

GLOBAL VARIATION IN THE DIVERSIFICATION RATE OF PASSERINE BIRDS

ROBERT E. RICKLEFS¹

Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121-4499 USA

Abstract. Net diversification rates were estimated for samples of primarily tribe-to-family-level clades of passerine birds, taking into account extinction as well as speciation. Two samples were used. The first consisted of 37 clades of primarily temperate North American and primarily tropical South American passerines; the second comprised a global set of 90 clades, each distributed within one or more zoogeographic regions. Circumscription and ages of clades were taken from Sibley and Ahlquist's phylogeny based on DNA hybridization, with updates from more recent sequence analysis. Under a homogeneous speciation (rate = λ) and extinction (rate = μ) process, the expected number of species (N) after t units of time can be described by the expression, $N(t) = [\exp(\lambda(1 - \kappa)t - \kappa)] / (1 - \kappa)$, where $\kappa = \mu/\lambda$. A nonlinear least-squares regression for the temperate and tropical American clades with more than one species estimated $\kappa = 0.938 \pm 0.076$ (mean \pm SE), suggesting a high rate of turnover of lineages within clades. Because of the broad confidence limits in κ , I used values ranging from 0.80 to 0.98 to calculate speciation rates in subsequent analyses, assuming that κ is uniform among clades and does not vary with latitude. Speciation rate among South American clades exceeded that among North American clades for all κ , whether monophyletic lineages were included or not. The estimated speciation rate was negatively related to clade age, suggesting that proliferation within clades slows with time. In the global data set, rate of speciation decreased with clade age and increased with the area of the region or regions within which a clade is distributed, and for any given value of κ the speciation rate was significantly higher in tropical than in temperate regions. Relaxing the assumption of latitude independence in κ , larger clade size in the tropics could be achieved by various combinations of relative speciation and extinction rates that obscure the underlying causes of global biodiversity patterns. Nonetheless, the results of this analysis clearly indicate that a higher rate of diversification in the tropics contributes to the pervasive latitudinal gradient in diversity observed in passerine birds.

Key words: *clades; diversification; extinction; global variation; latitudinal diversity gradient; passerine birds; speciation; species richness.*

INTRODUCTION

Ecologists recently have become interested in the role of history and large-scale processes in establishing global patterns in species richness, particularly the trend of increasing diversity toward the tropics (Hillebrand 2004). Tropical environments dominated the early Tertiary history of the earth, providing deeper roots for tropical diversity compared to temperate and boreal regions with seasonally cold environments (Terborgh 1973, Latham and Ricklefs 1993, Wiens and Donoghue 2004, Ricklefs 2005a). Several authors have further argued that rates of diversification are higher in tropical latitudes (Fischer 1960), suggesting that (1) higher temperature or energy flux promotes more rapid evolution (Rohde 1992, Allen et al. 2002, Brown et al. 2004, Davies et al. 2004a, b, Evans and Gaston 2005); (2) more equitable climate favors habitat specialization leading to reduced dispersal and gene flow (Pianka 1966,

Stevens 1989); or (3) more intense biological interactions drive adaptive change (Dobzhansky 1950, Schemske 2002, Currie et al. 2004). The "null" hypothesis for these scenarios is that rates of diversification do not differ between temperate and tropical regions. Initial attempts to test this hypothesis involved sister-taxon comparisons (Farrell and Mitter 1993, Cardillo 1999, Davies et al. 2004b). Because sister taxa have identical ages, differences in number of species must reflect differences in the realized net diversification rate (speciation minus extinction). The qualifier "realized" is made necessary by the stochastic nature of speciation and extinction, according to which a single process can lead to a wide range of outcomes, making large samples of independently evolving clades necessary to achieve reasonable statistical power. However, because sister taxa tend to retain ancestral ecological relationships, it is often difficult to find pairs that differ primarily in latitudinal distribution. Indeed, the first such analysis, by Farrell and Mitter (1993), included only five sister pairs of clades of herbivorous insects, three of which favored the temperate lineage in species number.

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¹ E-mail: ricklefs@umsl.edu

In a widely cited paper, Cardillo (1999) compared a larger number of sister clades of butterflies and passerine birds (Passeriformes). Of the 11 comparisons involving birds, the tropical clade was more diverse in 10 cases (binomial test, $P < 0.001$). However, as Cardillo et al. (2005b) later acknowledged, the constraints imposed on identifying appropriate sister clades severely limit such comparisons. For example, seven of the smaller passerine clades in Cardillo's (1999) study, including six of the higher latitude members of the sister pairs, belonged to a category of small lineages (Ricklefs 2003) that apparently persist with low rates of diversification at the geographical and ecological margins of the space occupied by most passerine birds (Ricklefs 2005b). Hence, the latitude comparisons in Cardillo's study might have been confounded by other factors.

To circumvent this problem of sister-clade comparisons, Ricklefs (2005b) and Cardillo et al. (2005b) analyzed variation in the net diversification rates of samples of clades of New World birds chosen without regard to relationship. Ricklefs (2005b) compared diversification at a regional level among clades in several tribe-to-family-level taxa of passerine birds that are endemic either to tropical South and Central America or to temperate North America. Cardillo et al. (2005b) compared diversification in genera of all types of birds as a function of their midpoint latitudes and other distributional (clade area) and environmental (temperature and productivity) attributes. In both studies, ages of clades were estimated from the depth of the nodes uniting them to sister lineages in the phylogeny of Sibley and Ahlquist (1990), supplemented by more recent molecular phylogenetic analyses where available. Both studies found higher diversification rates in clades at lower latitudes (i.e., South and Central America > North America in Ricklefs's study). However, when five monotypic clades were dropped from Ricklefs's (2005b) analysis of 36 clades, and 14 monospecific genera were dropped from the analysis by Cardillo et al. (2005b) of 37 genera, the latitudinal and regional differences in net diversification rate disappeared, once more raising the possibility of confounded variables associated with small clade size.

Both Cardillo et al. (2005b) and Ricklefs (2005b) estimated the net rate of diversification as the logarithm of the number of species (N) divided by the age of the clade (t). This is suitable for a pure speciation process, in which case speciation rate λ can be estimated by $\ln(N)/t$. However, this estimate is biased where extinction occurs because $\ln(N)/t$ decreases with increasing t under a homogeneous speciation–extinction process (Kendall 1948, Nee et al. 1994b, Magallón and Sanderson 2001). Thus, comparisons of $\ln(N)/t$ between clades of different age are inappropriate and potentially misleading.

In this analysis, I compare the diversity of clades of passerine birds in large zoogeographic regions to determine the effects of the predominant environment (tropical vs. temperate) and the area of the region on

rates of diversification. I reanalyze the data of Ricklefs (2005b), treating diversification as a speciation–extinction process. A larger global data set is then evaluated in the same manner. The present analysis differs from that of Cardillo et al. (2005b) in (1) considering a larger number of (2) predominantly tribe-level clades, (3) examining the effects on diversification of regional factors rather than clade-specific factors, and (4) incorporating, to the extent possible, the influence of extinction on estimates of net diversification rate. The primary conclusion, which is strongly supported by the data, is that the net rate of diversification in passerine birds is higher in both larger and more tropical regions, consistent with a strong role for regional factors in the origin of global patterns in diversity. A second result of the analysis of the global data set is that net diversification rates appear to decrease with clade age, supporting the hypothesis that the filling of ecological space constrains further diversification.

