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Global diversification rates of passerine birds

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The distribution of species richness in families of passerine birds suggests that the net rate of diversification was significantly higher than average in as many as 7 out of 47 families. However, the absence of excess species richness among the 106 tribes within these families indicates that these high rates were transient, perhaps associated in some cases with tectonic movements or dispersal events that extended geographical ranges. Thus, large clade size among passerine birds need not represent intrinsic key innovations that influence the rate of diversification. Approximately 17 families and 30 tribes have too few species relative to other passerine taxa. Many of these are ecologically or geographically marginal, being especially over-represented in the Australasian region. Observed intervals between lineage splitting suggest that extinction has occurred *ca.* 90% as frequently as speciation (waiting times of 1.03 and 0.93 Myr) and that the 47 modern families comprising 5712 species descended from approximately 430 passerine lineages extant 24 Myr ago. Speciation and extinction rates among small, marginal families might be 1–2 orders of magnitude lower.

Keywords: cladogenesis; diversification; geometric distribution; key innovation; species richness

1. INTRODUCTION

Non-random variation in species richness among clades (Dial & Marzluff 1989; Nee *et al.* 1992; Slowinski & Guyer 1993; Magallón & Sanderson 2001) has supported the idea that key innovations promote diversification (Barraclough *et al.* 1995; Heard & Hauser 1995; Bond & Opell 1998; Hunter 1998). Among birds, several comparisons of sister taxa suggest that high species richness is associated with promiscuous mating (Mitra *et al.* 1996) and plumage dichromatism (Barraclough *et al.* 1995; Møller & Cuervo 1998; Owens *et al.* 1999), which are indicators of sexual selection. However, such comparisons have included a wide range of species with diverse ecology, life history and geographical distribution, and it is therefore difficult, in the search for key innovations, to separate attributes of organisms from the environments that shape them.

To test for non-randomness in the distribution of species richness among clades, one may compare observed distributions to patterns expected from uniform speciation and extinction rates. When probabilities of speciation (b) and extinction (d) are uniform across lineages, the number of species in a clade assumes a geometric probability distribution (Kendall 1948; Nee *et al.* 1992, 1996). Accordingly, the probability of n species in an extant clade ($n > 0$) at time t is

$$P(n|t) = (1 - u)u^{n-1}, \tag{1.1}$$

where

$$u = \frac{b(L - 1)}{bL - d} \tag{1.2}$$

and L, the expected size over all clades at time t, whether extant or not ($n \geqslant 0$), is

$$L = e^{(b-d)t}. \tag{1.3}$$

For geometrically distributed data, the average species richness of extant clades ($n > 0$) is $N = 1/(1 - u)$, or

$$N = \frac{(bL - d)}{(b - d)}. \tag{1.4}$$

Hence, when $d = 0$, $N = L$. From equation (1.3), when $d = b$, $L = 1$, as required when new lineages exactly replace extinct ones. The standard deviation of the number of species per extant clade, $(N(N - 1))^{1/2}$, is approximately equal to the mean (N). This relationship provides a simple test of the null model of rate homogeneity that is independent of the absolute rates of speciation and extinction, including the case in which the rates are equal. Variation in these rates affects only the proportion of extinct lineages for a particular value of N, according to $P(n = 0 \mid t) = (d/b)(N - 1)/N$.

In addition to testing for non-randomness in the net rate of diversification, analysis of the distribution of species richness can show whether non-randomness has produced an excess of small or large clades. Nested analyses can reveal whether non-randomness exhibited at a higher level appears at the lower level as well, as expected when intrinsic clade properties influence diversification. Finally, because they are inherited from ancestors, such intrinsic clade properties should also exhibit phylogenetic non-independence.

