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Metabolic theory and elevational diversity of vertebrate ectotherms

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Abstract. The Metabolic Theory of Ecology (MTE) posits that the temperature-dependent kinetics of metabolism shape broad-scale patterns of biodiversity. Here we test whether the MTE accounts for patterns of diversity using 102 elevational diversity gradients of reptiles and amphibians. In particular, we examined the support for the two key predictions of the MTE: that the reciprocal of absolute temperature ($1/kT$) and diversity are linearly related and that the slope of that relationship is −0.65. We also tested two underlying assumptions of the MTE in cases with appropriate data, namely, that abundance is invariant among samples, and that behavioral thermoregulation influences the MTE predictions. We found that few studies supported the predictions of the MTE for the relationship between environmental temperature and elevational diversity using previous methods on individual gradients and using meta-analysis. The predominant relationship was curvilinear, and the slopes were steeper than predicted. In analyses of individual gradients, only 6% followed the MTE predictions in the strictest application, and 25% in the broadest. We found violations of the assumption of invariant abundances in all five test cases. All four herpetofaunal groups, regardless of behavioral thermoregulatory abilities, demonstrated poor fits to the MTE predictions. Even when arid gradients are removed, ameliorating the potential effects of water limitation, the MTE did not account for herpetofaunal elevational diversity. We conclude that an interplay of factors shapes elevational diversity gradients rather than the simple kinetics of biochemical reactions.

Key words: abundance; amphibians; mountains; reptiles; species richness; temperature.

INTRODUCTION

Numerous hypotheses have been suggested to explain why biodiversity varies geographically. Recently, an application of the Metabolic Theory of Ecology (MTE) has been proposed as a mechanistic explanation for geographic variation in species number (Allen et al. 2002, 2007, Brown et al. 2004, Gillooly and Allen 2007). Based on the biochemical kinetics of metabolism, an early version of the MTE extended the well-known energetic equivalence rule (Damuth 1987) to predict changes in diversity of ectotherms along temperature gradients by linking ecological and evolutionary processes to an organism's metabolic rate (Allen et al. 2002, Brown et al. 2004). The initial mechanisms largely focused on linking energy use, metabolism and body size to species richness in a defined area and argued that the activation energy of metabolism was 0.78 eV, but later versions of the MTE have argued that increasing temperature also increases speciation rate (Brown et al. 2004, Gillooly and Allen 2007) and assumed an activation energy of 0.65 eV. These links between temperature, metabolic rate and diversity also depend upon several important assumptions: (1) metabolic rate varies with body size and environmental temperature, (2) the total number of individuals in the community is invariant along the temperature gradient, (3) energetic use is equivalent for each population, and (4) the mean derived from the body size distribution is invariant. If each of these assumptions is met, though most have not been systematically tested, then the MTE makes two predictions about diversity: the reciprocal of absolute temperature ($1/kT$, where k is the Boltzmann's constant and T is temperature in degrees Kelvin) and diversity should be linearly related and the slope of that relationship should be −0.65 (Brown et al. 2004). In this paper, we test those two predictions and examine two assumptions: invariant community abundance and whether metabolic rate varies with environmental temperature under varying levels of behavioral thermoregulation.

The original examples supporting the MTE as an explanation for diversity focused on regional-scale diversity gradients and elevational diversity gradients (Allen et al. 2002, Brown et al. 2004). Hawkins and colleagues (2007*a*) recently tested 46 regional-scale data sets against the MTE diversity predictions and found only two data sets supporting the MTE predictions in the strict application. Importantly, however, these analyses did not include elevational gradients, even though the theory should account for variation in diversity along both elevational and latitudinal gradients

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(Allen et al. 2002, Brown et al. 2004). Hawkins et al. (2007*a*) suggested that data from smaller-scale gradients like elevation might support the MTE predictions better than data from regional-scale gradients. Therefore, whether the MTE can account for elevational diversity remains an open question (but see Sanders et al. 2007).

Here, we analyze 102 elevational gradients of reptiles and amphibians to test whether the MTE can account for spatial variation in ectotherm diversity. In addition, we test a fundamental assumption of the MTE, that abundance is invariant among communities or samples (Allen et al. 2002). Most empirical tests of the MTE violate this assumption, as pointed out in several recent papers (e.g., Allen et al. 2002, Brown et al. 2004, Hawkins et al. 2007*a*, Kreft and Jetz 2007, Buckley et al. 2008). Here, for five studies, we test whether violating the assumption of invariant abundance affects the fit to the MTE predictions about spatial variation in diversity. To examine the potential violation of the assumption of behavioral thermoregulation, we contrast the four groups of herpetofauna from lizards with the strongest abilities to behaviorally thermoregulate to salamanders with the weakest abilities (Pianka 1967, Feder and Lynch 1982, Huey 1982). In addition, Gillooly and Allen (2007) argued for the importance of additional factors when testing the MTE: water limitation, taxonomic breadth (e.g., orders vs. genera), data quality, and consistency of temperature measurements. To address these concerns, we contrast the fit of the MTE to gradients with and without strong water limitation; we control for taxonomic spread by focusing solely on herpetofaunal diversity; and we use only robustly sampled data and a consistent methodology to estimate temperature.

