTB as a broader framework in which the metabolic basis of macroevolutionary rates and patterns is an emergent property of dynamic feedbacks between ecological and evolutionary processes (see also Gillooly & Allen 2007). We next show how this eco-evolutionary MTB can be explicitly implemented.

TOWARDS A TRAIT-BASED, ECO-EVOLUTIONARY MTB

A trait-based (McGill *et al.* 2006), eco-evolutionary (Champagnat *et al.* 2006; Fussmann *et al.* 2007) approach can extend MTB by explicitly linking limiting resource supply, ecological interactions and evolutionary rates. This approach emphasizes how MTB's key functional trait (body mass) and environmental gradient (temperature) both fundamentally determine ecological interactions and long-term evolution (Box 1). More specifically, we define mutation rate to be dependent on both body mass and temperature (Gillooly *et al.* 2005, 2007; Allen *et al.* 2006) and allow selection on genetic variation in body mass to emerge from mass-dependent ecological interactions (Loeuille & Loreau 2005, 2006; Stegen & Swenson 2009). Our aim is to examine how temperature-dependent mutation rate and trait(mass)-dependent ecology influence speciation rate, extinction rate and species richness.

Box 1 Body size is allowed to evolve along temperature gradients and is a key functional trait influencing ecological and evolutionary processes

Body size, here to be understood as the expected body mass of a reproductive individual in its local community, is a pivotal influence of both ecological and evolutionary processes that shape community structure and dynamics. So far, metabolic theory has not detailed all of the ways that size influences ecological interactions and evolves under selection generated by these interactions (McGill *et al.* 2006; but see Brown *et al.* 1993; Kelt & Brown 1998). In this study, we follow the path lead by Loeuille & Loreau (2005, 2006) to embed organism metabolism into an eco-evolutionary dynamical model in which body size, ecological interactions and community structure evolve jointly. We thus make the key assumptions that body size is a strong determinant of competitive and trophic interactions, and that the evolution of body size is a primary axis upon which species diverge.

On the ecological side, body size influences the survival and reproductive potential of an organism. Reproduction and mortality rates are well known to correlate across species with mass-specific metabolic rates (Peters 1983; Savage *et al.* 2004), and the scaling of organism metabolic rate with body mass is the fundamental tenet of the metabolic theory of ecology (Brown *et al.* 2004). Secondly, body size has a major influence over trophic links between species – who eats who, and with what intensity (Petchey *et al.* 2008; Berlow *et al.* 2009). There is also strong evidence that trophic webs can be usefully represented by a single niche axis such as body size (Williams & Martinez 2000). Thirdly, interference competition is common (e.g. Robertson & Gaines 1986; Skalski & Gilliam 2001) and occurs because of overlap in resource use (Case & Gilpin 1974) such that inteference is expected to occur among similarly sized species.

On the evolutionary side, as emphasized in the Allen *et al.* (2006) evolutionary model of speciation rate, the effect of body size on individual metabolism translates into a body size-dependence of the rate of genetic mutation. Secondly, reproductive isolation is promoted by disruptive selection on ecologically important organismal traits, like body size (Dieckmann & Doebeli 1999). Indeed, macroevolutionary patterns of speciation often involve body size differentiation (Coyne & Orr 2004). Finally, since competitive and predatory interactions will determine the direction and strength of natural selection acting on genetic variation in body size, selection on body size will depend on and vary with the community size distribution (Loeuille & Loreau 2005; Lewis & Law 2007).

The adaptive dynamics framework

Eco-evolutionary, and more specifically adaptive dynamics, theory provides a general mathematical framework to merge the current MTB with trait-based ecological processes and eco-evolutionary feedbacks. Adaptive dynamics theory combines simple population genetics with explicit ecological interactions to predict the long-term evolution of quantitative traits under the assumption of rare mutation (Metz *et al.* 1992). The current trait distribution defines the ecological structure of the community and hence the selection gradient acting on variation around any current trait value. For unstructured populations characterized by trait values M_i (M is the trait, e.g. body mass; i is the species identity number), the canonical equation of adaptive dynamics predicts the rate of phenotypic change per unit time of each species in the community, as long as selection is directional:

$$dM_i/dt = \Delta f_+ \alpha(M_i, \tilde{M}, T) J_s(M_i, \tilde{M}, T) s(M_i, \tilde{M}, T) \qquad (4)$$

where Δ is the mutation step variance (change in mass squared per mutation), f_+ is the fraction of mutations that are beneficial (unitless), α is the mutation rate (mutations per time per reproducing individual), J_s is the number of reproducing individuals, and s is the selection gradient (per mass), which is derived from the fixation probability of mutants with body sizes around M_i. Here we use notations similar to Allen *et al.* (2006) to emphasize that the canonical eqn 4 shares its evolutionary foundations with the MTB speciation rate model. Our notations also emphasize potential dependencies of variables on temperature, T, species body mass, M_i, and the body mass distribution, $\tilde{M}$, in the community.

Adaptive dynamics theory predicts that directional selection described by eqn 4 can turn disruptive at particular trait values named 'evolutionary branching points' (Geritz *et al.* 1998; Waxman & Gavrilets 2005) where mutant invasion results in coexistence instead of fixation. Adaptive dynamics theory also provides general insight into the process of extinction. The interplay of ecological and evolutionary processes can lead to 'evolutionary suicide' (Dieckmann & Ferriere 2004), that is, the extinction of an established phenotype and potentially a whole lineage. Like speciation, this also happens at special points in trait space, where an established species can be invaded by ecologically non-viable mutants (Dieckmann & Ferriere 2004).

Adaptive dynamics theory is a special case of the more general theory of eco-evolutionary dynamics (Champagnat *et al.* 2006) in which the assumption of small and rare mutation is relaxed. Eco-evolutionary dynamics theory suggests that variation in speciation-extinction dynamics may originate from trait- and environment-dependent mutation rate (Champagnat *et al.* 2006). Quantitative analysis of a specific model demonstrates this in the next sections.

A metabolic eco-evolutionary model of biodiversity

We use the adaptive dynamics framework to integrate metabolic 'rules' into a simple eco-evolutionary model, described conceptually in Fig. 2. In our model body mass varies genetically, and the body mass distribution determines resource partitioning and energy flow among species. The community originates as a single species consuming only the basal resource (inorganic nutrients). This ancestral species can diversify into a species network in which trophic structure self-organizes and ecological niches emerge (Loeuille & Loreau 2005, 2006). The basal resource pool is dynamic and varies because of external inputs and outputs and direct consumption and recycling. Consumer biomass depends on intrinsic mortality, feeding, interference competition and predation.