Analyses presented here of species richness in similar-aged families and tribes of passerine birds (the monophyletic order Passeriformes, which includes more than half of all bird species) provide no evidence for clades with excessive species richness resulting from intrinsic attributes that accelerate diversification. A few species-rich families have diversified transiently during periods that were probably associated with major expansions of geographical distribution (Mercer & Roth 2003). Although ecology, mating system and other aspects of behaviour vary, such clade-specific traits apparently do not consistently influence species formation and extinction in passerine birds (Gage *et al.* 2002; Morrow *et al.* 2003).

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2. MATERIAL AND METHODS

(a) *Data*

I examined variation in species richness of passerine birds (the monophyletic order Passeriformes) among 47 clades designated as 'families' and 106 clades nested within these families and designated as 'tribes' by Sibley & Ahlquist (1990), together comprising 5712 species. I restricted this analysis to passerines to reduce the potential effects of body size and habitat (i.e. aquatic versus terrestrial) on rates of diversification. At each level, the clades are of similar age according to the genetic divergence between sister clades sharing a common ancestor. Sibley and Ahlquist quantified genetic divergence by DNA-hybridization and reported the difference between the midpoint temperatures of the melting curves for homoduplexed and heteroduplexed (hybridized) DNA ($\Delta T_{\rm H}50$). Clades were identified as lineages that descended either from a node within the range of $\Delta T_{\rm H}50 = 9$–11 °C for families or 4.5–7 °C for tribes, or from a single branch in either of these ranges. In the latter case, Sibley and Ahlquist gave the clade higher rank, but extant representatives diversified after the time-range for newly arising family-level or tribe-level clades. Although direct sequencing has refined the Sibley–Ahlquist avian phylogeny, the topology has held up reasonably well (Mooers & Cotgreave 1994; Irestedt *et al.* 2001; Barker *et al.* 2002). Nevertheless, incomplete sampling, inaccuracies in phylogenetic reconstruction, and ambiguities in monophyly of taxa are bound to add the appearance of randomness to distributions of species richness and may reduce our ability to extract the underlying structure. At this point, we can only accept this uncertainty and wait upon improved phylogenies for future refinements. Family-level and tribe-level taxonomy of birds, as well as the number of species in passerine families and tribes, was obtained from the treatment of the birds of the world by Sibley & Monroe (1990).

(b) *Simulations*

The observed data were compared with simulations assuming different models of speciation and extinction. I simulated speciation and extinction by using a program written in SAS language (SAS Institute 1989). The program generated species within a clade by randomly causing each lineage to either split, with probability b, or terminate, with probability d, at each of $t = 1000$ time-steps from the beginning to the end of the simulation. For most simulations, either 47 (families) or 106 (tribes) clades were simulated simultaneously. Each set of simulations over clades was repeated either 100 or 1000 times. From the values generated by these replicates, I calculated the means for average number of species per clade (N), the standard deviation of clade size n, and the ratios of s.d.(n) and maximum clade size ($n_{\rm max}$) to the average. All simulations and statistics were carried out by SAS version 6.12 software (SAS Institute 1989).

Speciation and extinction probabilities did not exceed 0.01 in most simulations. At each time-step, two random uniform variates (R_1 and R_2, range of 0–1) were generated for each lineage within the clade and an event occurred when $R_1 < b$ or $R_2 < d$. Speciation events were tabulated before extinction events, and so the rare (less than 10^{-4}) cases of double events resulted in no change in species number. For a particular average clade size (N), the distribution of clade size (u) is independent of the relative speciation and extinction rates. Thus, for this analysis, most simulations were run with $d = 0$. Hence $N = L$ and bt was estimated by $\ln(N)$.

For a particular speciation rate, repeated simulations over a fixed number of clades produce variation in the total number of species. However, because the observed total number of species is fixed, Nee *et al.* (1992) suggested that the expected distribution of species among clades should be produced by randomly subdividing the observed total number. For a given number of species in a prescribed number of clades, species abundances resulting from a homogeneous birth–death process assume a broken-stick distribution (Pielou 1977; Nee *et al.* 1992). I obtained broken-stick distributions by randomly distributing $x - 1$ (46 or 105 for families and tribes, respectively) points over an interval length of 5712 units (species) and calculating the increments between each random point.

