IDEAS AND PERSPECTIVES

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

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Abstract

Broad-scale variation in taxonomic richness is strongly correlated with climate. Many mechanisms have been hypothesized to explain these patterns; however, testable predictions that would distinguish among them have rarely been derived. Here, we examine several prominent hypotheses for climate–richness relationships, deriving and testing predictions based on their hypothesized mechanisms. The 'energy–richness hypothesis' (also called the 'more individuals hypothesis') postulates that more productive areas have more individuals and therefore more species. More productive areas do often have more species, but extant data are not consistent with the expected causal relationship from energy to numbers of individuals to numbers of species. We reject the energy–richness hypothesis in its standard form and consider some proposed modifications. The 'physiological tolerance hypothesis' postulates that richness varies according to the tolerances of individual species for different sets of climatic conditions. This hypothesis predicts that more combinations of physiological parameters can survive under warm and wet than cold or dry conditions. Data are qualitatively consistent with this prediction, but are inconsistent with the prediction that species should fill climatically suitable areas. Finally, the 'speciation rate hypothesis' postulates that speciation rates should vary with climate, due either to faster evolutionary rates or stronger biotic interactions increasing the opportunity for evolutionary diversification in some regions. The biotic interactions mechanism also has the potential to amplify shallower, underlying gradients in richness. Tests of speciation rate hypotheses are few (to date), and their results are mixed.

Keywords

Climatic gradients, latitudinal gradients, productivity, speciation, species richness, species-energy theory.

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INTRODUCTION

One of the strongest patterns in ecology is the statistical relationship between broad-scale variation in taxonomic richness and climate. The numbers of species, genera or families in broad functional or taxonomic groups (class level or higher) that occur in quadrats spread over large areas (continental to global) show strong geographical patterns (see, for example, global maps of angiosperm richness: Francis & Currie 2003, or bird richness: Hawkins *et al.* 2003b). These geographical patterns typically covary with temperature and/or water availability (or related variables) with coefficients of determination between 70 and 90% (Wright *et al.* 1993; Hawkins *et al.* 2003a). Richness–climate relationships have been documented for terrestrial plants (Currie & Paquin 1987; O'Brien 1993), terrestrial vertebrates (Turner *et al.* 1988; Currie 1991), insects (Turner *et al.* 1987; Kerr *et al.* 1998), aquatic invertebrates (Patalas 1990), freshwater fish (Guégan *et al.* 1998), human pathogens (Guernier *et al.* 2004), corals (Fraser & Currie 1996) and other taxa. Moreover, richness–climate relationships in different parts of the globe are generally similar to one another (Adams & Woodward 1989; Francis & Currie 2003; Hawkins *et al.* 2003b), suggesting consistent underlying mechanisms.

Many mechanisms have been hypothesized to account for broad-scale patterns in taxonomic richness (reviewed by Huston 1994; Rosenzweig 1995; Willig *et al.* 2003). These hypotheses all predict (and derive apparent support from) geographical variation in richness. However, few efforts have been made to reduce the list of hypotheses by deriving additional predictions, and using the predictions that differ among hypotheses to test them. Although observed richness–climate relationships may result from multiple mechanisms, the first step is to test the predictions of individual hypotheses. The ways in which simple hypotheses fail (if they do so) informs development of later, more complex, hypotheses.

The present paper addresses three prominent climate-based hypotheses for broad-scale richness patterns: the 'energy–richness hypothesis' (a.k.a. species-energy hypothesis; the more individuals hypothesis, Srivastava & Lawton 1998), the 'physiological tolerance hypothesis', and the 'speciation rates hypothesis'. We develop each hypothesis in a mechanistic form, we derive as many predictions as possible from each one, and we assess agreement with extant evidence.

This study focuses specifically on mechanisms to explain geographical covariation of climate and taxonomic richness. This work is not intended as a comprehensive review of hypotheses about broad-scale richness patterns. We do not consider non-climatic mechanisms (e.g. disturbance, habitat heterogeneity, history). Nor do we address hypotheses intended primarily to explain high tropical richness: e.g. the mid-domain hypothesis (the tropics are diverse because they are in the middle; Colwell & Lees 2000) or the area hypothesis (the tropics are diverse because they are big; Rosenzweig 1992). It is possible that these factors contribute to latitudinal gradients of richness. However, our concern here is with geographical variation in taxonomic richness in general, including patterns more complex than the latitudinal gradient (e.g. Francis & Currie 2003; Hawkins *et al.* 2003a). Hypotheses such as mid-domain and area are not intended to explain these more complex geographical patterns.

METHODS

We began by elaborating the mechanism underlying each of the three hypotheses given above, and we then derived predictions from these mechanisms (e.g. expected relationships between productivity and numbers of individuals, predicted geographical variation in speciation rates, correlations among other variables, etc.). We derived as many predictions as possible for each hypothesis in order to perform multiple tests of each one.

Predictions were compared with published results whenever we could locate studies that analysed relationships predicted by one of our hypotheses. The number of relevant published studies was too limited to warrant a formal meta-analysis.

We also analysed three broad-scale data sets to test predictions dealing with geographical variation in productivity, abundance of individuals and species richness. The first set, the North American Breeding Bird Survey (BBS), censuses bird abundance along *c.* 3000 routes in the US and Canada (Sauer *et al.* 2004). On each route, 3-min point counts are carried out at 50 stops along a 40 km route. The second set, gathered by Alwyn Gentry (Phillips & Miller 2002), censused trees in 220 plots (0.1 ha) on several continents, but concentrated in the neotropics. The third data set, the fourth of July butterfly count, is a 1-day count of all butterflies seen in 25-km diameter circles at 514 sites across North America (Kocher & Williams 2000). These three data sets each include numbers of individuals and of species at sites over broad geographical areas. Sampling was non-random: e.g. Gentry chose sites of regional interest; BBS routes follow secondary roads, etc. In each case, we used annual actual evapotranspiration as a surrogate for primary productivity (Rosenzweig 1968; Lieth 1975).

Trends in the data were shown using locally weighted sums of squares plots (LOWESS), and standard, non-spatial correlations and regressions. There is spatial autocorrelation in these data sets; however, we are interested in broad patterns of richness variation that are related to spatially structured climatic variables. It was therefore preferable not to use techniques that mask those

variations (Diniz-Filho *et al.* 2002). Because sample sizes were very large, the relationships reported below remain significant if even small portions of the observations are statistically independent. All analyses were done using SYSTAT v. 10.

H$_1$: ENERGY–RICHNESS HYPOTHESIS

Hypothesis: *Species richness varies as a function of the total number of individuals in an area. Net primary productivity (NPP) limits the number of individuals, and climate strongly affects NPP. If the fraction of total NPP secured by broad taxonomic groups (e.g. birds) varies little with NPP, then there will be more species in a given taxonomic group in areas of higher productivity (Hutchinson 1959; Brown 1981; Wright 1983).*

It has often been hypothesized that, in reasonably large aggregations of individuals of many species, the total number of species varies as a function of the total number of individuals. Fisher *et al.* (1943) observed that the number of individuals per species in large samples of lepidoptera followed a negative binomial frequency distribution. Based on this distribution, they proposed that the total number of species S in a sample depends upon the number of individuals I, and a fitted, empirical constant α (the 'index of diversity'):

$$S \cong \alpha \ln\left(1 + \frac{I}{\alpha}\right) \qquad (1)$$

Fisher *et al.* noted that α varied both seasonally and geographically. More recently, Hubbell (1997, 2001) proposed a mechanistic model that leads to the exactly the same predicted relationship between S and I. In Hubbell's model, θ, which is mathematically equivalent to Fisher's α, is equal to the number of individuals in the metacommunity from which the sample is drawn, times twice the per capita speciation rate. Hubbell (2001, chap. 5) notes that the components of θ are unobservable in practice.