MATERIALS AND METHODS

Delineation of clades

I identified clades in the phylogeny of Sibley and Ahlquist (1990), updated by more recent information on relationships based on sequence data, particularly from Barker et al. (2004). Each clade was assigned to one or more regions based on the predominance of its species distributions in those regions. In some cases, species outside the designated region or regions were deleted to circumscribe the contemporary diversity of each clade geographically. Some clades with broad distributions were assigned to concatenated regions, including the entire globe (“cosmopolitan”) in a few cases. Each clade was assigned a relative age based on DNA hybridization (Sibley and Ahlquist 1990), expressed as the temperature difference between the mid-melting points of monoduplexed and heteroduplexed DNA (ΔT_{50H} , °C). The age of each clade was the stem age measured from the node connecting to the nearest sister taxon. Because Sibley and Ahlquist's sampling was relatively complete at the level of tribes, missing taxa would have minimal effect on these estimates.

Comparison between temperate North America and tropical South America

Ricklefs (2005b) compared the number of species in 14 clades of passerine birds restricted to South America (primarily tropical) and 23 clades restricted to North America (primarily temperate; see Appendix A), including five monotypic clades in North America (Cinclidae, Aegithalidae, Silviinae, Alaudidae, Motacillidae).

Global comparison

I extracted 90 monophyletic, primarily tribe-to-family-level clades of passerine birds (see Appendix B). Numbers of species were determined from Monroe and Sibley (1993). Using distributional information in

Monroe and Sibley (1993), species were assigned to a single region or were split between two or more regions, and then the total number of species in each region was tabulated for each clade used in the analysis. The regions were based on Edwards (1974) and correspond to the major zoogeographic regions of the earth (Brown and Lomolino 1998:24 ff.): HN, Nearctic; N, neotropics; NI, Neotropical islands; HP, Palearctic; E, Africa (Ethiopian); EI, African islands; O, Oriental (south and southeast Asia); OI, Oriental Islands (Greater Sundas, Phillipines, etc.); AI, Australasian islands (New Guinea, Lesser Sundas, Oceania); AU, Australia, AZ, New Zealand. On the basis of these distributions, I assigned each clade to one or a combination of zoogeographic regions (see Appendix B): Nearctic (two clades), Eurasia (Palearctic, five), Holarctic (Nearctic + Palearctic, six), Neotropical (15), Western Hemisphere (Nearctic + Neotropical, seven), Ethiopian (sub-Saharan Africa, seven), Madagascar (two), Oriental (southern Asia + Greater Sunda Islands, five), Paleotropical (Ethiopian + Oriental, nine), Eastern Hemisphere (Palearctic + Paleotropical, seven), New Guinea (five), Australasia (Australia + New Guinea + Lesser Sunda Islands + Pacific Islands, 15), New Zealand (one), Cosmopolitan (four). Some of these regions are primarily tropical or subtropical (Neotropical, Ethiopian, Madagascar, Oriental, Paleotropical, New Guinea, Australasia), others are primarily temperate (Nearctic, Eurasia, Holarctic), whereas Eastern Hemisphere, Western Hemisphere, and Cosmopolitan include both tropical and temperate regions.

Consistency of time scaling

To determine whether the ages of nodes in the Sibley and Ahlquist (1990) phylogeny compare well with ages determined by phylogenetic analysis based on sequence data, I used values for both presented in Barker et al. (2004:Table 2), with minor modifications (see Appendix C). In order to account for heterogeneity in nucleotide substitutions among branches, Barker et al. (2004) used both nonparametric rate smoothing (NPRS; Sanderson 1997) and penalized likelihood (PL; Sanderson 2002) approaches, which gave similar estimated nodal ages. Barker et al. (2004) calibrated their genetic distances against time by setting the basal passerine split of the Acanthisittidae to coincide with the separation of New Zealand from the East Gondwanan land mass (82 Ma [mega annum, or 10^6 yr]). Barker et al. (2004) used a conversion of 4.7 Ma/°C melting point difference recommended by Sibley and Ahlquist (1990:254 = 4.5 Ma/°C), based on the splitting of ratite lineages coinciding with the breakup of Gondwana. However, Sibley and Ahlquist (1990) also suggested that genetic divergence might have proceeded more rapidly among small passerine birds with comparatively short generation times. Ages of nodes in either type of phylogeny are poorly calibrated at this point and provide only a relative time scale.

Diversification under a homogeneous speciation–extinction process

The probability that a lineage either splits into two or becomes extinct can be described as a rate (time^{-1}) that is inversely related to the average waiting time before each event. The difference between the rates of speciation (λ) and extinction (μ) is the net proliferation rate of a clade (r). In a pure speciation process, the expected number of lineages (N) present at time t is

$$N(t) = e^{\lambda t}. \quad (1)$$

Accordingly, the logarithm of the number of species increases linearly at a constant rate ($d \ln N / dt = \lambda$). However, when lineages can become extinct, and speciation and extinction rates are constant over time, the expected number of lineages increases as

$$N(t) = \frac{\lambda e^{(\lambda - \mu)t} - \mu}{\lambda - \mu} \quad (2)$$

(Kendall 1948, Harvey et al. 1994, Nee et al. 1994b, Magallón and Sanderson 2001). For a given speciation–extinction process where $\mu > 0$, the logarithm of the number of species initially ($t = 0$) increases at rate $d \ln N / dt = \lambda$, but subsequently slows to approach $d \ln N / dt = \lambda - \mu$ (Harvey et al. 1994). Consequently, for a given speciation–extinction process, estimating net proliferation rate by $\ln N / t$ (Cardillo et al. 2005b, Ricklefs 2005b) can bias results, particularly when the extinction rate is close to the speciation rate (Paradis 2004).

When μ is defined as a proportion (κ) of the speciation rate λ , i.e., $\mu = \kappa \lambda$, the equation for $N(t)$ becomes

$$N(t) = \frac{e^{\lambda(1 - \kappa)t} - \kappa}{1 - \kappa}. \quad (3)$$

Note that Magallón and Sanderson (2001) set $\mu = \epsilon \lambda$, but κ avoids potential confusion with the base of the natural logarithms (e). Using Eq. 3 in nonlinear regression, I estimated λ and κ for a sample of clades from North and South America to obtain a rough approximation for the rate of extinction relative to that of speciation. Then, assuming a particular value of κ , Eq. 3 can be rearranged to obtain

$$\lambda = \frac{\ln[N(t)(1 - \kappa) + \kappa]}{(1 - \kappa)t}. \quad (4)$$

In practice, the value of κ cannot be estimated accurately, so I conducted ANOVAs in λ using a range of values of κ .

