RESEARCH PAPER

A test of Metabolic Theory as the mechanism underlying broad-scale species-richness gradients

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ABSTRACT

Aim To test whether the temperature dependence of individuals' metabolic rates is the mechanism shaping broad-scale species-richness gradients as proposed in the Metabolic Theory of Ecology recently proposed by Allen, Gillooly and Brown.

Location North America, north of Mexico.

Methods Metabolic Theory predicts that the natural logarithm of species richness will be a linear function of environmental temperature ($(kT)^{-1}$, where k is Boltzmann's constant and T is temperature in K) with a slope of -0.78. We tested these predictions using the broad-scale variation in richness of amphibians, reptiles, trees, tiger beetles, butterflies and blister beetles. We tested whether the temperature–richness relationship was linear or curvilinear, and determined the range of temperature values (and geographical area) where the instantaneous slope of the curvilinear temperature–richness relationship was statistically indistinguishable from -0.78, after correcting for spatial autocorrelation.

Results We found that for all taxa, temperature–richness relationships were curvilinear. Moreover, for five of six taxa, the slope of this relationship was close to the predicted value for only a narrow range of temperatures. Blister beetles displayed the widest temperature range that is consistent with the Metabolic Theory, covering 45% of the study's geographical area. For the remaining taxa, the geographical range in which the slope is consistent with the predicted value amounts to only 10–20% of North America.

Main conclusions For a wide array of taxa in North America, temperature–richness relationships deviate from the pattern predicted by Metabolic Theory. These results demonstrate that the temperature dependence of individuals' metabolic rates is not the sole cause of broad-scale diversity gradients. Even in areas where factors other than temperature do not influence productivity, the data do not suggest that richness patterns are determined by the temperature dependence of metabolic rate.

Keywords

Allometry, climate, diversity gradients, ectotherms, latitudinal gradients, macroecology, Metabolic Theory, North America, species richness, temperature gradients.

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INTRODUCTION

Broad-scale species-richness gradients are among the most prevalent patterns in ecology. The mechanism(s) responsible for these patterns, however, are still a matter of debate (e.g. Currie *et al.*, 2004; Ricklefs, 2004). Proposed hypotheses include geometric models, e.g. mid-domain effects (Colwell *et al.*, 2004), historical factors (Latham & Ricklefs, 1993; Ricklefs *et al.*, 2004)

and climatic explanations (Currie *et al.*, 2004). Evidence consistent with aspects of all these hypotheses has been found, in one form or another. However, rejection of any particular hypothesis is difficult, because while the mechanisms proposed by these hypotheses differ, their primary predictions are not mutually exclusive. Historical and climatic hypotheses predict increasing species richness towards the equator, because of either the tropical origin of a clade, or the correlation between climatic factors and

latitude. When distance from the domain edge is collinear with climatic factors, mid-domain and climatic hypotheses can also make similar predictions (e.g. Romdal *et al.*, 2005). If this controversy is to be resolved, hypotheses must make additional, unique predictions that can potentially be falsified, rather than simply predicting a richness gradient (Currie *et al.*, 1999).

The strong correlation between energy-based climatic factors, i.e. temperature and potential evapotranspiration (see Hawkins *et al.*, 2003 and references therein), has led to energetic explanations of the richness–climate relationship (Wright, 1983; Currie, 1991). Energetic explanations can be divided into two groups: those dependent on ambient energy (i.e. temperature or potential evapotranspiration) and those based upon net primary productivity (Evans *et al.*, 2005). The most prominent energetic explanation has been the energy–richness (or more individuals) hypothesis, which suggests that higher-energy areas can support more individuals, which in turn results in more species (Wright, 1983). Tests of the energy–richness hypothesis have shown that species richness does not increase as a simple function of the total number of individuals (Currie *et al.*, 2004; Hurlbert, 2004). Numerous other mechanistic links between climate and species richness have been suggested (see Evans *et al.*, 2005), including physiological tolerance (e.g. Kleidon & Mooney, 2000) and variation in diversification rates across broad spatial extents (Cardillo, 1999, but cf. Kerr & Currie, 1999; reviewed in Evans & Gaston, 2005). Neither of these hypotheses has yielded unequivocal results, though rigorous tests are rare (Currie *et al.*, 2004). Therefore, although climate has been shown consistently to be the strongest predictor of species richness at broad scales (Hawkins *et al.*, 2003), a mechanistic link from climate to species richness has not yet been identified.