To simulate differences in speciation rate among clades, variation in b was generated by $b_{\rm var} = b\exp(kx)$, where k is a random normal deviate (mean = 0, s.d. = 1) and x is a coefficient controlling the magnitude of the variation. For small x, the proportional variation in b is approximately equal to x. Because Sibley & Ahlquist's (1990) minimum and maximum values of $\Delta T_{\rm H}50$ for family-level or tribe-level designation were arbitrary, variation in t was generated by adding a random uniform number ($0 < y < t_{\rm max}$) to a baseline value $t_{\rm min}$, hence $t_{\rm var} = t_{\rm min} + y$. Results for variation in t are not reported because the effect is small. For example, varying the number of time-steps randomly between 900 and 1100 to match the family-level range of 9–11 °C $\Delta T_{\rm H}50$ increased the ratio of the s.d. of clade size to the mean from 0.95 ± 0.12 to 1.05 ± 0.17 s.d.

Phylogenetic independence of clade size was tested by using the program Phylogenetic Independence (PI) (Abouheif 1999; Reeve & Abouheif 1999). When h observations of variable y are serially independent, the sum of squares of the $n - 1$ differences (Σd^2) between adjacent observations is twice the sum of squares of the values (Σy^2). Defining $\eta = \Sigma d^2/\Sigma y^2$, the value of $C = 1 - (\eta/2)$ is equal to 0. Values of $C > 0$ indicate serial autocorrelation, which one would expect when related lineages share traits (phylogenetic effect). Because the order of the tips of a phylogeny is constrained only by the rotation of branches about nodes, the significance of the observed value of C must be evaluated by a randomization test. The program Phylogenetic Independence performs 1000 random rotations of the phylogenetic topology to obtain an observed value of C and 1000 random shuffles of the tip data to obtain a null distribution of serial independence.

3. RESULTS

The variation in species richness among families is clearly non-random. The standard deviation of species richness is 1.67 times the mean (figure 1), which is outside the range of values produced by simulation of a homogeneous speciation–extinction process (0.952 ± 0.116 s.d., 100 trials) or by a 'broken-stick' distribution, which reproduces the geometric distribution for a fixed number of species (Pielou 1977; Nee *et al.* 1996). This reflects a small number of family-level clades having more species than predicted and a larger number of such clades having fewer species. The observed distribution of the number of species is consistent with variation among clades of *ca.* ± 20% of the mean in the net rate of diversification (figure 1).

For tribes, the ratio of the standard deviation to the mean (1.35) is also outside the range of variation of simulated clades (0.97 ± 0.11 s.d.; figure 1), however, this does not reflect instances of excessive species richness. Rather, many tribes have fewer species than expected under a

