

TESTING FOR LATITUDINAL BIAS IN DIVERSIFICATION RATES: AN EXAMPLE USING NEW WORLD BIRDS

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Abstract. Study of the latitudinal diversity gradient to date has focused largely on pattern description, with relatively little work on the possible mechanisms underlying the pattern. One proximate mechanism is a latitudinal bias in the discrepancy between speciation and extinction rates, leading to higher rates of species diversification toward lower latitudes. Despite being central to many explanations for high tropical diversity, this mechanism is tested very rarely. We discuss some of the problems involved in testing for latitudinal bias in diversification rates and present an example phylogenetic analysis for endemic bird genera of the New World. The results provide evidence for higher diversification rates in clades inhabiting lower latitudes, both when genera are considered independent and when phylogeny is controlled for using independent contrasts. High rates of diversification are also associated with larger geographic area and higher net primary productivity, although these do not fully account for the latitudinal effect. The latitudinal pattern is stronger in younger clades, supporting the prediction of a simple model in which the signal of latitudinal bias in diversification rates diminishes as clades age and become saturated with species. Our study demonstrates that a clade-based approach can help answer important questions that a geographic approach cannot, but large phylogenies and geographic databases are needed to cope with the large amount of noise inherent in this type of analysis.

Key words: diversification; extinction; latitudinal diversity gradient; New World birds; speciation; species richness.

INTRODUCTION

Explaining why there are more species in the tropics compared to higher latitudes is one of the great contemporary challenges of ecology. The continuing strong interest in the latitudinal diversity gradient is demonstrated by the large number of papers recently published on the topic, the frequent publication of reviews (Rohde 1992, 1999, Rosenzweig 1995, Gaston 2000, Willig et al. 2003), and the regular emergence of novel hypotheses to explain the pattern (Stevens 1989, Colwell and Hurtt 1994, Dynesius and Jansson 2000, Guernier et al. 2004). Although the pattern remains famously poorly explained, slow progress towards a solution is being made. For example, recent analyses of large data sets point increasingly towards climate rather than geographic area as the major driving force of higher tropical species richness (Hawkins and Porter 2001, Macpherson 2002, Francis and Currie 2003, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b, Hawkins and Porter 2003). However, much uncertainty remains. In particular, the mechanisms by which latitudinal variation in climate determines species numbers largely remain a mystery: far less effort

has been spent on empirical testing of possible mechanisms than on pattern description and correlative tests.

In this paper, we focus on the idea that the proximate mechanism for the latitudinal diversity gradient is a higher rate of species diversification at lower latitudes, where diversification is defined as the discrepancy between speciation and extinction rates. A latitudinal bias in diversification rate is central to a number of high-profile explanations for high tropical species richness. Rosenzweig's (1992, 1995) area hypothesis states that the larger geographic distributions attainable by tropical species serve both to elevate speciation rates (by increasing the likelihood of allopatric subdivision) and reduce extinction rates (by providing a buffer against range or population decline). The species–energy hypothesis (Wright 1983, Wright et al. 1993) proposes that extinction rates are reduced in lower latitude species as a result of the higher populations sustainable by the greater amount of available energy. Rohde (1992, 1999) suggests that speciation rates at lower latitudes are elevated by shorter generation times driven by higher temperatures. Other authors have predicted higher extinction rates at high latitudes due to “harsher” or more variable climatic conditions (Craft 1985, Dynesius and Jansson 2000).

Despite being central to many explanatory hypotheses, faster diversification is not a necessary precondition for higher species richness at lower latitudes.

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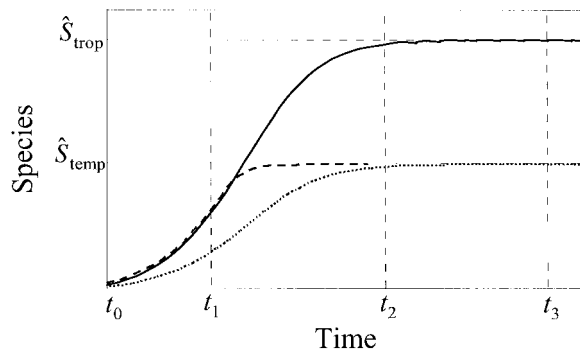


FIG. 1. Simple model of the growth in the number of species in tropical and temperate regions or clades, from zero to saturation levels (\hat{S}_{trop} and \hat{S}_{temp}). The solid curve represents diversification of tropical groups, the dotted curve represents diversification of temperate groups when a latitudinal bias in diversification rate exists, and the dashed curve represents diversification of temperate groups when there is no latitudinal bias.