Recently, Allen *et al.* (2002) proposed that broad-scale diversity patterns result from the temperature dependence of individuals' metabolic rates. This relationship is a prediction of the developing 'Metabolic Theory of Ecology' (Brown *et al.*, 2004; Allen *et al.*, in press). To predict richness gradients, Metabolic Theory connects two previously recognized relationships: the temperature dependence of metabolic rate (e.g. Gillooly *et al.*, 2001) and the energetic-equivalence rule of population energy use (Damuth, 1981; Enquist *et al.*, 1998). Assuming that the body temperature of ectotherms is equal to ambient environmental temperature, Metabolic Theory predicts a positive correlation between temperature and species richness by the following mechanism. As body temperature increases, so does metabolic rate, resulting in higher energy use per individual. If population energy use remains approximately constant, then fewer individuals can be supported in a population, i.e. the carrying capacity is reduced (Brown *et al.*, 2004). Considering that the total number of individuals in a community remains relatively constant across geographical space, the result is higher species richness in warm areas. Allen *et al.*'s (2002) hypothesis, however, does not merely predict an increase in richness towards the tropics; it predicts the exact form of the relationship. Specifically, the hypothesis predicts that, for ectothermic taxa, $\ln S = -E(kT)^{-1} + C$ where E is the activation energy of metabolism, 0.78 eV, k is Boltzmann's constant, 8.62×10^{-5} eV K^{-1}, and T is environmental temperature

in K. The intercept term, C, incorporates the effect of mean body size of the study taxon, area and total community abundance (see Allen *et al.*, 2002, for details). In other words, $\ln S$ should vary as a function of $(kT)^{-1}$ (the form more recently used in the Metabolic Theory; Brown *et al.*, 2004) with a slope of $-E$ or -0.78. This relationship is not expected to be equivalent for endotherms as their metabolic rate does not vary with temperature in a manner similar to ectotherms (Allen *et al.*, 2002).

The Metabolic Theory of Ecology is currently a topic of much debate. The lack of consensus is perhaps not surprising considering the theory's potential to explain a broad suite of ecological processes and patterns. Several of the theory's premises have been challenged, including the existence of universal metabolic scaling (Bokma, 2004; Kozlowski & Konarzewski, 2004), the mechanism underlying metabolic allometry (Darveau *et al.*, 2002), the activation energy of metabolism (Clarke & Fraser, 2004) and the energetic-equivalence rule (Russo *et al.*, 2003). The theory's applicability to broad-scale richness gradients has also been questioned (Storch, 2003). Many of these comments have been addressed by the authors of Metabolic Theory (e.g. West *et al.*, 2003; Brown *et al.*, 2005). However, hypotheses are not refuted because their premises are untrue; all models represent over-simplifications of the complexities of nature (e.g. Box, 1976). Rather, a hypothesis is refuted when observations fail to agree with its predictions. Departures from predicted patterns can then be used as a starting point for the development of new process-based hypotheses.

The Metabolic Theory's quantitative predictions of ectotherm species richness allow for particularly rigorous tests of its proposed mechanism. Because both the temperature dependence of metabolic rate and the energetic-equivalence rule potentially apply to a broad spectrum of organisms (Enquist *et al.*, 1998; Gillooly *et al.*, 2001), the mechanism of Metabolic Theory, if correct, should drive species richness of ectothermic taxa despite divergent evolutionary histories and/or habitat requirements. In this study, we test whether the slopes of $\ln S - (kT)^{-1}$ relationships are consistent with the predictions of Metabolic Theory in richness gradients in North America, north of Mexico. To test Allen *et al.*'s (2002) hypothesis, we assessed richness–temperature relationships for six ectothermic taxa, including reptiles, amphibians, trees and three insect taxa.

METHODS

We used the quadrat system of Currie (1991) to examine temperature–species-richness relationships. This quadrat system divides North America, north of Mexico, into 336 quadrats. Quadrats spanned $2.5° \times 2.5°$ (latitude $\times$ longitude) south of 50° N latitude and $5° \times 2.5°$ (latitude $\times$ longitude) north of 50° N. Coastal quadrats were included in the analysis and we included quadrat area in regression analysis to account for their reduced size. Quadrat area was not strongly correlated with either temperature (Pearson's $r < 0.06$) or latitude (Pearson's $r < 0.12$). Allen *et al.* (2002; Fig. 3a,c) used the same quadrat system, and the tree and amphibian data from Currie (1991) in the original development of Metabolic Theory. Our test, therefore considers

the identical spatial resolution and geographical extent as Allen *et al.* (2002). The mean annual temperature for each quadrat was also obtained from Currie (1991). Species richness per quadrat was acquired for four additional ectothermic groups: reptiles (Currie, 1991), blister beetles (Coleoptera: Meloidae: *Epicauta*; Kerr & Packer, 1999), tiger beetles (Coleoptera: Cicindelidae; Kerr & Currie, 1999) and butterflies (Lepidoptera: Papilionoidea and Hesperioidea). Butterfly richness data were obtained by scanning and georeferencing range maps from *The butterflies of North America* (Scott, 1986). In all cases, species-richness data were generated by overlaying relatively coarse range maps. Species are not expected to be found at all locations within their range (Hurlbert & White, 2005). However, the resolution of grid cells in our analysis is somewhat coarser than the resolution of the data (as judged by the smallest areas or presence or absence discernible on the maps). This greatly reduces the potential influence of range-filling procedures on measures of species richness. Treating each taxon separately, we found the lowest temperature at which at least one species was present and we excluded quadrats with lower temperatures from the analysis (where the slope of the richness–temperature relationship is clearly 0). To avoid taking the logarithm of zero, we added 0.5 to all species-richness values prior to transformation.

