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WHAT CAN MULTIPLE PHYLOGENIES SAY ABOUT THE LATITUDINAL DIVERSITY GRADIENT? A NEW LOOK AT THE TROPICAL CONSERVATISM, OUT OF THE TROPICS, AND DIVERSIFICATION RATE HYPOTHESES

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We reviewed published phylogenies and selected 111 phylogenetic studies representing mammals, birds, insects, and flowering plants. We then mapped the latitudinal range of all taxa to test the relative importance of the tropical conservatism, out of the tropics, and diversification rate hypotheses in generating latitudinal diversity gradients. Most clades originated in the tropics, with diversity peaking in the zone of origin. Transitions of lineages between latitudinal zones occurred at 16–22% of the tree nodes. The most common type of transition was range expansions of tropical lineages to encompass also temperate latitudes. Thus, adaptation to new climatic conditions may not represent a major obstacle for many clades. These results contradict predictions of the tropical conservatism hypothesis (i.e., few clades colonizing extratropical latitudes), but support the out-of-the-tropics model (i.e., tropical originations and subsequent latitudinal range expansions). Our results suggest no difference in diversification between tropical and temperate sister lineages; thus, diversity of tropical clades was not explained by higher diversification rates in this zone. Moreover, lineages with latitudinal stasis diversified more compared to sister lineages entering a new latitudinal zone. This preserved preexisting diversity differences between latitudinal zones and can be considered a new mechanism for why diversity tends to peak in the zone of origin.

KEY WORDS: Ancestral area reconstruction, evolutionary time, latitudinal zone transitions, sister-group analysis, tropical origination..

The mechanisms behind the increase in species richness from the poles toward the equator remain an enigma despite 200 years of scientific study since first described (Hawkins 2001; Willig et al. 2003; Hillebrand 2004). In recent years, methodological advances in biogeography and phylogenetics, along with greater availability of biodiversity data, have made feasible the testing of alternative hypotheses for why tropical latitudes are more diverse. Recent studies using phylogenetic data have found support for some of the hypotheses suggested to explain the latitudinal diversity gradient (LDG), but have generally focused on single clades (e.g., Stephens and Wiens 2003; Wiens and Donoghue 2004; Hawkins et al. 2006). Although LDGs have been documented in most higher taxa, to our knowledge, there has been no study attempting to test the relative importance of mechanisms generating LDGs using phylogenetic data for a wide array of taxa.

Some of the most discussed explanations for LDGs make predictions on the phylogenetic evolution of clades (Table 1): (1) the "evolutionary time hypothesis" (ETH) (Fischer 1960)

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Table 1. Characteristics of phylogenetic trees showing a latitudinal diversity gradient expected if they are generated by each of four different mechanisms.

	Evolutionary time	Tropical conservatism	Out of the tropics	Rate of diversification
Geographic origin of the clade	Tropical	Tropical	Tropical	Anywhere
Frequency of lineages switching latitudinal zones	No prediction	Low[1]	High[1]	No prediction
Type of latitudinal zone transition most common	No prediction	All rare	Range expansion of tropical lineages to encompass temperate latitudes	No prediction
Position in the phylogeny of switching events	Anywhere	Recent, near tips	Anywhere	Anywhere
Tropical-temperate contrasts in diversification	No latitudinal trend expected	No latitudinal trend expected	No latitudinal trend expected	Higher toward lower latitudes

[1] The frequency of latitudinal zone transitions would be deemed low if few temperate lineages would be derived from tropical ancestors, or if the tropical ancestry lies far back in time. Conversely, transition frequencies would be deemed high if a significant proportion of temperate taxa is derived from tropical ancestors.

suggests that tropical environments are more species-rich because they are older, providing more time for lineages to accumulate species. (2) A variation of the ETH, the "tropical conservatism hypothesis" (TCH), advocates that most clades originate in the tropics (because tropical environments are old or cover large areas) and that transitions of lineages from tropical to temperate latitudes are rare, leaving more species in the tropics (Latham and Ricklefs 1993; Wiens and Donoghue 2004). (3) The "out-of-the-tropics model" (OTM) (Jablonski et al. 2006) suggests that although most clades originate in the tropics, they tend to expand their ranges to encompass temperate latitudes, making latitudinal range transitions of lineages common and causing a large proportion of temperate taxa to have tropical origins. The TCH and the OTM can be considered opposite ends along a gradient in the frequency of latitudinal zone transitions of tropical taxa. (4) Alternatively, diversification rates (i.e., speciation minus extinction) might be higher at tropical than temperate latitudes (Rohde 1992; Cardillo 1999; Dynesius and Jansson 2000; Allen et al. 2006; Wright et al. 2006) resulting in the tropics being more diverse (i.e., the "diversification rate hypothesis," DRH). These mechanisms are not mutually exclusive, and their relative importance may vary among clades, regions, and time periods.

Individual studies support these hypotheses within single clades, but the relative importance of the mechanisms across clades is not known. Fossil (Crane and Lidgard 1989; Jablonski 1993; Jablonski et al. 2006) and phylogenetic (Stephens and Wiens 2003) evidence demonstrate that many clades originated in the tropics and hence have accumulated more taxa over time, consistent with the ETH. Patterns consistent with the TCH, with tropical origins and few events of extratropical colonization have been reported for many terrestrial clades including flowering plants (Latham and Ricklefs 1993; Wiens and Donoghue 2004), frogs (Wiens et al. 2006, 2009), birds (Hawkins et al. 2006, 2007), mammals (Buckley et al. 2010), and butterflies (Hawkins and DeVries 2009). Using fossil data, Jablonski et al. (2006) found that the OTM best explained the evolution of biodiversity in marine bivalves. Many studies have also found support for the DRH: Sampling phylogenies across large, inclusive clades of birds (Cardillo 1999; Cardillo et al. 2005; Ricklefs 2006), amphibians (Wiens 2007), and flowering plants (Davies et al. 2004) have consistently demonstrated higher diversification in the tropics. In contrast, most studies of a single family or assemblages encompassing relatively few taxa did not find diversification to be faster in tropical than temperate latitudes (Farrell and Mitter 1993; Stuart-Fox and Owens 2003; Böhm and Mayhew 2005; Wiens et al. 2006, 2009). If there are slowdowns in diversification with increasing diversity, these sister-group comparisons might not correctly estimate the net rate of species diversification per time, but the important point for LDGs is whether more taxa have accumulated in tropical versus temperate clades. If diversification slowed down to reach a diversity equilibrium, the analyses test whether the equilibrium tends to differ significantly between the latitudinal zones. In addition, many paleontological studies have found support for higher tropical diversification, as reviewed by Mittelbach et al. (2007). Despite empirical evidence for the different hypotheses on the LDG, it is still unclear how representative these mechanisms are across taxonomic groups, and how they interact to generate the present global distribution of species.

Many clades exhibit a LDG, and if the phylogenetic structure within each clade is taken as an independent sample, they may collectively help uncover the causes of the gradient. The structure of phylogenetic trees is expected to differ depending

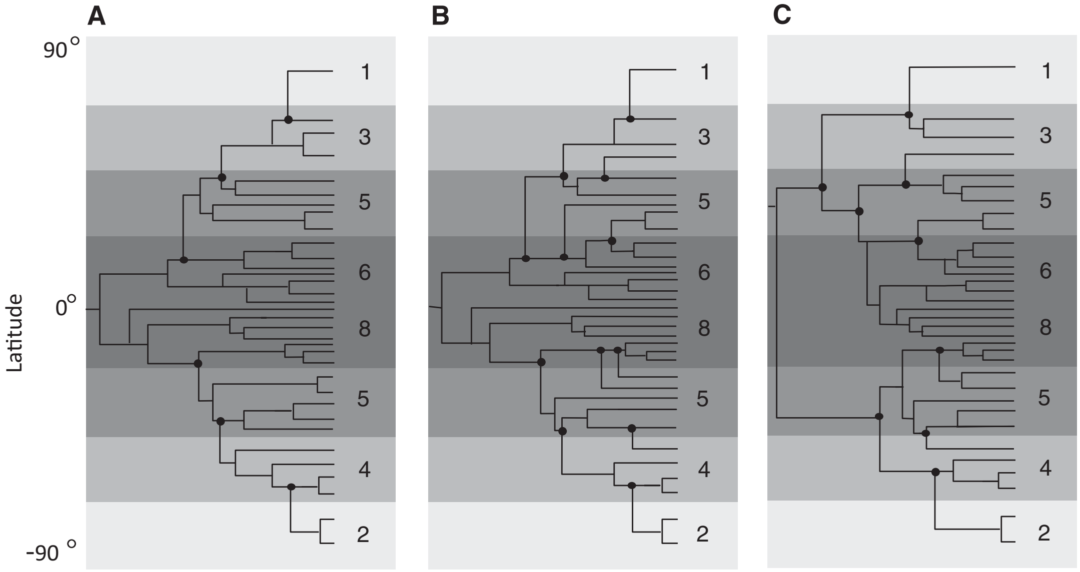

Figure 1. Three alternatives for the generation of latitudinal gradients in species richness for phylogenetic trees of extant taxa mapped across a pole-to-pole gradient. Gray bands indicate latitudinal bands, becoming paler toward higher latitudes. Each terminal branch in the trees represents an extant species, and figures give the number of species per latitudinal band. Dots mark nodes where one lineage has made a transition into a new latitudinal zone. All trees have similar numbers of species per latitudinal band, but differ in their branching patterns. (A) The TCH (Wiens and Donoghue 2004), in which there are more species in tropical regions because the clade originated there and has difficulty in colonizing extratropical climatic zones (few latitudinal zone transitions). This results in more time available for lineages to accumulate in the tropics. In (B), the clade originated in the tropics but lineages frequently expanded their ranges to extratropical latitudes (many latitudinal zone transitions), according to the OTM (Jablonski et al. 2006). In (C), there are more species in the tropical zone because net diversification rates (speciation–extinction) increase toward lower latitudes. After transitions to new latitudinal zones, the lower latitude sister clade diversifies more than its higher latitude sister clade.