METHODS

Elevational diversity of herpetofauna was compiled from the literature, field guides, faunal surveys, and online databases. These data, therefore, are a combination of field transects and of regional-scale compilations of field surveys and specimen records from montane areas. Elevational gradients were selected based on a priori sampling criteria: sampling was substantial, unbiased elevationally, covered $\geq$70% of the gradient, and was not influenced by large-scale habitat disturbance (McCain 2007, 2009, *in press*, Nogués-Bravo et al. 2008; C. M. McCain, *unpublished manuscript*). Of ~200 data sets, 102 met the a priori criteria: 6 reptile, 17 snake, 17 lizard, 20 salamander, and 42 frog (see Plate 1) gradients (see Appendix A), which vary in latitude (36°30′ S–49°30′ N), mountain height (1300–6800 m), and herpetological diversity (5–691 species).

Most studies did not document variation in temperature. Therefore, average annual temperature was calculated at each mountain base using WorldClim data (1-km^2 scale; *available online*).[4] For standardization, temperature was assumed to decrease monotonically by 0.6°C per 100 m elevational gain (Barry 1992). Slight variation might exist among and within data sets due to adiabatic cooling rates and local conditions (Fridley 2009), but standardization assures that differences in the MTE fits are not due to differences in temperature estimation. We note that a similar procedure to estimate temperature was adopted in previous tests of the MTE along both latitudinal and elevational gradients.

The MTE makes two specific predictions. First, ln-transformed species richness should be linearly associated with the reciprocal of absolute temperature. Second, and more specifically, the slope of the relationship between ln-transformed richness and $1/(kT)$, where k is the Boltzmann's constant (0.0000862 eV/K) and T is temperature in degrees Kelvin, should fall between −0.60 and −0.70 (Brown et al. 2004). We tested these predictions using ordinary least-squares (OLS) regression for each gradient following previously established methods (Allen et al. 2002, Brown et al. 2004, Hawkins et al. 2007*a*). These analyses detail how well the MTE predictions conform to local diversity patterns and allow comparisons to previous results. To get an overall trend in relationship and slope we used a meta-regression approach for each group (all reptile data, lizards, snakes, all amphibian data, salamanders, and frogs) by combining temperature and diversity values for each elevational band on each gradient. Such an analysis then weights the regression by the number of samples in each gradient. We assessed whether taxonomic groups differed significantly in the relationship between diversity and $1/(kT)$ by examining overlaps of 95% confidence limits for slopes. We did not analyze the slope of each gradient within the meta-regression. The variance would be pooled in the combined analyses, therefore narrowing the confidence limits of slopes for each gradient and increasing the probability of rejection.

For both individual gradients and meta-regressions, a linear relationship was assumed when (1) richness and temperature were significantly related ($P < 0.05$), and (2) the slope did not vary significantly along the gradient. Two gradient segments were defined by a breakpoint detected with linear piecewise polynomial regression (PPR). Slopes of each segment were calculated with OLS. Linearity was assumed if the 95% confidence intervals of each slope overlapped. A curvilinear relationship was assumed when the slopes of the two segments from the PPR did not overlap. No relationship was detected in cases of an insignificant OLS for the complete data set and the segments.

We tested whether the 95% confidence interval (CI) of the predicted slope fell between −0.60 and −0.70. We also broadened the MTE tests along individual gradients in three ways. First, we broadened the range for the predicted slopes to between −0.55 and −0.75. Second, we tested if the CI for the slopes of either segment defined by PPR fell within the predicted range. Third, we employed relationship categories: monotonically de-

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[4] ⟨www.worldclim.org⟩

creasing, low plateau, hump-shaped, monotonically increasing, and no relationship. The linear category was expanded to encompass monotonically decreasing relationships with minor (although significant) curvature. Low plateau patterns are defined by a shallow slope across the lower portion of the gradient, then a much steeper slope on the upper portion. Hump-shaped patterns are strongly curvilinear with a lower increasing slope and an upper decreasing slope.

Spatial autocorrelation within data sets could lead to smaller confidence intervals for the slopes leading to overly restrictive analyses of the MTE fits. We lack the appropriate distance and geo-referenced locality data to test explicitly for spatial autocorrelation. However, because we broadened the range of allowable slopes to –0.55 to –0.75, we argue that we are providing a buffer against overly conservative tests.