Magallón and Sanderson (2001) estimated $r = \lambda - \mu$, the net diversification rate, rather than λ , using

$$r = \frac{\ln[N(t)(1 - \kappa) + \kappa]}{t} \quad (5)$$

which is equivalent to Eq. 4. For a given value of κ , r and λ are directly proportional to each other. The relative merits of using estimates r and λ will be taken up in the *Discussion*, where I shall also demonstrate a small

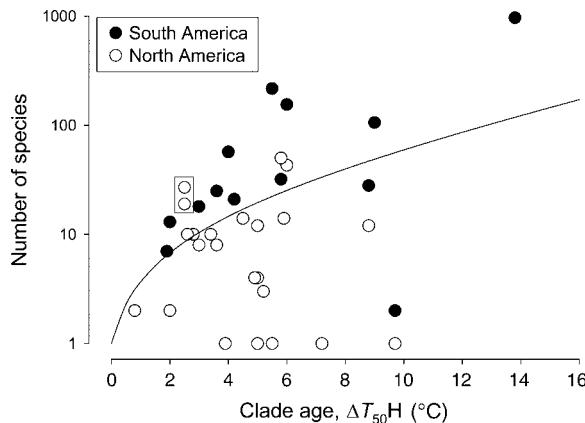


FIG. 1. Relationship between clade size and age in North and South American clades of passerine birds. The line represents Eq. 3 fitted to the data, excluding the five monotypic North American clades, with parameters $\lambda = 2.47$ and $\kappa = 0.938$ (λ , speciation rate; μ , extinction rate; $\kappa = \mu/\lambda$). The small vertical box encloses two points representing the North American Tyranninae and Icterini, both of which might include more than one independent lineage. Clade age is measured as the temperature difference between the mid-melting points of monoduplexed and heteroduplexed DNA (ΔT_{50H}).

but consistent bias in the estimation of λ and κ owing to the stochasticity of speciation and extinction.

Statistical analyses

Various simulations of clade diversity (Ricklefs 2003) were performed with SAS software or within Excel spreadsheets. All statistical analyses were carried out with the Statistical Analysis System, version 8.12 (SAS Institute, Cary, North Carolina, USA), procedures GLM and NLIN.

RESULTS

Net proliferation rates of passerine clades in North and South America

I initially conducted an analysis based on a pure speciation model for comparison with Ricklefs (2005b) and Cardillo et al. (2005b) and, subsequently, with results from a speciation–extinction model. The slope of the relationship between the natural logarithm of number of species and clade age (Fig. 1) did not differ significantly between North American and South American clades (interaction $F_{1,33} = 2.9$, $P = 0.10$), especially when the monotypic North American clades were deleted (interaction $F_{1,28} = 0.05$, $P = 0.83$). With the interaction deleted from the analysis, clade age was not a significant effect on $\ln(N)$ when monotypic clades were included ($F_{1,34} = 1.2$, $P = 0.28$), but was significant when these clades were excluded ($F_{1,29} = 6.7$, $P = 0.015$). In the first case, average $\ln(N)$ in South American clades exceeded that in North American clades by 1.68 natural log units ($F_{1,34} = 12.4$, $P = 0.0013$). In the latter case, with smaller clades excluded and differences in age accounted for, average $\ln(N)$ in South American clades

exceeded that in North American clades by 0.96 natural log units (a factor of 2.6), but the statistical significance of this result was marginal ($F_{1,29} = 5.0$, $P = 0.033$). The observed patterns parallel those of Cardillo et al. (2005b) and Ricklefs (2005b), namely, that finding a significantly slower rate of proliferation at higher latitudes largely depended on including several monospecific clades in the temperate sample.

Pairs of related, but not necessarily sister, temperate and tropical clades compiled by Ricklefs (2005b; see Appendix A) can be compared with respect to values of $\ln(N)/t$, which account for differences in clade age. Among 14 pairs of clades in the same tribe-to-family-level taxa, $\ln(N)/t$ was higher in nine South American members of the pair and tied in one, leaving four comparisons favoring the North American member of the pair. This result does not differ significantly from a random distribution, having no bias between regions (9.5 vs. 4.5; $G = 0.88$, $df = 1$, $P = 0.35$). The comparison included only one monospecific clade (Cinclidae in North America); four other monospecific clades in North America were not matched in South America. When $\ln(N)/t$ was compared between regions, regardless of phylogenetic pairing, by a nonparametric rank-order Kruskal-Wallis test, the rates were marginally higher in South America ($n = 14$ and 23 clades [for South and North America, respectively], $\chi^2 = 4.75$, $df = 1$, $P = 0.029$). When the five North American clades with single species were deleted from the comparison, the difference between regions was no longer significant ($n = 14$, 18, $\chi^2 = 1.72$, $df = 1$, $P = 0.19$).

The net proliferation rate, $\ln(N)/t$, is not corrected for the rate of extinction relative to that of speciation (κ). Here, I estimated κ and λ by nonlinear least-squares regression of the \ln -transformed version of Eq. 3, $\ln(N) = \ln(\exp[\lambda(1 - \kappa)t] - \kappa) - \ln(1 - \kappa)$. When applied to the 18 North American and 14 South American clades having more than one species (Appendix A), the estimated parameters were $\kappa = 0.938 \pm 0.076$ (mean \pm SE; 95% CI = 0.783–1.094) and $\lambda = 2.47 \pm 1.10$ (95% CI = 0.23–4.71), with $F_{2,30} = 92$, $P < 0.0001$, and $R^2 = 0.860$. The effect of region can be included in this analysis by using the model $\ln(N) = \ln(\exp[\lambda(1 - \kappa)t] - \kappa) - \ln(1 - \kappa) + \alpha$ region, where region = 1 for South American clades and region = 0 for North American clades. In this case, the estimated parameters (mean \pm SE) were $\kappa = 0.969 \pm 0.086$ (95% CI = 0.793–1.146), $\lambda = 1.99 \pm 0.93$ (95% CI = 0.094–3.89), and $\alpha = 0.974 \pm 0.426$ (95% CI = 0.102–1.846), with $F_{3,29} = 72$, $P < 0.0001$, and $R^2 = 0.881$. The positive contribution of a South American distribution to $\ln(N)$ suggests that, for a given age (t), South American clades are larger, by a factor of $\exp(0.974) = 2.65$, than North American clades.

The apparent, or realized, diversification rates of North and South American clades can be compared by calculating λ from $\ln(N)$ and t , assuming a particular value of κ . Because κ and λ had broad confidence limits, I used a range of values of κ (0.80, 0.85, 0.90, 0.95, 0.98)

TABLE 1. Estimated values of λ (mean with SD in parentheses) for North American (NA) and South American (SA) clades of passerine birds over a range of values of κ (where $\kappa = \mu/\lambda$ and μ is extinction rate).

