Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity

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I. Introduction

Understanding the causes and consequences of variation in biodiversity has long been a central focus of research in ecology and biogeography (von Humboldt, 1808; Hutchinson, 1959; MacArthur, 1969; Brown, 1981; Tilman, 1999; Hubbell, 2001; Clarke, 2006). Ecologists have been particularly fascinated by the latitudinal gradient of increasing biodiversity from the poles to the equator since at least the time of Darwin (1859) and Wallace (1878). Contemporary data indicate that this gradient holds for nearly all major groups of terrestrial, aquatic, and marine ectotherms, both plant and animal, and for endothermic birds and mammals (Rohde, 1992; Gaston, 2000; Allen, Brown & Gillooly, 2002; Willig, Kaufman & Stevens, 2003; Currie, Mittelbach, Cornell et al., 2004; Pautasso & Gaston, 2005; Clarke, 2006; Currie, 2006). Furthermore, fossil data indicate that this gradient has been maintained for over 200 million years (Stehli, Douglas &
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Newell, 1969). Despite more than 150 years of inquiry, the mechanisms responsible for the gradient are still not well understood (Allen, Brown & Gillooly, 2003; Hawkins, Field, Cornell et al., 2003; Huston, Brown, Allen et al., 2003; Storch, 2003; Currie et al., 2004; Clarke, 2006; Currie, 2006), but a large and growing list of hypotheses has been proposed to explain it (Rohde, 1992; Gaston, 2000; Hawkins et al., 2003; Currie et al., 2004).

In recent years, particular attention has focused on what we will refer to as the “species-energy hypothesis”, which proposes that the latitudinal biodiversity gradient has somehow been generated and maintained as a direct consequence of greater energy availability towards the equator. The species-energy hypothesis is consistent with extensive empirical work showing strong positive correlations between geographic gradients in biodiversity and climatic measures that directly or indirectly reflect energy availability in the environment (Currie, 1991; Wright, Currie & Maurer, 1993; Hawkins et al., 2003; Currie et al., 2004, Clarke, 2006 #2568; Currie, 2006). These climatic measures can be classified into one of two distinct classes: (i) those that directly reflect fluxes of solar radiation, such as temperature and potential evapotranspiration; and (ii) those that are directly or indirectly related to the rate of conversion of solar radiation to reduced carbon compounds through photosynthesis, such as precipitation, net primary production, and actual evapotranspiration.

Several mechanisms have been proposed to account for species-energy relationships; these include the effects of temperature on biochemical reaction rates (Rohde, 1992; Allen et al., 2002), the effects of temperature on the ability of organisms to maintain homeostasis (Currie, 1991; Hawkins et al., 2003; Currie et al., 2004), and the
effects of ecosystem productivity on total community abundance (Hutchinson, 1959; Brown, 1981; Wright, 1983; Allen et al., 2002; Clarke, 2006). Despite the strength and ubiquity of species-energy correlations, no consensus has yet emerged about the mechanisms that generate them (Hawkins et al., 2003; Currie et al., 2004).

Here we suggest that our present gap in knowledge about the origins of species-energy relationships stems from three interrelated issues. First, “energy” comes in not one, but two basic forms – kinetic and potential – that affect biota in different ways. Second, as a consequence, while both forms of energy may influence biodiversity, they necessarily do so through different mechanisms. And third, while we recognize that biodiversity is ultimately an integrated measure of speciation-extinction dynamics, we still have only limited understanding of how speciation rates, extinction rates, and the standing stock of species are dynamically linked to each other (Hubbell, 2001), and to the availability of kinetic and potential forms of energy in the environment (Allen et al., 2003; Huston et al., 2003; Storch, 2003). Together, these three issues highlight the need to recast the species-energy hypothesis in terms of the two basic forms of energy in nature – kinetic and potential – and the different ways they affect biota. (See also Clarke (2006), this volume.)