Many other models have been proposed relating species richness and distribution of individuals among species (reviewed by Chave 2003). Among the most influential is Preston's (1948, 1962) 'canonical log-normal' frequency distribution. Based on this distribution, Preston noted that, in assemblages with 100–1000 species, the number of species varies as a function of the number of individuals and m, the minimum number of individuals required for a species to persist.

$$\log S = 0.262 \log(I/m) + 0.317 \qquad (2)$$

Preston discussed m only briefly, noting that it must be at least two in a sexually reproducing population, although perhaps much higher. Like Hubbell's θ, estimates of m are difficult, and it is not obvious that it shows clear geographical variation (Reed *et al.* 2003).

These models all postulate a relationship between species richness and the total number of individuals. The familiar species richness–area relationship (e.g. MacArthur & Wilson 1967) is a corollary of this postulate. If the number of individuals per unit area ρ (density of individuals) remains approximately constant (e.g. on a set of neighbouring islands), then larger areas contain more individuals:

$$I = A \cdot \rho \qquad (3)$$

(where A is area) and therefore more species (Preston 1962). Moreover, as Hutchinson (1959) proposed, if the density of individuals varies as a function of primary productivity (ε), then richness should covary with climate. Broad-scale variation in primary productivity correlates strongly with climate (water, temperature, potential evapotranspiration or a combination of them such as actual evapotranspiration: Rosenzweig 1968; Lieth 1975). Metabolic costs that affect net productivity also covary with the same variables (e.g. Kleidon & Mooney 2000; Allen *et al.* 2002). It follows that richness in a given region should covary with both area and primary productivity per unit area:

$$\log(S) \propto \log(I) \propto \log(A \cdot \rho) \propto \log(A \cdot \varepsilon) \qquad (4)$$

Based on this logic, Wright (1983) showed that the variation in bird and angiosperm species richness among a global set of islands covaries strongly with total primary productivity per island (estimated from actual evapotranspiration, AET). This has come to be called 'species-energy theory'.

Predictions (P) and evidence (E)

If $\log(S) = f(I)$ and if $\log(\rho) = g(\varepsilon)$, then in equal area quadrats:

P$_{1,1}$: Density ρ and productivity ε must covary through space over broad spatial scales: density of individuals should be greatest in warm, wet places.

E$_{1,1}$: Evidence on this prediction is limited and contradictory. In Gentry's tree plots, the density of individuals is weakly positively related to AET (Spearman $r_s = 0.35$, $n = 191$, $P \leq 10^{-5}$: Fig. 1a). However, the number of individual trees per unit area shows no systematic variation through most of the tropics, and there are few points in the Southern Hemisphere outside the tropics (Fig. 1b). Enquist & Niklas (2001) noted similar relationships between abundance and latitude in the same data set.

In the North American breeding bird data, total abundance of birds observed also increases weakly with AET (Fig. 2a, $r_s = 0.35$, $n = 2948$, $P < 10^{-5}$) and seems to flatten out in the subtropics (Fig. 2b). Using the fourth of July butterfly data, Kocher & Williams (2000) found that the density of
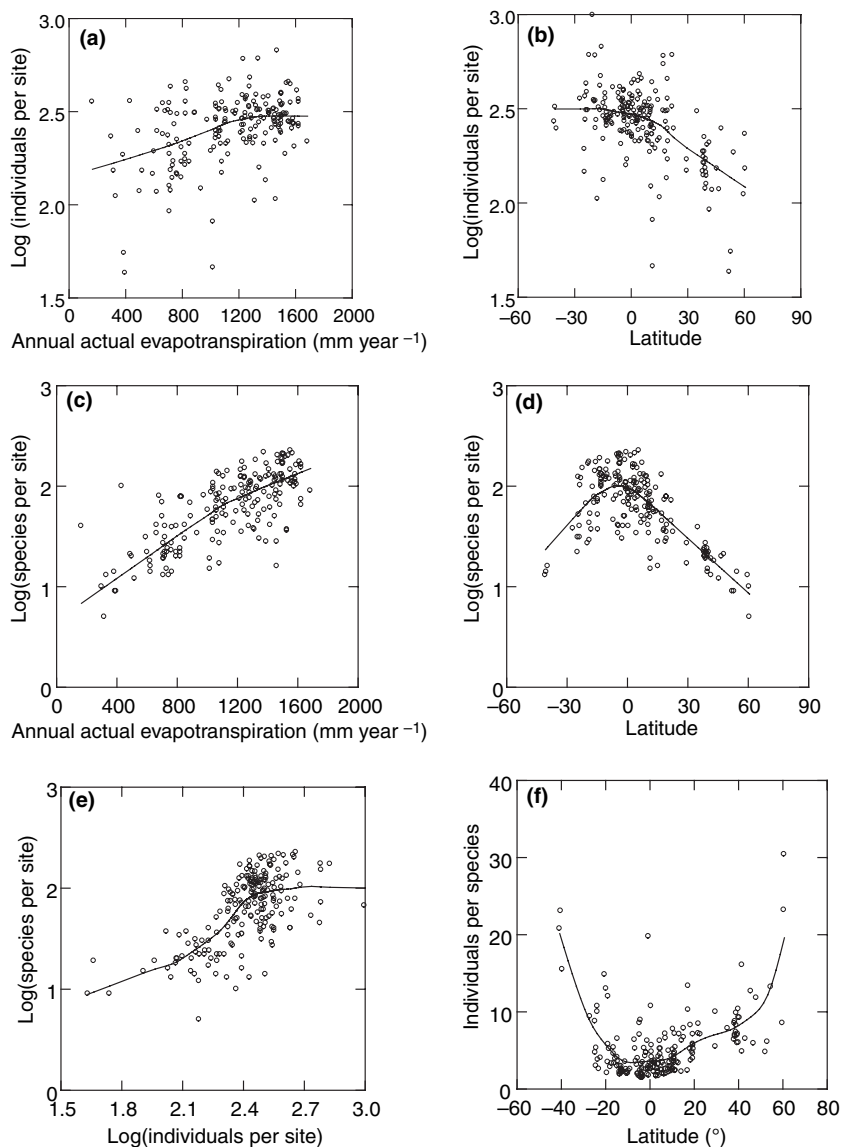
Figure 1 Using Gentry's counts of individual trees in 0.1 ha plots (Phillips & Miller 2002), the relationships among the number of individuals per site, the number of species, the number of individuals per species, latitude and annual actual evapotranspiration (AET). Lines are LOWESS trend lines, tension = 0.8.

individuals was unrelated to climatic variables, while species richness was strongly correlated with temperature and elevation. Thus, extant relationships between geographical variation in the density of individuals and productivity over broad spatial scales are weak and do not strongly support $P_{1,1}$.

$P_{1,2}$: Species richness S and the density of individuals ρ in equal areas must covary through space. Expected relationships, based on Fisher *et al.* (1943) and Preston (1948, 1962), are shown in Fig. 3. The predicted log–log slope from Preston (from eqn 1) is 0.26: a 6600-fold difference in abundance would yield a 10-fold difference in richness (eqn 1). The slope of Fisher's relationship depends upon abundance, but it is close to Preston's.