Intrinsic, mass-specific mortality rate is assumed to scale with body mass because of the influence of body mass over

metabolic rate. That is, mass-specific mortality is assumed to scale with body mass to $-1/4$ power, as observed empirically in Savage *et al.* (2004), such that:

$$m(M_i) \propto M_i^{-1/4} \tag{6}$$

Likewise, mass-specific feeding rate is assumed to be metabolism-dependent. Therefore, the mass-specific feeding rate of species i scales with its body mass to the $-1/4$ power, as observed empirically (Peters 1983; Moloney & Field 1989; Hansen *et al.* 1997). To focus on the influence of temperature-dependent mutation rate (see below) we exclude the temperature dependencies on mortality and feeding rates. These additional temperature dependencies can and should be incorporated into future versions of our model. In addition, feeding rate varies with the body mass of prey such that there is an optimal prey body size and around this size feeding rate declines (Sala & Graham 2002; Loeuille & Loreau 2005, 2006; Cozar *et al.* 2008). Feeding rate
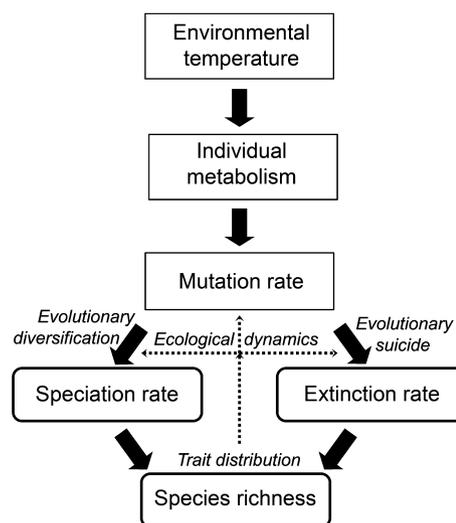
Figure 2 Conceptual diagram of the trait-based, eco-evolutionary metabolic model studied here. As inputs (square boxes) our model has environmental temperature and temperature-dependent individual metabolism, and therefore a temperature dependence on the supply rate of mutations in body mass, which is the key functional trait that varies between species. The supply of mutants leads to speciation through the diversification in body mass, therefore linking temperature to speciation rate. Likewise, the supply of mutants may also lead to extinction through evolutionary suicide (see text), therefore linking temperature to extinction rate. The balance of speciation and extinction rates determine species richness and the distribution of trait(mass) values, therefore linking temperature to community structure. The distribution and abundance of trait values define the ecological system and its dynamics. The structure and dynamics of the ecological system feedback (dashed arrows) onto the evolutionary dynamics by directly or indirectly influencing realized mutation, speciation and extinction rates.

therefore depends on the body mass of prey-species j following a Gaussian function (see Fig. S1 and above references) centered at an optimal body mass difference, d, and spreads with variance σ^2 such that

$$f(M_i, M_j) \propto M_i^{-1/4}\sigma^{-1}\exp[-(M_i - M_j - d)^2\sigma^{-2}] \qquad (7)$$

The ratio σ^2/d defines the width of a species' trophic niche (mass) (Loeuille & Loreau 2005, 2006). Trophic interactions can also be influenced by interference competition (Skalski & Gilliam 2001), the strength of which is determined by species' body mass differences:

$$c(M_i, M_j) = \begin{cases} c_0 & \text{if } |M_i - M_j| < \beta \\ 0 & \text{if } |M_i - M_j| > \beta \end{cases} \qquad (8)$$

(Loeuille & Loreau 2005, 2006). This formulation of interference competition assumes that species interfere with conspecifics and other species of similar body mass. These metabolic ecology eqns 6–8 are further incorporated into a dynamic ecological model described in Appendix S1.

An evolutionary component is layered over the dynamic ecological model by allowing body size to mutate and subsequently be selected for or against based on the ecological rules described in Appendix S1. As for the ecological rates discussed above, the supply rate of body mass mutants is assumed to be dependent on individual metabolism. However, here we include temperature as an additional driver of individual metabolism. Mass-specific mutation rate is therefore assumed to scale to the −1/4 power of the progenitor's body mass and to increase exponentially with temperature (Gillooly et al. 2005; Allen et al. 2006; Gillooly et al. 2007; see also Martin & Palumbi 1993). The probability of a mutant produced by species i per unit time is thus $N_i \propto (M_i, T)$, where N_i is population biomass and

$$\alpha(M_i, T) \propto M_i^{-1/4}e^{-E/kT} \qquad (9)$$

In this study, we follow previous metabolic theory models such that mutation rate is on a per nucleotide basis and we assume that genome size increases with body mass. There is a great deal of empirical variation in the relationship between genome size and body mass (Gregory 2005), so no single assumption is universally correct. Our model builds directly from Loeuille & Loreau (2005), who showed that emergent model communities have very similar structure to natural communities, so for consistency we have chosen to follow their formulation and assume that genome size increases with body mass. More importantly, model predictions should be robust to changes in this assumption because we examine *gradients* (i.e. relative values) in

speciation, extinction and species richness across communities rather than patterns within communities.

The proportional change in body mass resulting from mutation is drawn randomly from a temperature-independent distribution (see Appendix S1). Mutants have either a negative population growth rate and immediately go extinct or increase and remain in the system as a new 'established' species. Established species are assumed to go extinct if their population size falls below a minimum threshold, which is also the population biomass of a new mutant (1e-20). Speciation and extinction rates measure the total number of unique body sizes establishing in or leaving the community per unit time respectively. Measuring total speciation and extinction facilitate comparison of the model's predictions to empirical speciation and extinction data. Species richness is taken as the number of unique body sizes present at a given time.

It is important to note that our model implicitly assumes a large spatial scale across which a temperature gradient is realized. Alternatively, our model could be said to assume niche conservatism with respect to temperature optima. In either case, dispersal is assumed to not result in successful colonization. In addition, extinction is not influenced by external perturbations. Incorporating stochastic extinction would not fundamentally change model predictions, but if frequent enough, would maintain the system in a state of relatively early community assembly.

We note that speciation and subsequent diversification in our model does not require local fitness minima and disruptive selection, which are required in more traditional adaptive dynamics models (see Geritz et al. 1998). Rather, an ancestor and a mutant it produces can co-exist without directional change in either's body mass (see Fig. S2 and fig. 2 in Loeuille & Loreau 2005). Furthermore, as the network diversifies, the system self-organizes into 'body size guilds' (Loeuille & Loreau 2005; Fig. S2). We take the trophic level of a species to be dependent on the trophic structure of its prey such that it is dynamic through time. Although the definition of speciation and extinction rates within trophic levels is problematic (species entering and leaving a given trophic level can be because of speciation and extinction into that trophic level and/or speciation and extinction at lower trophic levels), the macroevolutionary dynamics of within-trophic level species richness can be quantified and analysed.