on which of the above processes are the most important (Fig. 1; Table 1). In Figure 1A, higher tropical diversity is generated by a tropical origin of the clade and few lineages colonizing higher latitudes (phylogenetic niche conservatism, Wiens and Graham 2005; Wiens et al. 2010), in accordance with the TCH. Figure 1B also exhibits a tropical clade origin, but consistent with the OTM, tropical lineages frequently expand their ranges to temperate latitudes, resulting in more latitudinal zone transitions. By comparison, Figure 1C depicts higher tropical diversity as a result of higher rates of diversification in tropical lineages. Higher tropical diversity results because lineages colonizing new latitudinal zones are expected to adjust diversification rates following transitions, such that rates increase when lineages colonize lower latitudes and vice versa. Predictions on the topology of phylogenetic trees made by the hypotheses (Table 1) mean that samples of trees could be used to infer the relative importance of each hypothesis.

The aim of this study was to use information from a large sample of phylogenetic trees representing multiple taxa to inform on the relative importance of common hypotheses to explain the LDG (Table 1). To date, generating a large number of time-calibrated phylogenetic trees or obtaining a more or less complete fossil representation of multiple taxa to test the generality of the mechanisms behind the LDG is not feasible. Hence, we did a literature search for phylogenies, mapped the geographic distribution of all included taxa, and collated data from multiple phylogenetic trees to test our hypotheses (Cooper 1998). To our knowledge, this has not been attempted before.

Methods

SELECTION OF PHYLOGENETIC TREES

We conducted a literature search for molecular-based phylogenies of mammals, birds, insects, and flowering plants. Our criteria for selection were that the tree included the majority of taxa in the clade, and that it encompassed both temperate and tropical latitudes. We did not limit tree selection to studies with only species at the tips, but also included trees resolved to the level of genera. Restricting the analyses to species trees would bias sampling against species-rich phylogenies because they seldom meet the completeness criterion, especially in tropical clades. Genera or higher taxa have frequently been used as units of analysis in studies of global patterns in biodiversity (Stehli et al. 1969; Roy et al. 1996; Francis and Currie 2003; Davies et al. 2004), making it appropriate also for evaluating hypotheses for how LDGs have been generated (Jablonski et al. 2006). We collected a total of

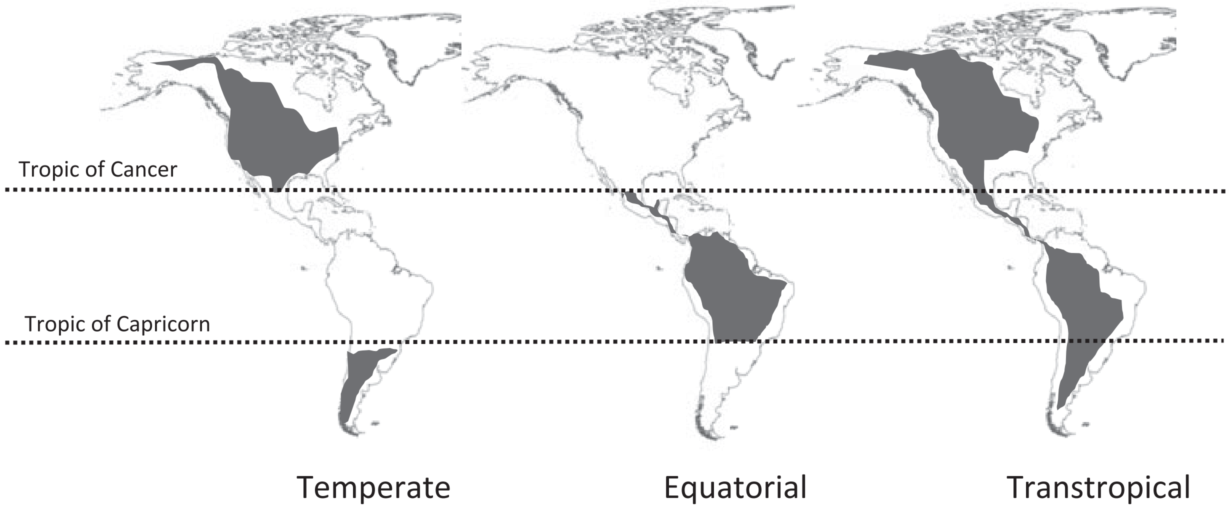

Figure 2. Examples of latitudinal ranges of taxa corresponding to our classification into temperate (geographic range on the poleward side of the Tropics), equatorial (geographic range contained within the Tropics of Cancer and Capricorn), and transtropical (range spanning across either or both of the Tropics of Cancer or Capricorn) latitudinal zones.

111 phylogenetic studies (33 mammal, 27 bird, eight insect, and 43 flowering-plant phylogenies; see Appendix S1). For each selected phylogenetic tree, we harvested information that allowed us to test predictions about the phylogenetic tree structure (Table 1). Because trees resolved to species- and genus-level might have different properties, results are reported separately for species-level trees. We note that although we made every effort to obtain an unbiased sample of published phylogenetic trees, published phylogenies may not yet include a complete or random representation of clades, because taxonomic interest and the availability of molecular data vary greatly within and among taxa.

LATITUDINAL RANGE OF TIPS AND NODES

For all tips in the phylogenetic trees, we classified taxa as "equatorial," "temperate," or "transtropical" according to the latitudinal range of their geographic distributions. Equatorial taxa had ranges contained within the Tropics of Cancer and Capricorn (between 23.5°N and 23.5°S), whereas temperate taxa had ranges on the poleward side of the Tropics (Fig. 2). Taxa whose range spanned either the Tropic of Cancer or Capricorn were classified as transtropical, rather than forcing them to fit a binary latitudinal classification with only tropical and temperate categories (Jablonski et al. 2006). Given limitations in the accuracy of some geographic range data (due to imprecision of range maps and scarcity of occurrence data for point locality data), geographic ranges had to range 1–2° across the tropics to be classified as transtropical. Because we intended to uncover causes for latitudinal differences in diversity, taxa were assigned to the three classes based on their latitudinal range and not the environmental conditions they inhabit. Thus, species at high elevations in tropical latitudes were classified as equatorial although aspects of their climatic niche could be considered temperate. We used reference literature on floras and faunas along with online databases, such as the Global Biodiversity Information Facility (www.gbif.org) to assign taxa to the correct latitudinal range class.

We attempted to reconstruct the latitudinal range class of all nodes in the trees under a parsimony framework using outgroup analysis for ancestral reconstruction of binary and multistate characters according to Maddison et al. (1984). Parsimony using outgroup analysis employs two rules to resolve the ancestral state of multistate clades: To resolve an ingroup, if the first outgroup and the first doublet (i.e., consecutive outgroups with matching character states) have the same character state, then that state is the most parsimonious ancestral state for the ingroup (first doublet rule). In case there are no doublets, if the first and the last outgroups have the same character state, that is the most parsimonious assignment for the ingroup (alternating outgroup rule). In case nodes could not be resolved according to these rules, we used a simple majority rule: if at least 80% of the daughter lineages belonged to a single latitudinal range class, that state was the most parsimonious state for the node. If the article presented fossil evidence for the latitudinal range of ancestral lineages, we took that into account. Otherwise, remaining nodes were left unresolved. A similar method of ancestral reconstruction of biome membership was used by Crisp et al. (2009).

Ancestral traits of nodes may also be inferred using maximum likelihood or Bayesian methods. Given the size of our metadata set, using such methods on all clades was not practical. To test the robustness of our parsimony reconstruction, we also reconstructed the nodes using maximum likelihood and parsimony optimizations in Mesquite (Maddison and Maddison 2011) for 19 out of 35 mammal clades (54%). For maximum-likelihood reconstruction, we used the MK1 model, shown to be suitable for discrete state data (Lewis 2001). We found that our parsimony method corresponded with maximum likelihood in 92% of the nodes. Our reconstruction was more similar to maximum-likelihood reconstruction than the parsimony reconstruction implemented in Mesquite (similarity in 84% of the nodes) because of our majority rule and the utilization of fossil information when available.