This can be visualized using the simple model shown in Fig. 1. The number of species in a region increases from zero to a saturation level where rates of speciation and extinction are in equilibrium. The inherent diversification rate of the temperate region may be equal to (dashed line) or lower than (dotted line) that in the tropics, but a lower saturation level keeps temperate species richness below that in the tropics. This model can be applied equally to the growth of individual clades. A regional assemblage of species consists of numerous clades, at different stages along this trajectory. Below saturation (e.g., at time t_1), any inherent variation in diversification rate between tropical and temperate clades should be easily detectable as latitudinal differences in mean diversification rates over the lifetime of clades (the period from t_0 to t_1). When saturation is reached (time t_2), the diversification rate of temperate and tropical clades at that point in time will be equal (speciation minus extinction = 0), but comparisons of mean diversification rates over the lifetime of clades (the period from t_0 to t_2) should still carry the signal of any inherent latitudinal bias. This signal will diminish in strength after long periods at saturation (time t_3). This model therefore predicts that any latitudinal bias in diversification rates should be most strong among younger clades, which have yet to become, or have only recently become, saturated with species. It also demonstrates that latitudinal variation in species numbers can arise without any latitudinal bias in diversification rates. Establishing whether or not diversification rates show latitudinal bias, therefore, is an important step in understanding the origin of the latitudinal diversity gradient.

TESTING FOR LATITUDINALLY BIASED DIVERSIFICATION RATES

Given its central position in many hypotheses to explain the latitudinal diversity gradient, it is surprising

that direct empirical tests for latitudinal bias in diversification rates are relatively scarce. Previous tests are almost entirely confined to the paleontological literature, and these have tended to support higher diversification rates in the tropics. Faster tropical diversification has been implied by lower average taxon ages or higher rates of first appearances in the tropics (Stehli et al. 1969, Durazzi and Stehli 1972, Hecht and Agan 1972, Jablonski 1993, Flessa and Jablonski 1996), or from a higher rate of diversity accumulation through time in tropical groups (Crame 2000, 2001, Buzas et al. 2002).

An alternative approach is to infer diversification rates using the information contained within phylogenies of extant taxa. Using phylogenetic methods allows tests to be done for groups with a poor or unreliable fossil record (e.g., the majority of terrestrial vertebrates). Whereas paleontological analyses are usually geographic (involving the comparison of assemblages across different geographic regions or grid cells), phylogenetic analyses are explicitly clade based. The mean diversification rate of a clade throughout its history is a function of its age and number of extant species. In the absence of dated phylogenies, sister-clade comparisons are often used to infer relative diversification rates, an approach that is now standard practice in comparative tests of the effects of life history or ecological traits on diversification rates (see Barraclough et al. 1998).

However, testing for geographic variation in diversification rates by this method presents additional difficulties and has received very little attention. As far as we are aware, only three times has latitude been tested explicitly as a predictor of diversification rates using phylogenetic methods. Farrell and Mitter (1993) attempted the first such test by identifying five tropical–temperate pairs of sister clades of phytophagous insects, but with such a small sample their result was inconclusive. Cardillo (1999) extended this approach to passerine birds and swallowtail butterflies, and increased the number of useful sister-clade comparisons by treating latitude as a continuous variable, measured as the midpoint between the northern and southern limits of the geographic range of each species. This study suggested that lower latitudes were indeed associated with higher rates of diversification. Most recently, Davies et al. (2004b) used a similar approach on a much larger data set for angiosperm families (see also Davies et al. 2004a). Again, this analysis suggested a link between latitude and diversification rates, although the test for latitudinal variation of Davies et al. (2004b) was incidental to an analysis of the effects of environmental energy. Taken together these three studies serve to highlight a number of challenges in doing comparative tests that are both phylogenetically and geographically explicit. These challenges may be summarized as follows. (1) *Phylogenetic accuracy*. As with any phylogenetic comparative analysis, the reliability of sister-

