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

Andrew P. Allen[1], James F. Gillooly[2], James H. Brown[3]

[1]National Center for Ecological Analysis and Synthesis, 735 State St., Suite 300, Santa Barbara, CA, USA, 93101, drewa@nceas.ucsb.edu

[2]Department of Zoology, University of Florida, Gainesville, FL, USA, 32611, gillooly@zoo.ufl.edu

[3]Department of Biology, University of New Mexico, Albuquerque, NM, USA, 87131 jhbrown@unm.edu

## 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 &

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

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

= 1 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, $P_i$,

$$CO_2 + H_2O \xrightarrow{P_i} CH_2O + O_2 \tag{1}$$

and the metabolic rate of a heterotroph is its total rate of respiration, $R_i$:

$$CH_2O + O_2 \xrightarrow{R_i} CO_2 + H_2O \tag{2}$$

Autotrophic metabolism is thus governed by the photosynthesis of chemical potential energy in the form of reduced carbon compounds ($CH_2O$), 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, $P_i$, 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, $R_i$. 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):

$$R_i = r_o M_i^{3/4} e^{-E/kT} \tag{3}$$

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 x 10$^{-5}$ 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 ($e^{-E/k313}/ e^{-E/k273} = 34$-fold from 273-313 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:

$$R_{Tot} = \frac{1}{A}\sum_{i=1}^{J} R_i = (J/A)\langle R_i \rangle_J = (J/A)r_o \langle M^{3/4} \rangle_J e^{-E/kT} \tag{4}$$

where $J/A$ is the abundance of individuals per unit area ($m^{-2}$), $\left\langle R_i \right\rangle_J$ is the average

metabolic rate of an individual ($= (1/J)\sum_{i=1}^{J} R_i = r_o \left\langle M^{3/4} \right\rangle_J e^{-E/kT}$), and $\left\langle M^{3/4} \right\rangle_J$ is an

average for body size ($= (1/J)\sum_{i=1}^{J} M_i^{3/4}$) (Enquist, Economo, Huxman *et al.*, 2003; Allen,

Gillooly & Brown, 2005).

Four issues arise in using Eq. 4 to derive and test predictions. First, while $R_{tot}$

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, $N(L_i)$, 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 $N(L_i)$.

One study supports this assumption by demonstrating that metabolic rates of a rodent

species declined by only ~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, $\left\langle M_i^{3/4} \right\rangle_J$, does not equal the arithmetic mean of body size raised to the 3/4-power, i.e.

$\left\langle M_i^{3/4} \right\rangle_J \neq \left\langle M \right\rangle_J^{3/4}$, where $\left\langle M \right\rangle_J = (1/J)\sum_{i=1}^{J} M_i$. This point is relevant because frequency

distributions of body size are often highly skewed in biological communities, resulting in

pronounced differences between $\left\langle M_i^{3/4} \right\rangle_J$ and $\left\langle M \right\rangle_J^{3/4}$ (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

$$R_{Tot} = (J/A)r_o\left\langle M_i^{3/4}\right\rangle_J e^{-E/kT} = N(L_i) \tag{5}$$

Rearranging the terms in Eq. 5 shows how the total abundance of heterotrophs is limited

by net primary production:

$$(J/A) = N(L_i)e^{E/kT}/r_o\left\langle M_i^{3/4}\right\rangle_J = N(L_i)/\left\langle R_i\right\rangle_J \tag{6}$$

Equation 6 yields different predictions for endotherms and ectotherms. For endotherms,

body temperatures, and hence average metabolic rates $\left\langle R_i\right\rangle_J$, are relatively high and

constant across global temperature gradients (Anderson & Jetz, 2005). Thus, after

controlling for body size, $\left\langle M_i^{3/4} \right\rangle_J$, 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 $\left\langle M_i^{3/4} \right\rangle_J$ 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,

$\left\langle R_i \right\rangle_J$ (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, $\left\langle R_i \right\rangle_J$, 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, $N(L_i)$ 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, $\overline{N}$, resulting in higher rates of stochastic extinction (Hubbell,

2001). Given that the stochastic extinction rate is expected to increase with decreasing $\overline{N}$