Severe water limitation along elevational gradients may influence the fit to the MTE predictions (Allen et al. 2002, Brown et al. 2004, Hawkins et al. 2007*a*). To test this influence, we delineated wet and arid montane gradients based on the habitat at the lowest elevations: arid vegetation types (humidity index < 0.50) and wet forest vegetation types (>0.50 humidity index); and contrasted their fits to the MTE predictions. Fit was expected to be higher among wet gradients than arid gradients (Gillooly and Allen 2007).

Last, we assessed the MTE assumption of invariant abundance for five gradients with both richness and abundance data, all from southern Europe. An invariant distribution was assumed if neither a linear nor a curvilinear relationship between abundance and elevation was detected using OLS and PPR. In cases of an abundance-elevation relationship, we use multiple regressions and Akaike's information criterion (AIC) to assess the strongest, most parsimonious model for diversity, using abundance and $1/kT$ as model predictors.

RESULTS

The 102 elevational gradients in reptile and amphibian diversity generally did not support the two predictions of the Metabolic Theory of Ecology (MTE). Meta-regression found a significantly curvilinear relationship between elevational diversity and $1/kT$ for combined reptiles, combined amphibians, salamanders and frogs (Fig. 1). Lizard and snake diversity each supported linear relationships but the slopes were significantly higher than predicted (95% confidence limits: –0.828 to –0.966 and –0.970 to –1.122, respectively).

We found similar results across the individual gradients. Seventeen exhibited the expected negative linear relationship between ln-transformed species richness and $1/kT$ (Fig. 2, Table 1, Appendix A). Among those, only six had confidence intervals that included slopes from –0.60 to –0.70, the range predicted by the MTE. On average, the negative linear slopes were steeper than predicted (–1.43). Most data sets were strongly curvilinear, and a few had positive or no detectable relationships. Thus, in the strictest application, only 6% of elevational herpetofaunal patterns met the MTE predictions, even when we relaxed the slopes to include –0.55 to –0.75. The variation among slope values was not attributable to the range of temperatures on each mountain (lizards, $r^2 = 0.02$, $P = 0.62$; snakes, $r^2 = 0.05$, $P = 0.41$; salamanders, $r^2 < 0.01$, $P = 0.90$; frogs, $r^2 = 0.11$, $P = 0.04$; frogs without two highest mountains, $r^2 = 0.07$, $P = 0.11$).

When considering gradient segments, 10 low-elevation and four high-elevation segments had confidence intervals including slopes of –0.60 to –0.70. When we expanded linearity to include 24 generally decreasing patterns, five met the stricter slope criteria and one additional pattern met the broader slope criteria. Again, on average, monotonically decreasing slopes were higher than predicted (–1.36). Under these broadest qualifications, about 25% of the data sets met the two diversity predictions of the MTE (Table 1).

The MTE fits varied among taxonomic groups and precipitation regimes. In the meta-regressions, the four herpetofaunal groups all differed significantly in their relationships between elevational diversity and $1/kT$; none of the 95% confidence intervals for slopes were overlapping (Fig. 1). For individual gradients with the much greater variability in diversity–temperature relationships, the slopes for lizards, snakes, and frogs were higher than predicted by the MTE, whereas slopes of salamanders were lower than predicted (Table 1, Fig. 3). Salamanders generally were the least likely to follow the MTE predictions. Wet gradients, in which water availability is presumably not limiting, did not exhibit better fits to the MTE predictions. Instead, and in contrast to Gillooly and Allen (2007), diversity gradients in dry habitats (where water is presumably limiting) had significantly more data sets that fit the predictions of the MTE (Mann-Whitney *U* test: $Z = 2.31$, $P = 0.02$). Dry gradients had more negative, linear fits, more monotonically decreasing fits, and more partial segment fits than did humid gradients (Table 1). Regardless, still only about 25% of the dry data sets support the broadest application of the MTE diversity predictions for individual gradients. By contrast, the meta-regressions of wet and dry gradients for lizards, snakes, salamanders, and frogs found that all groups contradicted the MTE predictions, except wet gradients of frog diversity. Dry gradients were significantly curvilinear for all four groups, whereas wet gradients were curvilinear for salamanders and linear for lizards, snakes, and frogs (Appendix B). Linear slopes were significantly higher than predicted except for frogs. The best fit curve for wet gradients in frogs was a quadratic-quadratic transformation, as both linear segments were curvilinear with wide confidence limits, which led to an erroneous "linear" fit.

