*Chapter 11*

# BIODIVERSITY AND ITS ENERGETIC AND THERMAL CONTROLS

## *David Storch*

### SUMMARY

**1** Biological diversity is affected by a multitude of evolutionary and ecological processes, but diversity patterns are quite universal across taxa; diversity generally increases towards low latitudes and towards environments characterized by high temperature and energy availability.

**2** The metabolic theory of ecology (MTE) assumes that diversity is affected both by amount or supply rate of resources which positively affects total number of individuals, and by the positive effect of temperature on diversification rates. Although these assumptions are reasonable, this theory has several conceptual problems and the empirical patterns support only some of its predictions.

**3** Species richness does not seem to be strongly affected by the total number of individuals.

**4** Diversity patterns are certainly also affected by processes which are not accounted for by the MTE, most importantly range dynamics associated with the evolution of species climatic tolerances, which is affected by the level of the conservatism of ecological niches of species.

**5** However, temperature appears as the most important driver of diversity patterns, possibly due to the temperature dependence of most biological processes.

## 11.1 INTRODUCTION

Biodiversity, or biological diversity, comprises all the variation of life on Earth, from genetic and molecular diversity, through diversity of species and higher taxa, to the diversity of whole ecosystems. Biological diversity is the most prominent feature of life on Earth, yet its distribution on the Earth's surface and across evolutionary lineages is unequal. Patterns in biological diversity have been affected by multiple processes acting at multiple scales, ranging from biotic interactions within local ecological communities to evolutionary radiations of evolutionary lineages within whole continents. All these processes potentially can be affected by energy availability and biological rates, and thus the considerations concerning organismal metabolism seem very appropriate when trying to understand them. However, the question is to what extent these simple considerations are useful for explaining or even predicting contemporary biodiversity patterns, given that their causes

are certainly complex. From this point of view I will mostly explore spatial patterns of biodiversity, as these have been the most thoroughly studied.

Perhaps the clearest ecological generality concerning spatial diversity patterns is that diversity closely correlates with climate (Fig. 11.1). In particular, abiotic variables related to energy availability and productivity (namely, temperature and water availability) appear to drive the most prominent biodiversity trend on land, the latitudinal diversity gradient (Currie
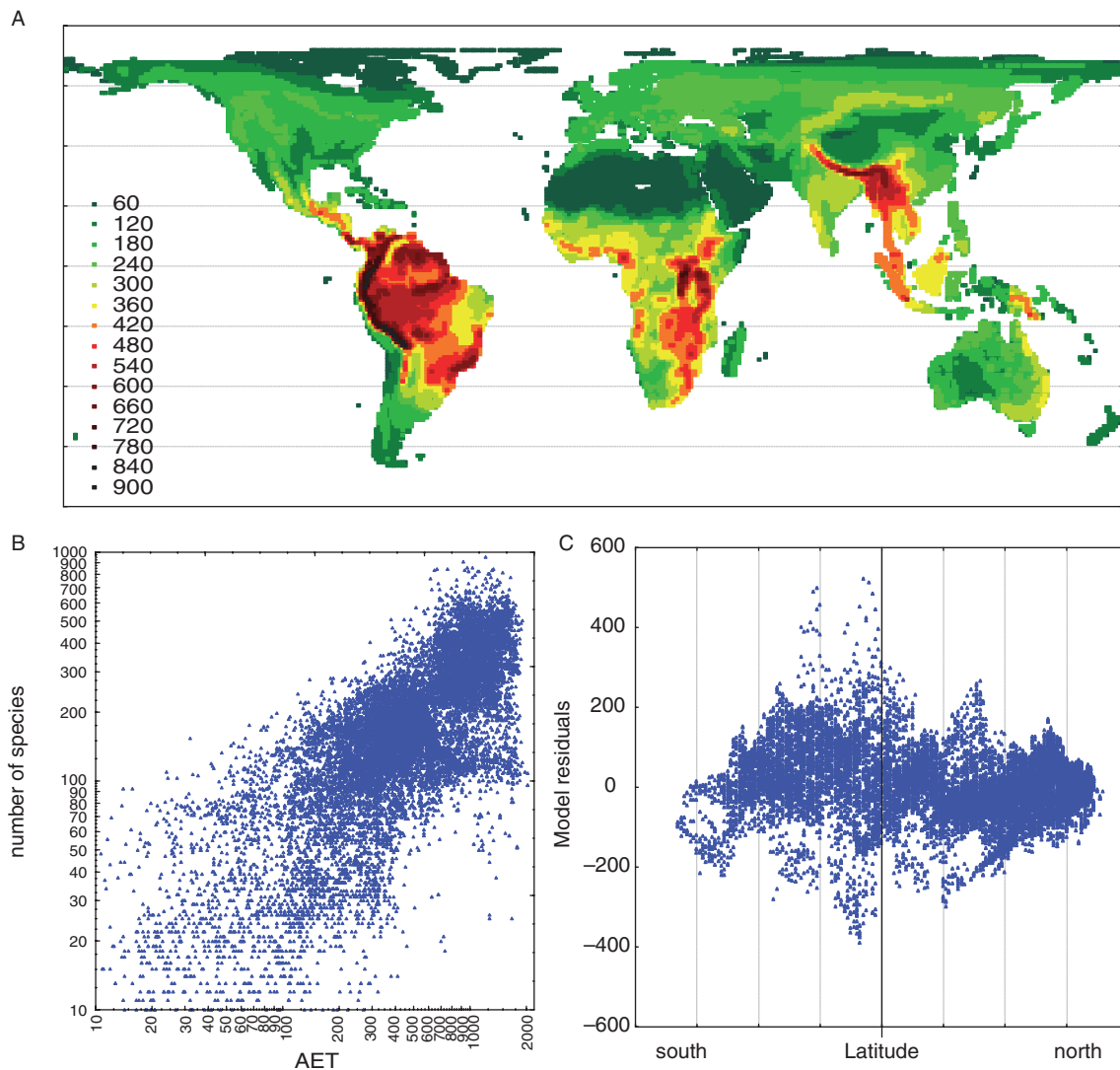


