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Energy gradients and the geographic distribution of local ant diversity

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Abstract Geographical diversity gradients, even among local communities, can ultimately arise from geographical differences in speciation and extinction rates. We evaluated three models—energy-speciation, energy-abundance, and area—that predict how geographic trends in net diversification rates generate trends in diversity. We sampled 96 litter ant communities from four provinces: Australia, Madagascar, North America, and South America. The energy-speciation hypothesis best predicted ant species richness by accurately predicting the slope of the temperature diversity curve, and accounting for most of the variation in diversity. The communities showed a strong latitudinal gradient in species richness as well as inter-province differences in diversity. The former vanished in the temperature-diversity residuals, suggesting that the latitudinal gradient arises primarily from higher diversification rates in the tropics. However, inter-province differences in diversity persisted in those residuals—South American communities remained more diverse than those in North America and Australia even after the effects of temperature were removed.

Keywords Species richness · Temperature · Area · Latitude · Biogeography

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Introduction

A key challenge in evolutionary ecology is understanding how and why local diversity [the number of species of a given taxon in ca. 1 ha (*S*), Kaspari et al. 2003] varies within and between biogeographic provinces (Rosenzweig 1995). Early approaches focused on how species traits and species interactions act to pack differing numbers of species into a community (reviewed in Tilman and Pacala 1993). Ricklefs' (1987) argued that biogeographic patterns of local diversity must have regional causes since communities cannot have more species than the region in which they are embedded. A major effort to test Ricklefs' hierarchy hypothesis has focused on ways that the net diversification rate varies at biogeographic scales (Rohde 1992; Rosenzweig 1995; Hubbell 2001). The net diversification rate arises from the balance of speciation rate and extinction rate; geographical trends in either can generate trends in diversity.

Here we test how three such models predict patterns of litter ant species richness generated from standardized sampling of four provinces. Ants are common in virtually every terrestrial habitat from tundra to rainforest (Holldobler and Wilson 1990; Kaspari et al. 2000a). Given their abundance and varied roles as predators, scavengers, seed dispersers, and competitors (Tilman 1978; Franks 1982; Beattie 1985; Cushman and Whitham 1991; Levey and Byrne 1993) and their impact as invasive species (Ward 1987; Porter 1988; Human and Gordon 1997; Holway 1998; Gotelli and Arnett 2000; Kaspari 2000a) the rules governing ant diversity should ramify throughout ecosystems. We explore how the best model for ant diversity accounts for two classic biogeographic patterns: the latitudinal gradient of diversity (Gaston 2000) and inter-province differences in diversity (Schluter 1986).

Three hypotheses based on net diversification at a biogeographic scale

The *area hypothesis* posits that speciation rates increase, and extinction rates decrease toward the equator. It has two key assumptions. First, taxa are specialized to “ecoclimate zones”—bands of relatively similar climate (Merriam 1898). Rosenzweig (1995) proposed five ecoclimate zones that subdivide continents: polar, boreal, temperate, subtropical and tropical. Second, the endemic biota from larger ecoclimate zones has a higher net rate of diversification. This happens for two reasons. First, as area increases, so does the likelihood of allopatric speciation (but see, Chown and Gaston 2000); second, as populations are distributed more widely they are less likely to suffer catastrophic extinction (Terborgh 1973; Rosenzweig 1995; Chown and Gaston 2000). The area hypothesis, for example, argues that the latitudinal gradient of diversity arises from the tropics’ larger size as it is the only zone with its North and South parts conjoined (Terborgh 1973). We test the area hypothesis’ prediction that S is proportional to the area of the community’s ecoclimate zone (Rosenzweig 1995).

The *energy-speciation hypothesis* posits that speciation rates limit S. It has two key assumptions. First, regardless of the many ways that speciation can occur (Otte and Endler 1989; McPeek and Brown 2000) the rate of speciation is ultimately limited by the introduction of new genetic variation (mutation) and how it is shuffled among individuals (sexual recombination, Rohde 1992; Roy et al. 1998). Second, mutation rates and generations/year both scale positively to temperature (Rohde 1992). Models of cellular metabolism have recently been used to accurately predict how generation time (Gillooly et al. 2002) and mutation rate (Gillooly et al., in review) scale with temperature. Allen et al. (2002) use the same mechanism of cellular kinetics to predict a slope of −9 for a plot of ln S vs. temperature^{-1} (1,000/K).