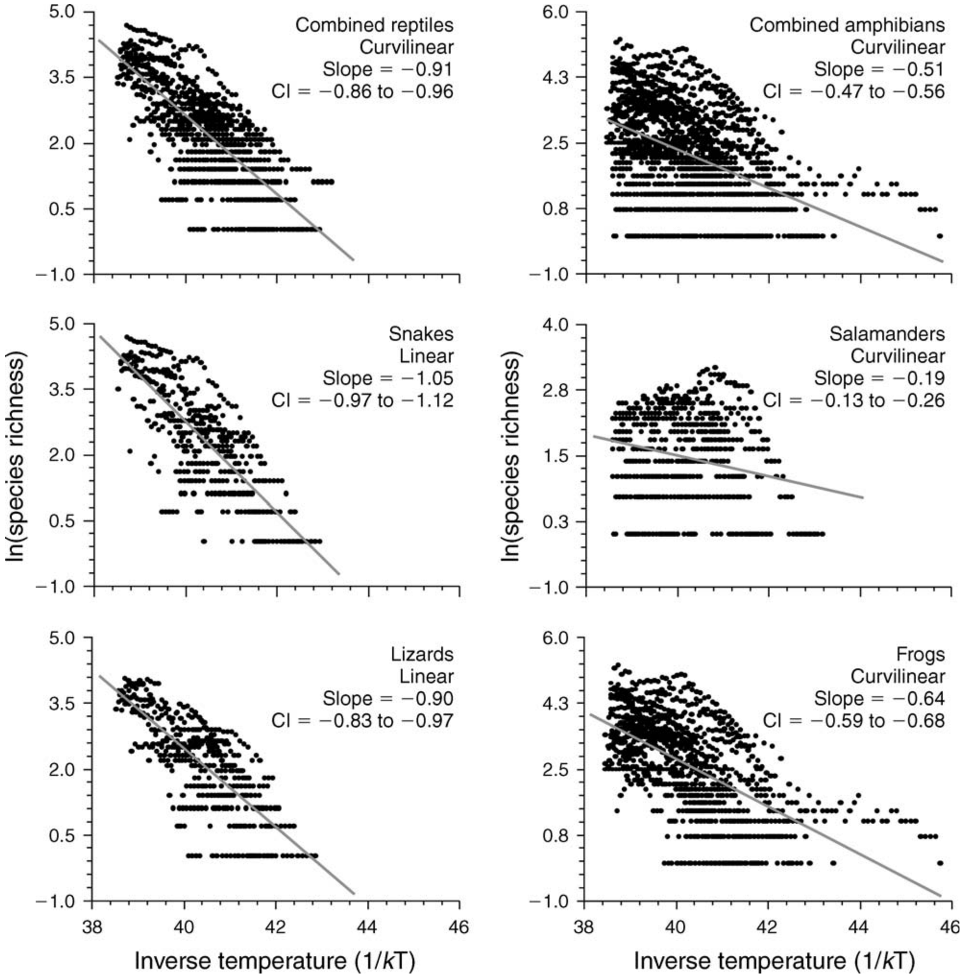

FIG. 1. Meta-regressions of the relationship between ln(species richness) and the inverse of absolute temperature (1/*kT*, where *k* is Boltzmann's constant [0.0000862] and *T* is temperature in degrees Kelvin) for combined reptiles, snakes, lizards, combined amphibians, salamanders, and frogs.

A significant abundance–elevation relationship was detected in all five test cases in which data were available. Of these five, four data sets exhibited curvilinear relationships and one showed a linear decreasing relationship (Fig. 4, Appendix C). Thus, the assumption of invariant abundance among samples was violated. Low-AIC, multiple regression models for four data sets included only abundance as the best predictor of diversity (Iberian Peninsula lizards, snakes, salamanders, and frogs). The fifth model (southern Italian reptiles) included significant effects of both abundance and temperature, but with a stronger abundance effect.

Discussion

We found only limited consistency between the diversity predictions of the Metabolic Theory of Ecology (MTE) and elevational diversity gradients of amphibians and reptiles. Most elevational relationships between herpetofaunal diversity and 1/*kT* were curvilinear, with diversity peaking at mid-elevations rather than linearly related to temperature. Those that supported a linear relationship generally had slopes that were significantly higher than predicted. Diversity gradients for salamanders deviated the most from the predictions, followed by frog gradients, in both the meta-regression and individual gradient analyses (Figs. 1 and 2; Table 1). Combined snake and lizard analyses supported linear relationships but with much steeper slopes than predicted by the MTE, and few individual gradients for snakes and lizards fit the prediction of a linear decrease with the inverse of temperature or a slope of −0.65 (Figs. 1 and 2; Table 1). These results are consistent with those found on larger spatial scales (latitudinal and regional), where similarly curvilinear relationships were documented between 1/*kT* and diversity, and slopes differed significantly from the predicted values (Algar et al. 2007, Hawkins et al. 2007*a*, *b*). For example, Wang et al. (2009) found negative linear relationships between ln-transformed