clade groupings and branch lengths (where used) are contingent on the quality of the phylogeny used. Different types of data and methods of phylogeny reconstruction may give conflicting results. However, the need for large phylogenies to identify a sufficient number of comparisons usually means there is little or no choice available in the selection of a phylogeny, and the limitations of the phylogeny used must be acknowledged and accepted. This is changing with the routine application of robust phylogenetic reconstruction methods. (2) *Loss of data*. In Cardillo's (1999) analysis, the use of pairwise comparisons required the imposition of strict criteria of latitudinal separation and overlap between sister clades. As a result, only a small subset of available sister-clade contrasts were permissible, so even with a large phylogeny, sample sizes were small and statistical power low. Restricting an analysis to comparisons between non-overlapping tropical-temperate sister clades, as attempted by Farrell and Mitter (1993), is unlikely to produce enough comparisons for an acceptable statistical test, even with the largest phylogenies currently available. However, this is changing with the increasing use of supertree methods to construct large phylogenies (e.g., Davies et al. 2004b). (3) *Summarizing clade latitude*. For use as a continuous predictor variable in statistical models, the range of latitudes inhabited by each clade must be summarized as a point estimate. Cardillo (1999) did this by using the mean of the latitudinal midpoints of all member species within a clade. Latitudinal midpoint is a relatively accurate point estimate for a species where its geographic range is small and circular, with a low perimeter:area ratio. However, many species have ranges that are irregularly shaped with respect to latitude. For example, a species may be found almost entirely in the tropics where it occupies a circular range, but with a narrow coastal band extending into high latitudes. In this case, latitudinal midpoint is a misleading summary of where the bulk of the area of the range of a species lies. (4) *Latitudinal overlap*. Even where latitudinal point estimates differ between two clades, there may still be substantial latitudinal overlap in their geographic ranges, although this probably elevates Type 2 rather than Type 1 statistical error (Cardillo 2002). The likelihood of substantial latitudinal overlap will be lower where geographic ranges are mostly relatively small. (5) *Accuracy of geographic range estimates*. Although distributions are well-known for some well-studied taxa in some parts of the world, other taxa have relatively few records and some parts of the world are poorly surveyed. Geographic distributions are often presented as the extent of occurrence (i.e., polygons drawn around a number of occurrence records from single, often widely separated, locations). This implies that the species inhabits a continuous distribution within the polygon boundaries, which may not be true. Even so, extent of occurrence maps may reflect historical distributions if the isolated populations have become

separated from a once continuous distribution (e.g., as a result of habitat fragmentation). (6) *Dynamic range boundaries*. Geographic ranges are unlikely to be static over long periods of time, but expand and contract in response to environmental changes or as the result of speciation events (Price et al. 1997, Gaston 1998). Even if the contemporary range of a species is mapped with accuracy, is difficult to know how well it represents the range that the species has occupied throughout its history. (7) *Environmental drivers of latitudinal patterns*. Although Cardillo's (1999) analysis supported a latitudinal bias in diversification rate, it went no further in testing possible causes of this pattern. Ultimately, it is not latitude itself, but the underlying environmental gradients or historical factors that are of interest in explaining the geographic distribution of species richness (Hawkins and Diniz-Filho 2004). As with latitude, there may be substantial error variance around a point estimate of the range of environmental conditions experienced by a species.

AN EXAMPLE USING NEW WORLD ENDEMIC BIRD CLADES

Methods

We present here an example of an approach to testing for latitudinal bias in diversification rates using phylogenetic methods, which attempts to improve on the analysis of Cardillo (1999) by dealing with some of the challenges (2, 3, and 7) shown in the previous section. We focused on endemic bird clades of the New World, since the geographic distributions of birds in the New World are relatively well-known, and restricting the analysis to the endemics of a single region provided a measure of control for possible biogeographic and historical influences (Hawkins et al. 2003b). We chose genus as the taxonomic level of the analysis, primarily for the larger number of endemic New World clades (hence larger sample size) available at lower taxonomic levels. In addition, species within genera tend to occupy a more restricted range of latitudes than species within higher taxa, so the problems of latitudinal overlap among clades and variation around the point estimate of the latitude of a clade are likely to be less severe.

To avoid the loss of data involved with choosing latitudinally separated pairs of sister clades from a phylogeny, we estimated absolute rates of species diversification of clades using a dated phylogeny. Using this approach allowed us to treat each clade as an independent observation in the analysis. Of course, any phylogenetic bias in diversification rates and latitude would violate this assumption of independence, so we repeated analyses using phylogenetically independent contrasts. We estimated clade ages using the DNA hybridization phylogeny of Sibley and Ahlquist (1990). The differences in melting temperatures of hybridized DNA between pairs of taxa (ΔT_{50H}) were converted to

millions of years (10^6 yr) using the calibration factors suggested by Sibley and Ahlquist: $\Delta T_{50}H 1.0 = 2.3 \times 10^6$ yr for passerines and $\Delta T_{50}H 1.0 = 4.2 \times 10^6$ yr for nonpasserines. Species diversification rate was then estimated for each clade as $\ln(\text{number of species})/\text{age}$ (Purvis 1996). We only accepted an age estimate for a clade from the Sibley and Ahlquist phylogeny if its sister clade was also present in the phylogeny, as the absence of the sister clade means that the age of a clade will appear artificially high, giving misleadingly low estimates of diversification rates. We established whether the sister of each clade was present in the Sibley and Ahlquist phylogeny by using the Sibley and Monroe (1990) classification of birds to determine the full list of genera within the next most inclusive taxon (usually a tribe or subfamily). If all other genera within the next most inclusive taxon were represented in the Sibley and Ahlquist phylogeny, we accepted the age estimate of the clade because its sister clade must be present. In some cases, if not all genera were present in Sibley and Ahlquist, we were able to refer to independent phylogenies to determine the sister of a clade. In this way, we were able to estimate ages for 37 New World endemic genera. We are conscious of the uncertainty of date estimates derived from DNA hybridization data, and of criticisms of some of the methods used by Sibley and Ahlquist (see O'Hara 1991). However, this phylogeny is currently the largest available for birds built using a single method, and thus the only one with which a test such as this can be carried out (see Bennett and Owens 2002). We emphasize that the analysis we present here is illustrative, and that the same approach can be applied with new and perhaps more rigorous dated phylogenies as they become available.