κ	Entire sample (SA, 14 clades; NA, 23 clades)								Clades with >1 species (SA, 14 clades; NA, 18 clades)							
	Speciation rate, λ				$\lambda - \mu$				Speciation rate, λ				$\lambda - \mu$			
	SA	NA	χ^2	P	SA	NA	SA/NA		SA	NA	χ^2	P	SA	NA	SA/NA	
0.80	2.09 (0.90)	1.12 (0.99)	8.05	0.0045	0.418	0.224	1.87		2.09 (0.90)	1.43 (0.89)	4.45	0.0350	0.418	0.286	1.46	
0.85	2.46 (1.09)	1.26 (1.15)	9.97	0.0027	0.369	0.189	1.95		2.46 (1.09)	1.61 (1.05)	5.28	0.0215	0.369	0.242	1.53	
0.90	3.05 (1.44)	1.46 (1.38)	9.73	0.0018	0.305	0.146	2.09		3.05 (1.44)	1.87 (1.29)	6.00	0.0143	0.305	0.187	1.63	
0.95	4.24 (2.32)	1.79 (1.79)	10.53	0.0012	0.212	0.090	2.37		4.24 (2.32)	2.28 (1.73)	6.77	0.0093	0.212	0.114	1.86	
0.98	6.10 (4.21)	2.13 (2.29)	10.94	0.0009	0.122	0.043	2.86		6.10 (4.21)	2.72 (2.25)	7.17	0.0074	0.122	0.054	2.24	

Notes: Kruskal-Wallis χ^2 values are presented for comparisons between the regions. SA/NA denotes the net diversification rate ($\lambda - \mu$) in South America relative to that in North America. Clade age was measured in units of ΔT_{50H} ($^{\circ}\text{C}$), the temperature difference between the mid-melting points of monoduplexed and heteroduplexed DNA.

to estimate λ for each clade (Eq. 4), and then compared the estimates of λ between regions by Kruskal-Wallis tests (Table 1). This approach assumes the same value of κ in tropical and temperate regions, which has not been ascertained. In these comparisons, the speciation rates, as well as the net diversification rates ($r = \lambda - \mu$), were significantly greater in South America than in North America, regardless of the value of κ or whether monospecific clades were included ($0.0009 < P < 0.0045$) or not ($0.0074 < P < 0.0350$). The greater significance levels in this analysis compared to those associated with $\ln(N)/t$ can be attributed to removing error variance generated by age-related bias in the estimation of the net rate of species proliferation.

If one allows κ to differ between North American and South American clades, it is possible to explain the difference in clade diversity solely by a higher extinction rate in North America or a higher speciation rate in South America. For example, when $\kappa = 0.80$ for South American clades and 0.98 for North American clades, the estimates of speciation rate are nearly identical for the two regions ($\lambda = 2.09$ and 2.13, respectively), but μ is greater in North America (2.09 vs. 1.67). Alternatively, when $\kappa = 0.80$ for South American clades and 0.95 for North American clades, estimated extinction rates are similar ($\mu = 1.67$ and 1.70, respectively) but λ is greater in South America (2.09 vs. 1.79).

Table 1 also presents the net diversification rate of clades in each region and their ratio between South and North America. Depending on the value of κ and whether small clades were included, the net diversification rate was 1.46 to 2.86 times more rapid among South American clades, assuming the same value of κ in both regions (see *Discussion*). The net diversification rate decreases as κ increases because the speciation rate must increase considerably to produce a particular expected clade size, more than compensating for the increasing extinction rate. Alternatively, if the net diversification rate ($r = \lambda - \mu$) were constant, the higher diversity of South American clades could be explained by an increase in speciation rate (λ) with a corresponding increase in the ratio $\kappa = \mu/\lambda$. For example, estimated $\lambda - \mu$ is about the same in North and South America (2.24

vs. 2.12) when the values of κ are 0.80 and 0.95, respectively.

Using Eq. 4 to estimate λ , given κ , the number of species, and the age of a lineage, presumes that speciation and extinction rates are constant over time. If diversification within a clade is constrained as ecological space becomes filled with species (Pybus and Harvey 2000), the rate of proliferation would decrease with time and the apparent average rate of speciation over the duration of a clade would decrease with increasing clade age. I tested whether the average net diversification rate decreased with lineage age by analysis of covariance with region as main effect and age of lineage as a covariate. Analyses were performed with and without monotypic clades, and over the same range of κ values as in Table 1. The interaction between age and region was not significant ($P > 0.05$). When this term was deleted from the model, the relationship between estimated λ and relative clade age was negative for all but one analysis, and the slopes were significant for $\kappa < 0.90$, but insignificant for $\kappa > 0.90$ (Table 2). The difference in estimated λ between regions significantly favored South America in all analyses.

Global data set

I used linear regression to compare Sibley-Ahlquist (1990) estimates of relative ages based on DNA-hybridization genetic distances with the estimates of Barker et al. (2004: Table 2) based on nuclear intron (RAG-1 and RAG-2) sequences. Fourteen points were compared, ranging in estimated age from 14 or 17 Ma to 82 Ma (see Appendix C). Clocklike phylogenetic trees obtained by nonparametric rate smoothing (NPRS) and penalized likelihood (PL) produced similar results. Using NPRS, the slope of the relationship between Sibley-Ahlquist estimates, assuming 4.7 Ma/ $^{\circ}\text{C}$ melting point difference, was 0.916 ± 0.073 (mean \pm SE; $t = 12.6$, $P < 0.0001$, $R^2 = 0.92$). Neither this slope, nor that for PL (0.946 ± 0.066 ; $t = 14.2$, $P < 0.0001$, $R^2 = 0.94$), differed significantly from 1. Thus, Sibley-Ahlquist genetic divergence agrees with an independent measure of relative time based on sequence analysis with respect to estimating the relative ages of clades. More impor-

TABLE 2. Relationship between estimated λ and clade age shown as slopes for North and South American clades of passerine birds and difference in λ (the intercepts of the regression lines) between South and North America over a range of values of κ .

κ	Entire sample (SA, 14 clades; NA, 23 clades)						Clades with >1 species (SA, 14 clades; NA, 18 clades)					
	Slope			λ , SA – NA			Slope			λ , SA – NA		
	Mean	SE	<i>P</i>	Mean	SE	<i>P</i>	Mean	SE	<i>P</i>	Mean	SE	<i>P</i>
0.80	-0.169	0.055	0.0040	1.18	0.30	0.0004	-0.142	0.057	0.019	0.90	0.31	0.0070
0.85	-0.178	0.066	0.011	1.42	0.36	0.0004	-0.146	0.070	0.045	1.10	0.38	0.0071
0.90	-0.184	0.085	0.037	1.82	0.46	0.0004	-0.143	0.091	0.13	1.43	0.50	0.0076
0.95	-0.160	0.126	0.21	2.65	0.69	0.0005	-0.098	0.140	0.48	2.12	0.76	0.0091
0.98	-0.034	0.202	0.87	4.02	1.11	0.0009	0.068	0.228	0.77	3.27	1.24	0.013

Note: Clade age was measured in units of ΔT_{50H} (°C).

tantly, regardless of the absolute age calibration, the relative ages of Sibley-Ahlquist clades parallel those derived from a sequence-based analysis.