Metabolic Theory predicts that the natural logarithm of ectotherm species richness will be a linear function of $(kT)^{-1}$ with a slope of −0.78. Simply performing linear regression to determine if the slope is equal to −0.78 is not an appropriate test of the hypothesis, as it assumes that one of the predictions, linearity, is true. To test this assumption we used two regression models:

$$\ln S = b_0 + b_1 (kT)^{-1} + b_2 \ln A \qquad (1)$$

$$\ln S = b_0 + b_1 (kT)^{-1} + b_2 \left[(kT)^{-1} \right]^2 + b_3 \ln A \qquad (2)$$

where S is species richness, T is mean annual temperature (K), k is Boltzmann's constant, 8.62×10^{-5} eV K^{-1} and A is quadrat area (km^2). We used the natural logarithm of quadrat area, as required by Metabolic Theory (Allen *et al.*, 2002). Equation 2 is a quadratic model, allowing for a curvilinear relationship between species richness and temperature.

To test Allen *et al.*'s (2002) first prediction, the linearity of the temperature–richness relationship, we used the Akaike information criterion (AIC) to choose the model that best fits the data. Although Allen *et al.* (2002) report that they used Type II regressions, our analyses of the same data yield slope estimates similar to theirs when we use ordinary least squares (OLS). Type II regressions yield much larger differences between predicted and observed slopes (not shown). We feel that OLS is to be preferred on theoretical grounds because the independent variable, mean annual temperature, can be measured with much less error than species richness. For these reasons, and because our use of Type I regression is less likely to reject Allen *et al.*'s (2002) hypothesis, we used OLS. To determine if quadrat area had an effect on model selection, we also compared AIC values after removing the area term from eqns 1 and 2. The effect of spatial

autocorrelation on analyses in geographical ecology is well documented (Dale & Fortin, 2002; Lichstein *et al.*, 2002; Tognelli & Kelt, 2004; Fortin & Dale, 2005). To minimize the possibility that spatial autocorrelation would lead to erroneous model selection, we also computed spatially corrected AIC values (AIC$_S$; A.J.F. Diniz-Filho *et al.*, unpublished). AIC$_S$ penalizes models with significant spatial autocorrelation remaining in their residuals (A.J.F. Diniz-Filho *et al.*, unpublished). We did not use conditional autoregressive models (CARs) because CARs can potentially confound model selection when the independent variable is strongly spatially structured (as is the case here), resulting in erroneous conclusions regarding the form of the true relationship (A.C.A., J.T.K. & D.J.C., unpublished data).

In the case of quadratic regressions, we tested whether the instantaneous slope of the temperature–species-richness relationship differs from −0.78. This procedure allows for the evaluation of the geographical extent over which the predictions of Allen *et al.* are met. The instantaneous slope of the temperature–species-richness relationship, given eqn 2, is found by taking the partial derivative of ln S with respect to $(kT)^{-1}$:

$$\frac{\partial \ln S}{\partial [(kT)^{-1}]} = b_1 + 2b_2 (kT)^{-1}. \qquad (3)$$

The standard errors of b_1 and b_2 and their covariance can all be estimated from the regression. However, the presence of spatial autocorrelation will result in variance estimates that are artificially small (Dale & Fortin, 2002; Fortin & Dale, 2005). To account for this, we calculated the geographically effective sample size (n_e), using the formula given by Cressie (1991):

$$n_e = n \frac{1 - \rho}{1 + \rho} \qquad (4)$$

where n is sample size and ρ is the autocorrelation coefficient of model residuals, which was calculated using the program Spatial Analysis in Macroecology (sam; Rangel *et al.*, 2005). Using n_e, we manually reconstructed the variances of the regression coefficients and their covariance to obtain geographically effective variances (var$_e$) and covariances (cov$_e$). These variances can be combined to give the corrected variance of the estimated slope (eqn 3) at a point $1/kT$:

$$\begin{aligned} &\text{var}_e [2b_2 (kT)^{-1} + b_1] \\ &= \text{var}_e [2b_2 (kT)^{-1}] + \text{var}(b_1) + 2\text{cov}_e [2b_2 (kT)^{-1}, b_1] \\ &= [2(kT)^{-1}]^2 \, \text{var}_e (b_2) + \text{var}_e (b_1) + 4(kT)^{-1} \text{cov}_e (b_1, b_2). \end{aligned} \qquad (5)$$