The *energy-abundance hypothesis* also links temperature to diversity, but by mitigating extinction rates (Wright et al. 1993; Kaspari et al. 2000b). It is based on a chain of three linked assumptions (Srivastava and Lawton 1998). First, temperature limits net primary productivity (NPP, g C/m^2 per year; Rosenzweig 1968). Second, NPP limits the total abundance of a taxon; for a given species abundance distribution this means that more NPP translates into a larger average population size for the species within that taxon (Kaspari et al. 2000a). Third, an individual population’s probability of demographic extinction is a negative decelerating function of its abundance (Leigh 1981; Pimm et al. 1988)—as NPP decreases, populations on the scarce end of the species abundance distribution are more likely to go locally extinct (Levinton 1979; Hubbell and Foster 1986; Kaspari et al. 2000b). If so diversity should be a positive function of NPP as high taxon abundance protects an area’s species from demographic extinction.

Despite such well-recognized patterns as the latitudinal gradient (Pianka 1966; Gaston 2000) and inter-province differences in species richness (Ricklefs and Schluter 1993, and references within) there is little agreement over their cause(s). This disconnection between pattern and cause arises for at least two reasons. First, the many different hypotheses for diversity gradients operate at different spatial, temporal, and taxonomic scales (Chase 2002; Rahbek and Graves 2002; Kaspari et al. 2003). The diversity of local assemblages, for example, will be shaped by more factors than the diversity of a 1°×1° grid cell (Ricklefs 1987). There is, however, a paucity of local diversity data at geographical distances (or *extents*) with which to test this assertion. Second, key independent variables from different diversity hypotheses often covary. In particular, the role of energy in shaping diversity has been clouded by the differing roles played by temperature in the energy-speciation hypothesis (where it enhances cellular metabolism) and the energy-abundance hypothesis (where it limits NPP, Rosenzweig 1968). Here we address these issues by: (1) testing three hypotheses for geographic distribution of local diversity of litter-inhabiting ants, (2) separating the different roles of temperature, and (3) measuring the ability of these mechanistic models to account for latitudinal and inter-province differences in litter ant diversity.

Materials and methods

We analyze ant species richness, S, from 96 of the 110 localities sampled by P. S. W. and described in detail elsewhere (Ward 2000). We use only samples from provinces in which Ward collected from at least ten communities. We use provinces sensu Rosenzweig (1995) to reflect land masses in which species arrive primarily via speciation. Two provinces, Australia and Madagascar, are islands. The other two, South America and North America (including Central America) fused 3.5 million years ago and have since experienced limited biotic exchange across the isthmus of Panama (Brown and Lomolino 1998).

In each locality 1 ha or less of forest or woodland was sampled by P. S. W. using a Winkler eclector (Besuchet et al. 1987). Winkler samples do not count ant colonies, but instead tally the “footprint” of each ant species in a community as reflected by the number of its workers distributed throughout 6 l of litter. The goal at each locality was to collect leaf litter from all available microhabitats, sifting it over a coarse mesh screen to concentrate fine litter (Ward 2000). A total of 6 l of sifted litter was collected in each community. This litter was pooled and suspended for ca. 2 days in mesh bags within a larger tapered cloth and wire frame. The ants that worked their way out of the mesh during that time fell into a vial of 95% alcohol. These ants were sorted to species or morphospecies by P. S. W. Voucher specimens are deposited at the Museum of Comparative Zoology, Harvard University.

We next converted the distribution of ant species from each locality’s sample into an estimate of total species richness had that sampling gone to completion. The computer program EstimateS (Colwell 1997) provides a variety of such diversity estimators. The most effective estimators (e.g., Chao and ACE) are based on the premise that the number of species missed in a sample increases at the ratio: number of species represented by a single individual/number of species represented by two individuals (Colwell and Coddington 1994; Chazdon et al. 1998). ACE is an estimator that tallies species based on the area that each occupies in the sampled community (Chazdon et al. 1998). It is thus particularly suited to plants and colonial organisms like ants that have a spatial “footprint” (Kaspari 2000b).