Stem ages of clades in this sample, based on Sibley-Ahlquist values, varied significantly among regions ($F_{13,76} = 4.4$, $P < 0.0001$, $R^2 = 0.43$). Clades restricted to single tropical zoogeographic regions were relatively old (SA, 8.83 ± 2.10 , $n = 15$; OR, 9.54 ± 2.76 , $n = 5$; AU, 8.99 ± 1.56 , $n = 15$; FR, 7.80 ± 2.19 , $n = 7$; GU, 7.88 ± 2.08 , $n = 5$) compared to one temperate region (UR, 7.44 ± 1.88 , $n = 5$). Clades widely distributed throughout the Western Hemisphere were the youngest (WH, 5.63 ± 1.38 , $n = 7$). Nonetheless, the overlap in clade ages between regions was broad.

When region was entered in an ANOVA as a main effect, the log-transformed number of species was independent of the age of a clade (interaction, $F_{12,63} = 0.63$, $P = 0.81$; with interaction removed, $F_{1,75} = 0.44$, $P = 0.51$; deleting clades with <5 species, $F_{1,64} = 2.4$, $P = 0.13$). Similarly, when age, logarithm of region area, and region latitude (tropical, mixed, temperate) were entered in a multiple regression with the logarithm of species richness as the dependent variable, age also was not a significant effect (interactions not significant, $P > 0.05$; latitude zone, $F_{2,84} = 11.8$, $P < 0.0001$; logarithm of region area, $F_{1,84} = 27.1$, $P < 0.0001$, slope = 0.73 ± 0.14 ; clade age, $F_{1,84} = 1.5$, $P = 0.22$; model $F_{4,84} = 10.7$, $P < 0.0001$, $R^2 = 0.33$). Deleting clades with <5 species, latitude zone ($F_{2,73} = 17.6$, $P < 0.0001$) and logarithm of region area ($F_{1,73} = 30.3$, $P < 0.0001$, common slope = 0.70 ± 0.13) remained highly significant effects; clade age was marginally significant and negative ($F_{1,73} = 5.1$,

$P = 0.027$, slope = -0.11 ± 0.05) (model $F_{4,73} = 12.9$, $P < 0.0001$, $R^2 = 0.41$). Thus, because $\ln(N)$ is linearly independent of age, clades appear to reach species saturation rapidly, after which speciation and extinction are balanced ($\lambda = \mu$) and net proliferation decreases with time. Accordingly, clade age should be entered as a covariate in comparisons of estimated λ among regions. Note further that the assumption of rate homogeneity through time is not strictly appropriate.

Taking the latitude zone and logarithm of area of each region into account, estimates of λ (Eq. 4) decreased with increasing clade age, regardless of the value of κ and regardless of whether clades with fewer than five species were excluded (Table 3). The latitude effect also was significant in all these analyses.

The average deviation of λ for each region from the regression of λ on clade age is presented in Table 4 and is plotted as a function of region area in Fig. 2. Only clades having five or more species were included and κ was set at 0.90. The regression of λ on clade age had an intercept of 5.89 ± 0.52 and a slope of -0.427 ± 0.061 (mean \pm SE; $F_{1,76} = 48.1$, $P < 0.0001$, $R^2 = 0.388$; mean $\lambda = 2.390$). Considering clade age, the highest average values of λ clearly belong to large regions either wholly within the tropics and subtropics (PT = +0.76, FR = +0.61, SA = +0.55) or that include large tropical areas (CO = +0.98, EH = +0.10, WH = -0.21). Eurasia and North America, together making up the large temperate region of the Holarctic, have low values (UR = -1.05, NA = -0.86). The importance of regional area is also apparent in the low values of adjusted λ in the smaller

TABLE 3. Slope (mean, with SE in parentheses) of the relationship between λ , estimated from Eq. 4, and both clade age and region area for a range of values of κ with and without small clades included.

κ	Entire sample (90 clades)					Clades with >4 species (78 clades)				
	Age slope	Area slope	Mean λ	Tropical–mixed	Tropical–temperate	Age slope	Area slope	Mean λ	Tropical–mixed	Tropical–temperate
0.80	-0.241 (0.035)	0.415 (0.074)	1.396	0.449	1.136	-0.270 (0.028)	0.412 (0.071)	1.567	0.652	1.142
0.85	-0.291 (0.044)	0.523 (0.093)	1.668	0.576	1.426	-0.327 (0.037)	0.526 (0.092)	1.877	0.833	1.448
0.90	-0.375 (0.060)	0.712 (0.126)	2.119	0.805	1.935	-0.421 (0.052)	0.730 (0.130)	2.390	1.158	1.990
0.95	-0.553 (0.098)	1.145 (0.208)	3.069	1.351	3.101	-0.622 (0.090)	1.208 (0.225)	3.472	1.928	3.253
0.98	-0.842 (0.175)	1.911 (0.371)	4.595	2.372	5.170	-0.947 (0.169)	2.078 (0.425)	5.213	3.358	5.535

Note: All effects, including latitude, were significant at $P < 0.0001$.

TABLE 4. Average residuals of λ from the regression of λ on clade age tabulated by region, with the area of the region (in millions of km²) and the latitude zone indicated.

Region	No. clades	Area (millions of km ²)	Latitude	Speciation rate, λ		
				Residual	SD	SE
AU	13	8.9	tropical	-0.28	0.90	0.25
CO	4	124.7	mixed	0.98	0.26	0.13
EH	7	76.6	mixed	0.10	1.09	0.41
FR	5	21.0	tropical	0.61	0.26	0.11
GU	3	0.8	tropical	-1.67	0.96	0.55
HA	6	67.0	temperate	-0.65	1.14	0.46
MA	1	0.6	tropical	-2.04		
NA	1	21.0	temperate	-0.86		
OR	4	9.6	tropical	-0.26	0.58	0.29
PT	9	30.6	tropical	0.76	0.73	0.24
SA	14	18.2	tropical	0.55	1.23	0.33
UR	4	46.0	temperate	-1.05	0.38	0.19
WH	7	39.2	mixed	-0.21	1.10	0.41

Notes: Clades with <5 species are not included. Blank cells indicate that no data are possible because there is only one clade.

tropical areas of New Guinea (GU = -1.67) and Madagascar (MA = -2.04).

DISCUSSION

The greater species richness of tropical regions potentially reflects a combination of greater lineage age and rates of diversification (Wiens and Donoghue 2004, Ricklefs 2005a, Hawkins et al. 2006). In this analysis, clades had similar rank in the taxonomic hierarchy defined by Sibley and Ahlquist (1990) and Sibley and Monroe (1990) on the basis of genetic divergence, which I have used as an estimate of time.