The 95% confidence interval of equation 3 is therefore given by:

$$2b_2 (kT)^{-1} + b_1 \pm$$
$$t_{(\text{d.f.}_e, \alpha/2)} \sqrt{4(kT)^{-2} \text{var}_e (b_2) + \text{var}_e (b_1) + 4(kT)^{-1} \text{cov}_e (b_1, b_2)} \qquad (6)$$

where d.f.$_e$ is the degrees of freedom calculated from n_e. We next calculated the range of temperatures for which the 95% confidence interval of the slope of the temperature–species-richness relationship included −0.78, i.e. the range that is consistent with Allen *et al.*'s (2002) prediction. We also determined the geographical extent of this range.

RESULTS

The temperature–species-richness relationship (Fig. 1) was curvilinear for all taxa, as determined from AIC values (Table 1). Since including the quadrat area term in regression improved the model fit, we present AIC values only from models that included this term. In all cases, quadratic terms remained statistically significant after computing corrected variances ($P < 0.01$ in all cases). Using AIC_S rather than AIC did not alter model selection: quadratic models provided a better fit to the data than linear models (Table 1). The only difference was that for amphibians, AIC_S indicated a better fit for a quadratic model excluding the area term, indicating that area does not provide additional information to the regression model for this taxon. Nevertheless, because of the well-established effect of area on species richness (the species–area relationship), its inclusion in Metabolic Theory (Allen *et al.*, 2002), and to retain consistency among taxa, we performed further analysis on amphibians using the quadratic model including the area term. Quadrat area was only weakly correlated with temperature (Pearson's $r < 0.06$), thus its inclusion, or exclusion, had virtually no effect on subsequent analyses of the temperature–species-richness relationship.

Because the relationship between ln S and $(kT)^{-1}$ is nonlinear, its instantaneous slope (eqn 3) varied substantially across space, for example the slope for amphibians ranged from −1.71 to +0.07 (Table 2). More importantly, for all taxa, with the exception of blister beetles, the 95% confidence interval (eqn 6) included −0.78 over only a narrow range of temperatures (Fig. 2). Geographically, this accounted for a low percentage of North America north of Mexico, ranging from 10% for reptiles, to 20% for amphibians (Fig. 3). Blister beetles showed the widest range of temperatures (Fig. 2) and geographical area (45% of the study area; Fig. 3) consistent with the predictions of Metabolic Theory. While the relationship was still curvilinear, the confidence interval of the slope estimate was large due to low spatially corrected degrees of freedom. For most taxa, the area within the range predicted by Metabolic Theory occurred near the centre of the temperature gradient. For blister beetles this range occurred in warm areas, while for butterflies the slope was similar to the predicted value in the coldest areas of North America.

DISCUSSION

A mechanistic link between climate and species richness has not yet been identified, despite the high predictive ability of climate-based empirical models of species richness (e.g. Francis & Currie, 2003). The link proposed by Metabolic Theory (Allen *et al.*, 2002) postulates that broad-scale species-richness gradients arise due to the temperature dependence of metabolic rate (Gillooly *et al.*, 2001) and the energetic-equivalence rule of population energy use (Damuth, 1981; Enquist *et al.*, 1998). Here, we tested this prediction using six ectothermic taxa in North America, north of Mexico.

Using Metabolic Theory, Allen *et al.* (2002) predict that, for ectotherms, the natural logarithm of species richness will be a linear function of $(kT)^{-1}$ with a slope of −0.78. For all six ectothermic taxa examined here, including amphibians, reptiles, trees, butterflies, tiger beetles and blister beetles, the slope of the richness–temperature relationship varied spatially. The temperature–species-richness relationships among these taxa were always curvilinear. Moreover, for all but one taxon (blister beetles), even after correcting for spatial autocorrelation, the slope of this relationship was statistically equivalent to −0.78 only over a small proportion of the study area that fell within a narrow temperature range. The curvilinear temperature–species-richness relationship and lack of correspondence with the predicted slope both provide strong evidence that the temperature dependency of metabolic rate is not the sole mechanism shaping broad-scale species-richness gradients.