(Lande, Engen & Saether, 2003) (arrow 7), and that

$$\overline{N} = \left(J/AS\right) \tag{7}$$

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):

$$g = g_o\left(R_i/M_i\right) = g_o r_o M_i^{-1/4} e^{-E/kT} \tag{7}$$

13

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$^{-1}$ 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):

$$\alpha = \alpha_o\left(R_i / M_i\right) = \alpha_o b_o M_i^{-1/4} e^{-E/kT} \tag{8}$$

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, $N(L_i)$, 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 $N(L_i)$ 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 $N(L_i)$, 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 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, $\overline{N}$, 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).
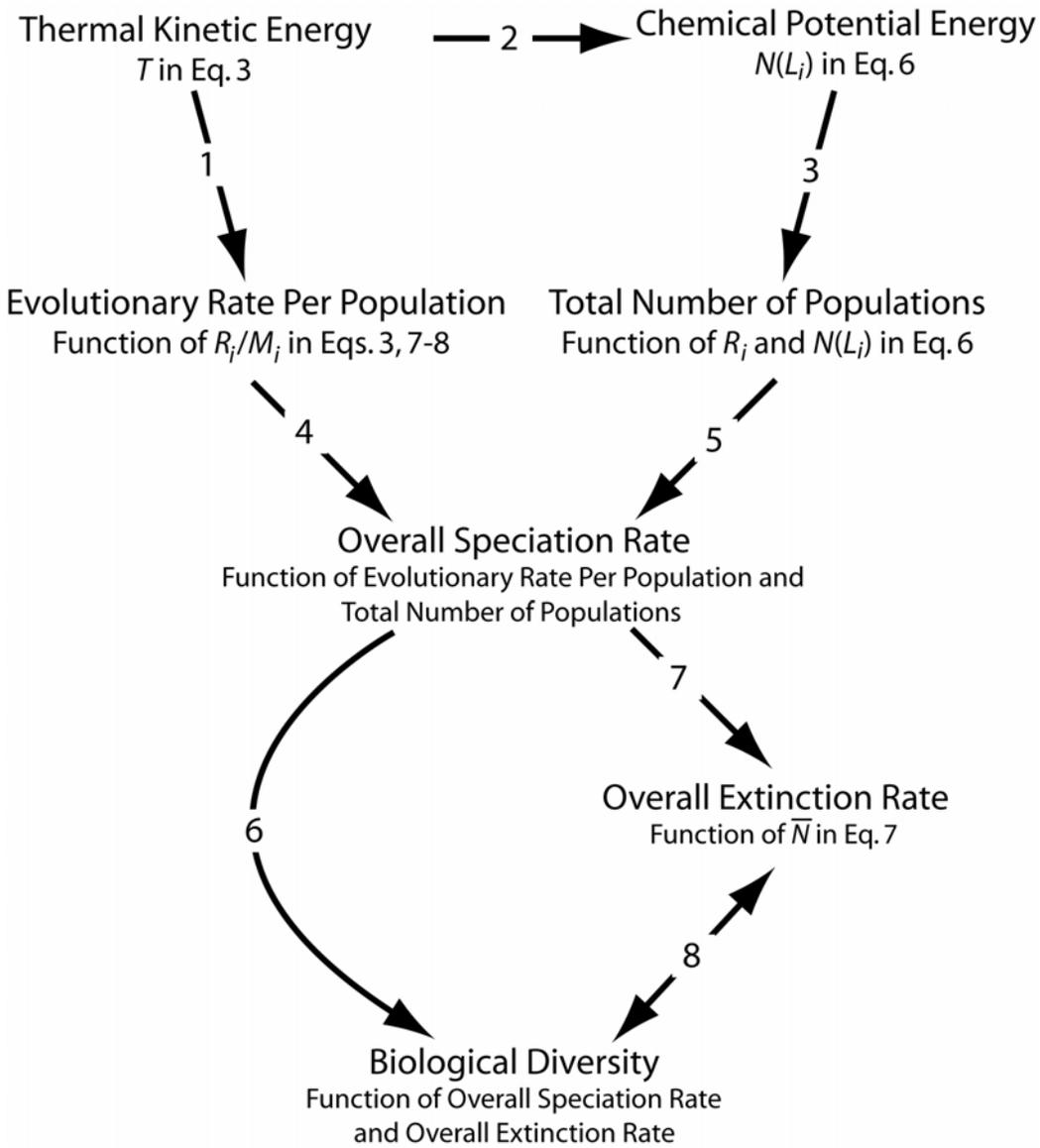
**Figure 2**. Effects of temperature, expressed as $1/kT$, on the natural logarithm of (A)