Therefore, it is not surprising that the ages of tropical and temperate lineages used in this analysis do not differ statistically ($F_{1,58} = 0.01$, $P = 0.93$; clades having five or more species that are exclusively tropical or temperate). Nonetheless, the influence of diversification deeper in the avian phylogeny is readily seen in the number of clades included in the analysis. In the global comparison, of clades with ≥ 5 species, 49 are tropical, 11 temperate, and 18 mixed; clades with <5 species add 9 to the tropical list and 3 to the temperate list. The difference in number of tribe-level clades could reflect greater age, more rapid diversification, or both, within tropical regions. Regardless, it is clear from the tribe-level analysis of diversification rate that species proliferate more rapidly in tropical regions, because of higher speciation or lower extinction, or both.

Under a homogeneous model of speciation and extinction, incorporating a relative extinction rate (κ) when estimating speciation rate (λ) reduces the "error" variance introduced by the systematic decrease in the uncorrected value, $\ln(N)/t$, over time. Consequently, the statistical power of detecting other effects, such as latitude or region area, increases, and biases resulting from different age distributions in different groups are minimized. Nonetheless, the validity of comparisons based on calculated net proliferation rates usually will depend on assumptions of homogeneity of the extinction rate relative to speciation rate (κ) across clades and the constancy of speciation and extinction rates through time. I shall return to these points.

In their study of the diversification of clades of flowering plants, Magallón and Sanderson (2001) estimated the net rate of species proliferation, $r = \lambda - \mu$. As in this study, the value of κ (their ϵ) was chosen somewhat arbitrarily as the upper bound to "reasonable" values and was given the same value for all clades. For a given value of κ , r is directly proportional to λ and, thus, the more appropriate measure could be argued either way. I have used λ in this study for two

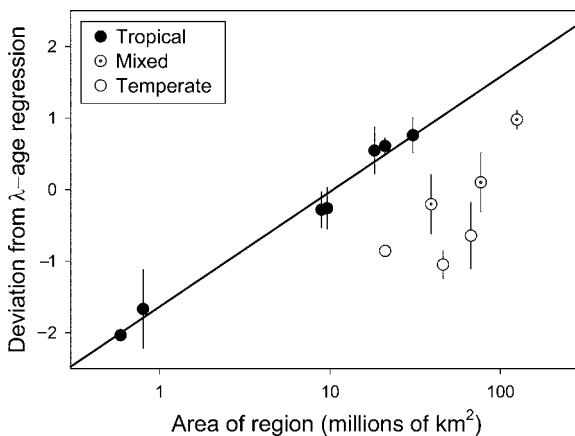


FIG. 2. Values of λ (mean \pm SE; see Table 4), adjusted by clade age and calculated with $\kappa = 0.90$ as a function of regional area for clades from tropical, mixed-latitude, and temperate regions. The regression of the age-adjusted λ on $\log_{10}(\text{area})$, weighted by the square root of the number of clades per region, had a common slope of 1.62 ± 0.15 ($F_{1,9} = 118$, $P < 0.0001$) with an intercept for tropical regions of -1.65 ± 0.17 ($t = -9.7$, $P < 0.0001$) (overall model, $F_{3,9} = 49.9$, $P < 0.0001$, $R^2 = 0.94$). Mixed regions were 1.10 ± 0.20 ($t = -5.6$, $P = 0.0004$) units below the tropical regression, and temperate regions were 1.90 ± 0.20 ($t = -9.6$, $P < 0.0001$) units below the tropical regression. The analysis was based on clades of five or more species.

TABLE 5. Comparison of rates of speciation (mean \pm SD) estimated from clade sizes drawn from geometric distributions produced by known values of λ .

κ	$\lambda (N = 100)$		$\lambda (N = 10)$	
	Known	Simulated	Known	Simulated
0.80	0.759	0.646 \pm 0.259	0.257	0.231 \pm 0.145
0.85	0.921	0.789 \pm 0.329	0.285	0.262 \pm 0.175
0.90	1.194	0.994 \pm 0.468	0.321	0.298 \pm 0.214
0.95	1.783	1.474 \pm 0.763	0.372	0.364 \pm 0.292
0.98	2.730	2.257 \pm 1.406	0.414	0.437 \pm 0.378

reasons. First, the role of diversification rate in creating patterns of species richness is discussed most often in the context of the production of new species (Currie et al. 2004). Although, extinction rate enters into the equation for diversification equally, many biologists subscribe to the view that recurrent, or background, extinction is driven by the appearance of new species in saturated communities (MacArthur and Wilson 1967, MacArthur 1972, Courtillot and Gaudemer 1996, Sepkoski 1998), in which case the rate of speciation would be more appropriate.

Second, the rate of diversification required to produce a particular number of species over a fixed time interval is inversely related to the speciation rate when the relative rate of extinction varies. For example, 200 species produced in 20 time units with $\kappa = 0.90$ implies a speciation rate of 1.52 and an extinction rate of 1.37 ($r = 0.15$). Producing the same number of species with $\kappa = 0.98$ implies $\lambda = 4.01$ and $\mu = 3.93$ ($r = 0.08$, or about half the value at $\kappa = 0.90$). Thus, when κ varies among clades, the value of the net diversification rate is inversely related to both the speciation and extinction rates.

Regardless of the value of κ employed, estimates of λ should be unbiased or at least uniformly biased to be useful in comparisons of diversification rate. I conducted a series of simulations to test this assumption. A homogeneous speciation–extinction process is associated with a geometric distribution of clade sizes N at

time t . Estimates of λ parallel variation in N (Eq. 4) and the mean of these estimates for a large number of independently produced clades should approximate the value used to produce them. To evaluate this proposition, I drew 1000 numbers at random from geometric distributions with means of 10 or 100 species and estimated λ for each clade assuming $t = 20$ and a range of values of κ (Table 5). In this exercise, the values of λ were approximately normally distributed (skew and kurtosis not significantly different from 0), but the average λ was significantly lower than the value estimated for the mean of the distribution.

I took a similar approach to generating clades by a speciation–extinction process and estimating λ and μ from the simulated data. The results presented in Table 6 pertain to simulations with $\lambda = 0.200$, $\mu = 0.180$ (i.e., $\kappa = 0.90$) for 500 trees generated over time intervals uniformly distributed from 50 to 150 (i.e., 0.2 increments for each successive tree within a trial). The simulations were repeated over 10 trials. Nonlinear curve-fitting of λ and κ (SAS Procedure NLIN) gave identical results to fitting λ and μ , which are reported here, along with the value of κ calculated from these estimates. The numbers in Table 6 are organized by increasing estimated λ , which ranged from 0.049 to 0.391, although half of the values were between 0.177 and 0.195. The average λ in the 10 trials was 0.175, which is 87.5% of the value used to simulate the clades. The calculated κ averaged only 0.81, and varied in close parallel with λ . The confidence limits on λ and μ (not reported) were broad and for the most part included zero. It appears, therefore, that speciation and extinction rates calculated from clade age and species number systematically underestimate the underlying rates of these processes. This bias should not, however, influence the comparisons between regions undertaken in this analysis.