$E_{1,2}$: In Gentry's tree data, species per plot increases approximately in proportion to the number of individuals per plot (log I), but with a log–log slope much higher than predicted: 1.19 ± 0.21 (mean ± 95% confidence interval; $r^2 = 0.41$, $n = 199$, $P < 10^{-5}$; Fig. 1e). The slope of a regional species–individuals relationship would probably be even steeper. Species per 0.1 ha plot almost certainly underestimates regional species richness to an increasing extant as richness increases. For example, in Mt St-Hilaire, Québec, five of 12 species (41%) in Gentry's sample were represented by a single individual, whereas in Rio Manso, Columbia, 164 of 221 species (74%) were singletons. Therefore, the slope of regional richness as a function of the density of individuals is probably greater than Fig. 1e suggests. In other words, species accumulate more quickly than the increase in individuals would predict, given either Fisher's or Preston's relationships.
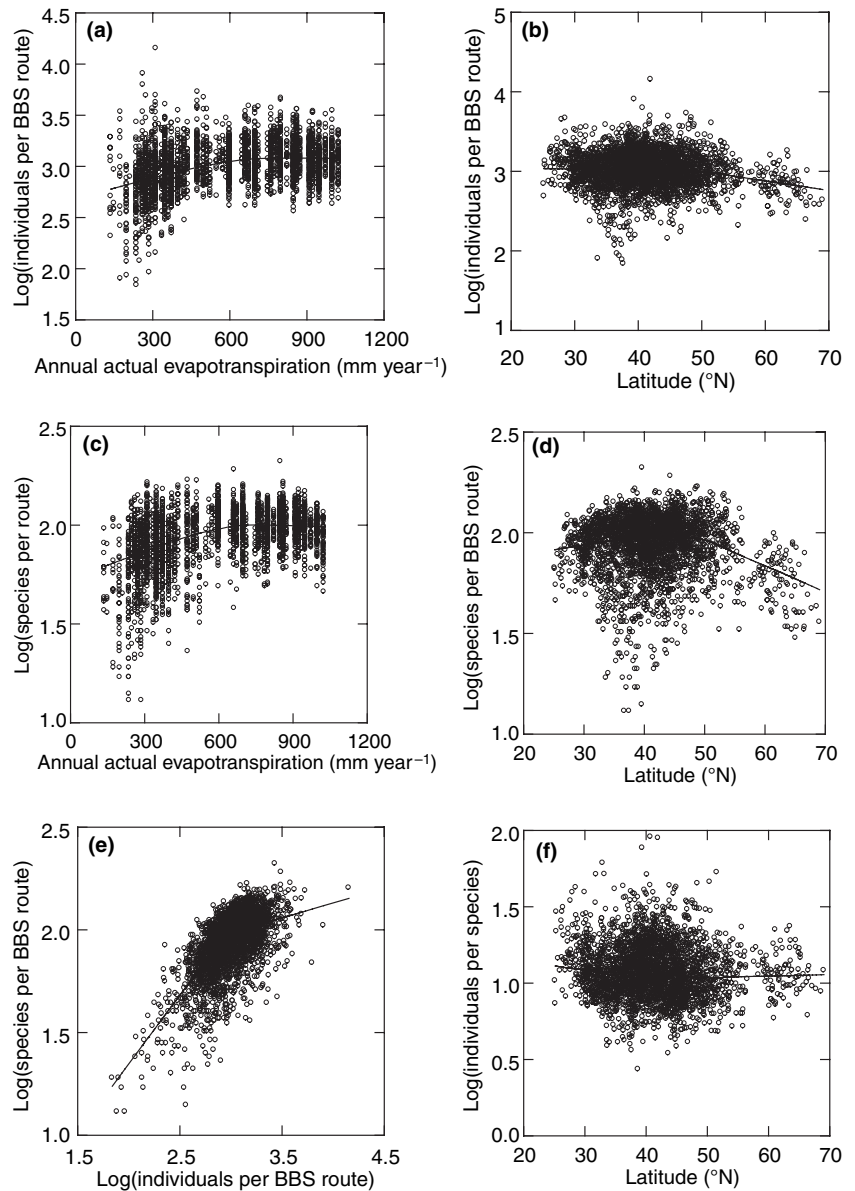
Figure 2 Using the North American Breeding Bird Survey (BBS) data for the year 2000, the relationships among number of individuals per BBS route, the number of species per route, the number of individuals per species, latitude and annual actual evapotranspiration. Lines are LOWESS trend lines, tension = 0.8.

In the Breeding Bird Survey data, log S per route is a positive decelerating function of log I ($r^2 = 0.44, n = 2948$, $P < 10^{-5}$; Fig. 2e) the slope of which decreases from 0.65 to 0.15 over the observed range of the data. Again, over most of the range of the data, species accumulate too quickly, compared with individuals, and (as in the case of Gentry's trees), regional richness is probably most dramatically underestimated at the high end of the relationship. Hurlburt (2004) recently examined the Breeding Bird Survey data within forest and grassland habitats, and found that log(S) increased with log(I) with a slope of 0.18 for forests and 0.33 for grasslands.

In the butterfly counts, Kocher & Williams's (2000) show a peaked richness–abundance relationship with a long right tail (their Fig. 8). Thus, butterfly richness is a negative

function of numbers of individuals over most of the range of the data. Underestimation of richness in high richness areas would accentuate this pattern.

Compiling data on the number of parasite species per host in tropical cichlid fish, Guégan (unpublished data) found that parasite species richness per fish increases as a function of the number of individual parasites, with a log–log slope close to the predicted slope [0.35 ± 0.13 (95% CI), $r^2 = 0.64$, $n = 20$, $P < 10^{-4}$; Fig. 3]. If fish are analogous to regions with respect to parasites, then this evidence is consistent with the prediction.

In sum, numbers of species and numbers of individuals covary in three of four data sets we investigated. The increase in richness as a function of the number of individuals is similar
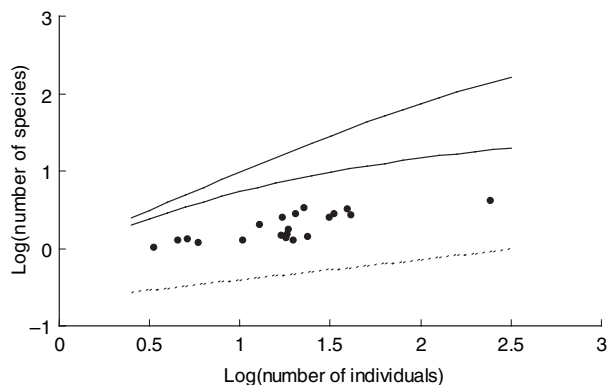
Figure 3 Relationships between the total number of species in an assemblage and the total number of individuals. (- - -) Preston's (1962) theoretical relationship, given the median minimum sizes of vertebrate populations studied by Reed *et al.* (2003). (——) The theoretical relationships of Fisher *et al.* (1943; and therefore Hubbell 2001) based on their highest and lowest observed α values in lepidopteran populations from England to Malaya. (•) The observed relationship between the number of individual parasites and the number of species of parasites observed in individual fish (J.-F. Guégan, unpublished data). All axes are $\log_{10}$ transformed. The slope of the trend in Guégan's data is at least qualitatively consistent with an increase in richness as a function of increasing numbers of individuals.

to Preston's and Fisher's predictions for parasites (Guégan's data) and for Hurlbert's (2004) analysis of breeding birds within habitat types. However, in most cases, rare species increase disproportionately with increases in the number of individuals (i.e. the species–individuals relationship is not constant, but instead varies between regions).

$P_{1,3}$: Richness and energy must also covary (eqn 6). The increase in species richness towards the tropics is the pattern that the energy–richness hypothesis was proposed to explain in the first place.

$E_{1,3}$: As summarized in the Introduction, most studies of broad-scale richness variation have shown strong positive correlations with climate. Earlier conflicting studies (e.g. Schall & Pianka 1978; Kerr & Packer 1997) usually did not consider both temperature and water. Residual regional differences in richness are generally small (Francis & Currie 2003; Hawkins *et al.* 2003a; but cf. Oberdorff *et al.* 1997; Kerr *et al.* 2001). The relationships in the Gentry ($r_s = 0.70$, $n = 191$, $P \leq 10^{-5}$, Fig. 1c) and BBS ($r_s = 0.41$, $n = 2937$, $P < 10^{-5}$, Fig. 2c) data sets are also consistent with $P_{1,3}$.