Metabolic Theory uses a single environmental variable, temperature, to generate its predictions. Empirical models have shown that, to predict species richness accurately, both water and temperature variables must be considered for most taxa (Currie, 1991; O'Brien, 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003). It is possible that temperature shapes species-richness gradients via its effect on metabolic rate, but this effect is distorted by the influence of water variables. It may be that the relationship between metabolic rate and temperature is not stationary across moisture gradients, or that water availability affects richness gradients via a mechanism unrelated to metabolic rates. Allen *et al.* (in press), for example, suggest that the species-richness–temperature relationship should be expected to hold only in areas where productivity is not limited by some factor other than temperature. Under either of these scenarios, if the relationship between temperature and metabolic rate was still a driving factor we would expect that in areas where water variables are statistically relatively unimportant, i.e. cold or low-energy areas (Hawkins *et al.*, 2003), the predictions of Metabolic Theory would be met. For five of the six taxa we examined, our results are inconsistent with this prediction. In these taxa, the observed slopes were more negative than −0.78 in cold areas, and for all but blister beetles, less negative in warm areas. For butterflies, the temperature range with a slope similar to the predicted value was in the coldest areas of North America, as expected. However, even for butterflies, it is not evident that there is a temperature threshold below which ln S varies linearly with $(kT)^{-1}$.