**Figure 11.1** Relationship between diversity and climate. (A) Global distribution of bird species richness (defined as number of species within grid cells of approximately 1° latitude × 1° longitude) shows the highest levels in tropical areas, especially in tropical mountains. (B) Relationship between actual evapotranspiration, a measure of water and energy flow through an ecosystem, and bird species richness. (C) After controlling for AET, there is no remaining latitudinal signal of species richness, indicating that AET fully accounts for the latitudinal variation in diversity. (Data from Storch et al. 2006 by permission of John Wiley & Sons, Ltd.)

1991; Francis and Currie 2003; Hawkins et al. 2003; Buckley and Jetz 2007; Kreft and Jetz 2007; Hortal et al. 2008). Although the importance of individual factors may vary regionally (e.g., water availability may be more important at lower and temperature at higher latitudes; Hawkins et al. 2003), the role of these major climatic factors appears to be globally consistent across taxa. Three major explanatory frameworks have recently emerged to address spatial diversity patterns.

### 11.1.1 Hypotheses based on environmental limits of species coexistence

This class of hypotheses assumes that the number of species which can coexist at a given site is constrained by the total number of available ecological niches or by the total number of individuals which can be sustained under given energy input. The total number of available niches is hard to estimate, given the circularities inherent in niche definitions (Chase and Leibold 2003, but see Walker and Valentine 1984). However, the possibility that the total amount of resources set by environmental productivity limits the total number of individuals is quite straightforward. A higher number of individuals can be divided into more species with viable populations, and sites which support more individuals will then tend to support more species (Wright 1983). This theory, which is referred to as the species-energy theory, has been refined and restated as the more-individuals hypothesis (Gaston 2000).

### 11.1.2 Hypotheses based on species diversification rates

According to this class of hypotheses, diversification rates are faster in hot and humid environments, resulting in higher number of taxa in the tropics (Rohde 1992). Diversification rate may be driven by mutation rate, which is in turn dependent on temperature-dependent metabolic rate (Allen et al. 2006, 2007; Gittleman and Stephens, Chapter 10).

### 11.1.3 Hypotheses based on historical climate and species niche and range dynamics

Diversity patterns are affected by Earth's history and the history of individual evolutionary lineages, their evolution and spread across the Earth's surface (Ricklefs 1987; Ricklefs and Schluter 1993). Most species may live in humid warm climates simply because tropical areas historically dominated the Earth, or were more stable over geological time, so that individual taxa had enough time to adapt to these environments (Latham and Ricklefs 1993; Ricklefs 2006a). This explanation necessitates the assumption of niche conservatism (i.e., species do not adapt too quickly to new environments; Wiens and Donoghue 2004), and represents in a sense a null explanation of diversity patterns, as it assumes no particular processes generating diversity besides historical legacy.

Clearly, all of these three explanatory frameworks are essentially incomplete. Hypotheses on environmental limits on coexistence ignore the findings that the diversity of each local community is strongly affected by regional/historical effects (Ricklefs and Schluter 1993; Caley and Schluter 1997; Ricklefs 2008), so that local environmental limits only partially affect diversity of species assemblages. Hypotheses on diversification rates ignore the fact that diversity is also given by species spreading out of evolutionary sources and by extinction dynamics (Jablonski et al. 2006), and that species richness is necessarily limited by limits of species geographic ranges. Hypotheses based on historical climate and species niche and range dynamics ignore unequal diversification rates in different regions and possible environmental limits of species richness. So none of the hypotheses are mutually exclusive and they complement each other.

Although biodiversity patterns have almost certainly emerged due to all the above-mentioned processes, the striking generalities concerning the role of climate and energy are challenging. The energetic and metabolic controls on biodiversity patterns are therefore worth exploring. I will first explore in more detail the energetic controls on the number of coexisting species, and then I will consider the role of metabolic control of diversification rate and diversity patterns.