We treated transtropical ranges as distinct from equatorial and temperate ones, and for simplicity, all transitions were considered to have equal probability. This could be considered an oversimplification because a range expansion from equatorial or temperate to become transtropical requires only one event (range expansion), whereas any shift between equatorial and temperate zones requires two steps (range expansion and extinction). On the other hand, geographic ranges of most taxa are determined by a constant balance between founding and extinction of populations in response to climatic conditions (McLaughlin et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003), making it hard to distinguish the number of steps required to make latitudinal transitions. Most taxa have shifted their latitudinal range in response to recurrent climatic oscillations (Dynesius and Jansson 2000), making it harder to infer ancestral latitudinal ranges from present-day distributions. However, we assume that the taxa studied shifted ranges in conjunction with climatic conditions, thereby preserving latitudinal zone contrasts.

TRANSITIONS BETWEEN GEOGRAPHIC RANGE CLASSES

Based on the latitudinal range classification, we identified all dichotomous nodes where a transition between latitudinal range classes had occurred, that is, when a daughter lineage switched to a latitudinal zone different from that inferred for the ancestral node. Because many nodes remained unresolved, our assessment of the latitudinal range transition frequency is likely to be an underestimate of true rates. We tested whether the method of reconstructing the latitudinal zone of nodes affected the frequency and type of transitions inferred by comparing trees reconstructed using our parsimony method with maximum-likelihood reconstruction in Mesquite (see above). For the 19 mammal phylogenies used, the transitions corresponded between our reconstruction and maximum likelihood in 77% of the cases. Many of the mismatches were caused by maximum likelihood leaving nodes unresolved (i.e., different latitudinal zones were equally probable), whereas we had resolved them with the help of the majority rule and in some cases fossil information. Excluding those cases, the similarity in transition frequency and type of transition rose to 87% between methods.

DATA OBTAINED FROM TREES

We recorded multiple variables from each selected phylogeny (Tables S1 and S2). Of principal interest was the number of tip taxa per latitudinal zone and the geographic origin of the clade (according to evidence presented in the article, or if such information was lacking, according to our ancestral range reconstruction). When determining the latitudinal origin of the clade, we relied on the judgment of the phylogeny authors to distinguish tropical and temperate paleolatitudes. For each tree, we recorded the total number of nodes and the number of nodes where ancestral states were reconstructed. We also recorded nodes where we inferred a latitudinal zone transition, the latitudinal zone of the two daughter lineages, the ancestral latitudinal zone of the node, the number of tip taxa in the two daughter lineages. In total, there are six possible latitudinal zone transitions: (1) temperate to equatorial, (2) temperate to transtropical, (3) equatorial to temperate, (4) equatorial to transtropical, (5) transtropical to equatorial, and (6) transtropical to temperate.

For bird trees resolved to the level of genera, many studies reported the number of species per genus. For these, we calculated the number of species per sister lineage, in addition to counting the number of genera. Given that the geographic ranges of bird species are well known in comparison with the other taxonomic groups, we recorded the extreme northern and southern latitudinal distribution of all taxa in the bird phylogenies to assess if latitudinal zone transitions resulted in latitudinal range expansions or contractions.

DATA ANALYSIS

Diversity and structure of phylogenetic trees

To test for differences in the number of equatorial, temperate, and transtropical taxa per tree, we applied two-way mixed-model analyses of variance (ANOVAs). We used log-transformed values of numbers of taxa (to account for the multiplicative nature of richness in diversifying clades), with the latitudinal range (equatorial, temperate, or transtropical) as a fixed factor and clade as a random factor. This analysis was done to establish whether there was a contrast in richness among latitudinal zones that could be explained by phylogenetic mechanisms. Therefore, we did not factor out any effect of phylogenetic nonindependence in the analysis.

Geographic origin of clades

To assess whether clades (each represented by a phylogenetic tree) more often had equatorial, temperate, or transtropical origins, we counted the number of clades by origin, and used χ^2-tests to see whether there was a bias in the representation of any of the latitudinal zones. We also tested whether clades tended to have more taxa in the latitudinal zone of origin than expected by chance using χ^2-tests.

Transitions between latitudinal zones

We calculated the frequency of latitudinal zone transitions as the number of transitions found in the clade divided by the total number of reconstructed nodes in the tree. We tested for a difference among taxonomic groups in the probability of transitions per tree using one-way ANOVA, with the proportion of transitions per tree as the predictor variable and taxonomic group as a factor. We also used one-way ANOVA to test for a difference among taxonomic groups in the proportion of nodes with the ancestral latitudinal zone reconstructed.

The effect of latitudinal zone transitions on the accumulation of lineages will differ depending on both the frequency and timing of occurrence. If transitions are rare and only occur late in the history of the clade, this will leave more time for accumulation of lineages in the latitudinal zone of origin (Fig. 1A). We recorded the estimated timing of latitudinal zone transitions for all clades for which time-calibrated trees were available (22 studies of which 10 dealt with mammals, four with birds, one with insects, and seven with plants). We recorded both the absolute age of nodes with transitions, and a relative age, dividing the age of the node with the age of the entire clade. We then tested for differences in the absolute or mean age of transitions among taxonomic groups using ANOVA. Finally, we tested whether certain types of latitudinal zone transitions were overrepresented using χ^2-tests. To simplify, we assumed all transitions had equal probability of occurring across the tree.

Latitudinal contrasts in diversification

We assessed differences in diversification among latitudinal zones by testing for differences in the log number of terminal taxa between sister lineages from different latitudinal zones using two-sample Wilcoxon's signed ranks tests (Vamosi and Vamosi 2005; Vamosi 2007). Sister-group comparisons largely avoid problems associated with age differences, nonindependence of taxa, confounding variables (sister clades will differ only in traits evolved since the last common ancestor) and noise (likely to mask any relationship between evolutionary variables) (Barraclough et al. 1998). Nodes with multiple transitions in the daughter lineages were left out such that only records of sister clades were included where each lineage in the pair belonged to a different latitudinal zone. Single transitions in daughter lineages were allowed, in case the majority of daughter lineages still belonged to the latitudinal zone immediately preceding the focal node. We tested for contrasts in diversification in two ways. First, we ignored the ancestral latitudinal zone of the node separating sister lineages and compared equatorial versus temperate, equatorial versus transtropical, and temperate versus transtropical sister groups. Next, we accounted for the ancestral state, comparing the number of taxa in lineages remaining in the ancestral latitudinal zone with lineages that switched to a new latitudinal zone, thus resulting in tests for six types of transitions as outlined above. We made separate tests for each taxonomic group and type of transition. We checked if ecological limits to diversification might have affected the sister-group analyses by testing for a correlation between the ratio of the unlogged sister clade diversities (N_1/N_2) and the age of their common ancestor, as proposed by Rabosky (2009). A positive correlation would indicate that sister-group contrasts are the result of speciation/extinction differences. Absence of correlation or a negative correlation would indicate that sister-group differences are due to factors setting limits to the number of taxa in the clades.

We also used GeoSSE, the Geographic State Speciation and Extinction model (Goldberg et al. 2011), a likelihood-based method estimating speciation and extinction rates, and geographic zone transitions, on a subset of the flowering-plant clades. The methods are described in Appendix S2.

We analyzed range expansions and contractions associated with latitudinal transitions using bird phylogenies. The latitudinal ranges of transtropical taxa are potentially larger than equatorial and temperate ones. All else being equal, wide-ranging lineages tend to diversify faster than range-restricted ones (Owens et al. 1999; Davies et al. 2004; Ricklefs 2006). For each type of transition, we tested whether the average latitudinal extent of species differed between lineages that switched latitudinal zone and lineages remaining in the zone of origin, using paired samples *t*-tests.

In all the above analyses, we considered clades represented by phylogenetic trees to be independent within taxonomic groups (mammals, birds, etc.). However, some clades are more closely related than others and might therefore share traits. This could potentially be accounted for by combining the trees into "supertrees" and calculating the phylogenetic dependence, but we considered this to be beyond the scope of the present article. Statistical tests were done using IBM SPSS Statistics version 20 (IBM, Armonk, New York) when not stated otherwise.

Results

Overall, the results drawn from published phylogenies supported the ETH, and specifically the OTM. Although mammal phylogenies were dominated primarily by temperate taxa, the majority of nonmammalian clades originated in the equatorial zone and were most diverse in the zone of origin. Transitions between latitudinal zones were frequent, with range expansions from equatorial to transtropical latitudinal range being most common. Transition of a lineage to a new latitudinal zone often resulted in reduced diversification compared to its sister lineage that remained in the zone of origin.