The species-richness prediction of Metabolic Theory relies on the assumption that, in general, the body temperature of ectotherms closely tracks environmental temperature. It is well established, however, that many ectotherms regulate their body temperature behaviourally to maintain it more closely to optimum levels (Angilletta *et al.*, 2002). It should be noted that the deviation between actual body temperature and environmental temperature may be reduced when examined at broad scales. Nevertheless, it does provide one potential explanation for the deviation from predictions that we have observed here. Trees, however, are unable to regulate their operating temperature behaviourally to the same extent as other groups, although like other organisms they can regulate their freezing point. Thus, if body temperature/environmental temperature discrepancies were distorting the richness–temperature relationship, trees should demonstrate the strongest agreement with predictions.
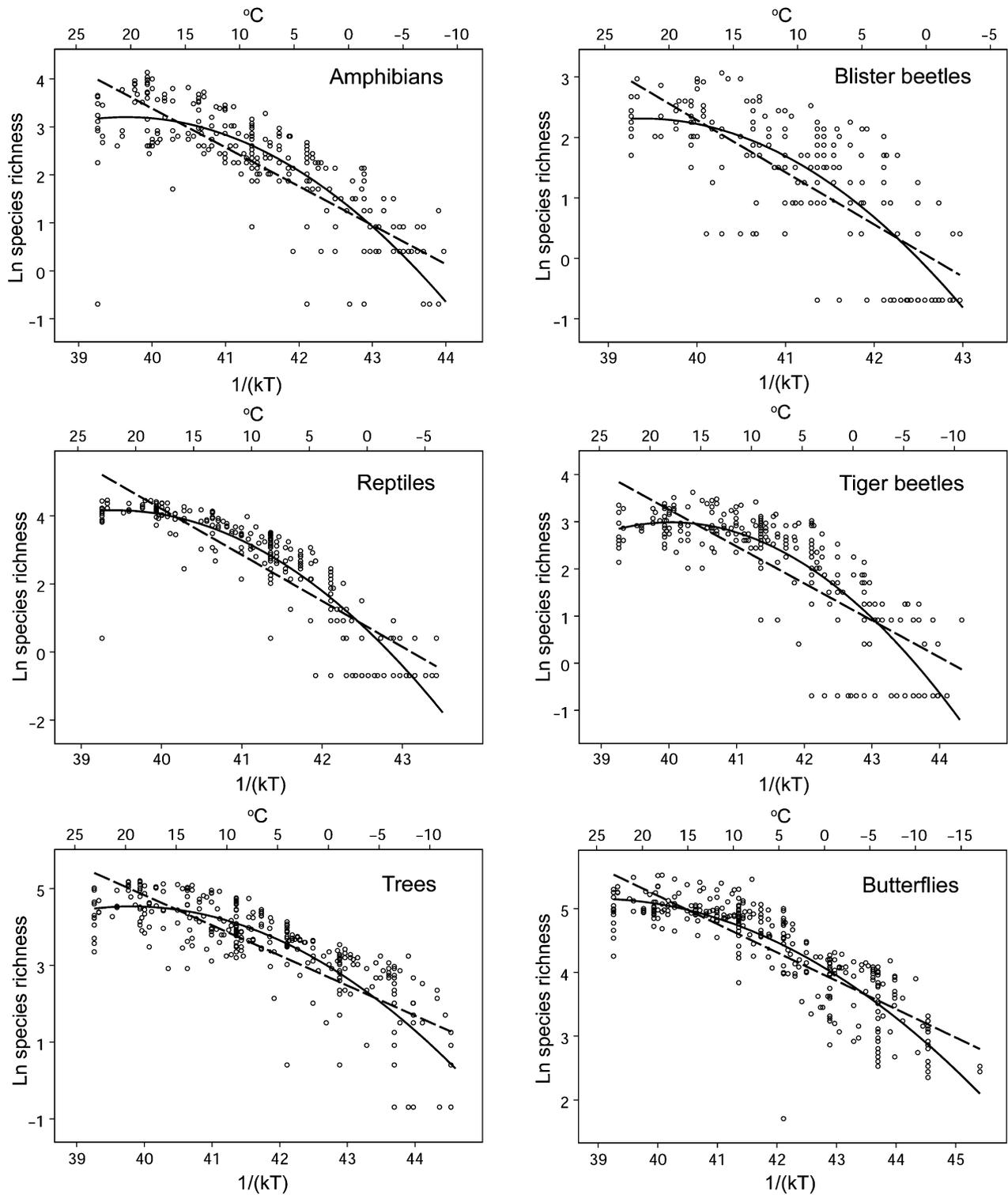
Figure 1 Temperature–species-richness relationships for six taxa in North America, north of Mexico. Solid lines are quadratic regressions: $\ln S = b_0 + b_1(kT)^{-1} + b_2[(kT)^{-1}]^2$, where S is species richness, k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) and T is mean annual environmental temperature (K). Dashed lines are linear fits. In all cases, Akaike information criterion values indicated that quadratic models provided a better fit to the data. Data are from 336 quadrats measuring 2.5° latitude × 2.5° longitude south of 50° N, and 5° latitude × 2.5° longitude north of 50° N.
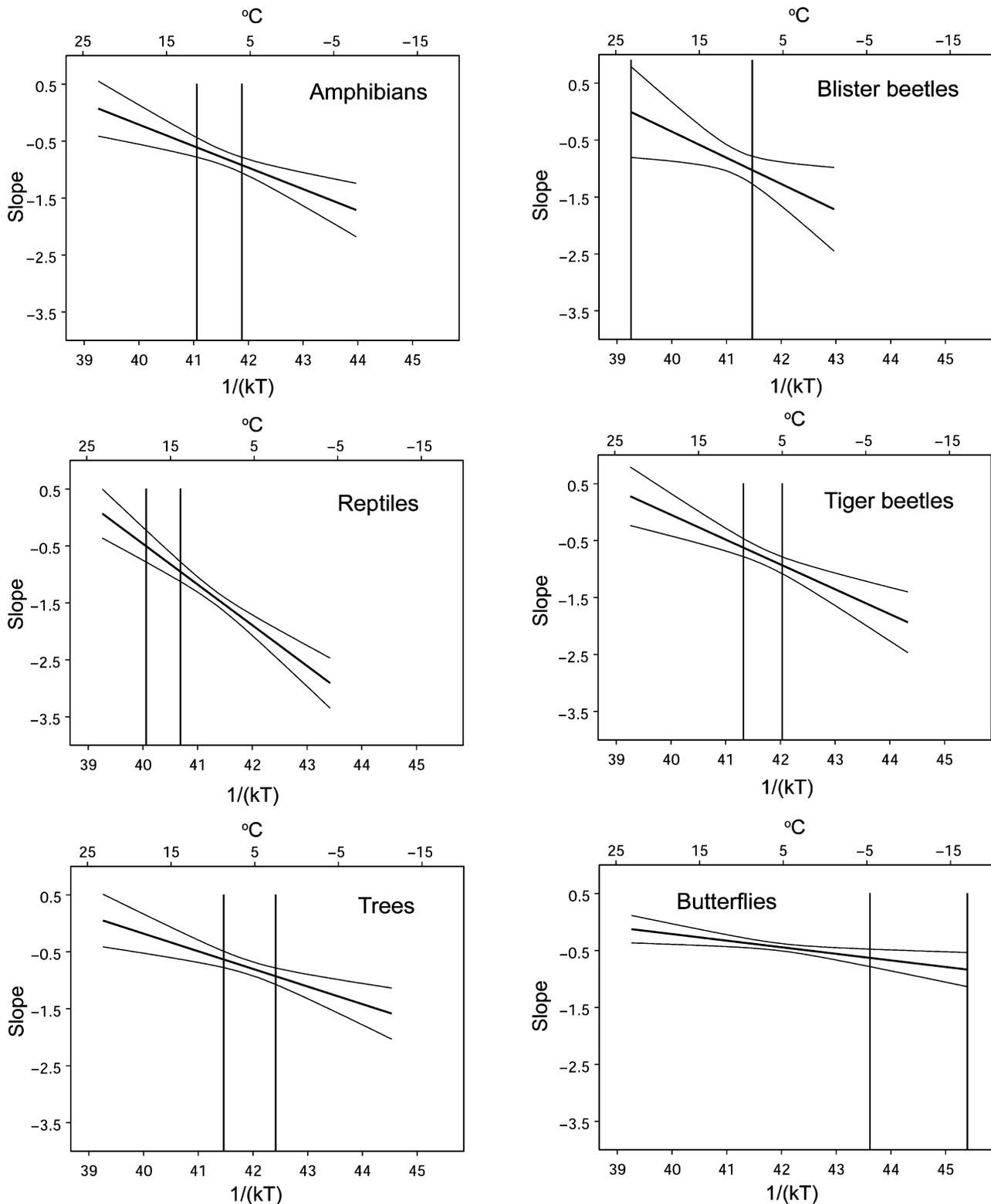
Figure 2 Instantaneous slopes and 95% confidence intervals of temperature–species-richness relationships for six taxa in North America, north of Mexico. 95% confidence intervals were computed using spatially corrected variances. Vertical lines depict the range of temperatures where the 95% confidence interval included –0.78, the value predicted by the metabolic hypothesis for ectotherms. Slopes were calculated by taking the partial derivative with respect to $(kT)^{-1}$ of a quadratic regression, $\ln S = b_0 + b_1(kT)^{-1} + b_2[(kT)^{-1}]^2 + b_3 \ln A$, such that $\partial \ln S/\partial[(kT)^{-1}] = b_1 + 2b_2(kT)^{-1}$, where S is species richness, k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), A is quadrat area, and T is mean annual environmental temperature (K).