In this chapter, we address these three key issues from the perspective of recent advances toward a metabolic theory of ecology (MTE) (Brown, Gillooly, Allen et al., 2004). This recent work indicates that the availability of both forms of energy, kinetic and potential, influences biodiversity, but through different mechanisms. The first mechanism is related to the constraint of thermal kinetic energy, characterized by environmental temperature, on cellular- and individual-level metabolic processes. It is
consistent with the “evolutionary speed” hypothesis (Rohde, 1992; Allen et al., 2002).
The second mechanism is related to the constraint of chemical potential energy, characterized by net primary production, on total community abundance. It is consistent with the “more individuals” hypothesis (Hutchinson, 1959; Brown, 1981; Wright, 1983; Allen et al., 2002). We argue that these mechanisms do not operate in isolation, but rather in concert, to help regulate biodiversity gradients. Furthermore, despite fundamental differences between these two mechanisms, we propose that they both influence biodiversity through their effects on speciation rates in biological communities.

We develop these ideas as follows in the remaining sections of this chapter. In section II, we define kinetic and potential energy, and discuss their relationships to rates of biological metabolism for individuals, communities, and ecosystems. In section III, we discuss mechanisms that may link biodiversity to energy availability in the environment through their effects on speciation rates in biological communities. Then, in section IV, we present empirical evidence that kinetic and potential energy each play important, but fundamentally different roles in regulating biodiversity. Finally, in section V, we discuss theoretical and empirical challenges that will need to be addressed in order to rigorously test the hypothesis that energy availability regulates biodiversity through its effects on speciation rates.

II. Relationships of kinetic and potential energy to biological metabolism

We propose that a more mechanistic understanding of species-energy relationships can be achieved by explicitly focusing on the two fundamental forms of energy in nature – kinetic and potential – and their different roles in sustaining life. We therefore begin this
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section by briefly reviewing basic energy concepts from physics. We then discuss biological metabolism in light of these concepts. We conclude this section by discussing how the availability of kinetic and potential forms of energy constrains the biological metabolism of individuals, communities, and ecosystems.

Energy is defined as the capacity of a system to do work. For a simple mechanical system, work involves moving a mass (kg) over a distance (m) by applying a force (m s\(^{-2}\)). Regardless of the type of work being performed, its magnitude can be expressed in energy units of joules (1 J = 1 kg m\(^2\) s\(^{-2}\)). From physics, we know that all energy comes in one of two basic forms, kinetic and potential. Kinetic energy is the energy of motion. Thermal kinetic energy is essential to life because, without it, biochemical reactions cannot proceed. Thermal kinetic energy is indexed by absolute temperature, \(T\) in degrees Kelvin (K), which is proportional to the average kinetic energy of randomly moving atoms and molecules in a system. At higher temperatures, atoms and molecules move at higher velocities, \(v\), and therefore have more thermal kinetic energy (\(T \propto v^2\)). Solar radiation, another type of kinetic energy, is also essential because it is used by plants to photosynthesize reduced carbon compounds. Once formed, these compounds represent the second basic form of energy, potential energy, which is defined as energy stored in an object. The chemical potential energy stored in reduced carbon compounds fuels virtually all biochemical reactions in the biosphere.

Metabolism is the process of transforming kinetic energy to potential forms (and vice versa) through biochemical reactions. The metabolic rate of an organism is equal to its total rate of energy transformation for fitness-enhancing processes of survival, growth, and reproduction (Brown et al., 2004). This rate can be expressed in units of Watts (1 W
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$= 1 \text{ J s}^{-1}$). As a point of reference, a human being has a metabolic rate about equal to the energy flux of a standard 100 W light bulb. Following the definition of biological metabolism, the metabolic rate of an autotroph is its total rate of photosynthesis, $P$, and the metabolic rate of a heterotroph is its total rate of respiration, $R$:

$$\text{CO}_2 + \text{H}_2\text{O} \xrightarrow{P} \text{CH}_2\text{O} + \text{O}_2 \quad (1)$$

$$\text{CH}_2\text{O} + \text{O}_2 \xrightarrow{R} \text{CO}_2 + \text{H}_2\text{O} \quad (2)$$

Autotrophic metabolism is thus governed by the photosynthesis of chemical potential energy in the form of reduced carbon compounds (CH$_2$O), whereas heterotrophic metabolism is governed by the utilization of chemical potential energy in respiration. Due to mass and energy balance, the gross rate of photosynthesis by a plant, $P$, can be expressed as the sum of two other individual-level rates, respiration plus growth. Thus, for autotrophic individuals, the metabolic rate exceeds the respiration rate. On the other hand, for heterotrophic individuals, the metabolic rate equals the respiration rate, $R$. This is because heterotrophs take in materials that have already been “prepackaged” by plants through photosynthesis, and because respiration fuels any additional energy transformations that are required to convert these prepackaged materials to heterotrophic biomass.