METABOLIC ECO-EVOLUTIONARY ANALYSIS

Having the above quantitative framework in place allows us to next integrate the eco-evolutionary network dynamics numerically to compute the relative influences of temperature-dependent mutation rate and ecological interactions on the generation and maintenance of biodiversity. To

facilitate comparison with empirical analyses we: (i) varied temperature across a range of biologically relevant values (5–45 °C); (ii) analysed the effect of temperature as the slope of the ordinary least squares linear regression relating log-transformed speciation rate, extinction rate, or species richness to $1/kT$; and (iii) examined the effect of different 'ecological scenarios' by varying two key parameters: trophic niche width and interference competition strength. These parameters were shown by Loeuille & Loreau (2005) to be the primary determinants of community structure and we investigate a similar parameter space as these authors, who also showed model communities to be structurally similar to natural food webs. Computational details are provided in Appendix S1.

Speciation and extinction rates

Model analyses show that speciation rates decline through time, tightly paralleled by extinction rates. Both rates initially take on larger values at higher temperature and approach zero as communities age (Figs 3a,b and S3). Similarly, slopes relating log-transformed rates to $1/kT$ are initially steeply negative and can reach −0.65, but as speciation and extinction rates approach zero, the slopes become shallower (Figs 3c,d and S4). Trophic niche width strongly influences the tempo of this pattern: the wider the niche, the longer steeper slopes are maintained (Figs 3c,d and S4).

Species richness of whole interaction networks

From an ancestral community that contains only one species, richness evolves and converges to a stationary level, and both ecology and temperature strongly influence species richness dynamics (Fig. 4). Temperature-dependent mutation rate drives more rapid diversification at higher temperature (Fig. 4), and higher temperature causes species richness to increase sharply and subsequently decrease towards the long-term equilibrium. Thus, a phase of species proliferation overshoots the community's emergent 'species carrying capacity,' and is followed by a phase dominated by extinction. Cooler temperatures result in a relatively smooth build-up of species richness towards the stationary level. With narrow trophic niches, the influence of temperature on the rate of diversification has no long-term effect on species richness (Fig. 4a). With broad trophic niches, the difference in species richness between temperatures persists and stabilizes (Fig. 4b).

Our model shows that the temperature dependence of species richness is temporally variable (Fig. 4c,d). The early phase of rapid diversification at high temperature and relatively slow diversification at low temperature (Figs 4a,b and S5) maximizes the temperature dependence of species richness. The slope of species richness (log-transformed) against $1/kT$ can approach Allen *et al.*'s (2002) prediction of −0.65 under conditions of wide trophic niches and strong interference competition (Fig. 4d). In all ecological scenarios, the steepest slope emerges in a brief evolutionary episode, followed by a decline in the temperature dependence of richness (Figs 4c,d and S6). The brief evolutionary episode in which steep slopes emerge is characterized by a rapidly changing slope, and as a consequence is also characterized by the greatest variation in slope values across replicate simulations (Fig. 4c,d). Through time, variation in slopes consistently declines (Fig. 4c,d; see Appendix S1 for methodological details). With narrow trophic niches, species richness converges to a stationary level that is temperature-invariant (Fig. 4a), so that the species richness-temperature gradient flattens completely (Fig. 4c). In contrast, wide trophic niches promote persistent, albeit small, differences in species richness across temperatures (Fig. 4b). As a result, a shallow, but evolutionarily persistent, species richness-temperature gradient emerges (Fig. 4d).

The influence of speciation on species richness also declines through time: the positive slope relating richness to speciation trends to zero (Figs 5 and S7a). The strong correlation between speciation and extinction rates causes the positive slope between richness and extinction to also trend to zero through time (Figs 5 and S7b). Therefore, the model predicts an initially strong effect of temperature-dependent mutation on species richness that is mediated by both speciation and extinction processes. However, as the self-organized trophic structure stabilizes, speciation and extinction, and thus species richness, become largely independent of mutation rate, and are primarily governed instead by ecological interactions.

Within-trophic level species richness

Our model shows that trophic level influences the evolution of the relationship between richness and temperature. The early emergence of a steep richness-temperature gradient followed by flattening of this gradient is commonly observed within each trophic level (Figs 4e,f and S8). However, the emergence and subsequent fading of the richness-temperature gradient is slower in higher trophic levels, and the steepest slopes (near −0.65) reached during eco-evolutionary assembly vary between trophic levels. Differences across trophic levels in how richness varies with temperature appear to persist (Fig. 4e,f). In particular, with wide trophic niches and strong interference competition, within-trophic level gradients converge to different non-zero, negative slopes (Fig. 4f). Replicated simulations confirm that these patterns are robust, and as for whole-community species richness, variation in slope values declines through time.
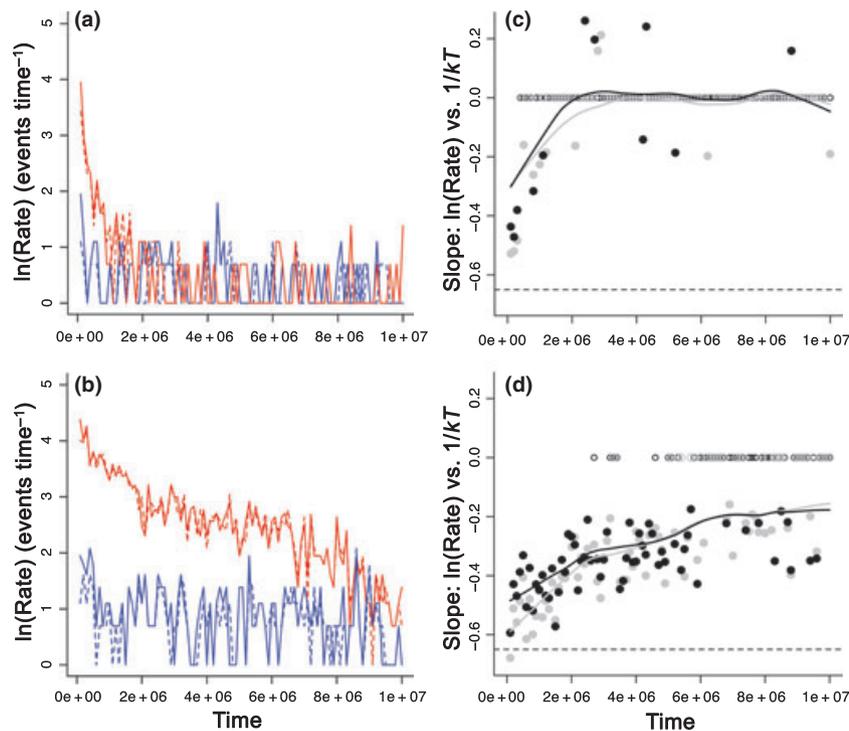
Figure 3 Temporal dynamics of speciation and extinction rates (a, b), and their dependence on temperature (c, d) throughout community assembly. Niche width (mass) is 0.5 in (a) and (c), and 5 in (b) and (d). Strength of interference competition is 0.5 in all panels. (a, b) Temporal dynamics of log-transformed speciation rate (solid) and extinction rate (dashed) at 45 °C (red) and 5 °C (blue) measured within 100 000 time step intervals. (c, d) Temporal dynamics of the slope from the linear regression of log-transformed speciation rate (black) or extinction rate (grey) (within 100 000 time step intervals) against inverse temperature, T, multiplied by Boltzmann's constant, k. Solid and open circles indicate significant and non-significant regressions ($P < 0.05$) respectively. Non-significant regressions are also indicated by a null slope. Solid lines are lowess curve fits to all data points, including non-significant regression slopes, and horizontal black dashed lines indicate a slope of −0.65. A value of one was added to all rates prior to analysis to allow log-transformation of null rates.