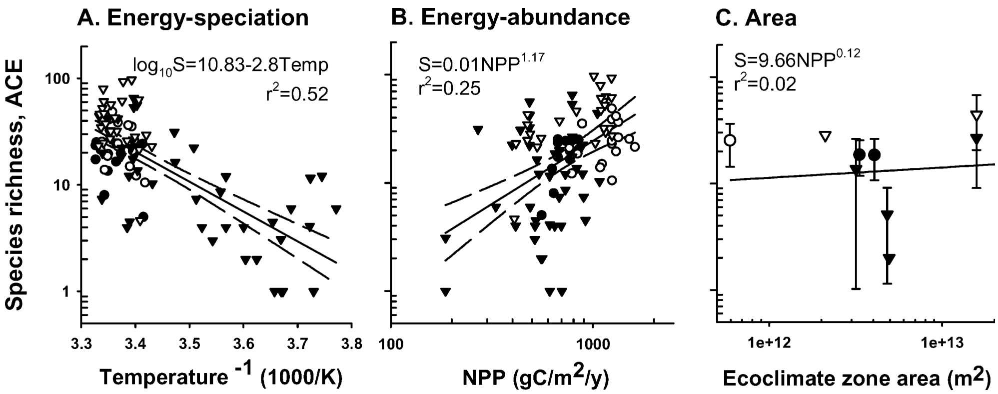


Fig. 1a–c Tests of three hypotheses—**a** Energy-speciation, **b** Energy-abundance, **c** Area for biogeographic gradients in diversity across 96 local litter ant communities. *Open circle* Madgascar (17 localities), *filled circle* Australia (12 localities), *open inverted triangle* South America (24 localities), *filled inverted triangle* North America (43 localities). Net primary productivity (*NPP*) and area, but not temperature, are $\log_{10}$-transformed to improve normality and equitably distribute values. *Lines* through scatterplots are fit by linear regressions. *Dashed lines* are 95% confidence bands; both extend beyond the *y*-axis in (**c**).

Independent variables were generated for each locality using GIS analysis (ArcView 1999). Sample localities were spatially overlain with data layers. Estimates were made through the bilinear spatial interpolation method (Richards 1993). Our three hypotheses required three independent variables. To test the energy-speciation hypothesis we regressed ln S on mean monthly temperature^{-1} (1,000/K to conform to Allen et al. 2002; Gillooly et al. 2002). Temperature was averaged from 1961 to 1990 at a 0.50°×0.50° resolution (IPPC 1988). To test the energy-abundance hypothesis, we regressed $\log_{10}S$ on $\log_{10}$ NPP (g C/m^2 per year) using output from CASA, a model that combines NDVI imagery and ecosystem and plant physiology submodels to generate productivity estimates at the 1°×1° scale (Field et al. 1995). To test the area hypothesis, $\log_{10}S$ was regressed on the $\log_{10}$ area of each ecoclimate zone in the tropics (26°S–26°N latitude), subtropical zone (26–36°), temperate zone (36–46°) and boreal zone (46–56°N) of the four provinces. Area was quantified with ArcINFO GIS. Log-transformation both improved normality and more evenly distributed values that spanned over 1 order of magnitude.

We compared the three models by first using least squares linear regression. We also used reduced-major-axis regression (Sokal and Rohlf 1981) to test Allen et al.'s (2002) prediction from the energy-speciation hypothesis. The hypotheses were then pitted against each other in a stepwise regression (P to enter<0.05, Draper and Smith 1981). As NPP and temperature were correlated (r_s=0.39, n=96, P<0.0001), we constructed a path analysis (Sokal and Rohlf 1981) to evaluate temperature's direct and indirect effect on S. Finally to explore how the temperature accounted for inter-province and latitudinal variation in S, we compared ANOVA and least square means regression results (respectively) on the original data and temperature–diversity residuals. If the pattern persisted in these residuals, then some other unaccounted for factor could reasonably be concluded to contribute to the pattern.

Results

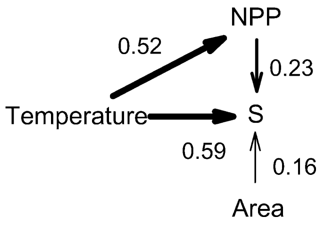
The number of ant species extracted from the litter of 96 forests varied from 1–75. With the ACE estimator, which calculates the predicted species richness of each site had sampling gone to completion, S varied from one (e.g., a hemlock ravine in Nova Scotia, Calif., USA) to 97 (an Ecuadorian rainforest). The raw data and the estimator were highly correlated (r_S=0.976, P<0.0001).