A problem with the estimation of diversification rates is the need to assume a relative rate of extinction, κ . The simplest approach, used in the analyses presented here, is to assume that the extinction rate is a fixed proportion

TABLE 6. Results of 10 trials generating 500 trees (most of which went extinct before the end of the simulation) using $\lambda = 0.200$, $\mu = 0.180$, and $t = 50$ –150.

Trial	Clades	No. species				λ	μ	κ	$N(t)$
		Mean	SD	Min.	Max.				
7	79	56.3	82.9	1	508	0.049	0.016	0.332	39.1
3	76	55.3	80.9	1	465	0.063	0.034	0.536	39.4
6	82	36.5	55.4	1	350	0.119	0.099	0.835	38.9
9	57	61.7	65.0	1	284	0.157	0.137	0.869	52.3
1	67	71.5	95.0	3	489	0.177	0.157	0.889	54.7
5	81	83.2	110.7	1	424	0.177	0.155	0.875	62.9
10	82	48.1	49.3	1	283	0.193	0.178	0.923	47.8
8	75	53.3	61.4	1	344	0.211	0.196	0.928	52.0
2	79	64.4	73.5	3	336	0.212	0.195	0.918	57.5
4	60	67.8	71.1	1	309	0.391	0.382	0.975	72.7
Mean	73.8	59.8	74.5	1.4	379.2	0.175	0.155	0.808	51.7
SD	9.2	13.0	18.6	0.8	85.1	0.095	0.101	0.207	11.0

Notes: The numbers for each trial represent the number of clades extant, the mean, standard deviation, minimum, and maximum number of species, fitted values of λ and μ , calculated κ , and the expected number of species for $t = 100$.

of the speciation rate. Accordingly, when both rates increase, the net proliferation rate $r = \lambda - \mu$ also increases in direct proportion and one can apply a fixed value of $\kappa = \mu/\lambda$ to all clades. When the value of κ is constant, the calculated value of λ varies in direct (although not linear) relation to the number of species, and comparisons among regions or other “treatments” are valid. However, when the relative extinction rate varies systematically between regions, one cannot distinguish the influences of variation in speciation and extinction rates. Holding speciation rate or extinction rate constant has nearly identical effects on κ and r for comparable differences between expected the number of species per clade. Without direct, independent measurements of λ and μ , one cannot distinguish between comparisons with constant λ , μ , κ , or r .

In the absence of fossil data, phylogenetic reconstructions provide the only way to estimate extinction rate directly, for example through the analysis of lineage-through-time (LTT) plots (Harvey et al. 1994, Nee et al. 1994b, Nee 2001). Ricklefs (2006) analyzed a LTT plot for South American sub-oscine passerines using the phylogeny of Sibley and Ahlquist (1990). The plot suggested time-invariant speciation and extinction rates with a value of κ of 0.82. However, because this is the largest avian clade endemic to a region (~966 species), it is not surprising that the apparent speciation rate is markedly higher than the apparent extinction rate. Smaller clades that are closer to the mean value of clade size for a region are more likely to suffer from stochastic factors, making the estimation of speciation and extinction rates more difficult.

Most analyses of LTT plots or branch lengths for small clades indicate a decline in the net diversification rate, suggesting the filling of ecological space and declining speciation rate or increasing extinction rate through time (e.g., Pybus and Harvey 2000; cf. Barraclough and Vogler 2002, Harmon et al. 2003, Kadereit et al. 2004, Zhang et al. 2004). The analyses presented here are similarly striking in that the apparent value of λ decreases with increasing clade age. This is consistent with declining speciation and extinction rates under constant κ , with increasing extinction rates under constant λ , and with decreasing speciation rates under constant μ . In addition, the sizes of clades are independent of their age, which suggests that clades quickly grow to some more-or-less stable size that is either clade specific or time specific. Lack of evidence that clade size is phylogenetically conservative (Ricklefs 2003) and failure to find convincing attributes associated with clade size (Bennett and Owens 2002, Ricklefs 2003) suggest that phases of diversification within clades might have limited life spans regardless of how many species are produced. If true, the underlying mechanism is not apparent.

I am grateful to Dolph Schluter for pointing out that the decline in apparent diversification rate with age could be a consequence of error in estimating the ages of

clades. In this case, younger estimated ages will tend to include more underestimated values and older estimated ages will include more overestimated values, reducing the dependence of $\ln(N)$ on clade age and causing a negative relationship between estimated λ and age. The error in clade age is difficult to estimate. Most of the clades in my global analysis had “ages” ranging uniformly between 5° and 12°C ΔT_{50H} . In a regression of Sibley and Ahlquist ages against penalized likelihood node ages estimated from genetic data (Appendix C), using values within the tribe range, the standard deviation about the regression line was 0.87°C ΔT_{50H} units, or about 11% of the mean. To test the effect of error in age on the relationships of $\ln(N)$ and λ to age, I simulated clade diversification with $\kappa = 0.90$, times drawn from a uniform distribution between 5 and 12, and yielding realistic distributions of clade sizes. I then calculated λ based on estimates of clade age with variation (standard deviations of 0%, 11%, and 22% of the actual clade age). I then regressed $\ln(N)$ and λ against estimated clade age. The slope of $\ln(N)$ as a function of estimated age decreased from 0.32 to 0.22 and 0.14 over this range ($0.002 < P < 0.004$), with the intercept increasing from 0.55 (not significant, NS) to 1.24 ($P = 0.05$), and 2.32 ($P < 0.0001$). The slope of λ vs. estimated age changed from 0.045 (NS) to -0.00 (NS) and -0.14 ($P = 0.004$) over this range. Thus, even with a substantial age error (22%), a signal of increasing $\ln(N)$ with age remains, and λ takes on a negative relationship to age only with the higher level of error. In the empirical analysis presented in *Results*, $\ln(N)$ was independent of age. Thus, although error in age estimation is a concern, it probably does not explain the apparent decrease in diversification with clade age.

The influence of regional area was very strong in these analyses. This suggests that unusually large clades of passerine birds might typically have broad geographic distributions rather than distinctive biological traits (Ricklefs 2003). Including tropical vs. nontropical as an effect, the logarithm of species number per clade was positively related to the log-transformed area of the region with a slope of 0.70 ± 0.13 , mean \pm SE ($F_{1,73} = 30.3$, $P < 0.0001$). The underlying causes of this relationship potentially include more ecological space, although Madagascar and New Guinea, the two smallest regions included in this analysis, probably are as diverse ecologically as the larger tropical regions. Large regions might provide more opportunities for isolation by distance and by geographic features that isolate populations by reducing dispersal across unsuitable habitat. Clades distributed among several zoogeographic regions also can increase in diversity through independent radiations in each region. The slope of the species–area relationship for clades substantially exceeds that for relationships within regions (Rosenzweig 1995), suggesting that the effect of area on the results of diversification differs from sampling- and extinction-

related effects on species richness (Losos and Schluter 2000).