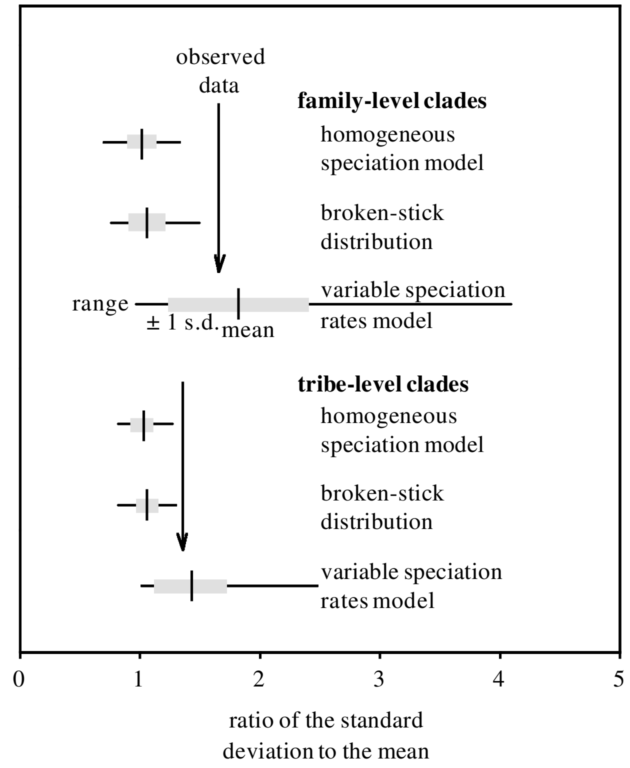

Figure 1. The average ratio of the standard deviation to the mean number of species (vertical marks), plus and minus 1 s.d. (grey boxes), and range of values (horizontal lines) for 100 simulations of the diversification of species richness among 47 family-level clades (above) and 106 tribe-level clades (below). For simulations of the homogeneous speciation rates model, $b = 0.004\,80$ ($u = 0.9918$) for families and 0.003 99 ($u = 0.9815$) for tribes over 1000 time-steps. Simulations of the variable speciation rates model used $b = 0.004\,30$ with exponential variation of 0.20 for families and $b = 0.003\,80 \pm 0.15$ for tribes. Vertical arrows indicate the observed ratios of the standard deviation to the mean.

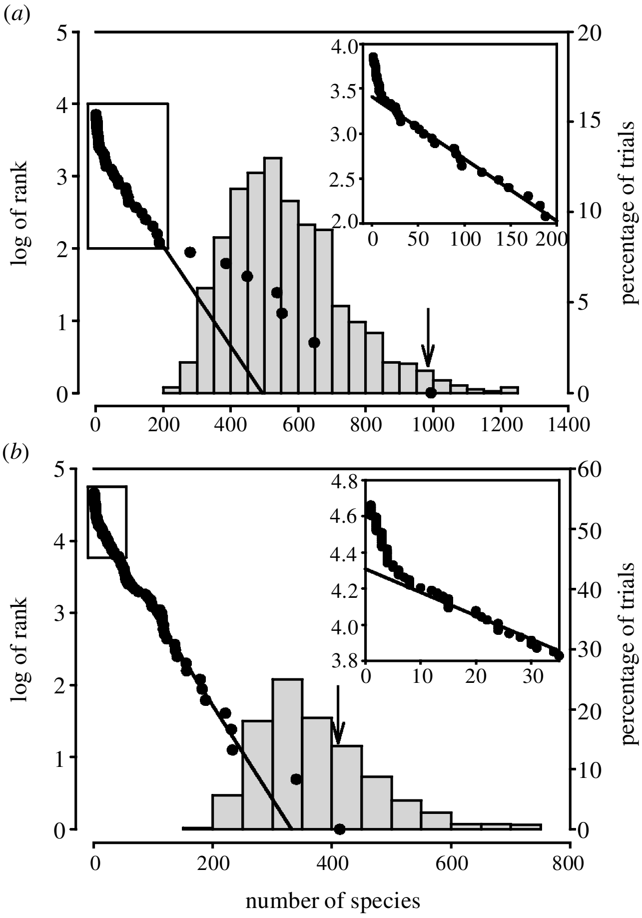

Figure 2. Relationship between the natural logarithm of rank (1 being the most species-rich clade, $\log_e(\text{rank}) = 0$) and number of species for (*a*) family-level clades and (*b*) tribe-level clades. The insets show close-ups of the relationship for less species-rich clades. The solid lines are fitted regressions for clades showing an approximately linear relationship between the logarithm of rank and species richness (11–200 species for family-level clades and 5–250 species for tribe-level clades). The fitted equation is $\log_e(\text{rank}) = \log_e[1 - C(n)] + \log_e(\text{number of clades}) = \log_e(u)n + \log_e(\text{number of clades})$. The histograms represent the distribution of maximum number of species per clade in 1000 trials, based on speciation rate and number of clades calculated from the regression for observed data (solid lines) ($b = 0.004\,98$, 30 families; $b = 0.004\,35$, 74 tribes).

model of homogeneous diversification (Nee *et al.* 1992; Owens *et al.* 1999).