For a heterotroph, the process of consuming chemical potential energy in respiration is primarily constrained by two variables: individual body size, $M_i$ (g), and temperature, $T$ (K) (Gillooly, Brown, West et al., 2001). The combined effects of these two variables on individual respiration, $R_i$ (W), can be described by the following equation (Gillooly et al., 2001):

$$R_i = r_o M_i^{3/4} e^{-E/kT} \quad (3)$$
where \( r_o \) is a normalization constant, independent of body size and temperature (W \( g^{-3/4} \)), that varies about 10-fold between multi-cellular animals and microbes (Gillooly et al., 2001). The 3/4-power scaling exponent on the body size term reflects geometric and biophysical constraints on the delivery of energy and materials to cells through biological distribution networks (West, Brown & Enquist, 1997). Based on this size dependence, Eq. 3 predicts a \( 10^{15} \)-fold increase in metabolic rate over the body size range \( 10^{-12} \) g to \( 10^8 \) g from microbes to whales ([\( 10^8/10^{-12} \)]^{3/4} = \( 10^{15} \)-fold). The Boltzmann-Arrhenius factor, \( e^{-E/kT} \), characterizes the exponential effects of temperature on individual metabolic rate, where \( E \) is the average activation energy of the respiratory complex (~0.65 eV), and \( k \) is Boltzmann’s constant \( (8.62 \times 10^{-5} \text{ eV K}^{-1}) \) (Gillooly et al., 2001). This Boltzmann-Arrhenius factor quantifies the relationship of temperature to the proportion of molecules in a system that have kinetic energies exceeding the activation energy, \( E \), required to react. Based on this temperature dependence, Eq. 3 predicts a 34-fold increase in metabolic rate over the biological temperature range 0-40°C from an Antarctic fish to an endothermic bird or mammal \( (e^{-E/k313}/e^{-E/k273} = 34\text{-fold from } 273\text{-313 K}) \).

By extending these basic energy concepts, we can quantify the relationship of the individual respiration rate, \( R_i \) (Eq. 3), to the respiratory flux of the entire heterotrophic community. Due to mass and energy balance, the total respiration rate per unit area for a heterotrophic community comprised of \( J \) individuals in an area of size \( A \), \( R_{Tot} \) (W m\(^{-2}\)), is equal to the sum of the individual respiration rates, \( R_i \), from Eq. 3:

\[
R_{Tot} = \frac{1}{A} \sum_{i=1}^{J} R_i = (J/A) \langle R_i \rangle_j = (J/A) r_o \langle M^{3/4} \rangle_j e^{-E/kT} \tag{4}
\]
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where $J/A$ is the abundance of individuals per unit area ($m^2$), $\langle R \rangle_j$ is the average metabolic rate of an individual $(= \left( \frac{1}{J} \sum_{i=1}^{J} R_i \right) = r_o \langle M^{3/4} \rangle_j e^{-E/RT} )$, and $\langle M^{3/4} \rangle_j$ is an average for body size $(= \left( \frac{1}{J} \sum_{i=1}^{J} M_i^{3/4} \right) )$ (Enquist, Economo, Huxman et al., 2003; Allen, Gillooly & Brown, 2005).