$P_{1,4}$: Because the causal pathway is from $\varepsilon \rightarrow I \rightarrow S$, and because other variables can potentially introduce unrelated variance in either of the links, the proximal $\varepsilon - I$ and the $I - S$ correlations must be stronger than the distal $\varepsilon - S$ correlation (see Shipley 2000 regarding the reasoning).

$E_{1,4}$: In general, published $\varepsilon - S$ correlations over broad spatial scales are strong (e.g. Adams & Woodward 1989;

Currie 1991; Wright *et al.* 1993; Francis & Currie 2003; Hawkins *et al.* 2003a), whereas $\varepsilon - I$ correlation are substantially weaker (Currie & Fritz 1993). This is also true in Gentry's tree data (Spearman $r_s = 0.70$ vs. 0.35, $n = 191$). In the BBS data, the correlation $\varepsilon - S$ is marginally stronger than the $\varepsilon - I$ correlations (Spearman $r_s = 0.40$ vs. 0.35, $n = 2948$). The evidence is inconsistent with $P_{1,4}$.

$P_{1,5}$: If ε, I and S are causally linked, then a change in primary productivity through time must lead to a proportional change in the two others (given sufficient time). For example, when climate changes, changes in the abundance of individuals and in the number of species consistent with contemporary climate–richness relationships must occur.

$E_{1,5}$: Testing $P_{1,5}$ would require a study of species richness when climate is changing. Climatic variables that influence primary productivity (e.g. temperature) change seasonally, and butterfly and bird richness follow these changes in the predicted directions (Turner *et al.* 1987, 1988). More recent work comparing bird species richness to a remotely sensed measure of productivity (NDVI, normalized difference vegetation index) also shows positive relationships between seasonal productivity and seasonal bird species richness (H.-Acevedo & Currie 2003; Hurlbert & Haskell 2003). Existing evidence on seasonal climate changes is thus consistent with $P_{1,5}$. To show that richness tracks climate change over geological time would be more convincing, but few such data appear to exist.

$P_{1,6}$: The average number of individuals per species must increase with energy. This follows from both Fisher's (eqn 1) and Preston's (eqn 2) models.

$E_{1,6}$: Except for some very rare species and host–parasite systems, there are few data on the total number of individuals of a species. However, as a first approximation, the total number of individuals per species equals population density (individuals/area) times range size (area).

Population densities are generally smaller in the tropics than at high latitudes. Currie & Fritz (1993) show this for several animal groups and also report density decreases with increasing potential evapotranspiration. Johnson (1998) observed similar patterns in Australian mammals. In Gentry's data, average per species abundances reach a minimum near the equator (Fig. 2f), as noted by Niklas *et al.* (2003).

Rapoport's rule (Stevens 1989) states that species ranges are generally smaller in the tropics (but see Rohde *et al.* 1993; Gaston *et al.* 1998 regarding exceptions). Together, these observations suggest that populations are smaller on average in the tropics, not larger. The evidence is inconsistent with $P_{1,6}$.

$P_{1,7}$: If richness varies as consequence of varying numbers of individuals, then new species can be introduced into an assemblage only if an equal number of existing species drop out, unless the total number of individuals

changes (eqns 1 and 2). $P_{1,7}$ is not strong for operational reasons: if extinctions are not observed, there are many alternative explanations (e.g. insufficient elapsed time).

$E_{1,7}$: Sax *et al.* (2002) found that the number of invasive bird species on oceanic islands was approximately equal to the number of extirpated species. In contrast, plant species richness has approximately doubled on islands as a result of invasions. There are many other examples demonstrating that species introductions may occur without concomitant losses in native species richness (e.g. Stohlgren *et al.* 1999, 2003). Because introductions of new species do not necessarily lead to loss of a similar number of native species, the evidence is inconsistent with $P_{1,7}$.

Summary for H_1

Extant evidence is largely inconsistent with the mechanism proposed for the energy–richness hypothesis by Hutchinson and elaborated by Brown (1981) and Wright (1983). Increased richness over broad spatial scales is not necessarily related to increased abundance, which in turn is not necessarily related to increased productivity. Most importantly, observed changes in the density of individuals with latitude or productivity are either too small, or in the wrong direction, to account for the observed changes in species richness. Thus, we reject the species–energy hypothesis as described here.

Possible modifications of the energy–richness hypothesis

Preston's model suggests that geographical variation in *m*, minimum viable population size could give rise to geographical patterns of richness. Equation 2 predicts a 10-fold increase in richness from a 6600-fold decrease in *m*. In vertebrate populations, Reed *et al.* (2003) did not observe any systematic latitudinal variation in *m*. It seems unlikely that variation in *m* would be sufficient to account for several orders of magnitude variation in species richness, but this remains to be tested more rigorously.

Hubbell's (2001, chap. 5) model suggests that geographical variation in metapopulation size or speciation rate could give rise to geographical gradients of richness. Following eqn 1, species richness is predicted to be far more sensitive to Fisher's α (Hubbell's θ, two times the product of the size of the meta-community and the speciation rate) than it is to the number of individuals present locally (Fig. 4). We explore the speciation rate hypothesis below.

The original version of the energy–richness hypothesis assumes that energy is partitioned among individuals that all use equal amounts of energy (or at least that mean energy use per individual does not vary systematically across geographical gradients). Because energy use scales as a function of body mass (Peters 1983), geographical variation in body mass
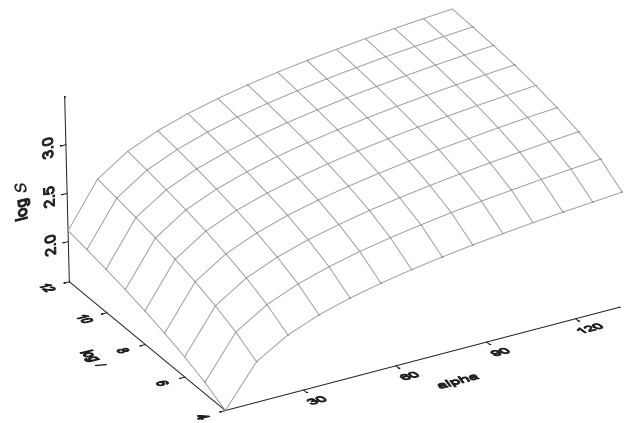

Figure 4 The predicted relationship between species richness (*S*), the number of individuals (*I*) and Fisher's (1943) α. Although this is an empirical constant in Fisher's work, it is identical to Hubbell's (1997, 2001) θ, which he defines as the number of individuals in the metacommunity times twice the per capita speciation rate. This model predicts that richness is far more sensitive to α (or θ) than to the number of individuals in the assemblage in question.

could alter the relationship between number of individuals and energy. Based on animal abundance and body size data gleaned from the literature, Currie & Fritz (1993) compared the geographical variation of species richness, individual body size and total energy use. They concluded that total energy use of all populations is nearly independent of latitude. Using Gentry's tree data, Enquist & Niklas (2001) argued that total community energy use is independent of plant size, and that total biomass is independent of latitude. Thus, variation in energy use per individual is unlikely to account for gradients of species richness.

Allen *et al.* (2002) propose that broad-scale geographical gradients of richness are the result of the temperature dependence of enzyme kinetics. Venevsky & Veneskaia (2003) develop similar predictions of patterns of vegetation diversity based upon latent heat of evaporation. Mechanistic approaches such as these hold promise for improved understanding of patterns of diversity, although at present the agreement between observed richness and theoretically predicted richness is not very different from purely empirical models.

H_2: TOLERANCE

Hypothesis: *Richness in a particular area is limited by the number of species that can tolerate the local conditions.*

Richness and climate may covary simply because fewer species can physiologically tolerate conditions in some places (cold and/or dry) than others (warm and wet). Many major taxa arose principally in the humid tropics (e.g. angiosperms in south-east Asia; Latham & Ricklefs 1993)

and progressively more adaptations were presumably required to occupy other habitats.