The three hypotheses differed in their ability to account for variation in S (Fig. 1). Localities varied in mean monthly temperature from −8.0°C in a deciduous forest in ON, Canada to 27.5°C in a rainforest in Queensland, Australia. Consistent with the energy-speciation hypothesis, linear regression shows that $\log_{10}S$ decreases with inverse temperature (1,000/K) and accounts for about half the variation in diversity ($F_{1,94}$=100.2, P<0.0001; Fig. 1). An analysis of covariance suggests that the slope fails to vary across the four provinces (Type III interaction between province and temperature: $F_{3,88}$=0.11,P=0.96). If the scatterplot is analyzed with reduced major axis regression (as directed by Allen et al. 2002), the resulting equation [ln$S$=33.62–8.98×(1,000/K)] has a slope close to that predicted by Allen et al., i.e., −9.0 (SE=0.28).

Estimates of NPP varied from 187 g C/m^2 per year in a Nevada pine forest to 1,611 g C/m^2 per year in a Madagascar rainforest. Consistent with the energy-abundance hypothesis, S increased with productivity and accounted for a quarter of the variance (Fig. 1, $F_{1,94}$=31.1, P<0.0001). In an analysis of covariance the slope failed to vary across the four provinces (Type III interaction between province and NPP: $F_{3,88}$=0.36, P=0.79). The exponent of 1.17 (SE=0.21) failed to deviate from unity ($F_{1,94}$=0.63, P=0.49) suggesting a linear relationship.

Localities were embedded in ecoclimate zones that ranged in area from 5.9E^{11} m for tropical Madagascar to 1.58E^{13} m for tropical America (Fig. 2). However, the linear regression of $\log_{10}S$ on $\log_{10}$ area was not significant ($F_{1,95}$=1.87, P=0.18; Fig. 1). This result is not altered if we treat each ecoclimate zone as a single sample and localities within each zone as subsamples (n=7, r^2=0.03, P<0.50).

Fig. 2 Path analysis highlights the relative strength of three independent variables temperature, area, and NPP, on patterns of local ant species richness (S). Thickness of the *arrow* is proportional to the magnitude of the effect



As the three hypotheses were not mutually exclusive we performed a stepwise regression with the three independent variables to predict $\log_{10}S$. All three variables entered the model but accounted for widely differing amounts of variation. Temperature entered first ($P<0.0001$), $\log_{10}$(NPP) second ($P<0.04$) and $\log_{10}$(Area) third ($P<0.03$), accounting for 52, 2, and 2% of the variation, respectively. As temperature limits NPP, we also performed a path analysis to separate the direct effects of temperature (as predicted by the energy-speciation hypothesis) from the temperature's indirect effect via NPP in the energy-abundance hypothesis (Fig. 2). The indirect effect of temperature via NPP ($0.52\times0.23=0.12$), was approximately one-fifth the strength of the direct effect of temperature on S, with temperature having an overall path coefficient of 0.72.

Mechanistic models and biogeographic patterns of diversity

Our results suggest that temperature is a driving variable generating biogeographic patterns of local ant diversity. If so, classic biodiversity patterns like the latitudinal gradient should disappear once the temperature effect is accounted for. Local litter ant diversity showed a latitudinal gradient (Fig. 3). A polynomial stepwise regression yielded a linear equation ($S=45-0.95\times$latitude, $r^2=0.34$, $F_{1,94}=48.3$, $P<0.0001$). However, the latitudinal gradient disappeared in the temperature-diversity residuals (S residuals: $r^2=0.03$, $F_{1,94}=3.03$, $P=0.09$).

An ANOVA also revealed significant heterogeneity among provinces in litter ant S ($F_{3,92}=13.01$, $P<0.0001$, Fig. 3). A Tukey's post-hoc test suggests that South American and Madagascar litter ant assemblages were more diverse than those of North America. These differences persisted even when the long tail of North American samples (which represented our coolest localities) was removed ($F_{3,69}=5.21$, $P<0.0026$). In contrast to the latitudinal gradient, inter-province differences persisted in the residuals left behind after temperature effects were removed ($F_{3,92}=4.15$, $P<0.0083$). The nature of these differences, revealed by Tukey's post-hoc tests, differed subtly from the raw data: once temperature effects were removed, South American communities were more diverse than communities from both North America and Australia.