SYNTHESIS AND KEY PREDICTIONS

The first part of our paper assessed the foundation of MTB and showed that Allen *et al.*'s (2002, 2006) seminal models can be extended to account for a broad range of relationships between temperature-dependent metabolism and speciation and species richness. There is thus no fundamental inconsistency between MTB and the breadth of empirical data on temperature-species richness patterns (e.g. Hawkins *et al.* 2007a; Fig. 1). Next, we showed how the broader MTB proposed by Allen *et al.* (2007) can be implemented by taking a functional trait approach. The evolution of body size is pivotal in this approach: body size determines resource partitioning and energy flow among species, and in return these ecological conditions shape selection on genetic variation in body size (Fig. 2).

In developing our model, we used a theoretical foundation similar to that in Loeuille & Loreau (2005, 2006), who focused on ecosystem properties at equilibrium, but incorporate the effect of temperature on mutation rate and focus on eco-evolutionary dynamics across the entire

history of communities (Fig. S2). From our model the mass and temperature dependencies of effective population and community size and the temperature dependence of selection emerge from the interplay between mutation, ecology, speciation, extinction and the diversification of body mass. This effectively relaxes MTB assumptions related to the temperature (in)dependencies of abundance, the distribution of body mass, and ecological interactions, and paves the way for a new suite of analyses of the influences of individual metabolism and resource supply on speciation, extinction and community structure. Hereafter we summarize and discuss the key predictions of our model.

Speciation and extinction rates are positively correlated and temporally declining throughout community evolutionary assembly (Fig. 3a, b). Classic 'birth–death' models of macroevolution often assume speciation and extinction rates to be diversity-dependent and/or extremely low extinction rates (Raup *et al.* 1973; Sepkoski 1978; Weir 2006; Rabosky & Lovette 2008a,b). McPeek (2007, 2008) took an ecologically explicit approach and showed that when the speciation rate is given and constant, ecological
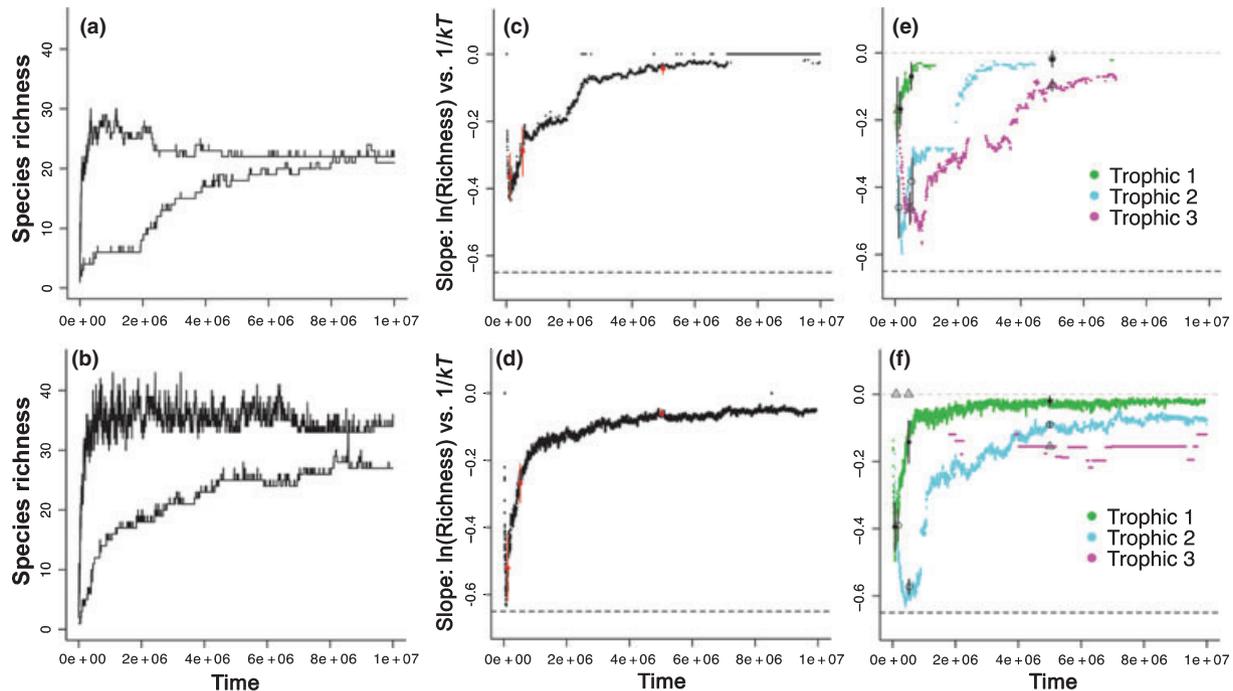
Figure 4 Temporal dynamics of species richness (a, b) and species richness-temperature gradients (c–f) throughout community assembly. Niche width is 0.5 in a, c, e and 5 in b, d, f. Strength of interference competition is 0.5 in all panels. (a, b) Species richness through time at 5 °C (lower trajectory) and 45 °C (upper trajectory). (c, d) Temporal dynamics of the slope from the linear regression of log-transformed whole community species richness against inverse temperature, T, multiplied by Boltzmann's constant, k. Non-significant correlations ($P > 0.05$) are indicated as null slopes. Mean slopes $\pm$ 2 SD at 100 000, 500 000 and 5 000 000 time steps are indicated in red. (e, f) Temporal dynamics of the slope from the linear regression of log-transformed species richness within trophic levels against $1/kT$. Non-significant correlations are not presented for clarity. Mean slopes $\pm$ 2 SD at 100 000, 500 000 and 5 000 000 time steps are indicated as solid circles (trophic level 1), open circles (trophic level 2), or open triangles (trophic level 3). Some symbols have been move horizontally for clarity. See Appendix S1 for details on quantification of slope means. In all panels species richness is measured every 1000 time steps. In (e) and (f) to allow log-transformation of null richness within a trophic level, all richness values were increased by one prior to analysis. Horizontal dashed lines indicate a slope of 0 (grey) or −0.65 (black).

interactions result in either low or slowly increasing extinction rates. In contrast, our metabolic, eco-evolutionary model *predicts* both speciation and extinction rates to decline during community assembly (Fig. 3a,b).