When variation in species richness is distributed geometrically, the cumulative frequency of clades with no more than n species is $C(n) = 1 - u^n$. Accordingly, u may be estimated from the slope of the linear relationship between the logarithm of $1 - C(n)$ and n, that is,

$$\log[1 - C(n)] = \log(u)n. \tag{3.1}$$

The term $[1 - C(n)]$ multiplied by the number of clades corresponds to the rank of the clade from largest to smallest. The log of rank as a function of clade size (n) is portrayed for families and tribes of passerine birds in figure 2. In both cases, the log of rank is linearly related to species number over most of the sample of clades. These clades may be used as a reference for homogeneous diversification against which the size of the largest clades and the number of the smallest clades can be compared.

Family-level clades within the range of 11–200 species follow a geometric distribution with $u = 0.9931$ and the estimated number of families for this value (the intercept at $n = 0$) equals to 30.3 (figure 2). Thus, approximately 17 out of 47 families deviate from the referenced homogeneous-rates model in having too few species. At the other end of the distribution, seven families apparently have too many species. The most diverse family (993 species) exceeds all but *ca.* 2% of the largest clades generated at random from the geometric parameters fitted to the referenced clades in figure 2. A test of phylogenetic independence indicated that species richness was not correlated among closely related family-level clades ($C = 0.052$, $p = 0.253$, 47 clades). Such a correlation would be expected if the rate of diversification were phylogenetically conservative. However, the most diverse family-level clades are broadly dispersed within the phylogeny of passerine birds.

Tribe-level clades within the range of 5–250 species follow a geometric distribution with $u = 0.9871$; the estimated number of tribes extrapolated from the referenced distribution is 74.3 (figure 2). One thousand sets of 74 clades generated at random using these parameters produced maximum clade size exceeding the observed 413