All geographic data were processed within a geographic information system. This had several important advantages over the analysis of Cardillo (1999): it allowed species latitudes to be measured more accurately, and it allowed us to include geographic area and climatic factors as covariates in the analysis. The geographic range characteristics for the clades were measured as follows, using polygon range data from Ridgley et al. (2003). First, we measured the latitude of the centroid of the breeding range of each species, a more accurate characterization of the latitude of a species than latitudinal midpoint when ranges are irregularly shaped. The latitude of each clade was then summarized as the mean of the species latitudinal centroids; effectively providing a measure that is weighted by species richness. We then measured the total geographic area occupied by each clade, a factor shown to be a significant predictor of diversification rates among bird families (Owens et al. 1999, Bennett and Owens 2002). The non-overlapping breeding ranges of species were combined into a single range for each clade, which was then reprojected into a Lambert Azimuthal Equal Area projection with central meridian and parallel set to the

centroid of the clade range. The area of the reprojected range was then recorded in km^2 . We included measures of three climatic factors, in order to test possible underlying causes of any latitudinal bias in diversification rates: mean annual temperature, annual actual evapotranspiration (AET), and annual net primary productivity (NPP), all of which have previously been shown to be correlated with species richness at large scales (Currie 1991, Wright et al. 1993, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b) or suggested to influence rates of speciation or extinction (Currie 1991, Rohde 1992, 1999, Wright et al. 1993). All three climatic variables were recorded as raster data on geodesic grids. The temperature and AET data (0.5° resolution) were from the United Nations Environment Program GRID databases (UNEP 2003), and the NPP data (1° resolution) were from Woodward et al. (1995). Estimates of climatic variables for each species were obtained by converting the breeding range for the species and each climatic variable onto a 0.05° grid and then calculating the mean value across the cells occupied by the species. We then summarized the variable for each clade as the mean of the member species values. All the above analyses were performed using ArcMap 8.2 (ESRI 2002).

We tested for associations between diversification rate and predictor variables using multiple linear regressions. We first examined histograms of all variables and univariate plots against diversification rate to determine the most suitable transformations to stabilize variances and normalize error distributions, and to test for second- and third-order polynomial effects. A minimum adequate model (MAM) was found by fitting all predictors, then sequentially removing each predictor that contributed the smallest amount of marginal variance to the model until all remaining predictors were significant at $P \leq 0.05$. We then reintroduced predictors, and interaction terms, one at a time and tested the model for significance each time.

Because of the possibility of phylogenetic bias in diversification rates, we repeated these tests using phylogenetically independent contrasts, calculated using software written in R by A. Purvis (*available online*).⁵ All regressions on independent contrasts were forced through the origin (Garland et al. 1992). Because we did not use a complete phylogeny, we could not test clade area as a predictor of diversification rate using independent contrasts calculated for internal nodes. Our independent-contrasts tests using clade area are therefore restricted to contrasts calculated for terminal nodes only.

A prediction of the model presented in the *Introduction* is that the strength of any latitudinal bias in diversification rates, measured as the mean rate over the lifetime of a clade, will depend on the point at which most clades appear along the trajectory shown in Fig.

⁵ <http://www.r-project.org/>

TABLE 1. (A) Cross-taxon results and (B) independent-contrasts results for separate effects of latitudinal centroid, clade area, mean annual temperature, annual actual evapotranspiration (AET), and net primary productivity (NPP) on bird diversification rates.

Variable	Entire data set			Monospecifics excluded		
	Coefficient	<i>t</i>	<i>r</i> ²	Coefficient	<i>t</i>	<i>r</i> ²
A) Cross-taxon results						
Latitude (degrees from equator)	-0.06	-2.31*	0.108	-0.04	-1.5	0.054
Clade area (km ² × 10 ⁶)	0.008	1.8†	0.059	0.007	1.68	0.077
Temp (°C)	0.05	0.61	0	0.05	0.56	0
AET (mm)	0.09	1.52	0.035	0.08	0.98	0
NPP (kg C/m ²)	0.11	1.93†	0.07	0.11	1.19	0.018
B) Independent-contrasts results						
Latitude (degrees from equator)	-0.06	-2.38*	0.118	-0.04	-1.64	0.074
Clade area (km ² × 10 ⁶)	0.02	3.02*	0.447			
Temp (°C)	0.05	0.57	0	0.04	0.59	0
AET (mm)	0.1	1.55	0.039	0.05	0.77	0
NPP (kg C/m ²)	0.16	2.83**	0.167	0.07	1.01	0.001

Notes: Results are shown for regressions of each variable using the entire data set ($n = 37$ clades and 35 contrasts for cross-taxon and independent-contrasts tests, respectively), and with monospecific clades excluded ($n = 23$ clades and 21 contrasts). Independent-contrasts results for clade area are for terminal nodes only ($n = 10$ contrasts; degrees of freedom was too low for the test with monospecific clades excluded). All predictors except clade area are ln-transformed; the diversification rate is square-root transformed.