$P_{2,1}$: As measures of temperature and/or water account for the bulk of broad-scale richness variation (Hawkins *et al.* 2003a), the same variables, or factors strongly collinear with them, must be the main limits on species' geographic ranges.

$E_{2,1}$: Clearly, at least some aspects of species' ranges respond to climate. Root (1988) found that the northern winter boundaries of 62 North American bird species were closely associated with a particular isotherm; however, the distributions of 191 other species she examined were not related to climate. Examining published studies of the ranges of > 1046 species or functional groups, Parmesan & Yohe (2003) found that 51% had shifted in accord with climate change predictions. The other half either had stable distributions, or showed changes unrelated to climate. Similarly Parmesan *et al.* (1999) found that 22% of 36 species of butterflies shifted ranges in the direction predicted by climate change. Over longer time scales, plant species' ranges shifted dramatically, mainly northward, since the last glacial retreat; however, assemblage composition did not remain constant with respect to climate (Davis 1981; Huntley & Birks 1983), even in small organisms that are unlikely to be dispersal-limited (e.g. Bennett *et al.* 2001). These results indicate that, while climatic variables can influence species' ranges, other factors do as well.

$P_{2,2}$: If tolerance limits richness, then the number of species that occur in a region should equal the number that can tolerate the climatic conditions there.

$E_{2,2}$: Kleidon & Mooney (2000) produced a model of plant growth with 13 linked functions describing productivity, respiration, energy allocation, etc. as functions of temperature, water and/or light availability. They then generated simulated species by assigning fixed values to eight parameters of these relationships and random values to 12 others. They assessed what proportion of these pseudo-species (i.e. sets of physiological parameters) could survive observed climates around the globe. The geographical pattern of predicted relative richness resembles the global plant species density map of Barthlott & Lauer (1996). The qualitative agreement between Kleidon and Mooney's model and observed patterns of richness is intriguing and is consistent with $P_{2,2}$. However, their model only predicts relative (not absolute) levels of richness, and they did not test quantitative agreement of their predictions and observed patterns of richness.

Francis (2003), in a recent thesis, assessed the degree to which angiosperms occupy the areas for which they are climatically suited. He generated a map of 'potential richness' of angiosperm families in 35 000 km² quadrats (i.e. 2° × 2° at 45° N or S) covering the world's land masses. Potential richness in a given quadrat was estimated as the total number of families that occur under the same climatic

conditions, and in same biogeographical subprovince (Brown & Lomolino 1998; North America, for example, is divided into five subprovinces). This assumes that there are no major barriers to dispersal within subprovinces. Although climatic variables explained > 80% of the spatial variation in richness in the same data set (Francis & Currie 2003), Francis (2003) found that observed richness was usually lower, often substantially lower, than climatically defined potential richness. In other words, any given quadrat typically has only a subset of the families of angiosperms that could be there, based on climatic tolerance. Thus, although species distributions may respond to climate, richness is not obviously limited by climatic tolerances. In sum, the evidence regarding $P_{2,2}$ is mixed.

$P_{2,3}$: If dispersal barriers have prevented a species from reaching a climatically suitable area, and if the species is subsequently introduced into that area, then its introduced range should expand until it reaches unsuitable climate or a dispersal barrier.

$E_{2,3}$: Sax (2001) compared native and non-native geographic ranges of successful invaders to new continents. He found that high latitude range limits were well correlated, although some species go farther poleward in non-native than in native habitats. Species do not generally approach the equator as closely in the non-native as in the native habitat. This is due, according to Sax, to biotic interactions at low latitudes. Duncan *et al.* (2001) reported that the range areas of birds introduced to Australia could be predicted from climate, although it is not clear whether the birds occur under the same climatic conditions in Australia as they do in their native ranges. Thus, it is not clear to what extent exotic species fail to colonize areas that they could tolerate climatically.

$P_{2,4}$: Invasion of species assemblages should be possible without loss of native species (cf. $P_{1,7}$).

$E_{2,4}$: As noted above, invasion by exotics does not necessarily cause compensatory losses of native species. See $E_{1,7}$. This is consistent with $P_{2,4}$.

Summary for H₂

Clearly, climatic tolerance can limit species distributions (Root 1988; Seip & Savard 1992). However, it appears that species are often absent from areas whose climate they can tolerate, and to which they apparently could disperse. This is inconsistent with, and thus apparently refutes, the hypothesis that climatic tolerance determines patterns of richness. Further direct tests of the hypothesis would be useful.

H₃: EVOLUTIONARY DIVERSIFICATION

Species richness–climate relationships could be driven by evolutionary processes as well as ecological mechanisms. In some cases, non-climatic factors have been proposed to give

rise to high richness in the tropics. For example, the large land area of the tropics may have provided more opportunity for speciation (Rosenzweig 1995), or the tropical origins of many taxa may have given more time for species to evolve in the tropics (Farrell & Mitter 1993; Latham & Ricklefs 1993). Other hypotheses postulate that speciation rates depend upon climate, and that species accumulate in areas with high speciation rates. We consider two such hypotheses. Because their predictions are largely identical, we group them and their supporting evidence together.

H₃ₐ: Evolutionary rates

Evolutionary rates are faster at higher ambient temperatures, due to shorter generation times, higher mutation rates, and/or faster physiological processes (Rohde 1992; Allen et al. 2002). If these processes result in higher rates of speciation (and extinction rates do not similarly vary with temperature), then net rates of diversification should vary with climate and latitude.

H₃ᵦ: Biotic interactions

Speciation rates are higher in warm, wet climates (i.e. the humid tropics) due to relatively stronger biotic interactions (Schemske 2002).

Schemske (2002) focused attention on how '…the selective forces experienced by organisms in tropical habitats might differ from those in temperate habitats, and how such differences might cause geographic variation in the opportunity for evolutionary diversification'. His argument runs like this. In the temperate zone, abiotic factors such as a killing frost or severe cold period provide predictably strong selective events. The precise timing of these events may differ from year to year, but their occurrence in any one year or place is nearly certain. Therefore, even geographically isolated populations will experience similar selection pressures and will evolve similar adaptations. In the tropics, the abiotic environment is milder. As a result, the portion of fitness variation due to abiotic factors decreases relative to biotic interactions (e.g. competition, predation, parasitism, mutualism). Because biotic interactions tend to be more spatially variable, geographically isolated populations will experience varying selection pressures, depending on the species composition of the surrounding community. Given limited gene flow between populations, reproductive isolation and speciation may result (Thompson 1994; McPeek 1996; Schluter 2001).

McPeek (1996) presented a graphical model illustrating how this process can produce evolutionary diversification (see Benkman 1999 for an empirical example). McPeek's (1996) model did not specifically consider the role of climatic gradients. However, we can easily modify it to illustrate how spatial variation in biotic interactions may be coupled with variation in the relative strengths of biotic and

abiotic interactions in temperate and tropical regions, as proposed by Kaufman (1995) and Schemske (2002) (Fig. 5). We refer to this as the 'biotic interactions' hypothesis for higher speciation rates in the tropics. Note that the 'biotic interactions' hypothesis is positively reinforcing: there should be higher rates of speciation in areas with stronger and more varied biological interactions, i.e. more species. Therefore, it should act in concert with other mechanisms to enhance and strengthen a climatic diversity gradient.

Predictions (P) and evidence (E)

P₃,₁: Speciation rates are greater in warm, wet areas (e.g. the humid tropics) than in cold or dry areas (e.g. high latitudes).

E₃,₁: This prediction has been little tested because of the difficulty in measuring speciation rates. However, Martin & McKay (2004) performed an mtDNA analysis of 60 vertebrate species and found that genetic divergence among populations within species is generally greater at low than at high latitudes. Genetic divergence is not a speciation event, but it may be an important precursor to future speciation if barriers to gene flow arise between populations. This is consistent with H₃ᵦ. Bromham & Cardillo (2003) tested for differences in the rate of molecular evolution between sister species of birds at different latitudes and found no latitudinal effect, which is inconsistent with H₃ₐ.