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.*

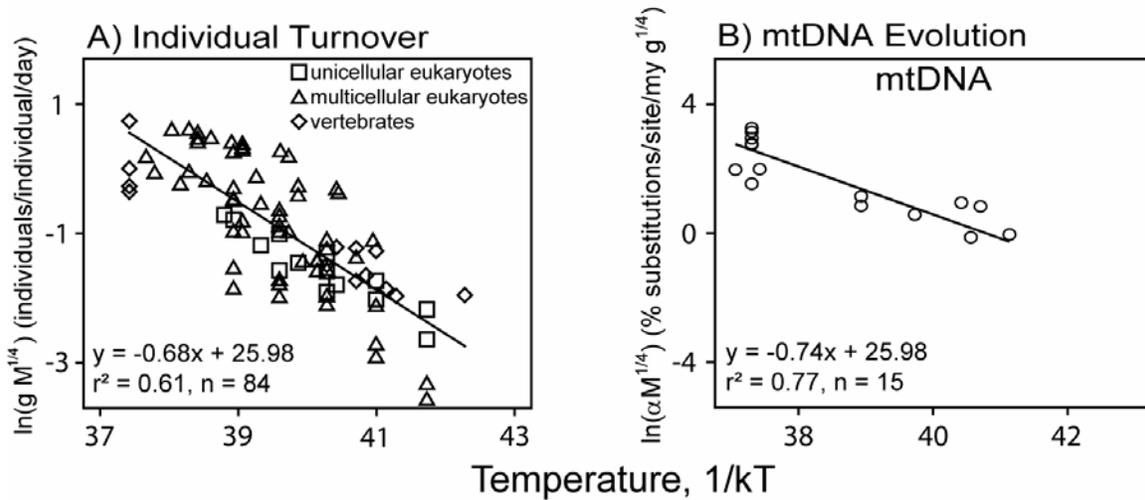(2004), and mitochondrial RFLP data are from Gillooly *et al.* (2005).

**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).
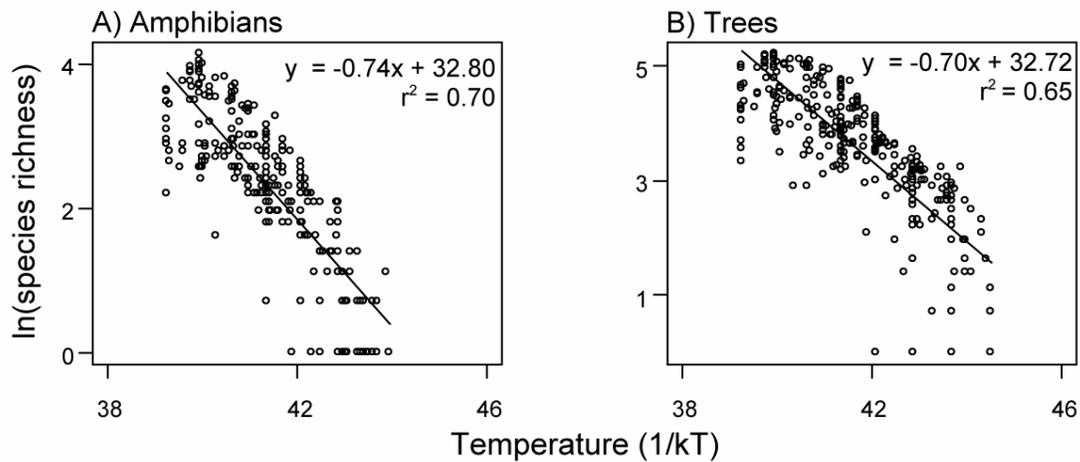
**Literature Cited**

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., Brown, J. H. & Gillooly, J. F. (2003). Response to comment on "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule". *Science*, **299,** 346c.