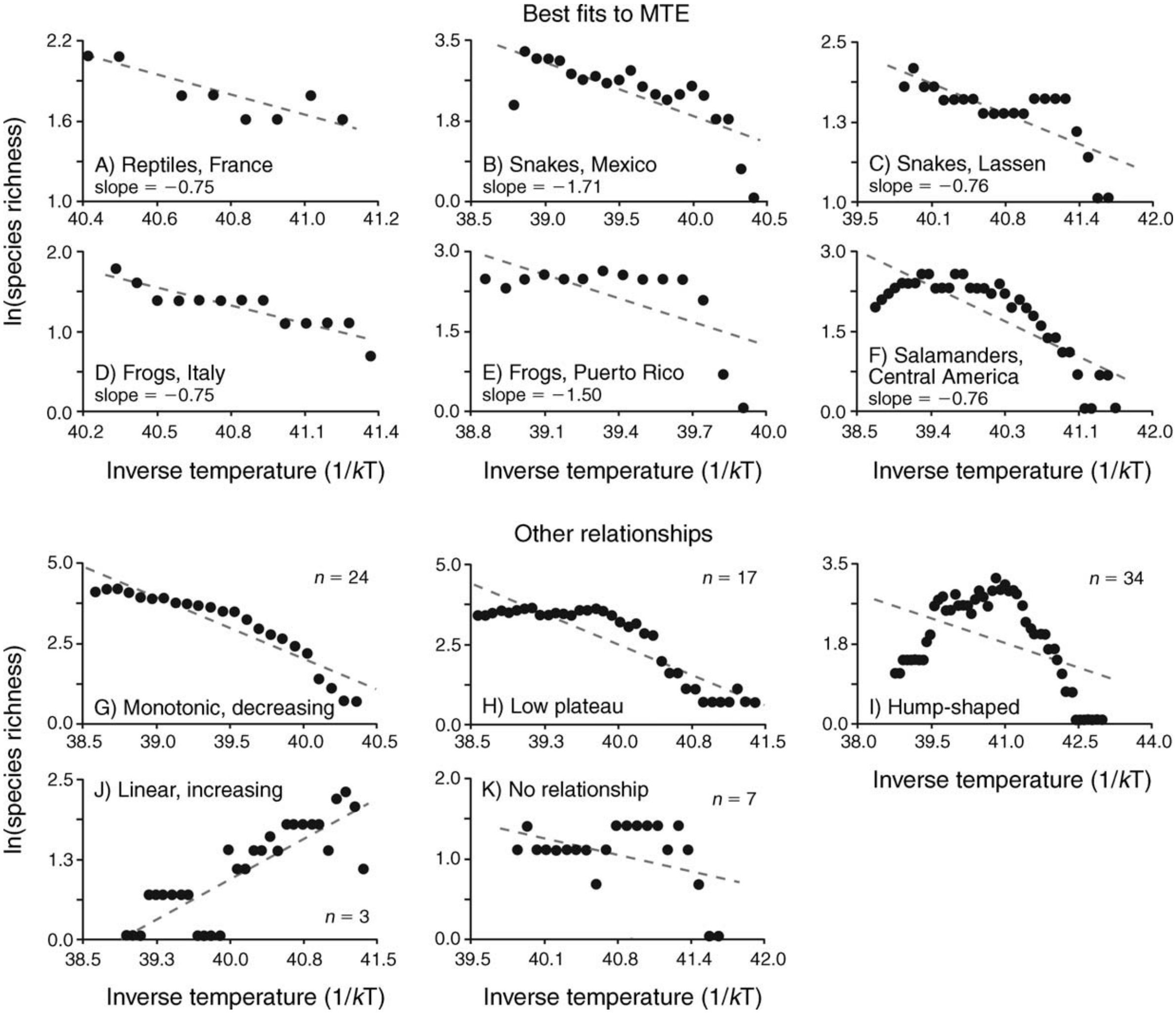

FIG. 2. Examples of linear regressions of ln species richness and the inverse of temperature along individual gradients, including (A–F) the six best fits, and (G–K) examples and frequency (*n*) of relationships that differ from the linear prediction. (A) Reptiles of La Montagne Noire, France; (B) snakes of Gomez Farias, Mexico; (C) snakes of Lassen National Park, California, USA; (D) frogs of Alburni Mountains, Italy; (E) frogs of Puerto Rico; (F) salamanders of Isthmian Central American highlands; (G) snakes of Peten region, Guatemala (slope = −1.92; curvilinear; monotonically decreasing); (H) frogs of Guatemala and Belize (slope = −1.27; curvilinear); (I) salamanders of Sierra Madre Oriental, Mexico (slope = −0.36; curvilinear); (J) salamanders of Northern Oaxaca, Mexico (slope = 0.84); and (K) lizards of Lassen National Park, California, USA (slope = −0.33).

tree species richness and temperature across spatial scales in both China and eastern North America. However, the slope of the relationship varied across scales and between continents, questioning the generality of the effects of temperature-dependent kinetics on spatial variation in biodiversity. If the MTE cannot explain elevational diversity gradients of ectotherm vertebrates, the question becomes, "Why not?"