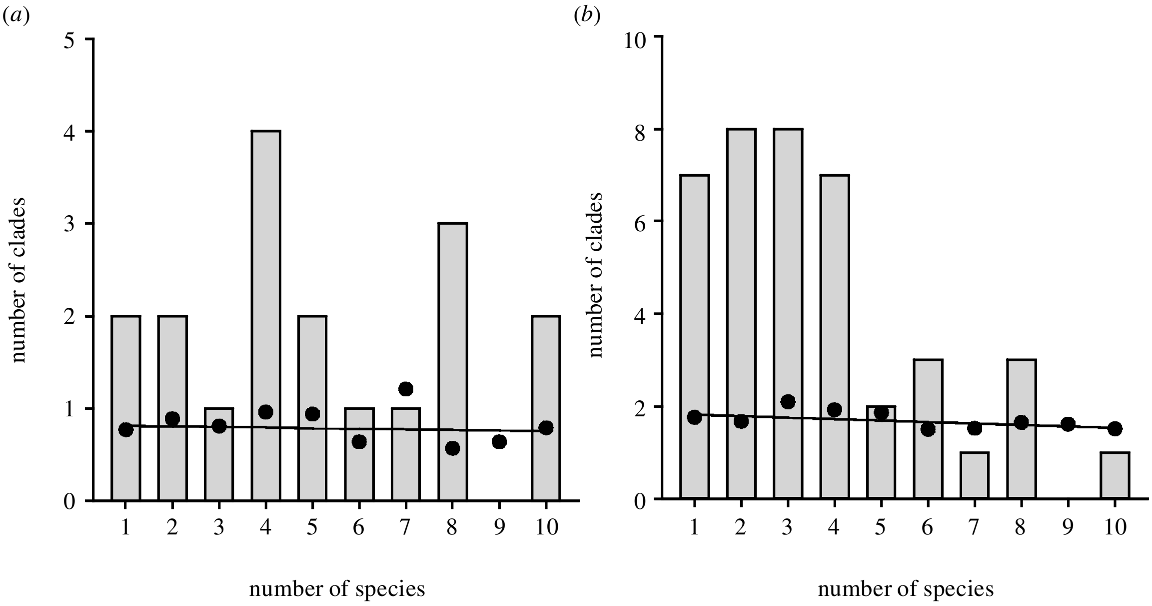

Figure 3. Observed number of (*a*) family-level ($u = 0.9918$, 47 clades) and (*b*) tribe-level ($u = 0.9815$, 106 clades) clades with 1–10 species compared to the expected number based on the geometric distribution (horizontal line) with the parameter u calculated from the observed (grey bars) mean number of species per clade (N). The means for 100 simulations with the same values of u are also presented. Simulated random speciation represented by filled circles.

species (Fringillidae: Thraupini) in almost 30% of cases, indicating an absence of excessive species richness among tribes. A test of phylogenetic independence also revealed no correlation of species richness among closely related tribe-level clades ($C = 0.110$, $p = 0.183$, 106 clades). Thus, the deviation of species richness among tribes from a homogeneous process is due to an excessive number of small clades, especially the 30 tribes having fewer than five species (figure 3), which are randomly distributed with respect to phylogenetic relationship.

Simulations using models with homogeneous rates of speciation or continuously variable rates of speciation do not reproduce the observed number of small tribe-level clades. For example, although a variable-rates model for tribes shown in figure 1 approximated the mean (56.6 versus 53.9 observed), standard deviation (79.3 versus 72.9), number of species in the 10 largest clades (2444 versus 2298), and number of clades with 5–9 species (9 versus 9), it produced only 10 clades with fewer than five species versus the 30 observed. The observed pattern is readily simulated, however, by a model with two discrete groups of clades with different rates of speciation. For example, applying $b = 0.004\,35$ to 70% of tribe-level clades and $b = 0.000\,435$ to 30% yields: mean = 53.6, s.d. = 70.7, 10 largest clades = 2240 species, 34 clades with less than five species, and seven clades with 5–9 species.

4. DISCUSSION

(a) *Transient high diversification rates*

Although extant passerines do not exhibit an excess of large tribe-level clades, several families with excessive species richness apparently experienced periods of higher-than-average net diversification of extant lineages between their origins and the time at which modern tribe-level clades arose and began to diversify. The average number of tribes per family is 2.26 ± 2.68 s.d. Five families out of the seven with the largest number of species have more than five tribes. Assuming a geometric distribution and using the mean of 2.26 tribes per family, the probability of six or more tribes is 0.030, which corresponds to approximately 1.5 families. Two families have nine or more tribes ($p = 0.005$) and one has 16 tribes ($p < 10^{-4}$). Thus, the larger numbers of tribes per family are unlikely to have been produced by a homogeneous process of diversification.

Conditions that led to high tribe-level diversity in a small number of families evidently were transient and probably were not related to the intrinsic qualities of the birds themselves. The lack of evident heterogeneity in rates of species proliferation among the larger tribes (figure 2*b*) and the absence of serial autocorrelation in species richness among families and tribes suggest that clade-specific traits that led to a proliferation of tribe-level lineages did not carry through to the tribe-level clades themselves.

Sibley & Ahlquist (1990) suggested that DNA-hybridization distances could be related to time according to 2.3 Myr per 1° $\Delta T_{\mathrm{H}}50$ for birds with the short generation times of most passerines. This would place the origin of family-level clades at 25–21 Myr (early Miocene), and the origin of tribe-level clades at 16–10 Myr (middle Miocene). Accordingly, the unusual proliferation of clades in some lineages during the late Tertiary could reflect unique episodes of expansion of geographical distribution or special ecological conditions that have not recently influenced the balance between species production and extinction. Significant events might have included the colonization of South America by several North American fringillid lineages (family Fringillidae, nine tribes), the escape of corvid lineages (family Corvidae, 16 tribes) from Australasia as the Australian plate approached Asia (Barker *et al.* 2002; Ericson *et al.* 2002), the closing of the Tethys seaway between Africa and Eurasia, and the rise