## 11.2 THE MORE-INDIVIDUALS HYPOTHESIS AND ITS LIMITATIONS

The assumption that energy availability constrains the total number of individuals which can coexist in an environment, consequently constraining the number of species, represents the most straightforward explanation of species richness patterns. Although this
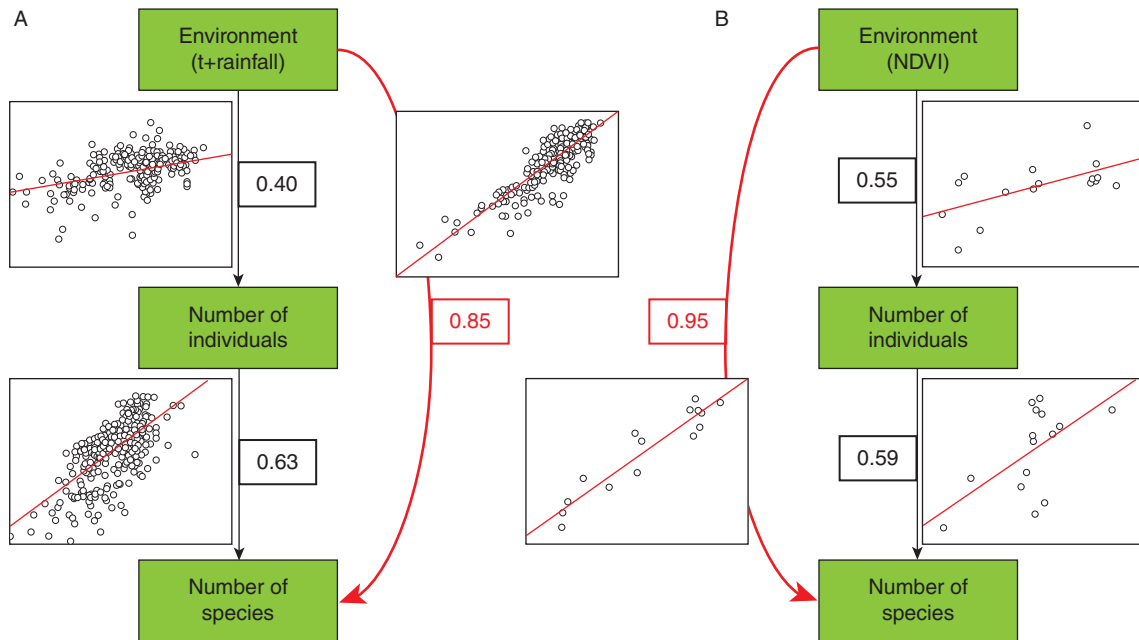
**Figure 11.2** Relationships between environmental variables, total assemblage abundance, and species richness for (A) global forest plots and (B) South African birds. The numbers in boxes refer to correlation coefficients for individual relationships. The *x*-axis in the biplots always refers to the variable (or the combination of variables in A) which is assumed to be independent and causally responsible for the dependent variable (note, however, that in fact this may not be the case, e.g., abundances may be higher due to higher species richness, and not vice versa). The relationship between environmental variables and species richness is apparently stronger than both the relationships between environment and total abundance, and between total abundance and species richness, casting doubt on the more-individuals hypothesis. Data from Šímová et al. (2011) by permission of John Wiley & Sons, Ltd, and Storch et al. (unpublished).

hypothesis has never been properly formalized (but see Wright 1983), it is reasonable to believe that a higher number of individuals can be divided into more species with viable populations, and conversely that decreases in the total number of individuals due to lower energy availability would lead to generally lower abundances and consequent extinction of populations of rarer species. Since the causal chain goes, according to the hypothesis, from energy availability to the total number of individuals, and then to the number of species, it predicts that the relationship between energy availability and number of individuals should be relatively tight, and that the relationship between the number of individuals and number of species should be tight as well. Conversely, the relationship between energy availability and species richness should be weaker, as these variables should be related only indirectly, through the number of individuals (Currie et al. 2004).

However, the opposite has been typically observed: species richness is quite tightly related to energy availability, whereas the number of individuals is only loosely related to both number of species and available energy (Currie et al. 2004; Šímová et al. 2011; Fig. 11.2). Moreover, the tight relationship between energy availability and species richness is observed even if the number of individuals is controlled for (Hurlbert 2004; Sanders et al. 2007; Šímová et al. 2011).

It thus appears that species–energy relationships are generally not mediated by the number of individuals. Although the very low numbers of individuals sustainable in extremely unproductive areas may limit the number of species found there, the more-individuals hypothesis does not seem to be the universal or even primary explanation of biodiversity patterns. The observation that the number of individuals is often correlated to the number of species (e.g., Kaspari et al.

2003; Evans et al. 2005) can be explained in other ways. For instance, the number of species may be determined by some other effects, and number of individuals is simply higher where the number of species is higher (see Long et al. 2006). The causal chain between number of species and number of individuals can thus in fact be reversed (Šímová et al. 2011).

On the other hand, regardless of the exact direction of causality, number of individuals is certainly linked to the number of species, and thus the pattern of relationships between climate (or energy availability) and number of individuals in an assemblage is worth exploring. Such patterns do not appear consistent between taxa. Whereas the total abundance of birds increases with productivity in approximately the same way as species richness (so that mean population size of species is more or less independent of productivity and of assemblage species richness; see Pautasso and Gaston 2005; Evans et al. 2008), total abundance does not vary much with climatic gradients in trees (Enquist and Niklas 2001; Šímová et al. 2011) nor, perhaps, in invertebrates (Novotny et al. 2006). This results in lower population densities of individual species of ectotherms at low latitudes and/or more productive

regions. This discrepancy can be addressed by the metabolic theory, for which the difference between endotherms and ectotherms is crucial.

## 11.3 METABOLIC THEORY OF BIODIVERSITY

The idea that temperature affects diversification rates, and consequently the major diversity gradients, is older than the metabolic theory of ecology (Rohde 1992). Interestingly, the first formal connection between the metabolic theory and diversity patterns was not explicitly based on evolutionary rates, but instead on the relationship between temperature-dependent metabolic rates and the controls of abundances (Fig. 11.3). Allen et al. (2002) derived the relationship between temperature and species richness within a given area, assuming a generalized version of the energetic equivalence rule (EER; see Isaac, Carbone, and McGill, Chapter 7). EER (Damuth 1987; Nee et al. 1991) states that population energy consumption of individual species per unit area is independent of body size, since species with larger body size (which have higher metabolic
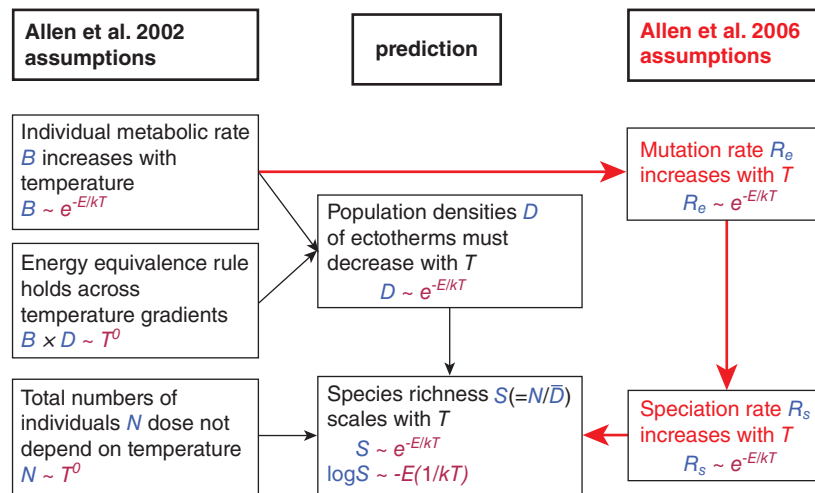