Molecular phylogenetic analysis holds great promise for using phylogenetic trees based on DNA sequences to measure rates of speciation amongst related taxa found in different areas (Barraclough & Nee 2001; Felsenstein 2004). For example, Losos & Schluter (2000) were able to compare speciation rates of *Anolis* lizards on Caribbean islands of different size. A similar approach could be taken with related taxa in different geographical areas. Webb *et al.* (2002) recently reviewed areas where community ecology should benefit from improved phylogenetic analyses – we would add comparisons of speciation rates across climatic gradients to their list.

P₃,₂: Diversification rates (speciation minus extinction) vary with precipitation and temperature (and, consequently, latitude). This is a weaker prediction than the one above, because higher diversification rates could result from lower extinction rates as well as higher speciation rates. However, it is questionable that extinction rates are generally lower at low latitudes and they may in fact be higher (Martin & McKay 2004). Moreover, this prediction is currently more testable.

E₃,₂: Buzas *et al.* (2002) showed that the increase in Cenozoic foraminiferan diversity over the past 10 million years was 150% higher on the tropical central American isthmus than on the temperate Atlantic coastal plain. Much of the difference is attributable to higher origination rates in
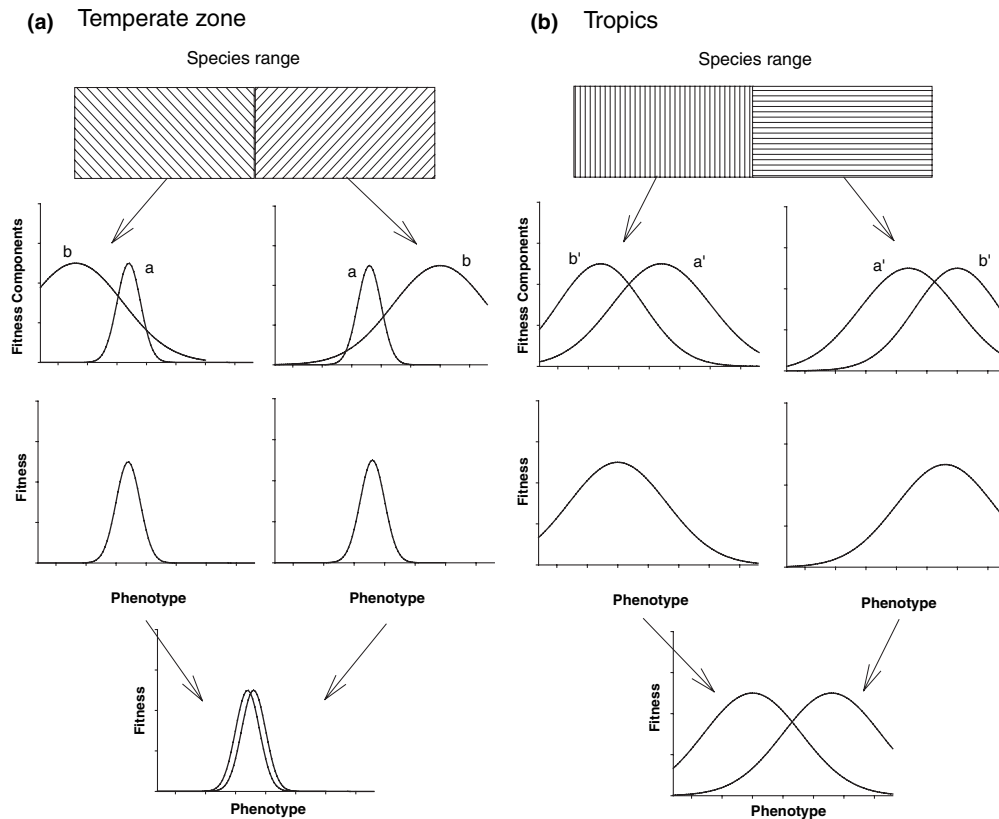
(a) Temperate zone **(b)** Tropics

Figure 5 (Modified from McPeek 1996). Hypothesized variation in the strength and direction of selective pressures experienced by a species in two parts of its range, and the resultant effects on phenotype fitness. In panel (a), representative of a temperate environment, the abiotic environment (curve a) exerts a strong and consistent selective pressure in both parts of a species range, whereas spatially variable biotic interactions exert relatively weaker selective pressures (curves b) on the species phenotype in the two parts of its range. As an example, if the phenotype space represents the activity times of a foraging bird in winter, the selective pressures exerted by different competitors or predators in the two parts of the species range could result in curves (b). However, the abiotic environment (e.g. ambient temperature) may exert a stronger selective pressure that acts similarly on the species phenotype across all parts of its range (curve a). The multiplicative combination of these two selective pressures (biotic and abiotic) would then lead to a similar distribution of fitness across phenotypes in the two parts of the species ranges (graph at bottom-left). As McPeek (1996) notes, curve (a) also may represent the consistent selective pressure exerted by a strongly interacting species (keystone species) found in all parts of a species range. Panel (b) provides a contrasting situation representative of the species-rich tropics, where biotic interactions are hypothesized to be stronger. In panel (b), the variable selective pressures exerted by different biotic interactions at two parts of a species range (curves b′) are of similar strength to the impact of the abiotic environment (curve a′). Therefore, the product of these two selective forces (a′ and b′) results in a divergence in the fitness of phenotypes across the species range (graphs at bottom-right) and an increased potential for speciation.

the tropics. Jablonski (1993) showed that the first appearance of orders of fossil marine invertebrates occurs more often in the tropics than would be expected by chance, which he interpreted as demonstrating that tropical regions 'have been a major source of evolutionary novelty and not simply a refuge that accumulated diversity owing to low extinction'. Flessa & Jablonski (1996) also conclude that fossil assemblages show higher rates of turnover, and therefore higher origination rates, in the tropics. Stehli *et al.* (1969) and Hecht & Agan (1972) found that tropical marine bivalve assemblages have, on average, a more recent evolutionary origin than temperate ones. Stehli *et al.* (1969) interpret these data as showing higher rates of familial and

generic origination in the tropics and therefore a latitudinal gradient in evolutionary rates (but see Stanley 1979 for a critique).

Recent phylogenetic studies looking at rates of species accumulation in sister groups provide a more direct test of $P_{3,2}$. Sister groups are by definition the same age and are therefore ideally suited to estimate rates of diversification in taxa centred at different latitudes (Barraclough *et al.* 1999). If species diversification is faster at lower latitudes, then a tropical clade should be more speciose than its temperate sister clade. Cardillo (1999) compared 48 clades of passerine birds and swallowtail butterflies whose centres of distribution differed in latitude and he found that the equatorial

clades were significantly more speciose. In contrast, Farrell & Mitter (1993) found no difference in species richness between tropical and temperate sister groups of phytophagous insects. As more sister group comparisons are conducted, we will be in a better position to examine the weight of the evidence for or against H_3. In addition, it may be possible in some situations to control for variation in extinction rates between sister-groups, providing a stronger test of the hypothesis (Barraclough & Nee 2001).

$P_{3,3}$: Areas with higher speciation rates should have, on average, younger species. For example, if 10% of the terminals (species) in a tropical phylogeny and only 5% of the terminals in a temperate phylogeny are new after each time step, then after 10 time steps, tropical richness has increased by 240% and temperate richness has increased by only 60%. More to the point, the average age of the additional tropical species (assuming extinctions occur randomly throughout the phylogenetic trees and at equal rates across latitudes) is 3.37 time steps and the average age of the additional temperate species is 3.67 time steps. Therefore, the average age of species within a taxon should change across climatic gradients.