Table 2. **The number of selected phylogenetic trees/clades, sorted by taxonomic group (vertical) and taxonomic hierarchy (horizontal). Taxonomic resolution refers to the type of taxa found at branch tips of the trees.**

							Taxonomic resolution	
	Genus	Tribe	Family	Order	Subclass	Total	Species	Genera
Mammals	22	2	9			33	30	3
Birds	13		12	2		27	20	7
Insects		1	6	1		8	1	7
Flowering plants	11	5	25	1	1	43	20	23
Total	46	8	52	4	1	111	71	40

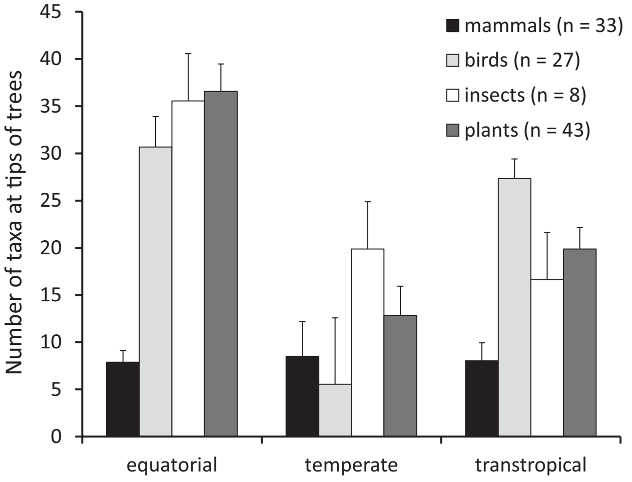

Figure 3. **Average (±SE, in error bars) number of taxa at the tips of phylogenetic trees per latitudinal zone. Equatorial taxa have their range within the Tropics of Cancer (23.5°N latitude) and Capricorn (23.5°S), temperate taxa have their distribution poleward from the Tropics (>23.5°), whereas transtropical taxa have ranges that span either the Tropic of Cancer or Capricorn. "*n*" gives the number of clades per taxonomic group (mammals, birds, insects, and flowering plants).**

PATTERNS IN DIVERSITY AND TAXONOMY AMONG PHYLOGENETIC TREES

The 111 selected phylogenetic trees encompassed subgenera to subclasses in the taxonomic hierarchy, but the majority considered either a genus or a family (Table 2). Overall, there were more equatorial and transtropical taxa per tree than temperate ones (Fig. 3, $F_{2,\,220} = 11.1$, $P = 0.0001$). When analyzing patterns of diversity separately for the taxonomic groups, we found no significant differences among latitudinal zones for mammals and insects ($P > 0.05$), although insects tended to be most diverse in the equatorial zone. For birds, the equatorial and transtropical zones were more diverse than the temperate one ($F_{2,\,52} = 23.4$, $P = 0.0001$), whereas for flowering plants, there were more equatorial than temperate taxa, with transtropical ones being intermediate (although the model was not significant; $F_{2,\,84} = 2.4$, $P = 0.10$). Restricting analyses to only species-level trees did not change results, except that there were significantly more flowering-plant species in the equatorial zone ($F_{2,\,57} = 4.2$, $P = 0.02$, $n = 20$).

GEOGRAPHIC ORIGIN OF CLADES

We inferred the geographic origin for 57 of 111 clades. Given that mammals did not differ in taxonomic richness among latitudinal zones (Fig. 3), these were analyzed separately. For birds, insects, and flowering plants, equatorial origins (15 clades) were statistically overrepresented compared to temperate (nine) and transtropical (four) origins ($\chi^2 = 6.5$, df = 2, $P = 0.039$; Fig. 4A). In contrast, more mammal clades originated in the temperate than the equatorial or transtropical zones (Fig. 4B), but the difference was not statistically significant ($\chi^2 = 3.4$, df = 2, $P = 0.19$). Seventy-nine percent of the 57 clades with a geographic origin inferred were most diverse in the latitudinal zone of origin. The clades peaking in diversity in their zone of origin were distributed randomly among latitudinal zones ($\chi^2 = 0.8$, df = 2, $P = 0.68$; the result did not change when excluding mammals). Results were similar when analyzing species-level trees exclusively, but differences were not significant due to smaller sample size.

TRANSITIONS BETWEEN LATITUDINAL ZONES

Transitions of lineages between latitudinal zones occurred at 16–31% of the nodes (Fig. 5), and more common in mammals than in birds and plants ($P < 0.05$, Tukey tests; $F_{3,\,107} = 10.6$, $P = 0.0001$). The proportion of nodes for which we could reconstruct the ancestral latitudinal zone also varied among taxonomic groups ($F_{3,\,107} = 4.5$, $P < 0.01$), being highest in mammals and lowest in flowering plants ($P < 0.05$, Tukey tests).

Latitudinal zone transitions occurred on average 7 ± 1.2 million years ago (Mya) in species-level phylogenies (mean ± SE, range 0.2–72, $n = 92$), and 28 ± 1.1 Mya (range 0.2–81, $n = 144$) in genus-level trees (Fig. 6A). The absolute age of transitions differed significantly between species- and genus-level phylogenies ($F_{3,\,231} = 18.4$, $P < 0.01$), as well as among taxonomic groups ($F_{3,\,231} = 6.9$, $P < 0.0001$), being younger in mammals than the other taxonomic groups (two-way ANOVA and Tukey tests). The relative age of transitions (age of transitions divided

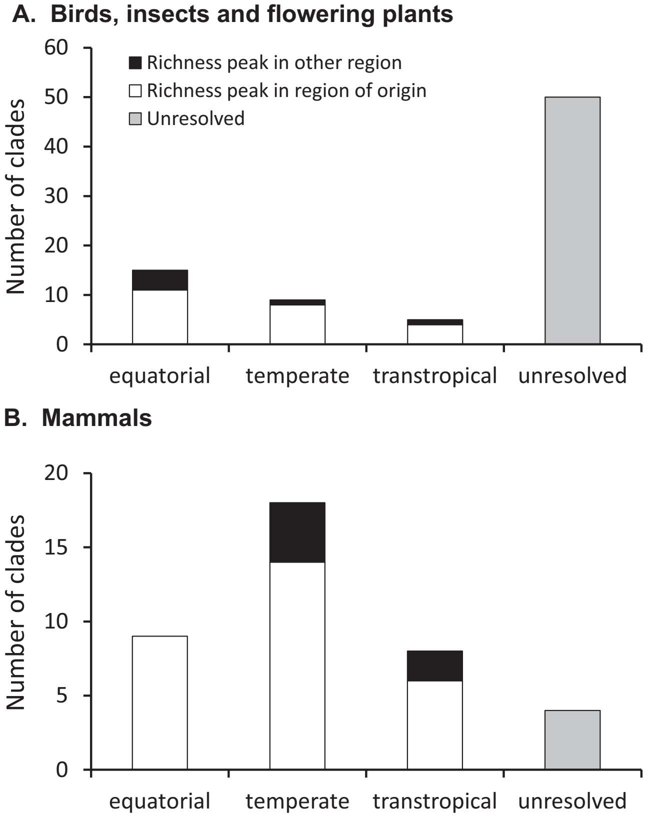

Figure 4. The number of clades originating in different latitudinal zones and the region in which they peak in richness for (A) birds, insects, and flowering plants, and (B) for mammals, according to information given in the publications containing the phylogenetic trees, or according to our reconstruction of ancestral states.

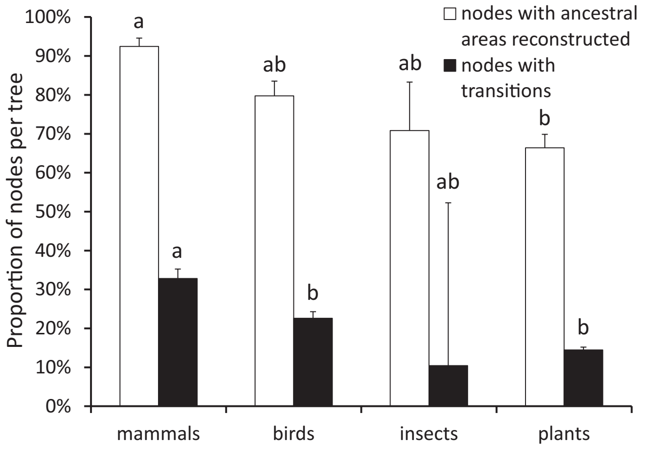

Figure 5. Proportion of nodes per phylogenetic tree for which we could reconstruct the ancestral latitudinal zone (equatorial, temperate, or transtropical), and the proportion of nodes where we inferred a transition to a new latitudinal zone in one of the daughter lineages. Error bars denote ±1 standard error, different letters above the bars indicate bars were significantly different according to one-way ANOVAs with post hoc Tukey tests ($P < 0.05$).