* $P \leq 0.05$; ** $P \leq 0.01$.

† $P \leq 0.1$.

1. We expect the signal of any latitudinal bias in diversification rate to be weaker among older clades that are more likely to have been at saturation levels for a long time, and stronger among younger clades. To test for any such age effects, we included clade age and latitude × clade age interaction terms in the models together with latitude. We also tested the effect of latitude on diversification rate separately for clades younger and older than the median genus age of 23.52×10^6 yr for cross-taxon tests, and the median nodal age of 39.48×10^6 yr for independent-contrasts tests.

Results

Latitude, clade area, and net primary productivity (NPP) were significantly associated with diversification rate as single predictors (Table 1, Figs. 2, 3). Diversification rate was significantly higher in clades with lower latitudinal centroids, both in cross-taxon tests ($P = 0.027$) and independent-contrasts tests ($P = 0.023$). For both clade area and NPP, positive associations with diversification rate were marginally nonsignificant in cross-taxon tests ($P = 0.08$ for clade area and $P = 0.062$ for NPP), but significant when independent contrasts were used ($P = 0.015$ and $P = 0.008$). Area explained a substantial proportion of the variance in diversification rate when independent contrasts were used (44.7%), although because only terminal nodes were used, the power of this test was low. Actual evapotranspiration (AET) and temperature were not significantly associated with latitude as single predictors in cross-taxon tests or in independent-contrasts tests.

One feature of our data set is the large proportion of genera with only one species, which tend to have higher latitudinal centroids than the majority of genera (Fig. 2). To examine the degree to which these genera

drive the negative association between latitude and diversification rate, we repeated the tests with the 14 monospecific genera dropped from the analysis. For most predictors, slopes became slightly flatter and the significant associations with diversification rate disappeared, although the power of the tests to detect significant associations also declined substantially (Table 1).

Latitude was significantly associated with diversification rate when included with other variables in multiple regression models (Table 2). In cross-taxon analyses, the only independent predictors included in the final minimum adequate model (MAM) were latitude, clade age, and a positive latitude × clade age interaction term. The positive interaction indicates that the slope of the latitudinal effect on diversification rate is more steeply negative for younger clades, supporting the prediction of the model shown in Fig. 1. In analyses using independent contrasts, the MAM included latitude and a positive, nonlinear effect of NPP on diversification rate.

The effect of clade age on the strength of the latitude–diversification rate association was corroborated by separate tests on young and old clades (Table 3, Fig. 2). In both cross-taxon tests and independent-contrasts tests, there was a significant positive association between latitude and diversification rate among young clades, but no significant association among old clades.

DISCUSSION

The analysis we present here is an example of how phylogenetic methods can be used to test for latitudinal or other geographic trends in species diversification rates. Within the limitations of the data set, our analysis points to faster diversification in clades of New World

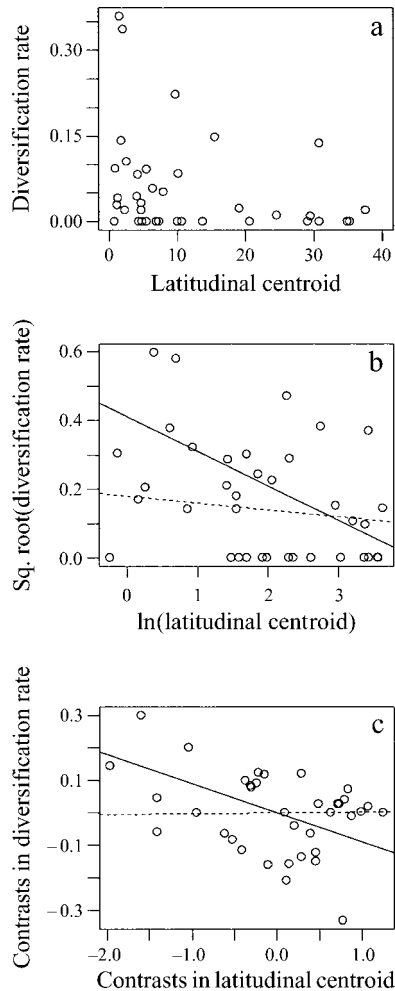


FIG. 2. Association between latitude (mean latitude of species geographic centroids) and diversification rate ($\ln[\text{species}]/10^6 \text{ yr}$), among New World endemic bird clades: (a) the association in arithmetic space; (b) the association with axes square-root transformed as in the analysis, with regression lines for young clades (solid line) and old clades (dashed line); (c) the association using phylogenetically independent contrasts, with regression lines for young and old clades.

endemic birds that inhabit lower latitudes. This pattern is found regardless of whether diversification rates are considered to be independent of phylogeny, or phylogeny is controlled for using independent contrasts. It also appears that the association between latitude and diversification rate is stronger among younger clades, supporting the prediction that the association should diminish as clades age beyond the point at which they become saturated with species.