The MTE might not explain elevational diversity gradients because the MTE's assumptions are violated. The MTE assumption of invariant abundance was violated in all testable cases (Fig. 4). In addition, abundance was more strongly related to diversity than was temperature in each of the cases we analyzed. Violation of the assumption of invariant abundance may invalidate the MTE tests, but previous MTE diversity tests did not examine abundance invariance, for the simple reason that abundance data are so rarely collected or robustly estimated, especially for macroecological data sets. Obtaining broad-scale, robust abundance data should be a priority for testing ecological theories of diversity, including the MTE (e.g., Kaspari 2004, Evans et al. 2005, Buckley et al. 2008).

The MTE may not account for variation in herpetofaunal diversity because other factors, such as water availability, primary productivity, or evolutionary history influence diversity as much, or more strongly, than do temperature-dependent kinetics alone. Allen et al. (2002) point out that they "... do not mean to imply that

TABLE 1. Distribution of OLS slopes and fits of the predictions of the Metabolic Theory of Ecology to patterns of diversity.

Category of analysis	N	Number of gradients with: MTE slope −0.6 to −0.7	Wider slope, −0.55 to −0.75	Lower segment slope −0.6 to −0.7‡	Upper segment slope −0.6 to −0.7‡	Slope: Mean	Upper CI	Lower CI
Linear relationship								
Decreasing	17	6	6	4 (3)	1	−1.43	−1.02	−1.84
Increasing	3	—	—	—	0	0.47	0.70	0.25
Curvilinear relationship								
Monotonic decreasing†	24	5	6	5 (4)	—	−1.36	−1.14	−1.58
Low plateau	17	8	—	1	—	−0.99	−0.75	−1.23
Hump-shaped	34	17	21	2	2	−0.73	−0.41	−1.05
No relationship	7	—	—	—	1	−0.15	0.11	−0.42
Taxon								
Reptiles	6	1	1	—	1 (1)	−0.82	−0.39	−1.24
Lizards	17	0	1	5 (5)	1 (1)	−1.13	−0.87	−1.39
Snakes	17	2	2	2 (1)	—	−1.28	−0.99	−1.58
Frogs	42	2	6	5 (4)	1 (1)	−1.13	−0.82	−1.43
Salamanders	20	1	2	–	1	−0.25	0.00	−0.50
Precipitation regime								
Wet gradients	46	2	5	4 (4)	1	−1.11	−0.83	−1.39
Dry gradients	49	4	7	5 (3)	3 (3)	−0.87	−0.56	−1.18
Wet/dry gradients	7	—	—	3 (3)	—	−0.61	−0.36	−0.86

Notes: See *Methods* for a description of MTE tests. N = total number of elevational gradients in each category of analysis, and the following four columns display the number of gradients meeting each MTE test criterion. Dashes indicate cases where no gradients met the test criteria. Finally, the last three columns give the average slope with the upper and lower confidence interval for all gradients in a category, MTE slope tests for taxonomic groups and precipitation regimes at the −0.6 to −0.7 level include only those gradients with a linearly decreasing relationship between diversity and MTE temperature, whereas those at the −0.55 to −0.75 level also include gradients that have a monotonically decreasing relationship between diversity and MTE temperature.

† Expanded definition of linear (decreasing).

‡ Numbers in parentheses indicate number of segments from data sets without an overall slope between −0.55 and −0.75.

temperature is the only variable that affects biodiversity." Gillooly and Allen (2007) recently suggested water, NPP, and nutrients can also limit diversity and have argued that the MTE is evolving to include these factors as drivers of diversity. Wang et al. (2009) highlight the importance of water availability as well. Indeed, several decades of research support the assertion that multiple factors can act to influence broad-scale diversity (e.g., Wright et al. 1993, Gaston 2000, Hawkins et al. 2003, Currie et al. 2004), and along elevational gradients (e.g.