Four issues arise in using Eq. 4 to derive and test predictions. First, while $R_{\text{tot}}$ exactly equals to the sum of the individual respiration rates, $r_o$ can vary among taxa (Gillooly et al., 2001). Accuracy of predictions may therefore be improved by aggregating organisms into different functional groups. Second, Eq. 4 assumes that $r_o$ is independent of resource availability, $N(L_t)$, but organisms sometimes depress their metabolic rates in response to food scarcity. Equation 4 will be robust to such facultative responses provided that the scope for change in $r_o$ is small relative to variation in $N(L_t)$. One study supports this assumption by demonstrating that metabolic rates of a rodent species declined by only $\sim$25% over a more than 10-fold decline in ecosystem net primary production (Mueller & Diamond, 2001). Third, the average for body size in Eq. 4, $\langle M_i^{3/4} \rangle_j$, does not equal the arithmetic mean of body size raised to the 3/4-power, i.e. $\langle M_i^{3/4} \rangle_j \neq \langle M \rangle_j^{3/4}$, where $\langle M \rangle_j = \left( \frac{1}{J} \sum_{i=1}^{J} M_i \right)$. This point is relevant because frequency distributions of body size are often highly skewed in biological communities, resulting in pronounced differences between $\langle M_i^{3/4} \rangle_j$ and $\langle M \rangle_j^{3/4}$ (Savage, 2004). Finally, fourth, Eq. 4 does not apply to long-term respiration rates of autotrophic communities. This is because plant metabolism is governed by photosynthesis (Eq. 1), which has a non-
exponential temperature dependence (Allen et al., 2005). Furthermore, photosynthesis may be limited or co-limited by other variables in addition to temperature (Farquhar, von Caemmerer & Berry, 1980; Allen et al., 2005); these variables include water (Lieth, 1973; Huxman, Smith, Fay et al., 2004), light (Monteith, 1972; Field, Behrenfeld, Randerson et al., 1998), nutrients (Vitousek, 1984; Chapin, Matson & Mooney, 2002), and space (Enquist & Niklas, 2001). (See also Clarke (2006)). For what follows, we will collectively denote those resources limiting photosynthesis by $L_i$, and we will denote the rate of net primary production of reduced carbon compounds by the function $N(L_i)$ (W m$^{-2}$) to reflect resource limitation on photosynthesis in ecosystems.

By imposing mass and energy balance on the production and consumption of chemical potential energy in ecosystems, we can extend Eq. 4 to predict the relationship of ecosystem net primary production to the total abundance and metabolism of heterotrophic individuals. If the total rate of respiration by all of the heterotrophs comprising a community, $R_{tot}$, is limited by the availability of reduced carbon compounds, $N(L_i)$, as indicated by recent work (Allen et al., 2005), then

$$R_{tot} = \left(\frac{J}{A}\right)r_o \langle M_i^{3/4} \rangle_j e^{-E_i/kT} = N(L_i)$$

Rearranging the terms in Eq. 5 shows how the total abundance of heterotrophs is limited by net primary production:

$$\left(\frac{J}{A}\right) = N(L_i) e^{E_i/kT} / r_o \langle M_i^{3/4} \rangle_j = N(L_i) / \langle R_i \rangle_j$$

Equation 6 yields different predictions for endotherms and ectotherms. For endotherms, body temperatures, and hence average metabolic rates $\langle R_i \rangle_j$, are relatively high and constant across global temperature gradients (Anderson & Jetz, 2005). Thus, after
controlling for body size, $\langle M_i^{3/4} \rangle_j$, community abundance is predicted to increase approximately linearly with the rate of consumption of net primary production, $N(L_i)$, in agreement with recent work (Pautasso & Gaston, 2005). By contrast, for ectotherms, abundance is predicted to decline exponentially with increasing temperature ($\propto e^{E/kT}$) if $N(L_i)$ and $\langle M_i^{3/4} \rangle_j$ are both held constant in Eq. 6 (Savage, Gillooly, Brown et al., 2004; Allen et al., 2005) because of increases in per-individual metabolic demands, $\langle R_i \rangle_j$ (Eq. 3). Thus, for the community abundance of ectotherms to even remain constant across global temperature gradients, the total rate of consumption of net primary production, $N(L_i)$, must increase with increasing temperature. Ecosystem net primary production does in fact increase with temperature (Lieth, 1973), but the response is not exponential (Allen et al., 2005). Modeling the overall global relationship between abundance and net primary production for heterotrophic ectotherms therefore requires explicit consideration of temperature and its differential effects on heterotrophic respiration versus autotrophic photosynthesis (Allen et al., 2005).