**Figure 11.3** The logic of the metabolic theory of biodiversity. Originally (black arrows) the prediction of the species–temperature relationship was based on a generalized energy equivalence rule and an assumption that total assemblage abundance is constant. However, more plausible causation comprises the effect of temperature on diversification rates (red arrows). The fundamental assumption (in both cases) is that individual metabolic rate, $B$, scales with temperature according to the relationship $B \sim e^{-E/kT}$, where $k$ is the Boltzmann constant ($8.62 \times 10^{-5}\,\mathrm{eV\,K^{-1}}$), $T$ is temperature in kelvin and $E$ is activation energy of metabolic reactions, which should vary between $-0.60$ and $-0.70\,\mathrm{eV}$ (Brown et al. 2004).

rate) have, on average, correspondingly lower population densities. Its generalized version according to Allen et al. (2002) assumes additionally that energy consumption of individual species' populations is independent of temperature. Ectothermic species living in warmer regions have higher metabolic rates (i.e., higher per-capita energy consumption; Gillooly et al. 2001); therefore, they need to have lower population densities in warmer regions to fulfill the generalized version of EER. Assuming additionally that the total number of individuals within an area, $N$, is independent of temperature, the total number of species, $S$, must be higher in warmer areas. The reason is that mean population density, $\bar{D}$, is given by $\bar{D} = N/S$, so that if $\bar{D}$ decreases with temperature and total assemblage abundance $N$ is constant, number of species, $S$, must increase to balance the decrease of mean population density, $\bar{D}$, with temperature. The number of species should thus scale with temperature in the same way as mean population density and metabolic rate (Fig. 11.3).

Allen et al. (2002) provided some evidence that mean population size of ectotherms indeed scaled inversely with temperature, as predicted by the generalized version of EER, as well as evidence of the predicted scaling of species richness with temperature. However, all the reasoning mentioned above is quite problematic. There is no reason to assume that the *total number of individuals per unit area, N*, is independent of temperature, and simultaneously that *per-species mean density* decreases with temperature (Storch 2003). If total densities of ectotherms do not depend on temperature, total supply rate of resources must increase with temperature to support the same total community size (total number of individuals), given that every individual consumes more resources. And if the supply rate of resources increases with temperature, there is no reason why the densities of individual species' populations should be lower in warmer regions to follow the generalized energy equivalence rule. In an effort to address these problems, the theory has been reformulated in terms of evolutionary rates (Allen et al. 2006, 2007): metabolic rate affects the rate of all biological processes including mutation (Gillooly et al. 2005b) and speciation (Allen et al. 2006), and higher speciation rates in warmer environments should lead to higher number of species (Fig. 11.3, red lines).

A current formulation of the metabolic theory of biodiversity (Allen et al. 2007) assumes that energy availability affects species richness in two independent
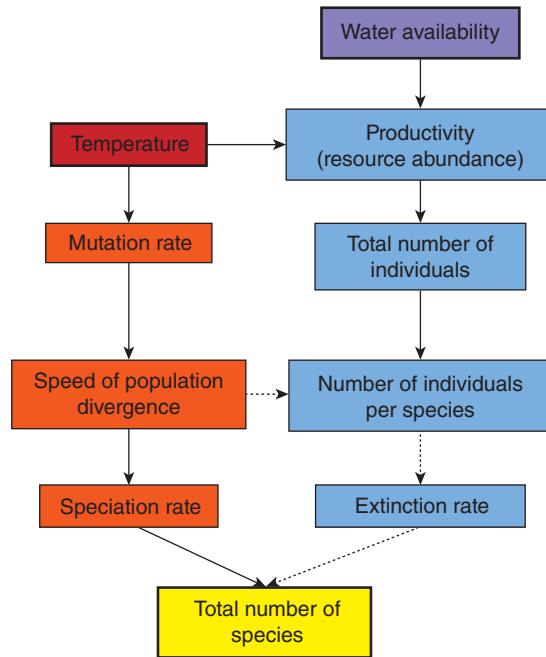


**Figure 11.4** Chains of causality showing how temperature and productivity can affect diversity (negative effects are marked by dashed lines; this scheme follows Allen et al. (2007) but differs in some respects). There are multiple and sometimes counteracting effects (e.g., temperature increases total number of individual due to its positive effect on productivity, but may lead to the decrease of abundance per species due to its positive effect on population divergence), so that exact predictions are difficult to formulate and test. Note that this is still a simplified picture of possible causal links. In fact, temperature may not only increase total number of individuals via increasing productivity, but may simultaneously exert a counteracting effect on the numbers of individuals, as individuals in warmer regions have higher energy consumption due to higher metabolic rate – and thus their population-carrying capacities may be lower in warmer environments (Allen et al. 2002).

ways, combining the more-individuals effect with the effect of temperature on speciation/diversification rates (Fig. 11.4). According to the theory, there are two fundamentally different forms of energy (see also Clarke and Gaston 2006): kinetic energy of molecules expressed as temperature, and potential energy of chemical bonds, i.e., energy stored in biomolecules. Whereas temperature affects mutation, and

consequently diversification rates, potential energy is equivalent to the amount or supply rate of resources (environmental productivity), and thus affects the number of individuals which can persist in an environment. However, environmental productivity is also affected by temperature, whose effect combines with the effect of nutrient and water limitation. Predictions of the theory are thus not straightforward. Population sizes of individual species are predicted to be generally positively affected by temperature through increasing productivity, but negatively by increasing diversification rates, so that the final expectation depends on the balance of these processes.