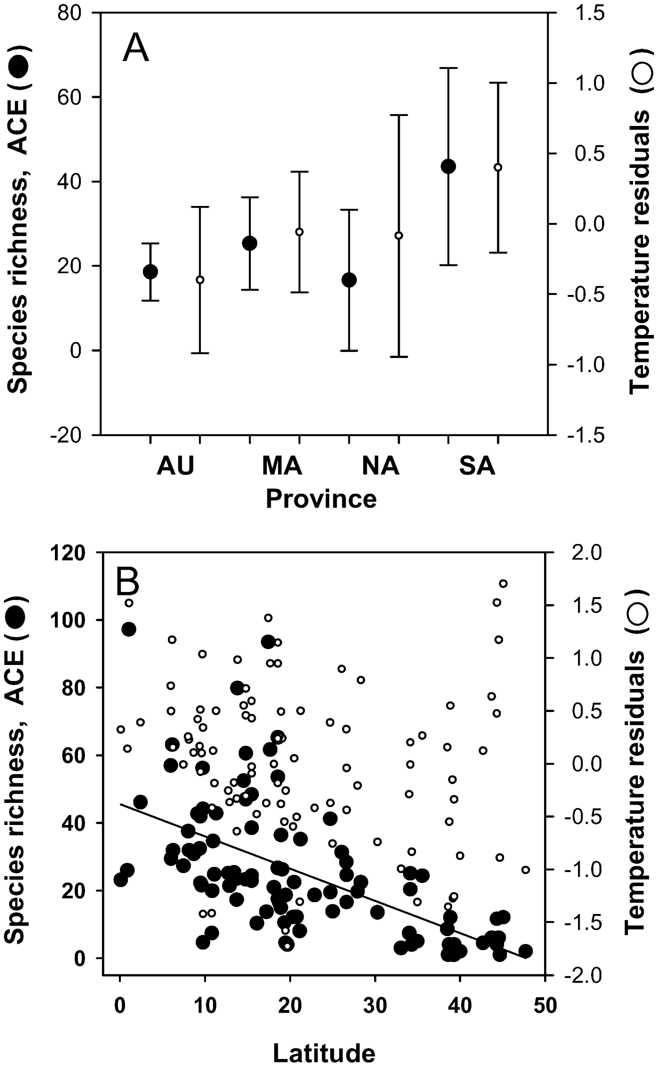


Fig. 3 Two geographic patterns of biological diversity, inter-province differences (**a**) and the latitudinal gradient (**b**). *Dark circles* give species richness, whereas *open circles* are residuals from the regression of species richness on latitude. *Error bars* are SDs, *lines* represent least square regression through the original data. *AU* Australia, *MA* Madagascar, *NA* North America, *SA* South America

Discussion

Our key finding is that the energy-speciation hypothesis is effective at predicting local litter ant diversity at a global extent since: (1) temperature accounts for half the variation in diversity, and (2) the slope of the temperature-diversity relationship deviated from the predicted value of −9.0 by 0.02. The hypothesis that S is ultimately limited by speciation rates, which are in turn driven by temperature-sensitive changes in taxa generation time and mutation rate, was first forcefully argued by Rohde (1992). The energy-speciation model has since been given added power via a common mechanism for these changes: cellular metabolic kinetics (Allen et al. 2002; Gillooly et al. 2002; Gillooly et al., in review). Our study is the first to independently test one of its key predictions: the slope of the temperature-S curve, which failed to differ over four biogeographic provinces.

Evidence continues to accrue for the role that a high net diversification rate (Cardillo 1999; Buzas 2002) plays in generating the temperature-S relationship (Currie 1991; Roy et al. 1998; Kaspari et al. 2003). Diversification rates can be decomposed into rates of speciation and extinction. While energy gradients can drive both processes, our data suggest that the energy-abundance hypothesis—which posits that NPP limits abundance and hence regulates extinction rates—plays a secondary role shaping global patterns of litter ant diversity. Although we did not measure colony abundance, NPP accounted for a much smaller fraction of the variation in diversity using both stepwise regression and path analysis. An earlier study of 15 soil ant communities that highlighted the link between abundance and diversity (Kaspari et al. 2000a) included deserts that were almost 100-fold more depauperate in NPP than our least productive site. It is thus likely that the energy-abundance hypothesis plays a larger role across all ant communities compared to the woodland and forest assemblages studied here (Kaspari et al. 2003).