The issues discussed above arise as direct consequences of differences in the controls on metabolism for plants, heterotrophic ectotherms, and endotherms, and can be quantified using Eqs. 3-6. More generally, these equations demonstrate that the availability of thermal kinetic energy in the environment, indexed by $T$, fundamentally constrains the consumption of chemical potential energy by heterotrophs at the individual level, $\langle R_i \rangle_j$, and that the net rate of production of chemical potential energy by autotrophs, $N(L_i)$, fundamentally constrains the consumption of chemical potential energy by heterotrophs at the community level, $R_{Tot}$. These ecosystem-level rates of energy
transformation, $N(L)$ and $R_{Tot}$, are, in turn, both constrained by the availability of resources, $L_i$, required for photosynthesis to proceed.

**III. Linking kinetic and potential energy to biodiversity through speciation**

In this section, we discuss processes and mechanisms that may link kinetic and potential energy to biodiversity through their effects on speciation rates. There is now significant theoretical and empirical support for the idea that comprehensive understanding of biodiversity gradients will require a synthesis of new approaches that explicitly link short-term species coexistence to long-term speciation-extinction dynamics. In particular, the recently proposed Neutral Theory of Biodiversity (NTB) demonstrates that increasing the overall rate of speciation in biological communities can result in higher steady-state levels of biodiversity (Hubbell, 2001). Furthermore, there exists fossil evidence indicating that biodiversity peaks in the tropics as a direct consequence of elevated speciation rates (Stehli *et al.*, 1969; Crane & Lidgard, 1989; Jablonski, 1993; Flessa & Jablonski, 1996; Crame, 2002), although this remains an important topic of debate. (See, for example, Chown and Gaston (2000) and Currie *et al.* (2004).)

We hypothesize that kinetic and potential forms of energy both help regulate biodiversity through their effects on speciation rates, but via different mechanisms (arrows 1-3, Fig. 1). The process of speciation involves the evolution of genetic differences among species populations, which accumulate to induce reproductive isolation and influence ecological roles (Coyne & Orr, 2004). The overall speciation rate in a community can therefore be increased in one of two ways (Fig. 1): (arrow 4) by increasing the rates of genetic divergence among species populations, or (arrow 5) by
increasing the total number of species populations. This reasoning implies that the overall rate of speciation in a community should be expressed as the product of a per capita rate (species individual$^{-1}$ time$^{-1}$) and total community abundance (Allen, Gillooly, Savage et al., in review). Characterizing speciation on a per capita basis runs counter to the long-standing tradition among evolutionists and paleontologists of expressing speciation on a per species basis (species species$^{-1}$ time$^{-1}$) (Yule, 1925; Coyne & Orr, 2004). Nevertheless, it is consistent with evolutionary theory because speciation occurs at the level of populations, not species (Coyne & Orr, 2004). It is also consistent with NTB, which predicts that the overall speciation rate determines the number of species maintained in a community of fixed total abundance, and not vice versa (Hubbell, 2001).

Biodiversity is an integrated measure of speciation-extinction dynamics because the number of species in existence at any given time equals the total number of speciation events minus the total number of extinction events (arrows 6, 8; Fig. 1). Recent work indicates that global biodiversity is at or near steady-state, and has been for hundreds of millions of years (Alroy, Marshall, Bambach et al., 2001). This implies that overall rates of speciation and extinction are approximately equal for many taxa. Following the early work of Rozensweig (1975) and Sepkoski (1978), among others, and the more recent work of Hubbell (2001) and Alroy et al. (2001), we assume here that biodiversity is at or near steady state. We also assume that this steady state arises because increasing the overall rate of speciation in a community of fixed size reduces the average abundance per species per unit area, $\bar{N}$, resulting in higher rates of stochastic extinction (Hubbell, 2001). Given that the stochastic extinction rate is expected to increase with decreasing $\bar{N}$ (Lande, Engen & Saether, 2003) (arrow 7), and that
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\[ \bar{N} = (J/AS) \] (7)

where \( S \) is species richness in a plot of area \( A \) (Allen et al., 2002), the extinction rate is directly related to species richness (arrow 8). This line of reasoning (Fig. 1) yields the hypothesis that the speciation rate is an important driving variable of speciation-extinction dynamics, and therefore of geographic gradients in biodiversity. For the remainder of this section, we will therefore speculate on how the availability of kinetic and potential forms of energy may help regulate biodiversity (arrows 1-3) through their effects on speciation rates (arrows 4-5), and the dynamic interplay between speciation, extinction, and the standing stock of species (arrows 6-8).