However, the theory does provide predictions for situations in which some effects are essentially constant. Most importantly, it predicts differences in species richness patterns between endotherms and ectotherms. Environmental temperature should not have a direct effect on diversification rates in endotherms, whose body temperature is constant, which may explain the observation that species' mean population sizes of birds do not change systematically with latitude or productivity (Pautasso and Gaston 2005). Conversely, population sizes of individual species of trees or insects may vary along these gradients due to the variation in diversification rate, as mentioned above. The other prediction concerns the situation in which the total number of individuals is constant, for example, due to resource limitation unrelated to temperature (e.g., forest trees limited by space). In such a case, the metabolic theory of biodiversity predicts that the causal chain which concerns potential energy (i.e., productivity effects; the right-hand column in Fig. 11.4) is not relevant, and species richness should be simply related to diversification rates, and should scale with temperature similarly to metabolic rate (Allen et al. 2006).

## 11.4  CONCEPTUAL PROBLEMS OF THE CURRENT FORMULATION OF THE METABOLIC THEORY OF BIODIVERSITY

Although the theory depicted above is compelling, because it deals explicitly with multiple pathways leading to observed relationships between climatic variables and biological diversity, it has several problems, both conceptual and empirical. One problem related to its original formulation using the generalized EER has been dealt with above, but this is not relevant to the current formulation of the theory. However, other problems are substantial, as follows.

### 11.4.1  Relationship between standing species richness and speciation rate

The metabolic theory assumes that speciation rate is proportional to metabolic rate per unit mass, and that species richness is proportional to speciation rate. Whereas the former proportionality has some empirical support (Allen et al. 2006), the relationship between speciation rate and species richness is much less straightforward. The equilibrium number of species is the net result of both speciation and extinction, similar to the way that equilibrium population size is the net result of natality and mortality. A direct proportionality between speciation rate and species richness is expected only under quite restrictive conditions (Fig. 11.5). If we assume that speciation rate is a variable which can be attributed to individual species, and that both speciation and extinction rates are dependent on mean population size (which is the case depicted in Fig. 11.5), both these rates should be dependent on species richness. The reason is that if there is a constant total number of individuals $N$ (determined by a constant supply rate of resources), then mean population sizes which drive speciation and extinction rate must decrease with increasing number of species (since mean populations size $= N/S$). Then the species richness is proportional to per-species speciation rate only in special cases of fine-tuned dependencies of both the rates on mean population size (Fig. 11.5). Allen et al. (2006, 2007) viewed speciation rate as a variable attributed to individuals (i.e., per-capita speciation rate) instead of species, following the formalism of the neutral theory of biodiversity and biogeography (Hubbell 2001). The situation is then somehow different, but the neutral theory does not predict the proportionality between speciation rate and species richness either. Instead, Hubbell's fundamental biodiversity number, theta, should be proportional to speciation rate, and thus this characterization of biodiversity could represent a better way to build a metabolic theory of biodiversity than by using species richness as the measure of biodiversity – with a caveat that the formalism of the neutral theory may not be universally valid and acceptable (McGill et al. 2006).
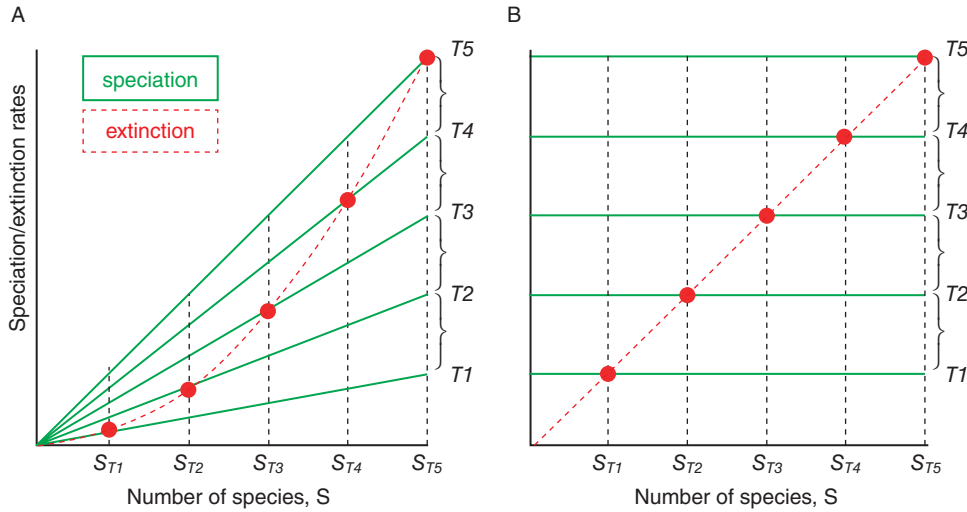
**Figure 11.5** Relationships between speciation and extinction rates and the number of species. Assume that per-species speciation rate increases linearly with some variable. In such a case, total speciation rate for the species assemblage increases with the number of species, and the lines denoting the relationship between the number of species and the total speciation rate for a given variable (here, different temperatures T1–T5) will be straight lines with slopes proportional to the temperature term (A). This is represented by constant increment of the endpoints of these lines on the vertical axis. The equilibrium number of species is given by intersection of the speciation curve with an extinction curve specifying the relationship between the number of species and total species extinction rate (i.e., number of species extinct in a given time interval). Clearly, equilibrium species richness is directly proportional to speciation rate only if the extinction curve intersects individual speciation curves/lines at points equally spaced on the horizontal axis. For other shapes of the extinction curve, equilibrium species richness is not proportional to speciation rate. Therefore, standing species richness may not be directly related to speciation rate. The same reasoning applies if we assume that total speciation rate does not vary with the number of species (B) (which is assumed in Hubbell's (2001) neutral theory in which total number of individuals is constant and speciation rate is defined on a per-capita basis). In this case, total extinction rate must increase linearly with the number of species to keep the proportionality between speciation rate and species richness.