The three processes driving speciation and extinction in our model are disruptive selection causing evolutionary branching, evolutionary suicide resulting in extinction (see also Dieckmann & Ferriere 2004; Loeuille & Loreau 2005; Ito & Ikegami 2006; Ito & Dieckmann 2007), and ecological disequilibrium. Overlap in timescales of population dynamics and genetic mutation results in ecological disequilibrium, which is more significant at higher temperatures/mutation rates (Champagnat *et al.* 2006). That is, a mutant with negative invasion fitness for equilibrium conditions may invade by taking advantage of transient ecological conditions (Ferriere & Gatto 1995; De Feo & Ferriere 2000). This may, in turn, lead to some established species being driven extinct (Champagnat *et al.* 2006).

The initially large difference between speciation/extinction rates at high versus low temperature (i.e. frequent vs. rare mutation) highlights the importance of ecological disequilibrium in the early phase of evolutionary assembly. The initially high rate of speciation is not surprising given that the environment is initially far from being saturated ecologically. More surprising is the similarly high extinction rate, which indicates a large contribution of ecological disequilibrium to the extinction process (see also Hall *et al.* 2002). In contrast, low speciation/extinction rates reached at all temperatures in the long run indicate a reduced influence of ecological disequilibrium. Once trophic niches have self-organized, the stationary species turnover is driven by low rates of branching and suicide within body size guilds (Bonsall *et al.* 2004).

Our prediction of positively correlated and temporally declining speciation and extinction rates is consistent with numerous empirical studies (Webb 1969; Flessa & Levinton 1975; Sepkoski 1978; Van Valen & Maiorana 1985; Stanley
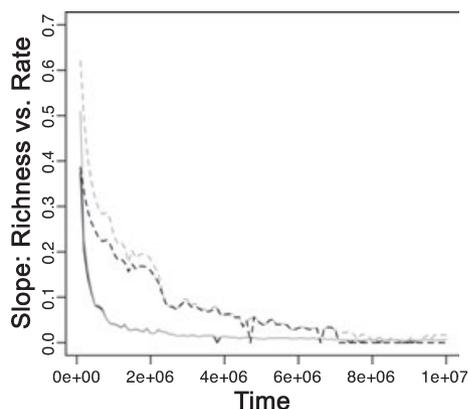
Figure 5 Temporal dynamics of the correlation between species richness and speciation rate or extinction rate across the temperature gradient throughout community assembly. Correlations are measured as the slope of the linear regression of species richness against total speciation or extinction rates (number of events) up to the time at which richness was measured. Black or grey lines indicate correlations with speciation or extinction respectively. Dashed or solid lines indicate correlations with niche width values of 0.5 or 5 respectively. Non-significant correlations are represented as null slopes.

1990; Hulbert 1993; Alroy 1998, 2008; Newman & Sibani 1999; McPeek & Brown 2007). Evaluating speciation and extinction as dynamical eco-evolutionary outcomes of trait (body mass) variation and species interactions therefore provides an important contribution towards reconciling macroevolutionary theory with empirical patterns.

Along temperature gradients, species richness correlates positively with both speciation rate and extinction rate. However, the correlations are not constant and decline to zero with community age (Fig. 5). Our results can be usefully compared with neutral models in which community assembly is driven by stochastic dispersal, speciation (or mutation) and extinction. In particular, neutral theory predicts species richness to be proportional to speciation rate (Hubbell 2001), and a positive empirical correlation of richness with speciation rate has been used as evidence for neutral community assembly (Allen & Gillooly 2006). Our model shows that the correlation between richness and speciation rate does not by itself, however, provide enough information to infer the processes underlying community assembly for two reasons.

First, our model is non-neutral because species are not demographically equivalent, yet it predicts a positive correlation between richness and speciation rate during diversification, consistent with empirical data (Allen & Gillooly 2006; Enquist *et al.* 2007). The model also predicts a positive correlation between richness and extinction rate. All of these correlations are explained by a stronger interaction between mutation and ecology at higher

temperature, which enhances ecological disequilibrium and results in greater species richness and higher speciation and extinction rates. Second, the model predicts lack of correlation between richness and speciation in the long term because of the stabilization of community structure and decline in macroevolutionary rates. Hence, a null richness-speciation correlation does not indicate that the entire history of a community was driven by 'pure' niche processes.

Temperature-richness gradients are evolutionarily dynamic. Steep slopes (close to −0.65) are achieved during the early diversification phase and flatten later on. The maintenance of non-zero slopes in the long run depends on the width of trophic niches (Fig. 4a–d). Our computation of temperature-related gradients assumes that all local communities along the temperature gradient begin their evolutionary history around the same time. Although this is not an unusual assumption (e.g. Allen & Gillooly 2006), different time origins for local evolutionary processes will affect the functional relationship between temperature and diversity. However, the steepest slopes occurred at the point in time when the difference between richness at high vs. low temperature is close to its potential maximum (Fig. 4a–d). Therefore, shuffling the time origins of local evolutionary trajectories will not produce steeper slopes than those reported here.

In contrast, a dependence of trophic niche width on temperature may have a significant effect on predicted slopes. A visual inspection of Fig. 4a,b suggests that steeper negative slopes are reached and maintained if trophic niches widen with increasing temperature; and positive slopes will emerge across sufficiently old communities if trophic niches narrow with increasing temperature.

Temperature-richness gradients vary between functional groups. Differences reduce though time, but persist in the long run if interference competition is strong and trophic niches are wide (Fig. 4e,f). The differential influence of temperature on species richness across functional groups leaves us with the question of where to look for empirical patterns of large-scale variation in species richness. Questions regarding the characteristics of appropriate data were raised early on (Allen *et al.* 2002), and continue to be discussed (e.g. Gillooly & Allen 2007; Hawkins *et al.* 2007a,b). Our trait-based, eco-evolutionary approach suggests broadening the search beyond taxonomic groups by taking ecological function into consideration, thus echoing pioneering work by Margalef (1978), among many others. In particular, evolutionary rates are 'translated' ecologically into patterns of functional composition that may not be legible when using a taxonomic approach. Adopting a functional trait perspective allows a community to be characterized as a frequency distribution of trait values so that patterns may be predicted and sought within and between functional groups.