Based on the MTE results presented in the previous section, and other MTE results discussed below, we propose that thermal kinetic energy influences speciation rates through its effects on rates of genetic divergence among species populations (arrow 1, Fig. 1), and that chemical potential energy influences speciation rates through its effects on the total numbers of individuals and populations that are maintained in an ecosystem (arrow 3, Fig. 1).

We hypothesize that the availability of thermal kinetic energy is linked to speciation rates through the constraints of environmental temperature, \( T \), on rate processes controlled by mass-specific metabolic rate, \( R_i/M_i \) (following Eq. 3; arrow 1, Fig. 1). The rate at which a population evolves is constrained by two individual-level variables, the generation time and mutation rate (Fisher, 1930; Kimura, 1983). Recent work has shown that the rate of turnover of individuals, \( g \) (generations sec\(^{-1}\)), increases directly with mass-specific metabolic rate, \( R_i/M_i \) (Gillooly, Charnov, West et al., 2002):

\[ g = g_o (R_i/M_i) = g_o r_o M_i^{-1/4} e^{-E/kT} \] (7)
where $g_o$ is a normalization constant that characterizes the number of generations per joule of energy flux through a gram of tissue ($J g^{-1} \text{ generation}^{-1}$) (Fig. 2a). More recently, we have shown that rates of mutation in nuclear and mitochondrial genomes, $\alpha$ (mutations nucleotide$^{-1}$ s$^{-1}$), also increase directly with mass-specific metabolic rate (Gillooly, Allen, West et al., 2005):

$$\alpha = \alpha_o \left( \frac{R_i}{M_i} \right) = \alpha_o b_o M_i^{-1/4} e^{-E_i/kT}$$

(8)

where $\alpha_o$ is a normalization constant that characterizes the number of joules of metabolic energy required to induce 1 mutation per site in a genome ($J g^{-1}$ mutations nucleotide$^{-1}$) (Fig. 2b). There are also population-level variables that influence how quickly populations evolve; these variables include effective population size, the migration rate among populations, and the intensity of natural selection (Fisher, 1930; Kimura, 1983). Furthermore, speciation requires not only evolution within populations, but also an ecological mechanism that facilitates genetic divergence among populations, e.g. a geographic barrier to dispersal in the allopatric mode of speciation (Mayr, 1942).

Speciation is thus an inherently ecological as well as evolutionary process. Nevertheless, using Eqs. 7-8, it can be shown that if the population-level variables affecting genetic divergence rates are held constant, rates of genetic divergence will increase exponentially with temperature in the same way as individual metabolic rate (Allen et al., in review).

We hypothesize that the availability of chemical potential energy is linked to the speciation rate through the constraints of ecosystem net primary production, $N(L_i)$, on total community abundance (following Eq. 6; arrow 3, Fig. 1). Our reasoning is that if the total abundance of individuals in a community is increased through enhancement of net primary production (Eq. 6), total rates of population subdivision via allopatric, parapatric,
sympatric mechanisms should also increase, resulting in higher speciation rates. We note one important complication with this argument. Equation 6 assumes that heterotrophs make use of all of the chemical potential energy made available by plants through net primary production. While this assumption is reasonable for the entire heterotrophic communities (Allen et al., 2005), only a small fraction of total net primary production in the ecosystem, \( N(L) \), is consumed by any of the more restricted heterotrophic “communities” that ecologists typically study (e.g., amphibians, birds, reptiles). Abundance for a restricted taxon is a function not only of ecosystem net primary production, but also of biotic and abiotic variables that interact with attributes of the taxon to uniquely determine its environmental niche (Kaspari, 2001). As a consequence, we would expect the relationship between \( N(L) \) and community abundance to be somewhat idiosyncratic for restricted taxa (Kaspari, 2005).