Table 1 Akaike information criterion (AIC) values of linear and quadratic models of the temperature–species-richness relationship. Spatially corrected AIC values (AIC$_S$; A.J.F. Diniz-Filho *et al.*, unpublished) are also presented. All models included ln(quadrat area) as a covariate. ΔAIC is AIC$_{quadratic}$ − AIC$_{linear}$. In all cases, quadratics have lower AIC values than linear models

Taxa	AIC			AIC$_S$		
	Linear	Quadratic	ΔAIC	Linear	Quadratic	ΔAIC$_S$
Amphibians	625	548	−77	374	226	−148
Reptiles	592	456	−96	380	44	−336
Trees	780	716	−64	502	325	−177
Blister beetles	551	517	−34	362	299	−63
Tiger beetles	727	628	−99	486	307	−179
Butterflies	326	290	−36	5	−90	−95

Table 2 Range of the instantaneous slope of the temperature–species-richness relationship for six ectothermic taxa in North America, north of Mexico. Slopes were determined by taking the partial derivative of ln S with respect to $(kT)^{-1}$ of the regression: ln $S = b_0 + b_1(kT)^{-1} + b_2[(kT)^{-1}]^2 + b_3$ln A, where S is species richness, k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}), A is quadrat area, and T is mean annual environmental temperature (K)

Taxa	Minimum slope (95% CI)	Maximum slope (95% CI)
Amphibians	−1.71 (−2.18, −1.24)	0.07 (−0.41, 0.55)
Reptiles	−2.91 (−3.35, −2.47)	0.07 (−0.36, 0.50)
Trees	−1.58 (−2.03, −1.14)	−0.05 (−0.41, 0.51)
Blister beetles	−1.71 (−2.45, −0.98)	−0.01 (−0.80, 0.79)
Tiger beetles	−1.93 (−2.47, −1.40)	0.28 (−0.24, 0.79)
Butterflies	−0.84 (−1.14, −0.54)	−0.12 (−0.37, 0.12)

Our results clearly show that tree species richness had a curvilinear relationship with temperature, and that the relationship's slope was close to −0.78 over a range similar to that of other ectothermic taxa. This suggests that Metabolic Theory's failure to explain broad-scale richness gradients in North America does not arise because of behavioural regulation of body temperature.