$E_{3,3}$: We know of only one direct (and currently unpublished) test of the prediction that within a clade, average species age should change across a climatic gradient. R. Stevens and K. Jones (unpublished data) found that sister species within the New World bats were younger (more derived) towards the equator than towards the poles (based on branch lengths in the bat molecular phylogeny). Other tests of $P_{3,3}$ are less direct. Stehli & Wells (1971) found that the generic richness of coral assemblages was negatively related to the average age of the genera present, based on the occurrence of corals in fossil strata. The relationships were strong, but they differed among regions. Kerr & Currie (1999) calculated a measure of evolutionary advancement (root distance – the number of nodes separating a species from the root of its phylogenetic tree) and correlated these root distances with various climatic variables. Root distances were calculated at the species level for the Cicindelidae (tiger beetles) and the Catastomidae (suckers), and at the genus level for the Cyprinidae (minnows) and Percidae (perch). They then plotted species richness as a function of average root distance in equal area quadrats that covered the family's range in North America. For the Percidae, more derived lineages (genera) generally occurred in areas of higher AET, the climatic variable most closely related to percid richness (Spearman $r_s = 0.56$, $n = 179$, $P < 10^{-5}$; see also Kerr & Currie 1999, Fig. 1). Tiger beetles and suckers showed the opposite trend: $r_s = -0.67$ and $r_s = -0.70$, $n = 263$, $P < 10^{-5}$), and there was essentially no relationship between AET and root distance for minnows ($r_s = -0.13$, $n = 255$, $P = 0.04$). Measures of advancement related to PET and latitude in qualitatively

similar ways. Kerr & Currie (1999) concluded that more-derived species or genera tended to be found at edges of clades' geographical ranges, and not in areas of higher species richness or in warmer climates. In contrast, Stevens (unpublished data) found that mean root distances in the New World bats followed the same pattern as shown by his analysis of branch lengths; i.e. root distances increased (i.e. species were more derived) moving from higher to lower latitudes.

Summary for H_3

While both evolutionary hypotheses predict higher speciation rates in the tropics, their underlying mechanisms differ. Specifically, the 'evolutionary rates' hypothesis predicts that higher mean temperatures lead to shorter generation times, higher mutation rates, and faster physiological processes that may result in accelerated selection and higher rates of speciation. In contrast, the 'biotic interactions' hypothesis predicts that speciation rates should vary amongst areas that differ in the relative importance of biotic interactions. Distinguishing these hypotheses is a challenge, but should be doable by: (1) testing their proposed mechanisms (e.g. does variation in mutation rate or generation time affect the rate of speciation), and (2) comparing speciation rates in geographical areas that contrast in either temperature or the intensity of biotic interactions.

The evidence available to test the predictions of the 'evolutionary rates' hypothesis and the 'biotic interactions' hypothesis is presently very limited. Prediction 1 is untested. The data are largely consistent with prediction 2, and mixed regarding prediction 3. Thus, it is premature to judge the success or failure of the two speciation rate hypotheses. The rapidly advancing field of molecular-based species-level phylogenies may soon shed more light on them.

CONCLUSIONS

Although patterns of richness are typically strongly correlated with climatic variables related to productivity or energy balance, the evidence is inconsistent with most of the predictions of the energy–richness hypothesis, the most-cited explanation of the richness–climate correlation (e.g. Wright 1983; Currie 1991). Most importantly, the generally observed increase in species richness with increased energy is manifested by an increased fraction of rare species. Therefore, a simple causal link between increased energy, increased individuals, and increased species is not supported. Revised energy–richness hypotheses must consider how an increase in available energy might lead to a disproportionate increase in the number of species per individual. The seductively simple hypothesis that climatic tolerances limit the distributions of individual species and therefore the sum

of these distributions produce patterns of richness, is also not entirely consistent with observation, although further tests are needed. Two evolutionary hypotheses based on changes in speciation rates with climate remain largely untested and the few existing tests show mixed results. However, these hypotheses may soon yield to more direct tests using species-level molecular-based phylogenies. Advances in the ability to measure geographical variation in speciation rates, along with advances in the ability to measure, map, and analyse fine-grain variation in climate and species richness over very broad spatial scales, will provide the tools to help solve the age-old riddle of global diversity patterns.

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REFERENCES

Adams, J.M. & Woodward, F.I. (1989). Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, 339, 699–701.

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.

Barraclough, T.G. & Nee, S. (2001). Phylogenetics and speciation. *Trends Ecol. Evol.*, 16, 391–399.

Barraclough, T.G., Vogler, A.P. & Harvey, P.H. (1999). In: *Evolution of Biological Diversity* (eds Magurran, S.E. & May, R.M.). Oxford University Press, Oxford, pp. 202–219.

Barthlott, W. & Lauer, W.P.A. (1996). Global distribution of species diversity in vascular plants: toward a world map of phytodiversity. *Erkunde*, 50, 317–327.

Benkman, C.W. (1999). The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.*, 153(Suppl.), S75–S91.

Bennett, J.R., Cumming, B.F., Leavitt, P.R., Chiu, M. & Smol, J.P.S.J. (2001). Diatom, pollen, and chemical evidence of post-glacial climatic change at Big Lake, south-central British Columbia, Canada. *Quaternary Res.*, 55, 332–343.

Bromham, L. & Cardillo, M. (2003). Testing the link between the latitudinal gradient in species richness and rates of molecular evolution. *J. Evol. Biol.*, 16, 200–207.

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

Brown, J.H. & Lomolino, M.V. (1998). *Biogeography*, 2nd edn. Sinauer, Sunderland, MA.

Buzas, M.A., Collins, L.S. & Culver, S.J. (2002). Latitudinal difference in biodiversity caused by higher tropical rate of increase. *Proc. Natl. Acad. Sci.*, 99, 7841–7843.

Cardillo, M. (1999). Latitude and rates of diversification in birds and butterflies. *Proc. R. Soc. Lond. B*, 266, 1221–1225.

Chave, J. (2003). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Colwell, R.K. & Lees, D.C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.*, 15, 70–76.

Currie, D.J. (1991). Energy and large scale patterns of animal and plant species richness. *Am. Nat.*, 137, 27–49.

Currie, D.J. & Fritz, J. (1993). Global patterns of animal abundance and species energy use. *Oikos*, 67, 56–68.

Currie, D.J. & Paquin, V. (1987). Large-scale biogeographical patterns of species richness in trees. *Nature*, 329, 326–327.

Davis, M.B. (1981). Quaternary history and the stability of plant communities. In: *Forest Succession: Concepts and Application* (eds West, D.C., Shugart, H.H. & Botkin, D.B.). Springer-Verlag, New York, pp. 132–153.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B. (2002). Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol. Biogeogr.*, 12, 53–64.

Duncan, R.P., Bomford, M., Forsyth, D.M. & Conibear, L. (2001). High predictability in introduced outcomes and the geographical range size of introduced Australian birds: a role for climate. *J. Anim. Ecol.*, 70, 621–632.

Enquist, B.J. & Niklas, K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.

Farrell, B.D. & Mitter, C. (1993). Phylogenetic determinants of insect/plant community diversity. In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 253–266.

Felsenstein, J. (2004). *Inferring Phylogenies*. Sinauer Associates, Sunderland, MA, USA.

Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.*, 12, 42–58.

Flessa, K.W. & Jablonski, D. (1996). The geography of evolutionary turnover: a global analysis of extant bivalves. In: *Evolutionary Paleobiology* (eds Jablonski, D., Erwin, D.H. & Lipps, J.H.). University of Chicago Press, Chicago, IL, pp. 376–397.

Francis, A.P. (2003). Broad-scale patterns of plant richness: patterns and mechanisms. PhD Thesis, University of Ottawa, Ottawa, Canada.

Francis, A.P. & Currie, D.J. (2003). A globally-consistent richness–climate relationship for angiosperms. *Am. Nat.*, 161, 523–536.

Fraser, R.H. & Currie, D.J. (1996). The species richness–energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *Am. Nat.*, 148, 138–159.

Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998). Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.*, 13, 70–74.