IV. The different roles of kinetic and potential energy in regulating biodiversity

In the preceding sections, we proposed that kinetic and potential energy each play important, but fundamentally different roles in regulating biodiversity. Specifically, we proposed that the availability of thermal kinetic energy, characterized by environmental temperature \( T \), helps regulate biodiversity through its effects on cellular- and individual-level processes (Eq. 3; arrow 1, Fig. 1), and that the availability of chemical potential energy availability, characterized by \( N(L) \), helps regulate biodiversity through its effects on community abundance (Eq. 6; arrow 3, Fig. 1). Furthermore, we speculated that both mechanisms contribute to the maintenance of biodiversity through their effects on speciation rates (arrows 4-5, Fig. 1).
Building on our proposed framework, it is possible to decompose energetic determinants of biodiversity into those that operate through their effects on individual metabolic rate, $R_i$, and those that operate through their effects on community abundance, $J/A$ (Allen et al. in preparation). However, it is important to note that these two sets of determinants are rarely if ever independent. For example, in terrestrial ecosystems, increasing the environmental temperature, $T$, not only enhances the metabolic rates of heterotrophic ectotherms ($R_i$, Eq. 3), it also enhances net primary production, $N(L_i)$ (Allen et al., 2005) (arrow 2, Fig. 1), which in turn interacts with $R_i$ to influence community abundance (Eq. 6). Marine ecosystems perhaps offer the greatest opportunity for disentangling the effects of kinetic and potential energy on biodiversity because broad-scale gradients in the net primary production of the world’s oceans are largely decoupled from temperature by nutrient limitation (Field et al., 1998).

The analysis of Currie (2006) illustrates the complexities involved in disentangling the determinants of biodiversity. In particular, Currie (2006) shows in Fig. 10a of his chapter that there exists an upper bound on tree diversity that is well fitted by the exponential Boltzmann temperature relationship predicted by Allen et al. (2002), but that there exists significant residual variation below this upper bound. Allen et al. (2002) were careful to point out in their derivation that the Boltzmann relationship is only predicted if total community abundance is held constant across temperature gradients. Thus, according to Allen et al. (2002), and to the framework proposed here (Fig. 1), this variation is largely attributable to variation in total plant abundance. Specifically, we hypothesize that upper bound in Fig. 10a of Currie (2006) is comprised predominantly of well-watered sites where plant abundance is high, relatively constant, and largely
independent of latitudinal gradients in temperature (Enquist & Niklas, 2001). Because plant abundance is held constant along this upper bound, the predicted exponential effects of temperature on plant diversity are manifested. By contrast, we hypothesize that points below this upper bound are predominantly water-limited sites that have lower total plant abundance and diversity. Furthermore, because precipitation and temperature interact to determine water deficit, and hence total plant abundance, we would also expect temperature and precipitation to strongly interact in determining the plant diversity of water-limited ecosystems. This is consistent with Eq. 3 and Fig. 8 of Currie (2006), the theoretical derivation of Allen et al. (2002), and the framework proposed here (Fig. 1). Thus, we strongly disagree with Currie (2006) that “plant richness does not vary with temperature in the manner predicted by metabolic theory.” Indeed, we feel that the analysis of Currie (2006) provides strong support for our arguments.

In spite of these issues, our framework predicts that the energetic determinants of biodiversity should fundamentally differ for ectotherms and endotherms. In general, for ectotherms, biodiversity should increase with increases in environmental temperature and total community abundance through the combined effects of these variables on speciation rates (Fig. 1). Importantly, even if community abundance is held constant across latitudes, and the “more individuals hypothesis” (Hutchinson, 1959; Brown, 1981; Wright, 1983; Allen et al., 2002) therefore does not apply, ectotherm diversity is predicted to increase exponentially with latitudinal gradients of increasing temperature (Allen et al. (2002), as demonstrated by Currie et al. (2004). According to our proposed framework (Fig. 1), this is a direct consequence of how temperature-induced increases in the metabolic rates of individuals (Eqs. 3, 7-8; arrow 2) influence the evolutionary rates
of populations (arrow 4). By contrast, for endotherms, which show only modest changes in metabolic rate across latitudinal gradients in environmental temperature (Anderson & Jetz, 2005), biodiversity should be regulated primarily by the availability of chemical potential energy through its effects on total community abundance (Eq. 6; arrow 3) and the total numbers of populations contributing to speciation-extinction dynamics (arrow 5).