Likewise, the size of the ecoclimate zone was of secondary importance in predicting the litter ant diversity from four biogeographic provinces. Relatively small provinces, like Madagascar, had higher diversities than zones in North America that were 10 times larger (Fig. 1c).

These data suggest the following working hypothesis. For ants, the warmer environments and higher predation rates of the tropics (Jeanne 1979; Kaspari and O'Donnell 2003) promote smaller colony mass (Cushman et al. 1993; Kaspari and Vargo 1995; Kaspari and Weiser, unpublished data), more generations/year (Kaspari et al. 2001), and higher abundance (Kaspari et al. 2000a). Warmer temperatures lead to higher mutation rates (Rohde 1992; Gillooly et al., in review), which, combined with shorter generation times, allow for higher rates of speciation. The increased abundance fostered by higher NPP and smaller body size plays a secondary role in reducing local extinction rates (Levinton 1979; Pimm et al. 1988).

This working hypothesis comes with provisos. First, a key assumption of Allen et al. (2002) is that, the average flux of energy/area for each population is roughly invariant (as metabolic rate and abundance scale with size to the 3/4 and −3/4 respectively, Damuth 1981). This "energy equivalence rule" is not true for all taxa (see Russo et al. 2003 and references within) and has yet to be tested for ants. Furthermore, there is little evidence at present for a latitudinal gradient in molecular evolution (at least among birds, Bromham and Cardillo 2003). Finally, the assumption that mutation and recombination rates limit speciation rates has yet to be verified, although there is a positive relationship between rates of neutral gene evolution and species diversity in some plant taxa (Barraclough and Savolainen 2001).

It is encouraging that two sampling protocols—this one aimed at collecting the maximum number of species in the minimum time (Longino and Colwell 1997; Ward 2000) and another (Kaspari et al. 2003) aimed at quantifying colony abundance over a wider range of habitats—yield qualitatively similar results. Kaspari et al.'s study of 49 New World sites found that temperature, area, and abundance accounted for 75% of the variance in ant species diversity. The decreased variation accounted for in this study may result, in part, from the mismatch of local diversity to more regional (e.g., latitude×longitude grid scale) measures of temperature and NPP. Furthermore, other hypotheses acting at geographic scales were not tested. For example, the mid-domain effect (Lees et al. 1999; Colwell and Lees 2000), which argues that diversity gradients arise from the random array of species ranges within a continent, was not evaluated due to the lack of range size information for ants and the non-uniform distribution of our samples across the four provinces.

Ecologists have long been fascinated by community convergence—the degree to which similar patterns of community structure arise on different continents (Gleason 1926; Elton 1927; Clements 1936; Elton 1958; Davis 1976; Orians and Pearson 1983; Pianka 1986). Early studies of convergence (Orians and Pearson 1983; Schluter 1986) often focused on comparing diversity and morphology in "matched habitats" from different provinces. We suggest that a more powerful measure of community convergence is the extent to which assemblages of taxa from different provinces respond to the same quantitative gradients. For example, Pianka's (1986) studies of desert lizard assemblages on three continents show qualitatively different diversity-rainfall relationships (low convergence). This study shows that global patterns of solar radiation drive about half the variation in local ant diversity—including the latitudinal gradient—in a similar fashion across four provinces. However, convergence is not absolute—provinces retain different average diversities even after this temperature-diversity relationship is removed. Why do South America litter ant communities still retain more species on average than those from North America and Australia? Perhaps this is where abundance and area effects play their modifying role—the South American ecoclimate zones we sampled are larger than those from Australia and more productive than those from North America.

In conclusion, we feel the energy-speciation hypothesis gains support based on its prediction of the diversity-temperature slope and the variance accounted for by this relationship across 96 litter ant communities (see also Kaspari et al. 2003). If it is a predominant factor shaping global diversity gradients it should apply for a variety of other ectotherm taxa as it does for gastropods, fish, and amphibians (Allen et al. 2002). Furthermore, the theory is rich in testable assumptions, most importantly that mutation and recombination rates: (1) limit speciation rates, and (2) are themselves limited by temperature.

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