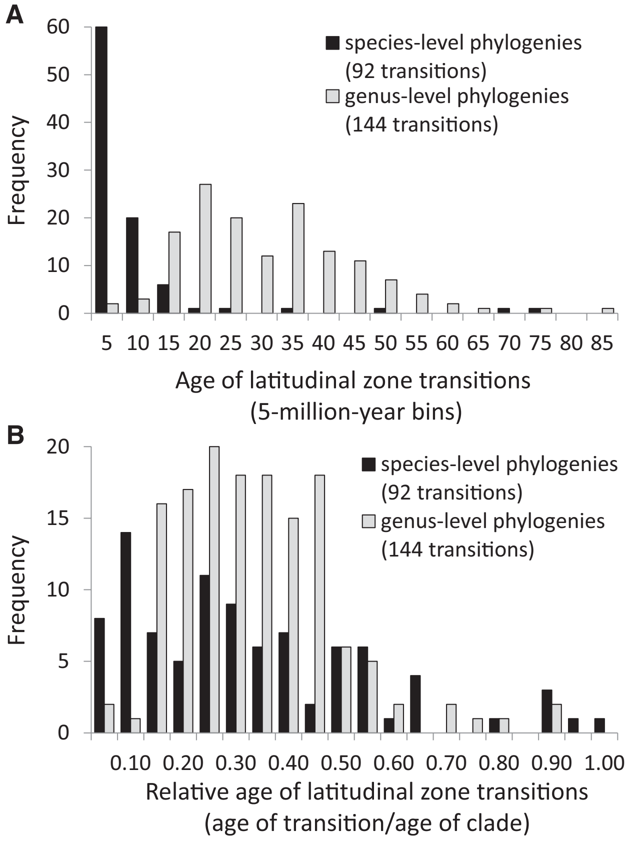

Figure 6. Age distribution of nodes where we inferred a latitudinal zone transition in phylogenetic trees with time-calibrated branch lengths and nodes. (A) Absolute age of latitudinal zone transitions. (B) Relative age of latitudinal zone transitions, scaled by the age of the clade in which the transition occurred.

by age of clade; Fig. 6B) did not differ significantly depending on whether trees were resolved to species or genus, or among taxonomic groups ($P > 0.1$, two-way ANOVA). Transitions occurred across the entire age range of the clades, with the majority of transitions in the younger 50% of the age range (Fig. 6B). The median relative age, where 0 represents the present and 1 the origin of the clade, was 0.27 for species-level transitions and 0.29 for genus-level transitions. Transitions from equatorial to transtropical (254 observed, 120 expected) as well as transitions in the opposite direction (180 observed, 120 expected) were more frequent than expected when assuming all transitions had equal probability of occurring ($\chi^2 = 293$, df $= 5$, $P < 0.0001$; Fig. 7). In contrast, we observed fewer transitions between equatorial ($n = 43$) and temperate zones ($n = 37$) than the 120 expected. These results held true also when excluding genus-level phylogenies ($\chi^2 = 115$, df $= 5$, $P < 0.0001$).

CONTRASTS IN DIVERSIFICATION RATES

When comparing sister lineages with tip taxa inhabiting different latitudinal zones, only flowering plants had higher diversification

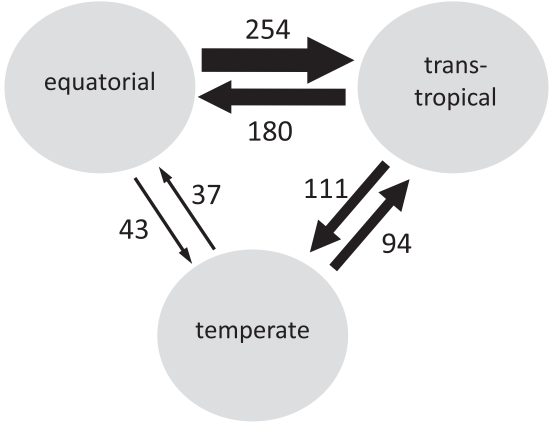

Figure 7. Frequency of different types of latitudinal zone transitions for all taxonomic groups combined. Direction of arrows denotes the type of transition (e.g., from equatorial to temperate latitudes), and the weight of arrows the frequency of the transition type, which is also given by the numbers.

in equatorial than temperate lineages as predicted by the DRH, although not significant at $\alpha = 0.05$ ($P = 0.08$, or $P = 0.12$ when excluding genus-level trees; Fig. 8E). Transtropical flowering-plant lineages diversified less than their transtropical counterparts ($P < 0.01$), and when excluding genus-level trees, also less than temperate lineages ($P = 0.027$, $n = 26$). For mammals, temperate lineages had accumulated more taxa than their equatorial sister lineages ($P < 0.05$, Fig. 8A). In birds, we found no significant differences in diversification between latitudinal zones when comparing the number of taxa at the tips of the phylogenies (Fig. 8B). However, when counting the number of species in genus-level phylogenies, we found that transtropical lineages diversified faster than equatorial and temperate ones ($P < 0.05$, Fig. 8C). Insects did not show significant differences in diversification rate between sister groups in different latitudinal zones ($P > 0.05$, Fig. 8D).

Lineages colonizing new latitudinal zones never exhibited significant increases in diversity over sister lineages remaining in the ancestral latitudinal zone and most nonsignificant differences were negative as well (Fig. 9). All significant contrasts in diversification demonstrated that lineages that switched to a new latitudinal zone diversified less ($P < 0.05$), and most nonsignificant differences were negative as well (Fig. 9). For flowering plants, higher diversification rates in equatorial lineages (Fig. 8E) were caused by constrained diversification in the lineages that shifted from equatorial to temperate or transtropical latitudinal zones (Fig. 9E). Likewise, the higher diversification in temperate than equatorial lineages in mammals (Fig. 8A) was caused by reduced diversification in lineages switching from temperate to equatorial regions (Fig. 9A). Four of the six possible geographic transitions in mammals resulted in significantly lower diversification compared to sister lineages remaining in the zone of origin. In birds, no transition resulted in significant contrasts in diversification, when counting tip taxa only ($P < 0.05$; Fig. 9B). The results remained similar when excluding genus-level phylogenies, but with lower statistical power due to smaller sample size.

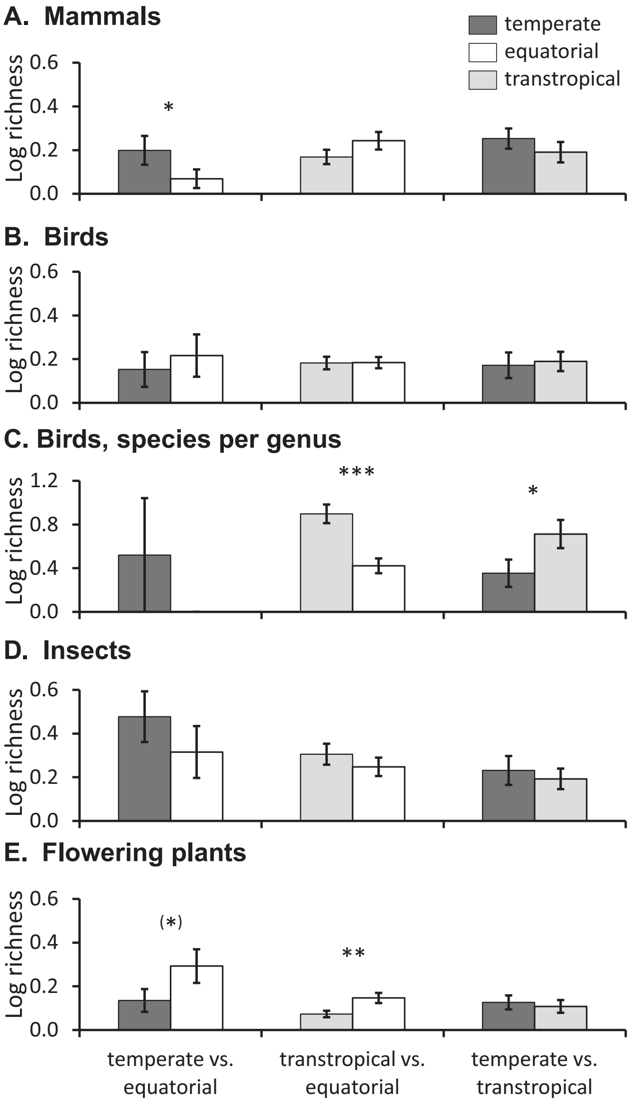

Figure 8. Log number of taxa compared pairwise between sister groups inhabiting different latitudinal zones for (A) mammals, (B) birds, (C) birds, species per genus, (D) insects, and (E) flowering plants. Error bars denote ±1 standard error. Stars denote level of significance according to Wilcoxon's signed ranks tests, testing for differences between sister taxa: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}0.01 < P < 0.05$; $(^{*})0.05 < P < 0.1$.