Community-level data strongly support the hypothesis that the controls on biodiversity fundamentally differ for ectotherms and endotherms. Our analysis of community-level data for ectotherms demonstrates that regional species richness increases exponentially with temperature in the same way as individual metabolic rate \( S \propto e^{-E/kT} \) when total community abundance is held constant (Allen et al., 2002) (Fig. 3). By contrast, another analysis of community-level data for endotherms has shown that the latitudinal gradient in bird diversity is driven largely by geographic variation in total community abundance (Pautasso & Gaston, 2005). Environmental temperature thus has little or no independent effect on biodiversity of the world’s avifaunas. Finally, our analysis of population-level data for ectotherms and endotherms supports this hypothesis (Allen et al., 2002). In that analysis, we showed that, after correcting for body size, average abundance per species per unit area, \( \bar{N} \), was independent of environmental temperature for endothermic mammal populations, but declined exponentially with increasing temperature for ectotherms. These population- and community-level data thus support the hypothesis that kinetic and potential forms of energy regulate biodiversity through fundamentally different mechanisms.
V. Conclusions and Caveats

Much remains to be done in order to establish the proposed chain of causality linking species diversity to energy availability (Fig. 1). Testing this proposed framework poses significant empirical and theoretical challenges. Empirical testing will require the analysis of regionally resolved data on contemporary gradients in biodiversity, combined with regionally resolved data on temperature, community abundance, speciation rates, and extinction rates over a time span comparable to the longest lived species in the taxon of interest. Species lifespans are often measured in millions to tens of millions of years (Stanley, 1998), so this will not be easy. Developing theoretical understanding of how community abundance, speciation, and extinction interact to control the standing stock of species will also be difficult. The NTB model may prove helpful in this regard because NTB incorporates separate terms for community abundance and per capita speciation rate to predict biodiversity (Hubbell, 2001). There are still important issues with NTB that need to be resolved regarding relevant time scales for stochastic changes in abundance and speciation (Clark & McLachlan, 2003; Hubbell, 2003; Ricklefs, 2003; Clark & McLachlan, 2004; Volkov, Banavar, Maritan et al., 2004). Nevertheless, synthesizing NTB with MTE appears to hold significant progress for the road ahead. Through such a synthesis, it is our hope that it will be possible to develop a more comprehensive understanding of biodiversity gradients that encompasses processes operating at the individual, population, and community levels of biological organization while remaining firmly grounded in rates of evolutionary change at the molecular level.
Figure 1. Framework proposed in this chapter for the relationship of biological diversity to the availability of kinetic and potential forms of energy in the environment. The arrows are numbered to facilitate discussion in the text. See Allen et al. (2005) for theory and data on how thermal kinetic energy, \( T \), influences net primary production, \( N(L_i) \), in terrestrial ecosystems (denoted by arrow 2).
**Figure 2.** Effects of temperature, expressed as $1/kT$, on the natural logarithm of (A) individual turnover of unicellular and multi-cellular eukaryotes, and (B) molecular evolution in mitochondria of multi-cellular eukaryotes. Rates were body size-corrected as described in (Brown et al., 2004) prior to logarithmic transformation. Negative linear relationships between the variables, with slopes close to $-E \approx -0.65$ eV, indicate that rates increases exponentially with temperature according to the Boltzmann-Arrhenius relationship for respiration ($\propto e^{-E/kT}$, Eq. 3). Turnover data are from Savage et al. (2004), and mitochondrial RFLP data are from Gillooly et al. (2005).
Figure 3. Effects of mean annual temperature, expressed as $1/kT$, on the natural logarithm of regional species richness for (A) amphibians and (B) trees of North America (Allen et al., 2002). Negative linear relationships between the variables, with slopes close to $-E \approx -0.65$ eV, indicate that species richness increases exponentially with temperature according to the Boltzmann-Arrhenius relationship for respiration ($\propto e^{-E/kT}$, Eq. 3). Data from Currie (1991).
Literature Cited


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Allen, Gillooly & Brown

*Proceedings of the National Academy of Sciences of the United States of America, 102*, 140-145.


Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical


G. Cotta, Tubingen, Germany.


biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology,

**41**, 496-506.

species richness on local and regional scales. In *Species Diversity in Ecological
Communities*, ed. R. E. Ricklefs and D. Schluter, pp 66-74, Chicago: University
of Chicago Press.

Yule, G. U. (1925). A mathematical theory of evolution, based on the conclusions of Dr.
J. C. Willis, F.R.S. *Philosophical Transactions of the Royal Society of London.