Allen, A. P., Gillooly, J. F. & Brown, J. H. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology*, **19,** 202-213.

Allen, A. P., Gillooly, J. F., Savage, V. M. & Brown, J. H. (in review). Kinetic effects of temperature on rates of genetic divergence and speciation in biotic communities.

Alroy, J., Marshall, C. R., Bambach, R. K., Bezusko, K., Foote, M., Fursich, F. T., Hansen, T. A., Holland, S. M., Ivany, L. C., Jablonski, D., Jacobs, D. K., Jones, D. C., Kosnik, M. A., Lidgard, S., Low, S., Miller, A. I., Novack-Gottshall, P. M., Olszewski, T. D., Patzkowsky, M. E., Raup, D. M., Roy, K., Sepkoski, J. J., Sommers, M. G., Wagner, P. J. & Webber, A. (2001). Effects of sampling standardization on estimates of phanerozoic marine diversification. *Proceedings of the National Academy of Sciences of the United States of America*, **98,** 6261-6266.

Anderson, K. J. & Jetz, W. (2005). The broad-scale ecology of energy expenditure of endotherms. *Ecology Letters*, **8,** 310.

Brown, J. H. (1981). Two decades of homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist*, **21,** 877-888.

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.

Chapin, F. S. I., Matson, P. A. & Mooney, H. A. (2002). Principles of Terrestrial
     Ecosystem Ecology. Springer-Verlag, New York.

Chown, S. L. & Gaston, K. J. (2000). Areas; cradles and museums: the latitudinal
     gradient in species richness. *Trends in Ecology & Evolution*, **15,** 311-315.

Clark, J. S. & McLachlan, J. S. (2003). Stability of forest biodiversity. *Nature*, **423,** 635-
     638.

Clark, J. S. & McLachlan, J. S. (2004). Neutral theory (communication arising): the
     stability of forest biodiversity. *Nature*, **427,** 696-697.

Clarke, A. (2006). Climate and diversity: the role of history.  In Scaling Biodiversity, ed.
     D. Storch and P. A. Marquet, pp #-#, New York: Cambridge University Press.

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

Crame, J. A. (2002). Evolution of taxonomic diversity gradients in the marine realm: a
     comparison of late jurassic and recent bivalve faunas. *Paleobiology*, **28,** 184-207.

Crane, P. R. & Lidgard, S. (1989). Angiosperm diversification and paleolatitudinal
     gradients in cretaceous floristic diversity. *Science*, **246,** 675-678.

Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant-species
     richness. *American Naturalist*, **137,** 27-49.

Currie, D. J. (2006). Regional- to global patterns of biodiversity, and what they have to
     say about mechanisms.  In Scaling Biodiversity, ed. D. Storch and P. A. Marquet,
     pp #-#, New York: Cambridge University Press.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A.,

    Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E. & Turner, J. R. G. (2004).

    Predictions and tests of climate-based hypotheses of broad-scale variation in

    taxonomic richness. *Ecology Letters*, **7,** 1121-1134.

Darwin, C. (1859). On the Origin of Species. John Murray, London.

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. & Niklas, K. J. (2001). Invariant scaling relations across tree-dominated

    communities. *Nature*, **410,** 655-660.

Farquhar, G. D., von Caemmerer, S. & Berry, J. A. (1980). A biochemical model of

    photosynthetic $CO_2$ assimilation in leaves of C3 plants. *Planta*, **149,** 78-90.

Field, C. B., Behrenfeld, M. J., Randerson, J. T. & Falkowski, P. (1998). Primary

    production of the biosphere: integrating terrestrial and oceanic components.

    *Science*, **281,** 237-240.

Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Clarendon Press,

    Oxford.

Flessa, K. W. & Jablonski, D. (1996). The geography of evolutionary turnover: a global

    analysis of extant bivalves.  In Evolutionary Paleobiology, ed. D. Jablonski, D. H.

    Erwin, and J. H. Lipps, pp 376-397, Chicago: University of Chicago Press.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, **405,** 220-227.

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.

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

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., Charnov, E. L., West, G. B., Savage, V. M. & Brown, J. H. (2002). Effects
of size and temperature on developmental time. *Nature*, **417,** 70-73.