One may then 'go beyond "How many species and why?" to ask "How much variation in traits and why?"' (McGill *et al.* 2006). However, while suitable data continue to accumulate (see McGill *et al.* 2006), we still know little about how community trait distributions are influenced by individual metabolism.

CONCLUSIONS

There is considerable disagreement with respect to the degree of support for the assumptions and predictions of MTB (e.g. Allen *et al.* 2002, 2006; Storch 2003; Gillooly *et al.* 2005, 2007; Algar *et al.* 2007; Gillooly & Allen 2007; Hawkins *et al.* 2007a,b; Latimer 2007). We propose that the question be recast from whether or not this theory is correct to, 'How can MTB be merged with other domains of ecological and evolutionary theory to provide testable, process-based predictions to account for observed macroevolutionary patterns?' We have moved towards answering this question by unifying trait-based metabolic ecology and evolution and shown that this provides an eco-evolutionary MTB similar to that envisioned by Allen *et al.* (2007) (Fig. 2).

The simple model investigated here yields general predictions that have specific implications regarding the interpretation of empirical patterns. We highlight five main predictions: (1) communities that are relatively young and thus unsaturated ecologically are expected to have temperature-richness gradients with negative slopes close to −0.65; (2) slope values are expected to change most rapidly during the early stages of diversification such that relatively young communities should be characterized by the most variation in slope values; (3) non-significant slopes reported for many taxa might in reality be negative but relatively small (as predicted by our model's long-term dynamics) and therefore difficult to detect; (4) functional heterogeneity (i.e. mixed trophic levels) in community data may obscure temperature-richness gradients evolving within functional groups; and (5) other factors not included in our model, e.g. niche width varying with temperature or coevolving with body size, must play a role in shaping strongly negative or strongly positive temperature-richness gradients.

The first prediction in the above list can be considered the most fundamental and testable prediction of our model. That is, the model predicts that ln(richness)-inverse temperature slopes should track towards zero the closer communities are to being saturated with species. This prediction can be tested by comparing ln(richness)-inverse temperature slopes for specific communities against their degree of saturation. The degree of saturation can be determined experimentally by supplying propagules from non-native species and quantifying the subsequent change in species richness (for a recent example of this experimental

approach see Lee & Bruno 2009). The general expectation is a positive relationship between ln(richness)-inverse temperature slopes and the degree of saturation. While the degree of saturation cannot be rigorously inferred from empirical slopes, it is intriguing to note that many communities are known to be far from saturation (Sax & Gaines 2008; Stohlgren *et al.* 2008; Lee & Bruno 2009), consistent with a peak near −0.65 in the distribution of empirical ln(richness)-inverse temperature slopes (Fig. 1). On the other hand, some empirical ln(richness)-inverse temperature relationships are non-significant (Hawkins *et al.* 2007a), and our model predicts that these groups are essentially saturated with species. If it could be shown that these groups are far from saturation, this would effectively reject the current realization of our model.

A non-experimental approach for testing the model's predictions could make use of fossilized communities to characterize richness-temperature gradients through time. Observed temporal dynamics could, in turn, be compared with the expected temporal patterns of the temperature dependence of species richness within and across trophic levels.

An additional, complementary approach would be to make use of techniques from the burgeoning field of experimental evolution to directly test the model's predictions. This could be achieved by evolving communities (e.g. Venail *et al.* 2008) at different temperatures and tracking genotypic and phenotypic diversity through time. Our model would be rejected if, for example, steep ln(richness)-inverse temperature slopes were maintained throughout all stages of diversification. Even in this case, however, rejection of the model's predictions would initiate a dynamic interplay between model development and empirical analyses, thus deepening our understanding of the processes that drive variation in biodiversity. Lastly, even stronger tests of the model can be developed by dissecting the underlying processes that drive the model's dynamical predictions and evaluate additional aspects of model community structure beyond species richness.

We emphasize that at this point the predictions of our model are by no means intended to be definitive. Rather, the metabolic eco-evolutionary approach presented here should primarily be taken as a foothold for advancing MTB. Further advancement of MTB can be achieved by studying the effects of additional metabolic temperature dependencies (e.g. ontogenic growth and life span) and temperature effects not directly related to metabolism (e.g. water availability). The influences of additional factors such as disturbance (Sousa 1979), spatially explicit dispersal (Loeuille & Leibold 2008), and the evolution of multiple functional traits (Ito & Ikegami 2006) are also important extensions. The eco-evolutionary framework allows for theoretical experiments in which these effects are progres-

sively included and assessed. In so doing, increasingly robust quantitative predictions will emerge from explicit physiological, ecological and evolutionary assumptions. A more complete understanding of how organism metabolism scales up to macroevolutionary patterns will be the result.

REFERENCES

Algar, A.C., Kerr, J.T. & Currie, D.J. (2007). A test of metabolic theory as the mechanism underlying broad-scale species-richness gradients. *Glob. Ecol. Biogeogr.*, 16, 170–178.

Allen, A.P. & Gillooly, J.F. (2006). Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.*, 9, 947–954.

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

Allen, A.P., Gillooly, J.J. & Brown, J.H. (2005). Linking the global carbon cycle to individual metabolism. *Funct. Ecol.*, 19, 202–213.

Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl Acad. Sci. USA*, 103, 9130–9135.

Allen, A.P., Gillooly, J.F. & Brown, J.H. (2007). Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In: *Scaling Biodiversity* (eds Storch, D., Marquet, P.A. & Brown, J.H.). Cambridge University Press, Cambridge, pp. 283–299.

Alroy, J. (1998). Equilibrial diversity dynamics in North American mammals. In: *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities* (eds McKinney, M.L. & Drake, J.A.). Columbia University Press, New York, NY, pp. 232–287.

Alroy, J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proc. Natl Acad. Sci. USA*, 105, 11536–11542.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl Acad. Sci. USA*, 106, 187–191.

Bonsall, M.B., Jansen, V.A.A. & Hassell, M.P. (2004). Life history trade-offs assemble ecological guilds. *Science*, 306, 111–114.

Brown, J.H. (1981). 2 Decades of homage to Santa-Rosalia – towards a general theory of diversity. *Am. Zool.*, 21, 877–888.

Brown, J.H., Marquet, P.A. & Taper, M.L. (1993). Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.*, 142, 573–584.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Case, T.J. & Gilpin, M.E. (1974). Interference competition and niche theory. *Proc. Natl Acad. Sci. USA*, 71, 3073–3077.

Champagnat, N., Ferriere, R. & Meleard, S. (2006). Unifying evolutionary dynamics: from individual stochastic processes to macroscopic models. *Theor. Popul. Biol.*, 69, 297–321.

Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer Associates, Sunderland, MA.

Cozar, A., Garcia, C.M., Galvez, J.A. & Echevarria, F. (2008). Structuring pelagic trophic networks from the biomass size spectra. *Ecol. Model.*, 215, 314–324.

Damuth, J. (1981). Population-density and body size in mammals. *Nature*, 290, 699–700.

De Feo, O. & Ferriere, R. (2000). Bifurcation analysis of population invasion: on-off intermittency and basin riddling. *Int. J. Bifurcat. Chaos*, 10, 443–452.

Dieckmann, U. & Doebeli, M. (1999). On the origin of species by sympactric speciation. *Nature*, 400, 354–357.

Dieckmann, U. & Ferriere, R. (2004). Adaptive dynamics and evolving biodiversity. In: *Evolutionary Conservation Biology* (eds Ferriere, R., Dieckmann, U. & Couvet, D.). Cambridge University Press, Cambridge, UK, pp. 188–224.

Enquist, B.J. & Niklas, K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.

Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D. & Gillooly, J.F. (2003). Scaling metabolism from organisms to ecosystems. *Nature*, 423, 639–642.

Enquist, B.J., Tiffney, B.H. & Niklas, K.J. (2007). Metabolic scaling and the evolutionary dynamics of plant size, form, and diversity: toward a synthesis of ecology, evolution, and paleontology. *Int. J. Plant Sci.*, 168, 729–749.

Ernest, S.K.M., Brown, J.H., Thibault, K.M., White, E.P. & Goheen, J.R. (2008). Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *Am. Nat.*, 172, E257–E269.

Ferriere, R. & Gatto, M. (1995). Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations. *Theor. Popul. Biol.*, 48, 126–171.

Flessa, K.W. & Levinton, J.S. (1975). Phanerozoic diversity patterns: tests for randomness. *J. Geol.*, 83, 239–248.

Frankham, R. (1996). Relationship of genetic variation to population size in wildlife. *Conserv. Biol.*, 10, 1500–1508.

Fussmann, G.F., Loreau, M. & Abrams, P.A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.*, 21, 465–477.

Geritz, S.A.H., Kiski, E., Meszena, K.E. & Metz, J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12, 35–57.

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

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293, 2248–2251.

Gillooly, J.F., Allen, A.P., West, G.B. & Brown, J.H. (2005). The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl Acad. Sci. USA*, 102, 140–145.

Gillooly, J.F., Allen, A.P., Savage, V.M., Charnov, E.L., West, G.B. & Brown, J.H. (2006). Response to Clark and Fraser: effects of temperature on metabolic rate. *Funct. Ecol.*, 20, 400–404.

Gillooly, J.F., McCoy, M.W. & Allen, A.P. (2007). Effects of metabolic rate on protein evolution. *Biol. Lett.*, 3, 655–659.

Gregory, T.R. (ed.) (2005). *The Evolution of the Genome*. Elsevier Academic Press, Burlington, MA.

Hall, M., Christensen, K., di Collobiano, S.A. & Jensen, H.J. (2002). Time-dependent extinction rate and species abundance in a tangled-nature model of biological evolution. *Phys. Rev. E*, 66, 011904.

Hansen, P.J., Bjornsen, P.K. & Hansen, B.W. (1997). Zooplankton grazing and growth: scaling within the 2-2,000-mu m body size range. *Limnol. Oceanogr.*, 42, 687–704.

Hawkins, B.A., Albuquerque, F.S., Araujo, M.B., Beck, J., Bini, L.M., Cabrero- Sanudo, F.J. *et al.* (2007a). A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, 88, 1877–1888.

Hawkins, B.A., Diniz, J.A.F., Bini, L.M., Araujo, M.B., Field, R., Hortal, J. *et al.* (2007b). Metabolic theory and diversity gradients: where do we go from here? *Ecology*, 88, 1898–1902.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Hulbert, R.C. (1993). Taxonomic evolution in North-American Neogene horses (Subfamily Equinae) – the rise and fall of an adaptive radiation. *Paleobiology*, 19, 216–234.

Hunt, G., Cronin, T.M. & Roy, K. (2005). Species-energy relationship in the deep sea: a test using the Quaternary fossil record. *Ecol Lett.*, 8, 739–747.

Ito, H.C. & Dieckmann, U. (2007). A new mechanism for recurrent adaptive radiations. *Am. Nat.*, 170, E96–E111.

Ito, H.C. & Ikegami, T. (2006). Food-web formation with recursive evolutionary branching. *J. Theor. Biol.*, 238, 1–10.

Kaspari, M., Ward, P.S. & Yuan, M. (2004). Energy gradients and the geographic distribution of local ant diversity. *Oecologia.*, 140, 407–413.

Kelt, D.A. & Brown, J.H. (1998). Diversification of body size: patterns and process in the assembly of terrestrial Mammal faunas. In: *Biodiveristy Dynamics: Turnover of Populations, Taxa, and Communities* (eds McKinney, M.L. & Drake, J.A.). Columbia University Press, New York, NY, pp. 109–131.

Kerkhoff, A.J., Enquist, B.J., Elser, J.J. & Fagan, W.F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Glob. Ecol. Biogeogr.*, 14, 585–598.

Kimura, M. (1983). *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge.

Kreft, H. & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proc. Nat. Acad. Sci. U.S.A.*, 104, 5925–5930.

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

Lee, S.C. & Bruno, J.F. (2009). Propagule supply controls grazer community structure and primary production in a benthic marine ecosystem. *Proc. Natl Acad. Sci.*, 106, 7052–7057.

Lewis, H.M. & Law, R. (2007). Effects of dynamics on ecological networks. *J. Theor. Biol.*, 247, 64–76.

Loeuille, N. & Leibold, M.A. (2008). Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. *Am. Nat.*, 171, 788–799.

Loeuille, N. & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proc. Natl Acad. Sci. USA*, 102, 5761–5766.

Loeuille, N. & Loreau, M. (2006). Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecol. Lett.*, 9, 171–178.

Margalef, R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, 1, 493–509.

Martin, A.P. & Palumbi, S.R. (1993). Body size, metabolic rate, generation time, and the molecular clock. *Proc. Natl Acad. Sci. USA*, 90, 4087–4091.

May, R.M. (1986). The search for patterns in the balance of nature – advances and retreats. *Ecology*, 67, 1115–1126.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

McPeek, M.A. (2007). The macroevolutionary consequences of ecological differences among species. *Palaeontology*, 50, 111–129.

McPeek, M.A. (2008). The ecological dynamics of clade diversification and community assembly. *Am. Nat.*, 172, E270–E284.

McPeek, M.A. & Brown, J.M. (2007). Clade age and not diversification rate explains species richness among animal taxa. *Am. Nat.*, 169, E97–E106.