The only exceptions to the trend of reduced diversification following transitions were observed within bird genera, with increased species diversification (Fig. 9C) when lineages expanded from equatorial to transtropical latitudes and decreased diversity when contracting from transtropical to equatorial latitudes ($P < 0.05$). These shifts in diversification were associated with similar

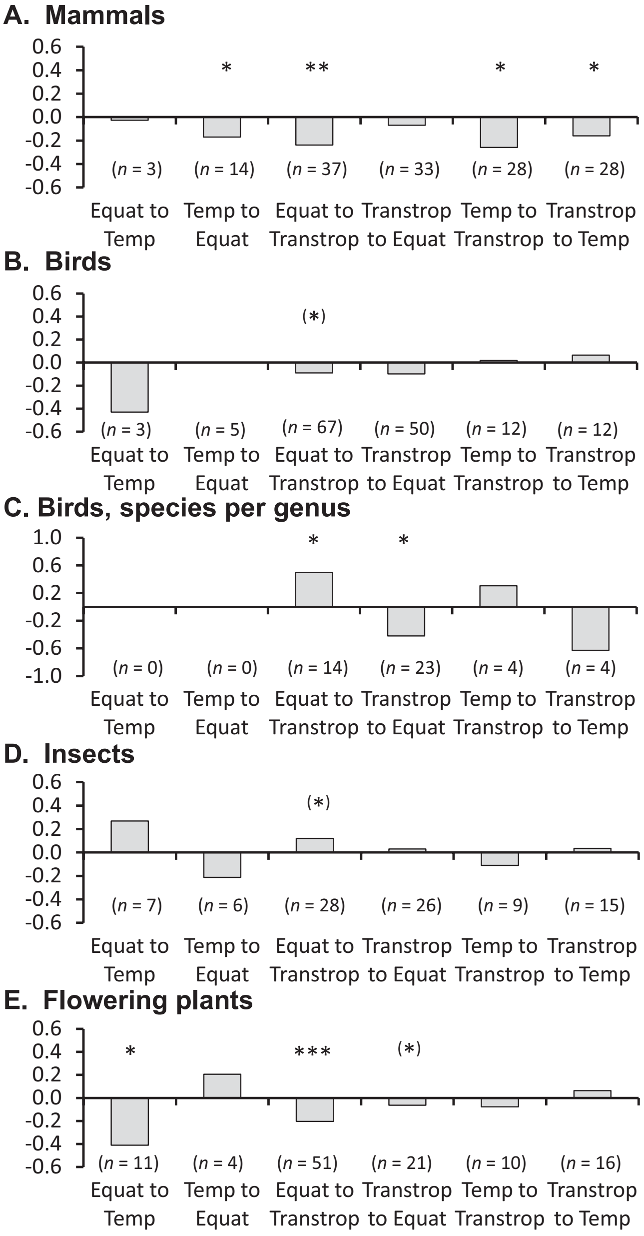

Figure 9. Ratio of log number of taxa in lineages following a transition from one latitudinal zone to another (e.g., from equatorial to temperate) over the log number of taxa in sister lineages remaining in the ancestral latitudinal zone. Equat = equatorial, Temp = temperate, and Transtrop = transtropical. Stars denote level of significance according to Wilcoxon's signed ranks tests, testing for differences between sister taxa: $^{***}P < 0.001$; $^{**}0.001 < P < 0.01$; $^{*}0.01 < P < 0.05$; $(^{*})0.05 < P < 0.1$.

shifts in the latitudinal ranges. There were enough time-calibrated phylogenies to test for a correlation between the ratio of the sister-group diversities and the age of their common ancestor for mammals and insects. We found a positive correlation for insects ($r_s = 0.33$, $P = 0.001$, $n = 87$, Spearman's rank correlation; Fig. S1A), whereas the correlation for mammals was not significant ($r_s = 0.22$, $P = 0.08$, $n = 61$, Fig. S1B). Inspection of the relationship for mammals revealed that it changed with age, with a positive correlation for sister groups ≤7 Myr old ($r_s = 0.41$, $P = 0.004$, $n = 46$), and no significant trend for older sister groups ($P > 0.05$).

The GeoSSE analyses showed that speciation and extinction rates were higher in temperate than equatorial latitudes, but diversification was positive in the equatorial zone, while close to zero in the temperate zone. Range shifts were more frequent from the equatorial to the temperate zone than vice versa (Appendix S2).

We recorded the mean latitudinal extent for 67% of the bird clades included in our study. Transtropical bird taxa at the tips of trees (either species or genera) had a latitudinal extent about twice that of equatorial ones. Lineages switching from equatorial to transtropical distributions had mean latitudinal ranges of 50.3 ± 3.6° latitude, compared to 24.5 ± 4.6° for their equatorial sister lineages ($P < 0.001$). Similarly, lineages contracting from transtropical to equatorial areas had average latitudinal ranges of 23.2 ± 2.8°, compared to 46.0 ± 4.9° for their sister lineages retaining transtropical distributions ($P < 0.0001$). Trends were similar for transitions between temperate and transtropical latitudes but not significant, due to small sample sizes.

Discussion

By sampling from a wide range of published phylogenies, we were able to infer the relative importance of longstanding hypotheses to explain the LDG, with predominant support for the OTM, whereas one or more of the predictions by the other hypotheses were rejected.

LDGS IN EXTANT TAXA

For birds, insects, and flowering plants, diversity of the selected clades peaked in the equatorial zone, in agreement with diversity patterns of the groups in general (e.g., Hillebrand 2004). A considerable proportion of taxa were classified as transtropical (Fig. 2), suggesting that such taxa are important for diversity dynamics. In the case of mammals, we found no significant difference in the number of taxa among latitudinal zones. However, the LDG in mammals is largely driven by bats, being shallow in slope if they are excluded (Buckley et al. 2010). We only had a few bat clades in our sample. Moreover, the lack of an LDG likely reflects the more extensive genetic sampling of holarctic species compared to equatorial taxa, resulting in few phylogenetic trees with significant representation of equatorial taxa in our sample.

EVOLUTIONARY TIME AND TROPICAL ORIGINS

We found strong support for the ETH (Table 1) with tropical origins of most clades and highest diversity in the latitudinal zone of origin (Fig. 4). Given that tropical habitats were more widespread during most of the Tertiary (Morley 2000), it seems likely that multiple tropical clades had a time-for-speciation-events advantage (Stephens and Wiens 2003). This result could, however, potentially be explained by the method of ancestral reconstruction, where an origin similar to the majority of taxa at the tips would be more parsimonious. Clade origins were, however, also inferred through fossils and other data presented in the phylogeny publications, and parsimony results were verified by maximum-likelihood reconstruction, making it unlikely to be an artifact.

An outstanding question is why clades tend to originate in the tropics. According to Wiens and Donoghue (2004), more clades originated in the tropics because more of the globe had tropical (or megathermal) climate early in the Tertiary than at present (Morley 2000), whereas temperate and boreal biomes have expanded in area later in the Tertiary in association with long-term global cooling (Fine and Ree 2006). Biomes having larger time-integrated area should experience higher speciation and lower extinction rates (Fine and Ree 2006), making it more likely that new clades originate. LDGs are documented also from the Palaeozoic and Mesozoic periods (Stehli et al. 1969; Crane and Lidgard 1989; Crame 2001; Leighton 2005), with first appearances of many clades in the tropics (Crane and Lidgard 1989; Jablonski 1993), and it is likely that the time-integrated area (sensu Fine and Ree 2006) was larger in tropical than temperate regions also during these periods (Willis and McElwain 2002).

Higher tropical origination rates might also be caused by other factors potentially resulting in more diversification toward lower latitudes as discussed below. Alternatively, higher tropical origination rates might result from more anagenetic change conferred by tropical environments. According to Sheldon (1996), anagenetic change is faster in more stable environments, such as the tropics, and Jansson and Dynesius (2002) argued that there is more anagenetic change in tropical lineages, experiencing less climatic variability compared to lineages at higher latitudes.

TROPICAL CONSERVATISM

The primary predictions distinguishing the TCH from the OTM were not supported: Transitions between latitudinal zones were relatively frequent, occurring at 16–31% of the nodes for which the latitudinal zone was reconstructed (Fig. 5). Moreover, latitudinal zone transitions occurred across the entire age range of trees (Fig. 6B), reflecting the age distribution of time-calibrated nodes in general. Thus, although diversity appears to be higher at equatorial compared to temperate latitudes because many clades originated there, tropical lineages frequently expanded their ranges to encompass also temperate latitudes. One should note that we did not sample clades with exclusively tropical ranges, which may exhibit the strongest niche conservatism. For example, half the families of flowering plants have no temperate representatives (Ricklefs and Renner 1994). Nevertheless, the frequency of transitions that we documented between latitudinal zones (22%) was considerably higher than that documented for transitions at plant speciation events between biomes in the Southern Hemisphere (3.6%; Crisp et al. 2009). It may be that expanding or shifting geographic range into another climatic zone requires fewer adaptations than switching to a new biome. Although it might suffice to adapt to novel temperatures when switching latitudinal position, switching biome might entail a host of adaptations to tolerate novel abiotic and biotic conditions.