### 11.4.2 Scale dependence of species richness

Metabolic theory predicts a particular quantitative relationship between temperature and species richness (Fig. 11.3), namely that the logarithm of number of species should decrease linearly with $1/kT$ (where $k$ is Boltzmann's constant and $T$ is temperature in kelvin), with the slope equal to the activation energy of metabolism (around 0.6–0.7 eV) (Brown et al. 2004; Allen et al. 2006, 2007; Brown and Sibly, Chapter 2). However, the spatial grain at which this prediction should hold is not specified. Species richness is scale-dependent, and if some richness–environment relationship holds for areas of, say, 100 km², a different slope would likely be observed in smaller or larger areas. In fact, a constant (area-independent) slope of the richness–temperature relationship could be observed only if the species–area relationship had a slope which was independent of temperature. If this is not the case, i.e., if number of species increases more rapidly with area in, for example, warmer regions, then the number of species would be relatively higher in larger areas in these regions, and the overall richness–temperature relationship would be steeper for large areas. This effect was demonstrated by Wang et al. (2009) for richness patterns of woody plants (Fig. 11.6). The slope of the species–area relationship is higher in warmer areas, and consequently, the species–temperature relationship is steeper for larger areas (in statistical terms, there is a positive interaction between temperature and area in their effects on
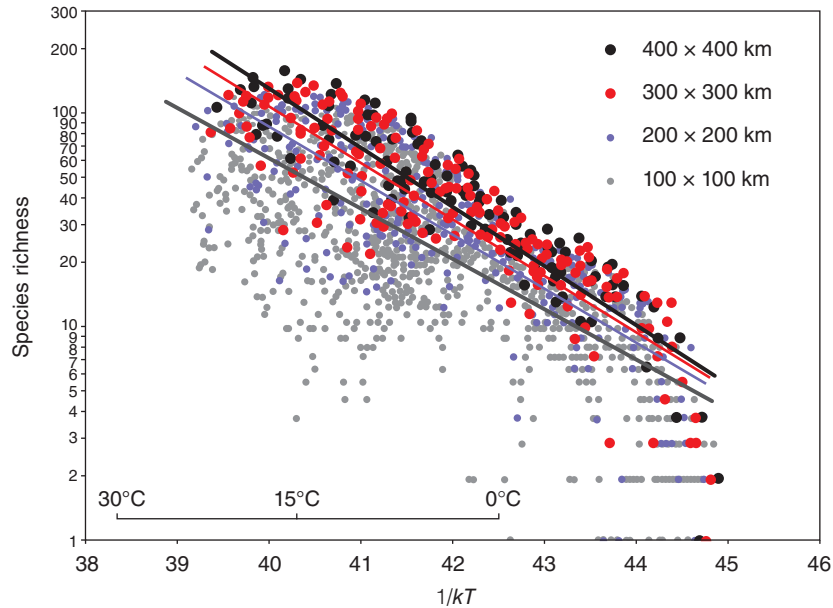
**Figure 11.6** The relationship between temperature expressed as $1/kT$ and tree species richness in North America for different grain sizes (grid areas). The slope of species–temperature relationship (which is equivalent to the activation energy $E$) increases with grain. There is thus a positive interaction between temperature and area in their effect on species richness, with the consequence that the slope of the species–area relationship increases with temperature. Data from Wang et al. (2009).

species richness). This concurs with the findings of Harte et al. (2009) that the slope of the species–area relationship depends on the ratio between the total number of individuals and number of species within a given assemblage ($N/S$, which is equivalent to mean population size, see above): the higher the ratio, the lower the slope of the species–area relationship. Since the number of species increases with temperature, whereas the total number of individuals (in this case the density of trees in forests) is not too sensitive to temperature, the ratio is lower in warmer regions, leading to a steeper species–area relationship. The exact relationship between temperature and species richness thus cannot be universal across spatial scales.

### 11.4.3   The problem of taxonomic invariance

Any macroecological pattern can be truly universal only if it is invariant against changing taxonomic delimitation, i.e., if it can simultaneously hold for a given taxon as well as for its subtaxa (Storch and Šizling 2008). This is hardly the case for the above-mentioned exponential relationship between temperature and species richness. Imagine a taxon composed of two or more subtaxa (such as South American mammals including placentals and marsupials). The exponential relationship between temperature and species richness mentioned above could hold for the taxon and all subtaxa only if the respective equations have exactly the same parameters. Whenever one of the subtaxa deviates, either having a different form of the relationship (e.g., linear instead of exponential), or the same form with a different slope (given by activation energy $E$), the resulting relationship for the larger inclusive taxon cannot be exponential, simply because the summation of exponentials for different subtaxa gives an exponential for a larger taxon only if the parameters are the same. Since some taxa certainly deviate from predicted patterns (see below), it is unlikely that the exact predicted relationship can hold for species richness of any larger taxon.