The pattern of higher rates of diversification at low latitudes that we have detected here does appear to be driven, at least in part, by the tendency for monospecific clades to inhabit higher latitudes. Although clades that are currently monospecific may well have undergone periods of rapid cladogenesis, they have an ap-

parent diversification rate of zero, since any speciation events have been balanced by extinctions. However, because these clades do vary in age and we have no way of knowing how imminent the next bifurcation event might be, any real variation in diversification rate among monospecific clades may be obscured. Nevertheless, weakening of the latitude–diversification rate association when monospecific clades are dropped does not, in our view, necessarily nullify the result obtained when all clades are included in the analysis. The tendency for monospecific clades to be found at higher latitudes than most other clades in our data set is consistent with latitudinal variation in diversification rates. Furthermore, there is still a positive latitude–diversification rate slope with monospecific clades excluded, and the fact that this slope is not significantly different from zero may result simply from the substantially reduced power of the test. This underscores the importance of large phylogenetic and geographic data sets in testing for geographic variation in diversification rate: with larger data sets, the influence of monospecific clades on patterns of diversification rate will be testable with more power.

A potential problem of using molecular data to estimate the ages of bird clades is the possibility of latitudinal bias in rates of molecular evolution, and thus in estimates of diversification rate. For example, higher temperatures at low latitudes may lead to faster individual growth rates and shorter generation times, which could speed the rate of molecular evolution (Rohde 1992). However, Bromham and Cardillo (2003) have recently examined this possibility and found no evidence for latitudinal bias in rates of molecular evolution in birds, using both DNA hybridization data and molecular sequence data. In any case, any such bias would be likely to be conservative, as a higher rate of molecular evolution at lower latitudes would increase estimates of node ages, making diversification rates of lower latitude clades appear artificially low. Therefore, we do not believe that our result could have been an artifact of latitudinal bias in rates of molecular evolution.

One assumption that many phylogenetically based analyses of geographic patterns must make is that contemporary geographic ranges of species represent, at least approximately, the distributions species have occupied throughout their histories. Unfortunately, we do not know the extent to which this is true, given that geographic ranges expand, contract, and shift over time (Price et al. 1997, Gaston 1998). Furthermore, climatic zones are also nonstatic: within the lifetimes of many of the genera included in our analyses, there have been periods when climatic conditions we now consider “tropical” extended to far higher latitudes than they do today (Brown and Lomolino 1998). Ideally, an analysis such as ours would make use of reliably reconstructed paleodistributions and paleoclimates to summarize the mean latitudinal position and climatic con-