Clearly, diversification of passerine birds has occurred more rapidly in tropical regions than in temperate regions. Whether this is due to higher rates of speciation or lower rates of extinction cannot be determined in this analysis, and both are possible. In either case, relatively higher rates of species proliferation should be associated with shorter branch lengths in a phylogenetic tree (e.g., Weir and Schluter 2004). At present, the only way to estimate absolute values of speciation and extinction rates is through the analysis of lineage-through-time plots or changes in branch length through time within phylogenies (Harvey et al. 1994, Nee et al. 1994a, b). Eventually, sufficient sampling of phylogenies might permit such comparisons, but this is not yet the case. Based on what we now know for passerine birds, the disparity in proliferation rates between tropical and temperate species suggests that appraisals of incipient speciation (e.g., Martin and McKay 2004) and incipient extinction (Manne et al. 1999, Purvis et al. 2000, Cardillo et al. 2005a) might reveal pervasive differences between tropical and temperate clades.

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LITERATURE CITED

- Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**:1545–1548.
- Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences (USA)* **101**:11040–11045.
- Barracough, T. G., and A. P. Vogler. 2002. Recent diversification rates in North American tiger beetles estimated from a dated mtDNA phylogenetic tree. *Molecular Biology and Evolution* **19**:1706–1716.
- Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds. Life histories, mating systems, and extinction. Oxford University Press, Oxford, UK.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771–1789.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society of London Series B* **266**:1221–1225.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005a. Multiple causes of high extinction risk in large mammal species. *Science* **309**:1239–1241.
- Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005b. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* **86**:2278–2287.
- Courtilot, V., and Y. Gaudemer. 1996. Effects of mass extinctions on biodiversity. *Nature* **381**:146–148.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**:1121–1134.
- Davies, T. J., T. G. Barraclough, V. Savolainen, and M. W. Chase. 2004a. Environmental causes for plant biodiversity gradients. *Philosophical Transactions of the Royal Society of London Series B* **359**:1645–1656.
- Davies, T. J., V. Savolainen, M. W. Chase, J. Moat, and T. G. Barraclough. 2004b. Environmental energy and evolutionary rates in flowering plants. *Proceedings of the Royal Society of London Series B* **271**:2195–2200.
- Dobzhansky, T. 1950. Evolution in the tropics. *American Scientist* **38**:209–221.
- Edwards, E. P. 1974. A coded list of birds of the world. Ernest P. Edwards, Sweet Briar, Virginia, USA.
- Evans, K. L., and K. J. Gaston. 2005. Can the evolutionary-rates hypothesis explain species–energy relationships? *Functional Ecology* **19**:899–915.
- Farrell, B. D., and C. Mitter. 1993. Phylogenetic determinants of insect/plant community diversity. Pages 253–266 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Fischer, A. G. 1960. Latitudinal variation in organic diversity. *Evolution* **14**:64–81.
- Harmon, L. J., J. A. Schulte, II, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* **301**:961–964.
- Harvey, P. H., R. M. May, and S. Nee. 1994. Phylogenies without fossils. *Evolution* **48**:523–529.
- Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography* **33**:770–780.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* **163**:192–211.
- Kadereit, J. W., E. M. Griebeler, and H. P. Comes. 2004. Quaternary diversification in European alpine plants: pattern and process. *Philosophical Transactions of the Royal Society of London Series B* **359**:265–274.
- Kendall, D. G. 1948. On the generalized birth-and-death process. *Annals of Mathematical Statistics* **19**:1–15.
- Latham, R. E., and R. E. Ricklefs. 1993. Continental comparisons of temperate-zone tree species diversity. Pages 294–314 in R. E. Ricklefs and D. Schluter, editors. *Species diversity: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species–area relationship. *Nature* **408**:847–850.
- MacArthur, R. H. 1972. *Geographical ecology. Patterns in the distribution of species*. Harper and Row, New York, New York, USA.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. *Evolution* **55**:1762–1780.
- Manne, L. L., T. M. Brooks, and S. L. Pimm. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* **399**:258–261.
- Martin, P. R., and J. K. McKay. 2004. Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution* **58**:938–945.
- Monroe, B. L., Jr., and C. G. Sibley. 1993. *A world checklist of birds*. Yale University Press, New Haven, Connecticut, USA.
- Nee, S. 2001. Inferring speciation rates from phylogenies. *Evolution* **55**:661–668.

- Nee, S., E. C. Holmes, R. M. May, and P. H. Harvey. 1994a. Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society of London Series B* **344**:77–82.
- Nee, S., R. M. May, and P. H. Harvey. 1994b. The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London Series B* **344**:305–311.
- Paradis, E. 2004. Can extinction rates be estimated without fossils? *Journal of Theoretical Biology* **229**:19–30.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**:33–46.
- Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B* **267**:1947–1952.
- Pybus, O. G., and P. H. Harvey. 2000. Testing macroevolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society of London Series B* **267**:2267–2272.
- Ricklefs, R. E. 2003. Global diversification rates of passerine birds. *Proceedings of the Royal Society of London Series B* **270**:2285–2291.
- Ricklefs, R. E. 2005a. Historical and ecological dimensions of global patterns in plant diversity. *Biologiske Skrifter [Royal Danish Academy of Sciences and Letters]* **55**:583–603.
- Ricklefs, R. E. 2005b. Phylogenetic perspectives on patterns of regional and local species richness. Pages 16–40 in E. Bermingham, C. Dick, and C. Moritz, editors. *Tropical rainforests. Past, present, and future*. University of Chicago Press, Chicago, Illinois, USA.
- Ricklefs, R. E. 2006. The unified neutral theory of biodiversity: do the numbers add up? *Ecology* **87**:1418–1431.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**:514–527.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Sanderson, M. J. 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* **14**:1218–1231.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution* **19**:101–109.
- Schemske, D. 2002. Tropical diversity: patterns and processes. Pages 163–173 in R. Chazdon and T. Whitmore, editors. *Ecological and evolutionary perspectives on the origins of tropical diversity: key papers and commentaries*. University of Chicago Press, Chicago, Illinois, USA.
- Sepkoski, J. J. 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London Series B* **353**:315–326.
- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and classification of the birds of the world*. Yale University Press, New Haven, Connecticut, USA.
- Sibley, C. G., and B. L. Monroe, Jr. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, Connecticut, USA.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**:240–256.
- Terborgh, J. 1973. On the notion of favorableness in plant ecology. *American Naturalist* **107**:481–501.
- Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society of London Series B* **271**:1881–1887.
- Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* **19**:639–644.
- Zhang, L. B., H. P. Comes, and J. W. Kadereit. 2004. The temporal course of quaternary diversification in the European high mountain endemic *Primula* sect. *Auricula* (Primulaceae). *International Journal of Plant Sciences* **165**:191–207.

APPENDIX A

Number of species and relative age of 14 South American and 23 North American clades of passerine birds. (*Ecological Archives* E087-149-A1).

APPENDIX B

Number of species and relative age of clades of passerine birds. (*Ecological Archives* E087-149-A2).

APPENDIX C

Inferred dates of major passerine divergences and dispersal events. (*Ecological Archives* E087-149-A3).