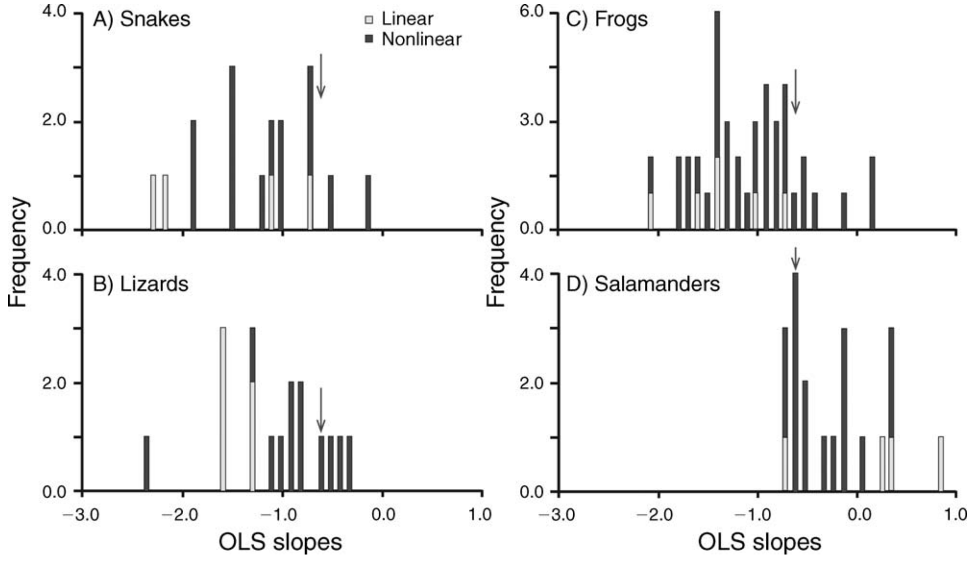

FIG. 3. Ordinary least-squares (OLS) slopes for each herpetological taxon and contrasting linear and nonlinear data sets. Arrows indicate slope predicted by the Metabolic Theory of Ecology (MTE).

Sanders 2002, McCain 2007, 2009). However, this newer version of the MTE for diversity that includes temperature, nutrients, precipitation, and NPP makes no quantifiable predictions. Thus, the latest versions of the MTE simply document correlations between temperature and species richness, thereby negating the strength and appeal of earlier versions.

Even if the newer version of the MTE applied to diversity allows for other factors to mediate the effects of temperature, we found that, in contrast to the revised predictions, the MTE was a better predictor of richness for individual *dry* gradients, where water is limiting, than it was for wet gradients. This divergence was not strong in meta-regressions, as there was little support among either dry or wet gradients for the MTE diversity predictions. Interestingly, the relationship between elevational diversity and temperature had a tendency to be more linear along wet gradients in reptiles than along dry gradients. This confirms other reptile diversity analyses showing a strong temperature effect mediated by radiant heat availability (sunning) that differs predictably on wet and dry elevational gradients (C. M. McCain, *in press*). The contrasting results across montane precipitation regimes suggest that attempts to rescue the MTE from a growing body of critical tests will be more challenging than simply arguing that the MTE works only when it is not too dry, or when other factors are not limiting.

The poor fits to the MTE diversity predictions do not negate the overall importance of temperature to herpetofaunal diversity on montane gradients. Temperature variation has been linked to large-scale diversity patterns in lizards, snakes, and frogs with various mechanisms underlying the trend including increased niche differentiation, resource use and specialization, indirect effects of plant diversity, and temperature-dependent activity times (e.g., Pianka 1967, Schall and Pianka 1978, Clarke and Gaston 2006). These temperature-related mechanisms have not been broadly tested along elevational gradients in herpetofaunal diversity, but some are addressed elsewhere (McCain, *in press*, C. M. McCain, *unpublished manuscript*). The variation in behavioral thermoregulation among herpetofauna from strong (e.g., lizards; Pianka 1967, Huey 1982) to weak (e.g., salamanders; Feder and Lynch 1982) may also influence the results found herein. Strong behavioral thermoregulation should weaken the fit to the MTE predictions because the individuals would not be as directly tied to environmental temperatures. In fact, the ability to thermoregulate violates an important assumption of the MTE, since metabolic rate would no longer be directly tied to environmental temperature. But the comparison of the MTE fits among the four herpetofaunal groups show that all four, regardless of thermoregulatory ability, have low fits to the MTE. In fact, Fig. 1 demonstrates that the best behavioral thermoregulators, lizards, showed the closest fit to the MTE among the four groups: a linear relationship with temperature and the lowest slopes (although still higher than predicted). Clearly the role of temperature and availability of radiant heat will influence the diversity of ectothermic vertebrates, but the underlying mechanisms and the strength of various factors from temperature, sunlight, and precipitation need more detailed analyses (e.g., Pianka 1967, Schall and Pianka 1978, Clarke and Gaston 2006).