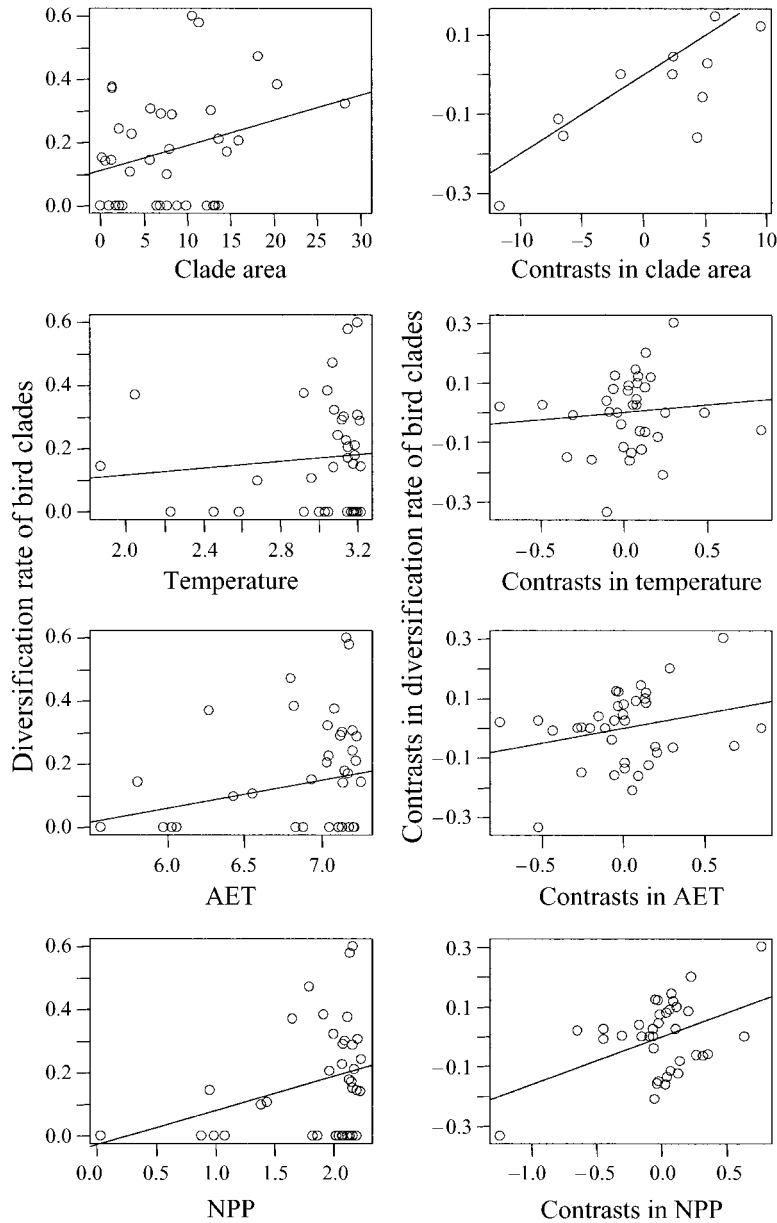


FIG. 3. Associations between clade area (millions of km²), mean annual temperature (°C), annual actual evapotranspiration (AET, mm), and net primary productivity (NPP, kg C/m²), and diversification rate of bird clades. Left-hand column: associations with bird genera treated as independent observations. Right-hand column: associations using phylogenetically independent contrasts. All predictors except area are ln-transformed; diversification rate is square-root transformed.

ditions within the range of each species throughout its history. For some groups that have a high-quality fossil record, such as marine bivalves, this may indeed be possible (e.g., Flessa and Jablonski 1996). For birds and other terrestrial vertebrates, however, the fossil record is relatively poor, and reconstructing paleodistributions for large numbers of species will never be possible. However, if there is a tendency for phylogenetic conservatism of ecological niches, as has been suggested (Peterson et al. 1999, Wiens 2004), it seems likely that geographic ranges track long-term expan-

sions and contractions of climatic zones; this has been demonstrated in birds (Price et al. 1997). Even if latitudinal positions of species have been dynamic, therefore, current distributions may at least provide a reasonable summary of climatic conditions experienced by species throughout their lifetimes.

If variation in diversification rates is a proximate mechanism for the origin of the latitudinal diversity gradient, what are the environmental gradients that underlie this mechanism? The two major contenders are geographic area and climate. Rosenzweig (1992, 1995)

TABLE 2. Cross-taxon tests ($n = 37$ clades) and independent-contrasts tests ($n = 35$ contrasts) for combined effects of latitudinal centroid, mean annual temperature, annual actual evapotranspiration (AET), and net primary productivity (NPP) on bird diversification rates.

Predictor	Cross-taxon results			Independent-contrasts results		
	Coefficient	t	Partial r^2	Coefficient	t	Partial r^2
Intercept	0.51	6.23***				
Latitude (degrees from equator)	-0.14	-3.91***	0.133	-0.06	-1.84†	0.143
Clade area ($\text{km}^2 \times 10^6$)						
Temp ($^{\circ}\text{C}$)						
AET (mm)						
NPP (kg C/m^2)				0.55	2.7*	0.065
(NPP) ²				-0.18	-2.42*	0.108
Clade age	-0.007	-3.48**	0.089			
Latitude \times AET						
Latitude \times clade age	0.002	2.74**	0.145			

Notes: Results shown are for minimum adequate models (see *An example using New World endemic bird clades; Methods*). Clade area was not fitted in the model using independent contrasts.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† $P \leq 0.1$.

has argued that because the tropics are the largest of the world's major bioclimatic zones, tropical clades are able to occupy larger areas, which promotes a higher speciation rate and a lower extinction rate. The area hypothesis has been controversial: for example, it has been argued that land area does not even increase towards low latitudes (Rohde 1997). The balance of empirical evidence seems not to favor the area hypothesis, with recent large geographic analyses offering little support for area as a major driver of the latitudinal diversity gradient (Hawkins and Porter 2001, Macpherson 2002). Climate, on the other hand, varies unarguably across latitudes, and there is strong support for associations between climatic factors and species richness of birds and other major taxonomic groups across latitudes (Currie and Paquin 1987, Currie 1991, Francis and Currie 2003, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b, Hawkins and Porter 2003).