Guégan, J.-F., Lek, S. & Oberdorff, T. (1998). Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, 391, 382–384.

Guernier, V., Hochberg, M.E. & Guégan, J.F. (2004). Ecology drives the worldwide distribution of human diseases. *PLoS Biol.*, 2, 740–746.

H.-Acevedo, J.D. & Currie, D.J. (2003). Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecol. Biogeogr.*, 12, 461–473.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M. *et al.* (2003a). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.

Hawkins, B.A., Porter, E.E., & Diniz-Filho, J.A.F. (2003b). Productivity and history as predictors of the latitudinal diversity gradient for terrestrial birds. *Ecology*, 84, 1608–1623.

Hecht, A.D. & Agan, B. (1972). Diversity and age relationships in recent and Miocene bivalves. *Syst. Zool.*, 21, 308–312.

Hubbell, S.P. (1997). A unified theory of biogeography and relative species abundance and its application to rain forests and coral reefs. *Coral Reefs*, 16 (Suppl.), S9–S21.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton and Oxford.

Huntley, B. & Birks, H.J.B. (1983). *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 years Ago*. Cambridge University Press, Cambridge.

Hurlbert, A.H. (2004). Species–energy relationships and habitat complexity in bird communities. *Ecol. Lett.*, 7, 714–720.

Hurlbert, A.H. & Haskell, J.P. (2003). The effect of energy and seasonality on avian species richness and community composition. *Am. Nat.*, 161, 83–97.

Huston, M. (1994). *Biological Diversity: The Coexistence of Species on a Changing Landscape*. Cambridge University Press, Cambridge.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.*, 93, 145–159.

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

Johnson, C.N. (1998). Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *J. Anim. Ecol.*, 67, 689–698.

Kaufman, D.M. (1995). Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *J. Mammal.*, 76, 322–334.

Kerr, J.T. & Currie, D.J. (1999). The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience*, 6, 329–337.

Kerr, J.T. & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385, 252–254.

Kerr, J.T., Vincent, R. & Currie, D.J. (1998). Lepidopteran richness patterns in North America. *Ecoscience*, 5, 448–453.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001). Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proc. Natl. Acad. Sci.*, 98, 11365–11370.

Kleidon, A. & Mooney, H.A. (2000). A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biol.*, 6, 507–523.

Kocher, S.D. & Williams, E.D. (2000). The diversity and abundance of North American butterflies vary with habitat disturbance and geography. *J. Biogeogr.*, 27, 785–794.

Latham, R.E. & Ricklefs, R.E. (1993). Continental comparisons of temperate-zone tree species diversity. In: *Species Diversity in Eco-*

logical Communities: Historical and Geographical Perspectives (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 294–314.

Lieth, H. (1975). Modeling the primary productivity of the world. In: *Primary Productivity of the Biosphere* (eds Lieth, H. & Whittaker, R.H.). Springer-Verlag, New York, pp. 237–263.

Losos, J.B. & Schluter, D. (2000). Analysis of an evolutionary species–area relationship. *Nature*, 408, 847–850.

MacArthur, R.H. & Wilson, E.O. (1967). *Island Biogeography*. Princeton University Press, Princeton, NJ.

Martin, P.R. & McKay, J.K. (2004). Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution*, 58, 938–945.

McPeek, M.A. (1996). Linking local species interactions to rates of speciation in communities. *Ecology*, 77, 1355–1366.

Niklas, K.J., Midgley, J.J. & Rand, R.H. (2003). Size-dependent species richness: trends within plant communities and across latitude. *Ecol. Lett.*, 6, 631–636.

O'Brien, E.M. (1993). Climatic gradients in woody plant species richness – towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeogr.*, 20, 181–198.

Oberdorff, T., Hugueny, B. & Guégan, J.F. (1997). Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *J. Biogeogr.*, 24, 461–467.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H. *et al.* (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.

Patalas, K. (1990). Diversity of zooplankton communities in Canadian lakes as a function of climate. *Verhandlungen der Internationale Vereinigung für theoretische und andgewandte Limnologie*, 24, 360–368.

Peters, R.H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Phillips, O. & Miller, J.S. (2002). *Global Patterns of Plant Diversity: Alwyn H.Gentry's Forest Transect Data Set*. Missouri Botanical Garden Press, St Louis, MO.

Preston, F.W. (1948). The commonness, and rarity, of species. *Ecology*, 29, 254–283.

Preston, F.W. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology*, 43, 185–215.

Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D. & Frankham, R. (2003). Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biol. Cons.*, 113, 23–34.

Rohde, K. (1992). Latitudinal gradients in species diversity – the search for the primary cause. *Oikos*, 65, 514–527.

Rohde, K., Heap, M. & Heap, D. (1993). Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *Am. Nat.*, 142, 1–16.

Root, T. (1988). Energy constraints on avian distributions and abundances. *Ecology*, 69, 330–339.

Rosenzweig, M.L. (1968). Net primary productivity of terrestrial communities: predictions from climatological data. *Am. Nat.*, 102, 67–74.

Rosenzweig, M.L. (1992). Species diversity gradients – we know more and less than we thought. *J. Mammal.*, 73, 715–730.

Rosenzweig, M.L. (1995). *Species Diversity in Time and Space*. Cambridge University Press, Cambridge, UK.

Sauer, J.R., Hines, J.E. & Fallon, J. (2004). *The North American Breeding Bird Survey, Results and Analysis 1966–2003*, Version 2004.1 USGS Patuxent Wildlife Research Center, Laurel, MD.

Sax, D.F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.*, 28, 139–150.

Sax, D.F., Gaines, S.D. & Brown, J.H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.*, 160, 766–783.

Schall, J.J. & Pianka, E.R. (1978). Geographical trends in the numbers of species. *Science*, 201, 679–686.

Schemske, D. (2002). Tropical diversity: patterns and processes. In: *Ecological and Evolutionary Perspectives on the Origins of Tropical Diversity: Key Papers and Commentaries* (eds Chazdon, R. & Whitmore, T.). University of Chicago Press, Chicago, IL.

Schluter, D. (2001). Ecology and the origin of species. *Trends Ecol. Evol.*, 16, 372–380.

Seip, D.R. & Savard, J.P.L. (1992). Comparison of bird, small mammal and amphibian abundance and diversity in old-growth and 2nd-growth forests of coastal British-Columbia. *Northw. Environ. J.*, 8, 230–231.

Shipley, W. (2000). *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations, and Causal Inference*. Cambridge University Press, Cambridge, UK.

Srivastava D.S. & Lawton, J.H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *Am. Nat.*, 152, 510–529.

Stanley, S.M. (1979). *Macroevolution: Pattern and Process*. W. H. Freeman and Company, San Francisco, CA.

Stehli, F.G. & Wells, J.W. (1971). Diversity and age patterns in hermatypic corals. *Syst. Zool.*, 20, 114–126.

Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969). Generation and maintenance of gradients in taxonomic diversity. *Science*, 164, 947–949.

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how do so many species coexist in the tropics? *Am. Nat.*, 133, 240–256.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A. *et al.* (1999). Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69, 25–46.

Stohlgren, T.J., Barnett, D.T. & Kartesz, J.T. (2003). The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.*, 1, 11–14.

Thompson, J.N. (1994). Evaluating the dynamics of coevolution among geographically structured populations. *Ecology*, 78, 1619–1623.

Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. (1987). Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48, 195–205.

Turner, J.R.G., Lennon, J.J. & Lawrenson, J.A. (1988). British bird species distributions and the energy theory. *Nature*, 335, 539–541.

Venevsky, S. & Veneskaia, I. (2003). Large-scale energetic and landscape factors of vegetation diversity. *Ecol. Lett.*, 6, 1004–1016.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.*, 33, 475–505.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Ann. Rev. Ecol. Syst.*, 34, 273–310.

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

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993). Energy supply and patterns of species richness on local and regional scales. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 66–74.