Allen *et al.* (2002) suggest that their theory may not apply to taxa whose body size and/or abundance is dependent on temperature (e.g. reptiles), or to groups that are narrowly defined (e.g. pine trees). Our data show that reptiles deviated from the theory's predictions in a manner similar to other groups, such as trees, whose abundance and biomass vary little with latitude (Enquist & Niklas, 2001; Allen *et al.*, 2002). Additionally, we
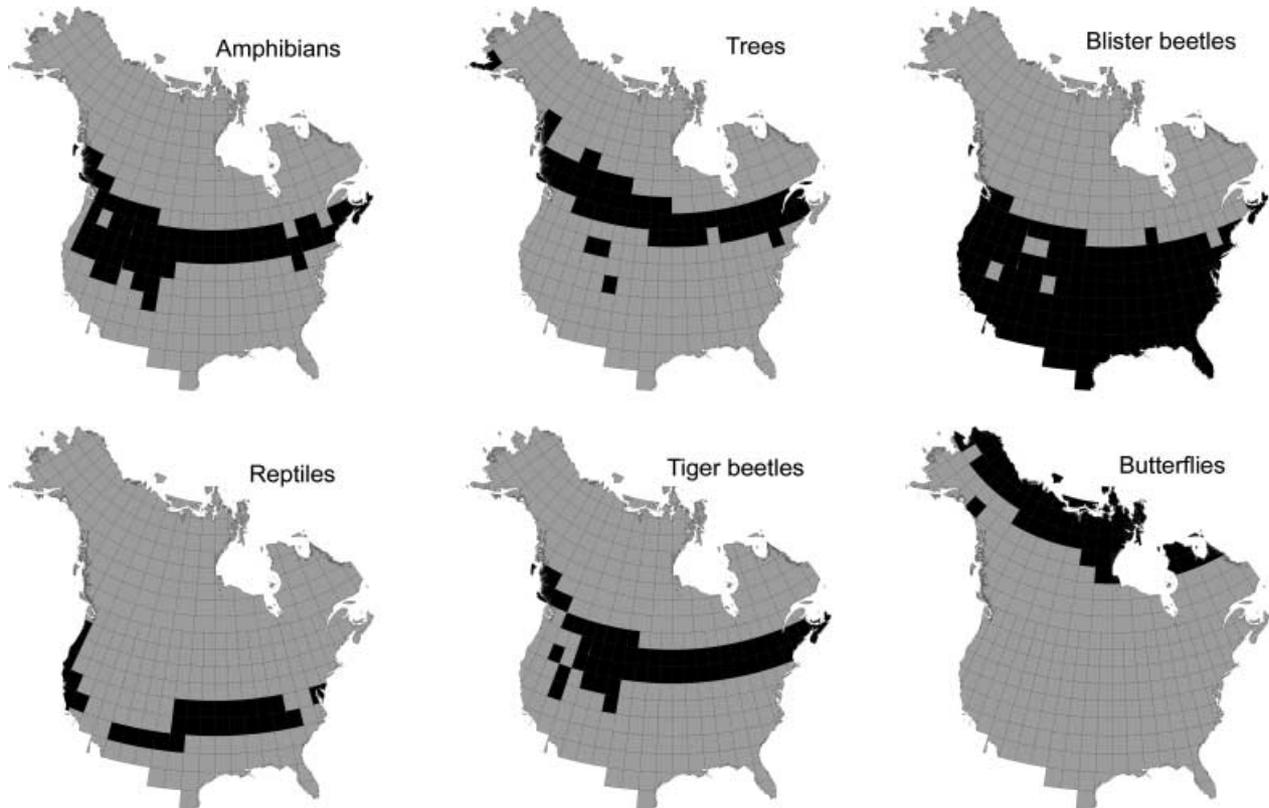

Figure 3 Areas of North America, north of Mexico, where the slope of the temperature–richness relationship is consistent with the metabolic hypothesis. Black quadrats are areas where the 95% confidence interval of the instantaneous slope of the temperature–richness relationship includes −0.78, the value predicted by the metabolic hypothesis. Data are for 336 quadrats measuring 2.5° latitude × 2.5° longitude south of 50° N, and 5° latitude × 2.5° longitude north of 50° N.

tested a variety of taxa which varied from broadly to narrowly defined: the tree data included both angiosperms and gymnosperms, amphibians and reptiles were defined at the class level, butterflies included two superfamilies, tiger beetles were defined at the family level, and blister beetles at the genus level. Departures from the theory's prediction were present, and similar, for all taxa. Indeed, the group that showed the greatest accordance with the theory's predictions (although still deviating from them) was the most narrowly defined group (blister beetles), exactly the opposite of Allen *et al.*'s (2002) expectation. Results for blister beetles do not generalize to tiger beetles, a larger assemblage of species, which show patterns very much like those observed for trees, vertebrates and butterflies (i.e. the predictions of Metabolic Theory apply across only a small area of North America).

Unlike other mechanisms proposed to explain climate–species-richness gradients, Allen *et al.*'s (2002) hypothesis is remarkable in the precise, quantitative and testable predictions that it makes. Although the predictions of Metabolic Theory have proven incorrect, it is impressive how close they come. It is possible that other metabolic mechanisms that incorporate the effects of water (e.g. Venevsky & Veneskaia, 2003) are required to predict species-richness gradients more accurately and over a wider geographical range. A critically important contribution of Allen *et al.*'s (2002) model is the way in which it fails. Why is the richness–temperature relationship nonlinear, but overlapping the slope predicted by Metabolic Theory? Can the metabolic model be modified to account for this pattern? For example, it has been suggested that both the three-quarter scaling of metabolism (Glazier, 2005) and the activation energy of metabolism (Clarke & Fraser, 2004) are variable. Systematic variation of these parameters, especially the latter, could result in the patterns observed here, though to be successfully integrated into the theory the variation in their values would preferably be defined a priori. Both the successes and failures of Metabolic Theory will provide invaluable clues to future efforts to resolve the long-standing controversy over what determines broad-scale variation in species richness.

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