## 11.5 EMPIRICAL PATTERNS: EVIDENCE AND COUNTEREVIDENCE

Allen et al. (2002, 2006) and Brown et al. (2004) published several graphs concerning the relationship between the logarithm of number of species and $1/kT$ in support of their theory. This has stimulated a wave of studies trying to support or refute it (e.g., Algar et al. 2007; Hawkins et al. 2007; Keil et al. 2008). Although some studies found the predicted relationship between species richness and temperature, including the slopes, it appears to be far from general (Hawkins et al. 2007). Species richness generally increases with temperature (the exceptions tend to be narrowly defined taxa with particular habitat requirements), but this increase may not always be exponential, and even in this case the slope varies much more than predicted by the theory. In fact, this is not surprising, given the conceptual problems mentioned above. Moreover, it seems that tests comprising just the exploration of the bivariate relationships between temperature and species richness are not appropriate. The theory makes specific assumptions concerning the absence of other factors affecting diversity, namely that the number of individuals does not vary due to variation in resource availability (Allen et al. 2007; Gillooly and Allen 2007; Cassemiro and Diniz-Filho 2010). These effects have rarely been controlled for (although, paradoxically, this was a problem in the original Allen et al. (2002) study as well). Šímová et al. (2011), however, have shown that the relationship between tree species richness and temperature in forest plots deviated from the predicted exponential relationship, even if water availability and number of individuals were accounted for.

The other problem with tests of the predictions of the metabolic theory of biodiversity comprises the conditions and scales under which the predictions should hold. Since the most recent formulation of the theory is based on evolutionary rates, we would expect that the relationship would have emerged during evolutionary timescales and should be observed mostly on large spatial scales. However, the cases in which the pattern did agree with the predictions often comprised much smaller scales, and apparently emerged in much shorter time intervals than would be necessary for evolutionary changes. Hunt et al. (2005) reported pronounced temporal changes of species richness of benthic Foraminifera associated with temperature changes (in the direction predicted by the theory) during the last 130 000 years, i.e., a much shorter timescale than would be enough for evolutionary changes such as altered speciation rates. Also, the diversity patterns observed in terrestrial organisms inhabiting the temperate regions of the Northern Hemisphere must be relatively recent, as the species have immigrated to these areas after the end of last glacial, i.e., during the last 12 000 years. One could argue that these recent patterns are driven by the differential immigration of species from large species pools, whose niches are conservative and whose evolution was determined by temperature as predicted. However, the relationship between richness of the species pool (i.e., regional richness) and local community richness is not straightforward (Ricklefs and Schluter 1993), and is confounded by all the scale issues mentioned above.

These issues can be generalized. The major problem of the theory is that it is focused exclusively on the temperature dependence of diversification rates. It ignores other effects, including migration from source areas and population spatial dynamics in general, as well as other processes which may also be temperature-dependent, albeit in a different manner (Stegen et al. 2009). It is therefore reasonable to ask what the true achievements of the theory are.

## 11.6 MERITS OF THE METABOLIC THEORY OF BIODIVERSITY

Despite many problems mentioned above, there are several insights and contributions of the metabolic theory of biodiversity which makes it a useful and lively approach to biodiversity science. Firstly, it is the only theory which gives exact quantitative predictions of species richness patterns. Most theories concerning biodiversity patterns provide only qualitative predictions (e.g., species richness should increase with productivity/area/temperature), and the predictions of individual theories are thus not distinguishable from each other. The possibility that the increase of species richness is predictable from the knowledge of the increase of temperature is intriguing, but even more important is the fact that this prediction provides opportunity to test the theory (with the caveats mentioned above).

Second, the metabolic theory of biodiversity is the only theory which explicitly predicts an exponential increase of species richness with temperature.

Although, as has been argued above, this pattern is not always observed, this exponential relationship occurs quite often (e.g., da Silva et al. 2007; Sanders et al. 2007; Wang et al. 2009; Cassemiro and Diniz-Filho 2010), so it is reasonable to consider it to be a rule rather than an exception. Moreover, although the slopes of the relationship between log (species number) and $1/kT$ cannot be the same for all taxa and all scales – indeed, they are not – the slopes seem to converge on the predicted value (Stegen et al. 2009). This is rather paradoxical, given that the theory is so far intrinsically incomplete, without the ability to fully address all the processes producing diversity patterns.

Third, the theory explicitly stresses the role of temperature in contrast to other energy-related variables such as productivity, or actual or potential evapotranspiration. Although these variables are often closely correlated in terrestrial environments, so that their effects are difficult to disentangle, it appears that the effect of temperature is more important than productivity. This can be more easily demonstrated in marine systems, where temperature and productivity are decoupled. Fuhrman et al. (2008a) have shown that the diversity of marine planktonic bacteria increased with temperature, but was independent of productivity or bacterial biomass. Temperature is generally a better predictor of marine diversity than other environmental variables (Tittensor et al. 2010). Within terrestrial forest plots, diversity correlates with productivity only if temperature is accounted for when estimating productivity; otherwise there is no effect of productivity on tree species richness (Šímová et al. 2011). Similarly, local ant diversity is predicted by temperature but not productivity (Sanders et al. 2007). Large-scale diversity patterns in vertebrates are related to both productivity and temperature, but the relative role of temperature is stronger at larger spatial scales (Belmaker and Jetz 2011), conforming to the metabolic theory, which involves evolutionary processes rather than factors affecting local species coexistence. On the other hand, temperature appears also to predict large-scale richness of endotherms (Davies et al. 2007; Belmaker and Jetz 2011), which contradicts the metabolic theory, and indicates that the role of temperature may be different and more complex than assumed by the theory so far.