Other studies may have failed to find many latitudinal transitions because they forced taxa into either a tropical or a temperate category (Jablonski et al. 2006). By adding a transtropical category and transitions to and from it, we added a geographic expansion and contraction component that may explain the deviation from the TCH. Indeed, the vast majority of transitions (84%) represented expansions of equatorial lineages into temperate latitudes or contractions of transtropical lineages to strictly equatorial distributions (Fig. 7).

OUT OF THE TROPICS

All predictions for the OTM were confirmed (Table 1). Although the model of Jablonski et al. (2006) was based on an analysis of fossil marine bivalves, our test was made using phylogenetic data. Most terrestrial clades have poor fossil records in comparison to marine bivalves, and the possibility of gleaning information from multiple phylogenies to evaluate the predictions of LDG models is important, often representing the only means of obtaining data to test hypotheses. Additionally, here we show that the OTM is relevant also in our diverse sampling of primarily nonmarine organisms.

A crucial prediction of the OTM is that a high frequency of lineages expands from equatorial latitudes to also include temperate ones. As pointed out by Jablonski et al. (2006), this distinction is made possible only by categorizing taxa that encompass both tropical and temperate latitudes separately from exclusively tropical or temperate clades.

DIVERSIFICATION RATES

Even though latitudinal zone transitions were associated with significant contrasts in diversification, we did not find support for transitions to the equatorial zone being associated with higher diversification as expected by the DRH (Table 1). The likelihood-based GeoSSE analyses on a subset of the data confirmed the results obtained by parsimony and sister-group comparisons, suggesting results were robust to choice of method (Appendix S2). We could not evaluate the results obtained for transtropical taxa due to differences in the treatment of multiregion taxa, but instead GeoSSE provided other insights: Both speciation and extinction rates were inferred to be higher at temperate than equatorial latitudes, whereas diversification did not differ significantly.

For all taxonomic groups, we found that the diversification rate often decreased following a latitudinal transition and was in no case higher for the lineage moving to a novel latitudinal zone, compared to sister lineages in the ancestral area (Fig. 9), even when lineages moved from temperate into equatorial regions. Thus, contrasts in diversification observed in the phylogenies appear to conserve ancestral differences in latitudinal diversity (reflecting clade origin). This result is counterintuitive because lineages colonizing new environments might be expected to exhibit bursts of diversification in response to novel ecological opportunity (Burbrink and Pyron 2010). Why then were most transitions between latitudinal zones associated with reduced diversification? Contrasts in diversification between sister groups may depend on the "type" of latitudinal transition: Unsurprisingly, when transitions resulted from range contraction (a clade contracting from a transtropical to an equatorial or temperate range), diversification decreased. Range contractions of mammals from transtropical to temperate latitudinal zones and from transtropical to equatorial zones in birds were associated with reduced diversification (Fig. 9A, C). Conversely, the response of lineages expanding latitudinal ranges depended on the taxonomic group. Although bird richness increased with range expansion from equatorial to transtropical zones (Fig. 9C), both mammals and flowering plants showed reduced diversification (Fig. 9A, E). This indicates that there may be a suite of ecological and evolutionary factors that influence rates of diversification with changes in latitude. In addition to diversification rates varying with the area occupied by the clade, we propose three hypotheses to explain lower diversification following latitudinal zone transitions:

(1) *The maladaptation hypothesis*—Presence of a lineage in a novel latitudinal zone may be enabled by some physiological adaptation to novel environmental conditions. Yet average clade fitness may be lower if lineages subsequently fail to respond to additional selection pressures and adapt because of constraints from other prominent characteristics or interactions (Futuyma 2010). For example, plants may adapt to tolerate frost, enabling tropical clades to colonize temperate zones, but continued diversification of the clade may be hindered by lack of adaptations necessary to outcompete or be on par in fitness with organisms having a longer history of evolution in the target latitudinal zone.

(2) *The biome affinity hypothesis*—Lineages may be able to enter a new latitudinal zone, but have niche constraints so that lineages can only occupy ancestral biomes or habitats with similar environmental conditions as in their ancestral zone. Recent evidence suggests that sister-species pairs of plants occur in the same biome as their most recent shared ancestor (>96% of cases), with biome shifts being rare even after transoceanic colonizations (Crisp et al. 2009). For example, equatorial lineages may be able to colonize warm, extratropical microclimates, and temperate lineages may colonize montane and alpine environments in the equatorial zone. However, these environmentally similar niches are likely to occupy only small areas in the novel latitudinal zones in relation to the lineage's ancestral area. Thus, given that availability of area controls diversification (Owens et al. 1999; Davies et al. 2004; Ricklefs 2006), diversification is constrained in relation to sister lineages in ancestral areas.

(3) *The high-vagility/generality hypothesis*—Taxa of high vagility (good dispersal ability and propensity) are more likely to colonize a new latitudinal zone. Likewise, generalist taxa are more likely to make transitions (Weir et al. 2009). High vagility and low specialization are often associated with strong gene flow and low divergence among gene pools, potentially reducing speciation rate (Vrba 1984; Jocque et al. 2010).

These three hypotheses are not mutually exclusive, and distinguishing among them is beyond the scope of the article. The maladaptation hypothesis could be tested by comparing traits of lineages that switched latitudinal zone with sister lineages remaining in the ancestral area and with coexisting taxa in the new latitudinal zone. The biome affinity and high-vagility/generality hypotheses are readily testable by investigating habitat associations, range sizes, vagility, and specialization in sister lineages following latitudinal zone transitions.

Previous studies have documented higher diversification in tropical than temperate clades (Cardillo 1999; Davies et al. 2004; Cardillo et al. 2005; Ricklefs 2006; Wiens 2007; Svenning et al. 2008). Furthermore, there are spectacular examples of radiation in lineages entering the tropics, such as those of plethodontid salamanders (García-Paris et al. 2000) and the plant clade Dipsacales (Moore and Donoghue 2007). Yet we failed to find increased diversification in lineages entering the equatorial zone. This could be an artifact of our sampling strategy as we only included phylogenies that contained a majority of known taxa in the clade and were well resolved (i.e., no large polytomies). In this way, we likely eliminated extremely diverse clades or groups undergoing explosive radiations, particularly in insects and plants, because they were only regionally sampled or contained large polytomies. Nevertheless, although being rare, such radiations may have profound influence on biodiversity patterns. For example, the only primarily tropical clade of salamanders, Bolitoglossinae, contains about half of all salamander species (García-Paris et al. 2000; Wiens 2007). Second, the documented examples of higher tropical diversification focused on relatively inclusive clades, such as families or higher taxa, whereas the sister lineages inhabiting different latitudinal zones identified by us were mostly nested within families or genera. This suggests there may be an interaction between the scale at which geographic patterns occur and those at which diversification contrasts are evident. First, long time periods may be needed for tropical clades to acquire a diversity advantage. Second, only few lineages in a clade may have the appropriate adaptive traits to successfully move between latitudinal zones and radiate, and inclusion of such lineages might require sampling at higher taxonomic levels. For example, frogs (order Anura) show higher diversification in tropical lineages (Wiens 2007) whereas individual frog families, such as Hylidae and Ranidae, do not. These families are inferred to be more species-rich in the tropics as a result of tropical origins and few extra-tropical colonization events (Wiens et al. 2006, 2009), but when analyzed at a higher taxonomic level, those clades contribute to a bias toward more tropical than temperate diversification.

Our finding that latitudinal zone transitions were often associated with reductions in diversification might have made our test of the DRH (Table 1) inappropriate. The logic of the test was that sister lineages should be similar in all respects except for the latitudinal distribution. However, if latitudinal zone transitions involve a penalty on the diversification of the lineage that made the transition, the comparison is not impartial. A remedy to this would be to sample lineages from each latitudinal zone across phylogenies, excluding those recently involved in transitions, record their geographic range as a proxy for ecological opportunity, and compare their diversification. This would also require having a comparable measure of diversification across lineages, for example, using only lineages with age estimates for branching events.

The fact that we found positive correlations between the ratio of sister-group diversities and the age of their common ancestors for insect sister groups evolving ≤ 7 Mya suggest that diversification grew unimpeded by ecological limits and that contrasts among sister groups could be interpreted as results of differences in speciation/extinction rates. However, the lack of relationship for mammal sister groups >7 Myr shows that, at least for organisms with large biomass, diversity does not grow unimpeded forever. However, the majority of sister groups were younger than 7 Myr, suggesting little overall influence of diversification slowdown on our results.

Conclusions

By sampling from many phylogenies, we were able to test predictions and elucidate patterns not possible in a detailed analysis of a single clade. Patterns within single clades do not give information about the generality of different mechanisms to explain large-scale diversity patterns. Moreover, data from 111 phylogenetic studies revealed novel patterns: That clade origin and decreased diversification in clades shifting to novel latitudes work in concert to preserve the latitudinal bias in biodiversity is evident in our collective phylogenetic sample. Although one may sacrifice some of the precision and sophistication common in focused phylogeographic analyses, pooling data extracted from topologies across a variety of taxa can reveal macroevolutionary processes driving global diversity patterns among clades.