Metz, J.A.J., Nisbet, R.M. & Geritz, S.A.H. (1992). How should we define 'fitness' for general ecological scenarios?. *Trends in Ecol. Evol.*, 7, 198–202.

Moloney, C.L. & Field, J.G. (1989). General allometric equations for rates of nutrient-uptake, ingestion, and respiration in plankton organisms. *Limnol. Oceanogr.*, 34, 1290–1299.

Newman, M.E.J. & Sibani, P. (1999). Extinction, diversity and survivorship of taxa in the fossil record. *Proc. R. Soc. B Biol. Sci.*, 266, 1593–1599.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA*, 105, 4191–4196.

Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Rabosky, D.L. & Lovette, I.J. (2008a). Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution*, 62, 1866–1875.

Raup, D.M., Gould, S.J., Schopf, T.J.M. & Simberloff, D.S. (1973). Stochastic-models of phylogeny and evolutionary of diversity. *J. Geol.*, 81, 525–542.

Robertson, D.R. & Gaines, S.D. (1986). Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology*, 67, 1372–1383.

Sala, E. & Graham, M.H. (2002). Community-wide distribution of predator-prey interaction strength in kelp forests. *Proc. Natl Acad. Sci. USA*, 99, 3678–3683.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). Effects of body size and temperature on population growth. *Am. Nat.*, 163, 429–441.

Sax, D.F. & Gaines, S.D. (2008). Species invasions and extinction: the future of native biodiversity on islands. *Proc. Natl Acad. Sci.*, 105, 11490–11497.

Sepkoski, J.J. (1978). Kinetic-model of phanerozoic taxonomic diversity. 1. Analysis of marine orders. *Paleobiology*, 4, 223–251.

Skalski, G.T. & Gilliam, J.F. (2001). Functional responses with predator interference: viable alternatives to the Holling Type II model. *Ecology*, 82, 3083–3092.

Sousa, W.P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, 60, 1225–1239.

Stanley, S.M. (1990). The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. In: *Causes of Evolution: A Paleontological Perspective* (eds Ross, R.M. & Allmon, W.D.). University of Chicago Press, Chicago, IL, pp. 103–127.

Stegen, J.C. & Swenson, N.G. (2009). Functional trait assembly through ecological and evolutionary time. *Theor. Ecol.*, in press.

Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C. & Kartesz, J. (2008). The myth of plant species saturation. *Ecol. Lett.*, 11, 313–326.

Storch, D. (2003). Comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule". *Science*, 299.

Van Valen, L.M. & Maiorana, V.C. (1985). Patterns of origination. *Evol. Theory*, 7, 107–125.

Venail, P.A., MacLean, R.C., Bouvier, T., Brockhurst, M.A., Hochberg, M.E. & Mouquet, N. (2008). Diversity and productivity peak at intermediate dispersal rate in evolving meta-communities. *Nature*, 452, 210–214.

Waxman, D. & Gavrilets, S. (2005). 20 questions on adaptive dynamics. *J. Evol. Biol.*, 18, 1139–1154.

Webb, S.D. (1969). Extinction-origination equilibria in late Cenozoic land mammals of North America. *Evolution*, 23, 688–702.

Weir, J.T. (2006). Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, 60, 842–855.

Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.

Wright, S.D., Gillman, L.N., Ross, H.A. & Keeling, D.J. (2009). Slower tempo of microevolution in island birds: implications for conservation biology. *Evolution*, in press.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Gaussian mass-specific feeding function.
Figure S2 Evolutionary emergence of food web.
Figure S3 Temporal dynamics of speciation and extinction rates.
Figure S4 Temperature dependence of speciation and extinction rates.
Figure S5 Whole food web species richness through time.
Figure S6 Temperature dependence of whole food web species richness.

Figure S7 Correlation between species richness and speciation or extinction.
Figure S8 Temperature dependence of within-trophic-level species richness.
Appendix S1 Description of eco-evolutionary model.

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APPENDIX 1

Consumers and nutrients are modeled as pools of 'biomass', N_i and N_0, respectively, and changes in the sizes of these pools are given by Eqs. A1 and A2, respectively, in which consumer species are ordered by body size from 1 to n.

$$\frac{dN_i}{dt} = N_i \left(\varepsilon \sum_{j=0}^{i-1} f(M_i, M_j) N_j - m(M_i) - \sum_{j=1}^{n} c(M_i, M_j) N_j \right.$$
$$\left. - \sum_{j=i+1}^{n} f(M_j, M_i) N_j \right) \tag{A1}$$

$$\frac{dN_0}{dt} = I - N_0 y + v \left((1 - \varepsilon) \sum_{i=1}^{n} \sum_{j=0}^{i-1} f(M_i, M_j) N_j N_i \right.$$
$$\left. + \sum_{i=1}^{n} m(M_i) N_i + \sum_{i=1}^{n} \sum_{j=1}^{n} c(M_i, M_j) N_j N_i \right)$$
$$- \sum_{i=1}^{n} f(M_i, M_0) N_0 N_i \tag{A2}$$

where the intrinsic mortality rate m and the feeding rate f are given by Eqs. A3 and A4, respectively, and Suppl. Fig. 1 provides a visualization of the feeding function.

$$m(M) = m_0 M_i^{-0.25} \tag{A3}$$

$$f(M_i, M_j) = f_0 M_i^{-0.25} \sigma^{-1} (2\pi)^{-0.5} exp(-(M_i - M_j - d)^2 \sigma^2) \tag{A4}$$

Table A1 Parameter values used in model simulations

Parameter	Description	Value (units)
α_o	mutation rate normalization	14722190 (mutation mass$^{0.25}$ time^{-1})
v	ecosystem nutrient retention efficiency	0.5 (unitless)
y	nutrient loss rate	0.1 (time^{-1})
I	nutrient influx rate	10 (mass.time^{-1})
β	interference competition max. body size difference	0.25 (mass)
c_o	interference competition rate constant	0.1 or 0.5 (time^{-1}mass^{-1})
m_o	mortality rate normalization	0.1 (mass$^{0.25}$time^{-1})
f_o	feeding rate normalization	1.189 (mass$^{0.25}$time^{-1})
σ	feeding function standard deviation	1 or 3.16 (mass)
d	optimal body size difference	2 (mass)
ϵ	assimilation efficiency	0.25 (unitless)

The population biomass of a new mutant is fixed to 1e-20. The value of the mutation rate 'normalization constant', α_o, gives a mutation probability of 10^{-4} at 25°C and for a body size of 5, the approximate median body size of interaction networks evolved under a body-size-independent mutation probability of 10^{-4}. Other parameters are set to values similar to those producing realistic interaction networks in Loeuille & Loreau (2005) (Table A1).