Regardless of the role of temperature on spatial diversity patterns themselves, diversification rates seem to be latitude- and thus temperature-dependent (Svenning et al. 2007; Wiens 2007; Jansson and Davies 2008; Wright et al. 2010). Although this generally conforms to MTE, similar temperature dependence was observed in endotherms (Cardillo et al. 2005; Ricklefs 2006b; but see Weir and Schluter 2007). This may indicate that diversification processes are more complex, being affected by temperature indirectly as well as directly. Moreover, Davies et al. (2004) have shown that although temperature was strongly associated with plant diversification rates as well as with plant species richness, diversification rates did not appear responsible for species richness patterns. Therefore, although the role of temperature is apparent in many aspects of ecology and evolution, the way MTE deals with these effects has so far been overly simplistic.

## 11.7 TEMPERATURE AGAIN: WHICH EFFECTS AND WHEN?

Temperature is a crucial abiotic factor affecting almost all aspects of organismal biology. Even the oldest considerations concerning global diversity patterns invoked temperature as an essential driver. Indeed, Alexander von Humboldt (1850) attributed higher species richness of tropical organisms to their limited cold tolerance (Hawkins 2001). Current findings support this conclusion. Minimum temperature, in contrast to mean values, appears to be the best predictor of tree species richness (Šímová et al. 2011; Wang et al. 2011). Biological diversity in terrestrial environments is obviously also limited by water availability, so that a combination of temperature and water availability predicts species richness patterns. However, minimum rainfall again appears more important than mean values (Šímová et al. 2011), indicating that, rather than simple multiplicative or additive effects of both variables, some nonlinear and threshold-like effects play a role. Additionally, species-poor regions are typically inhabited by a subset of higher taxa, which are often younger, more derived and phylogenetically clustered (Hawkins 2010; Machac et al. 2011), suggesting that only a few evolutionary lineages were able to overcome climatic constraints. All these findings can be interpreted as evidence for the role of climatic limits of individual species distributions, i.e., as support for the third of the above-mentioned hypotheses, comprising history of niche evolution and the spreading of species out of the tropics and their lower diversity in colder and drier

climates limited by the difficulty of adapting to extreme abiotic conditions. Species niches are to a large extent conservative (Wiens and Donoghue 2004), and it is reasonable to assume that many species are adapted to historically prevailing warm humid conditions (but see Algar et al. 2009).

Temperature will thus undoubtedly have several independent and interacting effects, influencing diversification of lineages, range dynamics, and the spreading of taxa, and potentially also the limits of species coexistence (i.e., the major processes affecting global diversity patterns mentioned in section 11.1). The effect of temperature on local species coexistence is much less clear than in the case of the other processes. One could argue that higher temperatures should increase the rate of all interspecific interactions including competitive exclusion, and thus decrease rather than increase diversity. However, organisms living at higher temperatures could also have greater potential to avoid competition (or predation), since temperature keeps all the physiological processes active, enhancing the range of possible strategies for thriving in an environment and how and when resources can be utilized (Sanders et al. 2007). Warmer environments thus promote multidimensionality and complexity of biotic interactions, all of which supports high biological diversity (Schemske 2009). Low temperature, on the other hand, simplifies the interactions between an organism and environment, promoting simple and directional changes in community composition. More generally, higher temperature may be associated with greater complexity in possible ways of life, thus enhancing diversity (see Anderson and Jetz 2005).

Even more generally, diversity of life can be universally understood as a result of the interplay of processes which enhance it (such as evolutionary diversification, coevolution, co-adaptation, and the emergence of novelties), and processes which suppress it, namely population extinction including competitive exclusion. It is reasonable to assume that the first set of processes will be more closely – and positively – related to temperature, as all these processes are essentially biological, and thus their rate is dependent on metabolic rate. On the other hand, the processes which reduce diversity are more closely associated with temperature-independent environmental stochasticity. Their speed will depend negatively on population sizes, the later being effectively independent of temperature, but positively dependent on energy availability, in accord with the basic framework of metabolic theory

of biodiversity (Fig. 11.4). Diversity patterns could thus be viewed as the outcome of differential rate of diversity-enhancing and diversity-suppressing processes, largely controlled by temperature.

## 11.8 CONCLUSIONS

A metabolic theory of biodiversity is a work in progress. It is helping to shed light on fundamental relationships between biological rates, resource supply and utilization, and numbers of individuals and species. But current versions of the theory (various MTE applications) have serious problems – logical inconsistencies and failures to account for empirical patterns. Although spatial biodiversity patterns are related to energy availability and temperature, the exact causal chains are difficult to disentangle. Energy availability apparently does not affect biological diversity simply through its effect on the number of individuals, as assumed by the more-individuals hypothesis. Metabolic theory provides a more elaborate explanation of biodiversity patterns, but so far it does not represent a logically consistent theory. It is mainly confined to temperature-dependent speciation rates, which seems reasonable, but far from complete. There is no universal slope of the relationship between temperature and species richness, and such a universal relationship cannot exist at all, given the scale dependence of species richness patterns. However, the role of temperature appears strong and essential, apparently more important than productivity (especially at large spatial scales), the form of the relationship between temperature and species richness roughly conforming to the MTE predictions. Temperature obviously is not the only factor affecting biodiversity patterns – water availability appears to be at least equally important – but it has potentially multiple effects, ranging from temperature-dependent diversification rates to limits of range expansions dependent on minimum temperature.