We were able to reject the primary predictions of both the TCH and DRH, whereas the OTM was supported. Our results shed new light on how LDGs are generated and maintained. First, most taxa originated in the equatorial zone, and most clades peak in diversity in the zone of origin, supporting the ETH. Second, we found transitions between latitudinal zones to be relatively frequent, suggesting that adapting to new climatic conditions per se may not be a major obstacle in many clades. However, most of these transitions represent range expansions out of the equatorial zone to encompass temperate areas, or extinctions from extratropical latitudes. Binning taxa in exclusively tropical and temperate categories would mask such dynamics.

Contrasts in diversification rate between sister lineages inhabiting different latitudinal zones were common, but did not conform to higher diversification in tropical lineages as expected with the DRH. In contrast, transitions were often associated with reductions in diversification rates, irrespective of the direction of the transition, suggesting an evolutionary cost or disadvantage to lineages involved in transitions. That latitudinal zone transitions are frequent, but that lineages fail to diversify following latitudinal zone switches can be considered a new mechanism for why diversity tends to peak in the zone of origin. Alternatively, it may be considered a different type of niche conservatism, in which lineages frequently expand their niches or geographic ranges to include new climatic zones, but fail to diversify as a result of the adaptations allowing range expansion. Future studies should investigate diversification contrasts between lineages involved in latitudinal zone transitions and those remaining in their zone of origin to formally test the implications of niche conservatism versus latitudinal range expansion on diversity.

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LITERATURE CITED

Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. Proc. Natl. Acad. Sci. USA 103:9130–9135.

Barraclough, T. G., A. P. Vogler, and P. H. Harvey. 1998. Revealing the factors that promote speciation. Philos. Trans. R. Soc. B. 353:241–249.

Böhm, M., and P. J. Mayhew. 2005. Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata: Cercopithecidae). Biol. J. Linnean Soc. 85:235–246.

Buckley, L. B., T. J. Davies, D. D. Ackerly, N. J. B. Kraft, S. P. Harrison, B. L. Anacker, H. V. Cornell, E. I. Damschen, J. A. Grytnes, B. A. Hawkins, et al. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proc. R. Soc. Lond. B. 277:2131–2138.

Burbrink, F. T., and R. A. Pyron. 2010. How does ecological opportunity influence rates of speciation, extinction, and morphological diversification in New World ratsnakes (tribe Lampropeltini)? Evolution 64:934–943.

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

Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in diversification rates: an example using New World birds. Ecology 86:2278–2287.

Cooper, H. M. 1998. Synthesizing research: a guide for literature reviews. 3rd ed. Sage Publications, Thousand Oaks.

Crame, J. A. 2001. Taxonomic diversity gradients through geological time. Divers. Distrib. 7:175–189.

Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246:675–678.

Crisp, M. D., M. T. K. Arroyo, L. G. Cook, M. A. Gandolfo, G. J. Jordan, M. S. McGlone, P. H. Weston, M. Westoby, P. Wilf, and H. P. Linder. 2009. Phylogenetic biome conservatism on a global scale. Nature 458:U754–U790.

Davies, T. J., V. Savolainen, M. W. Chase, J. Moat, and T. G. Barraclough. 2004. Environmental energy and evolutionary rates in flowering plants. Proc. R. Soc. Lond. B 271:2195–2200.

Dynesius, M., and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Natl. Acad. Sci. USA 97:9115–9120.

Farrell, B. D., and C. Mitter. 1993. Phylogenetic determinants of insect/plant community diversity. Pp. 253–266 *in* R. E. Ricklefs, and D. Schluter, eds. Species diversity in ecological communities. Chicago Univ. Press, Chicago.

Fine, P. V. A., and R. H. Ree. 2006. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. Am. Nat. 168:796–804.

Fischer, A. G. 1960. Latitudinal variation in organic diversity. Evolution 14:64–81.

Francis, A. P., and D. J. Currie. 2003. A globally consistent richness-climate relationship for angiosperms. Am. Nat. 161:523–536.

Futuyma, D. J. 2010. Evolutionary constraint and ecological consequences. Evolution 64:1865–1884.

García-Paris, M., D. A. Good, G. Parra-Olea, and D. B. Wake. 2000. Biodiversity of Costa Rican salamanders: implications of high levels of genetic differentiation and phylogeographic structure for species formation. Proc. Natl. Acad. Sci. USA 97:1640–1647.

Goldberg, E. E., L. T. Lancaster, and R. H. Ree. 2011. Phylogenetic inference of reciprocal effects between grographic range evolution and diversification. Syst. Biol. 60:451–465.

Hawkins, B. A. 2001. Ecology's oldest pattern? Endeavour 25:133–134.

Hawkins, B. A., and P. J. DeVries. 2009. Tropical niche conservatism and the species richness gradient of North American butterflies. J. Biogeogr. 36:1698–1711.

Hawkins, B. A., J. A. F. Diniz, C. A. Jaramillo, and S. A. Soeller. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. J. Biogeogr. 33:770–780.

Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170:S16–S27.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163:192–211.

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

Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314:102–106.

Jansson, R., and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annu. Rev. Ecol. Syst. 33:741–777.

Jocque, M., R. Field, L. Brendonck, and L. De Meester. 2010. Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? Glob. Ecol. Biogeogr. 19:244–252.

Latham, R. E., and R. E. Ricklefs. 1993. Continental comparison of temperate-zone tree species diversity. Pp. 294–314 *in* R. E. Ricklefs, and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

Leighton, L. R. 2005. The latitudinal diversity gradient through deep time: testing the "Age of the Tropics" hypothesis using Carboniferous productidine brachiopods. Evol. Ecol. 19:563–581.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50:913–925.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. Available at http://mesquiteproject.org.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.

McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. Proc. Natl. Acad. Sci. USA 99:6070–6074.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10:315–331.

Moore, B. R., and M. J. Donoghue. 2007. Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. Am. Nat. 170:S28–S55.

Morley, R. J. 2000. Origin and evolution of tropical rain forests. John Wiley and Sons, Chichester.

Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proc. R. Soc. Lond. B. 266:933–939.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Rabosky, D. L. 2009. Ecological limits and diversifcation rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecol. Lett. 12:735–743.

Ricklefs, R. E. 2006. Global variation in the diversification rate of passerine birds. Ecology 87:2468–2478.

Ricklefs, R. E., and S. S. Renner. 1994. Species richness within families of flowering plants. Evolution 48:1619–1636.

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

Roy, K., D. Jablonski, and J. W. Valentine. 1996. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. Philos. Trans. R. Soc. Lond. B. 351:1605–1613.

Sheldon, P. R. 1996. Plus ça change—a model for stasis and evolution in different environments. Palaeogeogr. Palaeoclimatol. Palaeoecol. 127:209–227.

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

Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. Am. Nat. 161:112–128.

Stuart-Fox, D., and I. P. F. Owens. 2003. Species richness in agamid lizards: chance, body size, sexual selection or ecology? J. Evol. Biol. 16:659–669.

Svenning, J. C., F. Borchsenius, S. Björholm, and H. Balslev. 2008. High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. J. Biogeogr. 35:394–406.

Vamosi, S. M. 2007. Endless tests: guidelines for analysing non-nested sister-group comparisons. An addendum. Evol. Ecol. Res. 9: 717–717.

Vamosi, S. M., and J. C. Vamosi. 2005. Endless tests: guidelines for analysing non-nested sister-group comparisons. Evol. Ecol. Res. 7:567–579.

Vrba, E. S. 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammailia: Bovidae). Pp. 62–78 *in* N. Eldredge, and S. M. Stanley, eds. Living fossils. Springer, New York, New York.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Weir, J. T., E. Bermingham, and D. Schluter. 2009. The Great American Biotic Interchange in birds. Proc. Natl. Acad. Sci. USA 106:21737–21742.

Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. Am. Nat. 170:S86–S106.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36:519–539.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19:639–644.

Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat. 168:579–596.

Wiens, J. J., J. Sukumaran, R. A. Pyron, and R. M. Brown. 2009. Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). Evolution 63:1217–1231.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J. A. Grytnes, S. P. Harrison, et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13:1310–1324.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34:273–309.

Willis, K. J., and J. C. McElwain. 2002. The evolution of plants. Oxford Univ. Press, Oxford.

Wright, S., J. Keeling, and L. Gillman. 2006. The road from Santa Rosalia: a faster tempo of evolution in tropical climates. Proc. Natl. Acad. Sci. USA 103:7718–7722.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Selection of phylogenetic trees.

Appendix S2. Rates of speciation, extinction, and latitudinal zone transitions compared between temperate and equatorial latitudes using GeoSSE.

Table S1. Data on the phylogenies and sister groups extracted from the 111 phylogenetic studies selected for study.

Table S2. Explanations for each column of data in Table S1.

Figure S1. Relationship between ratio of sister group diversity and age of common ancestor for insects and mammals.