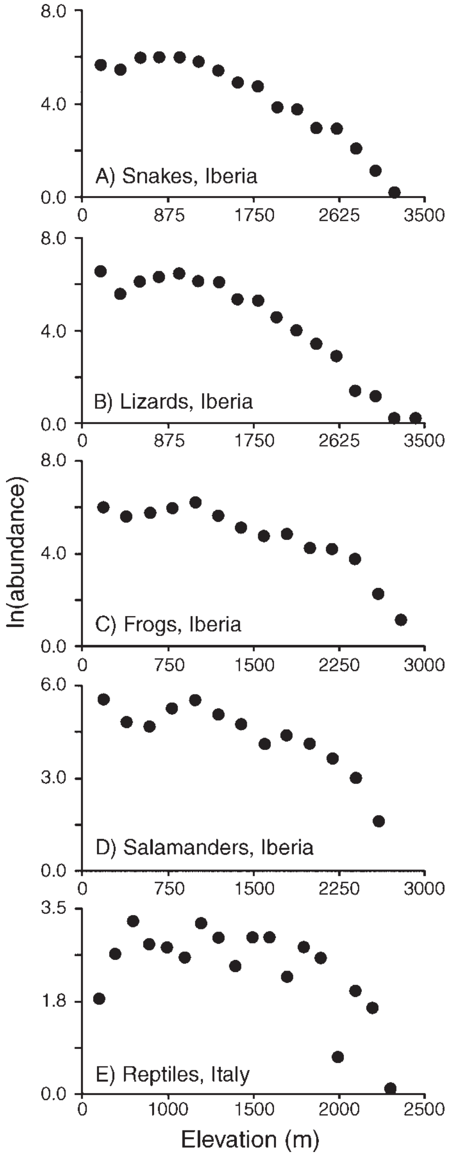

FIG. 4. Five relationships between ln-transformed abundance and elevation: (A–D) various ectotherm taxa, Iberian Peninsula; (E) reptiles, Paneveggio, Italy.

In sum, there has been a long history in ecology and biogeography of documenting the multitude of interacting factors that shape patterns of biodiversity. These factors, including evolutionary history, contemporary and historic climate, biotic interactions, and niche

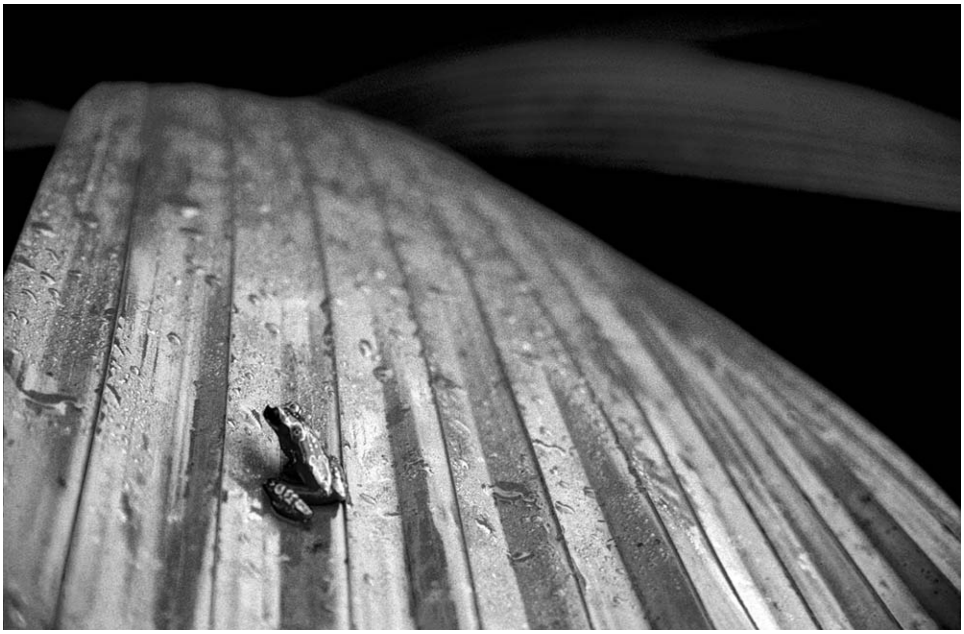

PLATE 1. *Dendrosophus ebraccatus* (hourglass treefrog), La Selva Biological Station, Costa Rica. Photo credit: C. M. McCain.

conservatism, may also interact to drive elevational diversity of amphibians and reptiles. Though there may be still some merit to the MTE and its ability to explain ecological patterns and processes, it is clearly not the key driver of elevational diversity gradients in reptiles and amphibians.

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APPENDIX A

List of all elevational gradients used to test the diversity predictions of the Metabolic Theory of Ecology including locality, citation, taxon, climate, number of species, and regression statistics (*Ecological Archives* E091-043-A1).

APPENDIX B

Meta-regressions between ln species richness and $1/kT$, contrasting dry and wet elevational gradients for snakes, lizards, salamanders, and frogs (*Ecological Archives* E091-043-A2).

APPENDIX C

Multiple regression models and AIC values for the relationship between elevational diversity, abundance, and the MTE temperature (*Ecological Archives* E091-043-A3).