Our study has taken a different approach from the majority of previous studies by examining area, climate, and latitude as properties of clades rather than of geographic entities such as grid cells. Although our data set is small and subject to a number of limitations, our results suggest that diversification rates may be influenced by both area and climate. The tendency for clades occupying larger areas to have higher diversification rates is consistent with previous findings for bird families (Owens et al. 1999, Bennett and Owens

2002), and may reflect an increased potential for population divergence or a greater buffer against extinction. The influence of climate on diversification rates is supported by a positive association with net primary productivity (NPP), but not with actual evapotranspiration (AET) or temperature. Compared to AET or temperature, NPP may be a closer indicator of the habitat features that promote speciation in birds, such as the structural complexity of tropical forests. It should be kept in mind, however, that NPP and AET are highly correlated across bird clades, that diversification rate also showed a positive trend against AET (Fig. 3), and that the overall power of the data set to detect significant patterns was relatively low.

If large clade area and high NPP are associated with high rates of diversification among bird clades, are these the factors driving the increase in diversification rates towards lower latitudes? Both clade area and NPP increase strongly towards lower latitudes (clade area: $P = 0.008$, $r^2 = 0.16$; NPP: $P < 0.0001$, $r^2 = 0.82$), so these two factors must certainly account for at least some of the latitudinal bias in diversification rates. However, the association between latitude and diversification rate is independent of clade area (Table 2), and largely independent of NPP, although when independent contrasts were used, the addition of NPP reduced the slope of the latitudinal effect considerably (Table 2). Clearly, there is a component of latitudinal

TABLE 3. Effects of clade age on the latitudinal bias in diversification rate, for young and old clades, using cross-taxon tests ($n = 18$ and 19 clades, respectively) and independent-contrasts tests ($n = 17$ and 18 contrasts, respectively).

Predictor	Cross-taxon results				Independent-contrasts results			
	Young clades		Old clades		Young clades		Old clades	
	Coefficient	t	Coefficient	t	Coefficient	t	Coefficient	t
Intercept	0.41	3.99**	0.18	4.41***				
Latitude	-0.1	-2.31*	-0.02	-1.05	-0.09	-2.52*	0.003	0.12

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

variation in diversification rate that is not accounted for by the environmental measures we have examined. It is possible that this is simply because our data set is prone to high Type 2 statistical error resulting from summarizing heterogeneous climatic conditions to a point estimate for each clade. Another possibility is that latitudinal variation in speciation or extinction rates are driven by environmental features we have not examined. For example, extinction rates may be elevated by a high degree of temperature variation, either annually or over longer time periods (Dynesius and Jansson 2000).

Our finding that the slope of the association between latitude and diversification rate was steeper in younger clades is consistent with the prediction derived from the model presented in Fig. 1. Although our division of clades into “young” and “old” was arbitrary, the model does not predict a discrete division of young and old clades. Rather, it predicts that the strength of any latitudinal bias in diversification rate should decline smoothly with clade age. Hence, the precise definition of young and old clades is relatively unimportant, and almost any division should produce a similar result. In fact, with a sufficiently large and robustly dated phylogeny, it may even be possible to estimate the function of the decline in slope with clade age, perhaps providing insight into the age (or range of ages) at which clades tend to reach saturation.

Hypotheses for the latitudinal diversity gradient assume either equilibrium or nonequilibrium regional species richness. If the former, the gradient must arise from latitudinal differences in the geographic equilibrium (saturation) level; if the latter, it must arise from latitudinal differences in diversification rate or clade ages (Rohde 1992). By focusing on clades rather than geographic entities, the model in Fig. 1 unites these opposing viewpoints by assuming simply that clades of a range of ages are present, that each has its own saturation level of species richness, and that some have reached saturation and some have not. The model therefore implies that among older, saturated clades, it is latitudinal variation in equilibrium levels of species richness, rather than diversification rates, that determine the latitudinal diversity gradient. Hence, the opposite prediction to that for diversification rate applies (i.e., that latitudinal variation in species richness per unit area among clades should be stronger among older clades). This should be another matter for investigation when larger phylogenies and geographic data sets become available.

CONCLUSION

There are two central messages that arise from the illustrative analysis we have presented. First, there should be more emphasis on clade-based approaches, to complement geographic approaches, in studying the latitudinal diversity gradient and other geographic patterns of diversity. Work to date has been dominated by

geographic analyses, whereas phylogenetic analyses, provided the limitations are recognized, can address different and important questions. As we have shown, latitudinal variation in diversification rates cannot be assumed to underlie the gradient in species richness, and must be explicitly demonstrated. At present, the best developed methods for doing so use clades rather than regions as the units of analysis. Second, there is an urgent need for large phylogenetic and geographic data sets. The data sets used in this type of study are inherently noisy, since clade diversification rates are likely to be determined by numerous environmental and biological factors, as well as unpredictable factors such as dispersal events or the evolution of key innovations. Hence, detecting the component of variation in diversification rates explained by latitude, then further decomposing this into components accounted for by different environmental factors, is a task best suited to large databases.

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