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

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

Hubbell, S. P. (2003). Modes of speciation and the lifespans of species under neutrality: a
response to the comment of Robert E. Ricklefs. *Oikos*, **100,** 193-199.

Huston, M. A., Brown, J. H., Allen, A. P. & Gillooly, J. F. (2003). Heat and biodiversity.
*Science*, **299,** 512-513.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of
animals. *American Naturalist*, **93,** 145-159.

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith,
S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E.,
Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E. & Williams,
D. G. (2004). Convergence across biomes to a common rain-use efficiency.
*Nature*, **429,** 651-654.

Jablonski, D. (1993). The tropics as a source of evolutionary novelty through geological time. *Nature*, **364,** 142-144.

Kaspari, M. (2001). Taxonomic level, trophic biology and the regulation of local abundance. *Global Ecology and Biogeography*, **10,** 229-244.

Kaspari, M. (2005). Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. *Proceedings of the National Academy of Sciences of the United States of America*, **102,** 5079-5083.

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

Lande, R., Engen, S. & Saether, B. E. (2003). Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford, UK.

Lieth, H. (1973). Primary production: terrestrial ecosystems. *Human Ecology*, **1,** 303-332.

MacArthur, R. H. (1969). Patterns of communities in the tropics. *Biological Journal of the Linnean Society*, **1,** 19-31.

Mayr, E. (1942). Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia University Press, New York.

Monteith, J. L. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, **9,** 747-766.

Mueller, P. & Diamond, J. (2001). Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. *Proceedings of the National Academy of Sciences of the United States of America*, **98,** 12550-12554.

Pautasso, M. & Gaston, K. J. (2005). Resources and global avian assemblage structure in

    forests. *Ecology Letters*, **8,** 282-289.

Ricklefs, R. E. (2003). A comment on Hubbell's zero-sum ecological drift model. *Oikos*,

    **100,** 185-192.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary

    cause. *Oikos*, **65,** 514-527.

Rosenzweig, M. L. (1975). On continential steady states of biodiversity.  In Ecology and

    evolution of communities, ed. M. L. Cody and J. M. Diamond, pp 121-140,

    Cambridge, MA: Belnap Press.

Savage, V. M. (2004). Improved approximations to scaling relationships for species,

    populations, and ecosystems across latitudinal and elevational gradients. *Journal

    of Theoretical Biology*, **227,** 525-534.

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. *American Naturalist*, **163,**

    E429-E441.

Sepkoski, J. J., Jr. (1978). A kinetic model of phanerozoic taxonomic diversity I. analysis

    of marine orders. *Paleobiology*, **4,** 223-251.

Stanley, H. E. (1998). Macroevolution, pattern and process. Johns Hopkins University

    Press, Baltimore, Maryland.

Stehli, F. G., Douglas, D. G. & Newell, N. D. (1969). Generation and maintenance of

    gradients in taxonomic diversity. *Science*, **164,** 947-949.

Storch, D. (2003). Comment on "Global biodiversity, biochemical kinetics, and the

    energetic-equivalence rule". *Science*, **299,** 346b.

Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for
general principles. *Ecology*, **80,** 1455-1474.

Vitousek, P. M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical
forests. *Ecology*, **65,** 285-298.

Volkov, I., Banavar, J. R., Maritan, A. & Hubbell, S. P. (2004). Neutral theory
(communication arising): The stability of forest biodiversity. *Nature*, **427,** 696.

von Humboldt, A. (1808). Ansichten der Natur mit wissenschaftlichen Erlauterungen. J.
G. Cotta, Tubingen, Germany.

Wallace, A. R. (1878). Tropical Nature and Other Essays. Macmillan, London.

West, G. B., Brown, J. H. & Enquist, B. J. (1997). A general model for the origin of
allometric scaling laws in biology. *Science*, **276,** 122-126.

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

Wright, D. H. (1983). Species-energy theory: an extension of species-area theory. *Oikos*,
**41,** 496-506.

Wright, D. H., Currie, D. J. & Maurer, B. A. (1993). Energy supply and patterns of
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.
Series B, Containing Papers of a Biological Character*, **213,** 21-87.