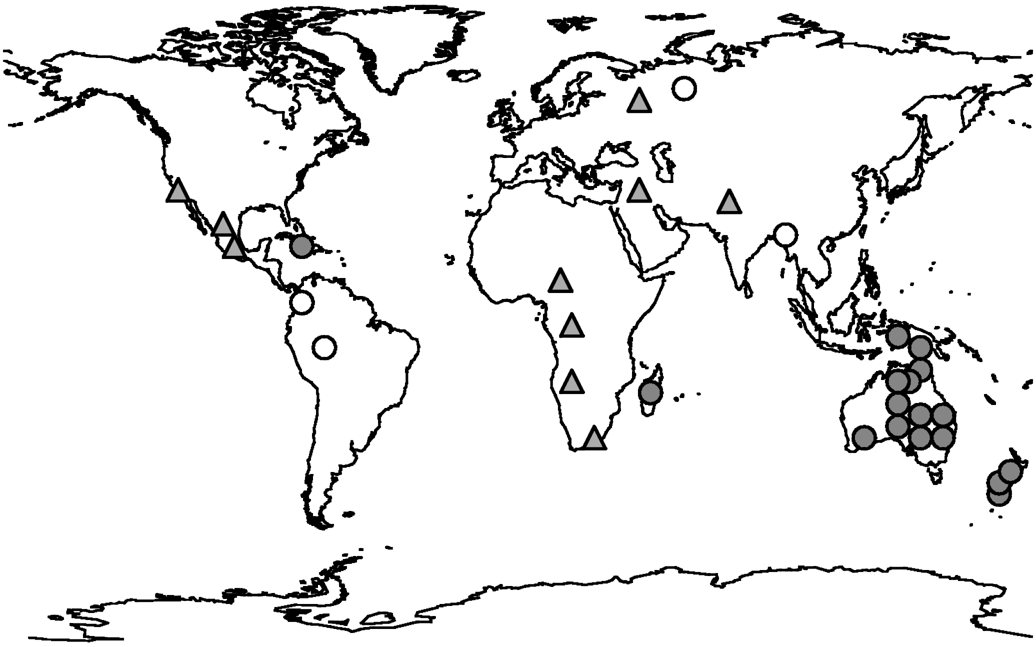

Figure 4. Approximate geographical distribution centres of small tribe-level clades of passerine birds. Seventeen non-continental endemics (filled circles) are restricted to Australasia (15 clades), Madagascar (Philepittini) and Hispaniola (Dulini). Seven occupy marginal habitats (filled triangles; dry woodland and scrub: African creeper, Salpornithini; wrentit, Chamaeini; hypocolius, Hypocoliini; river-martin, Pseudochelidonini; montane pine forest: olive warbler, Peucedramini; rock outcrops: wall creeper, Tichodromini; rock dweller, Picathartini). Two sister tribes (subfamily Bombycillinae: waxwings, Bombycillini; silky flycatchers, Ptilogonatini) include a high proportion of waxy fruit in their diets. The remaining four small tribes (open circles; the monotypic *Sapayoa*, northwestern South America; *Schiffornis*, tropical America; Fringillini, Palaearctic; ioras, Aegithinini, southeastern Asia) do not have notably unusual traits.

Table 1. Distribution of small tribes among the major biogeographic regions of the Earth.
(Australasia and the Neotropics have an excess of endemic tribes (overall G statistic for heterogeneity $= 21.4$, d.f. $= 5$, $p = 0.0007$); the proportion of small tribes among all regions except Australasia is homogeneous ($G = 1.8$, d.f. $= 4$, $p = 0.76$) but Australasia differs significantly from the other regions ($G = 7.5$, d.f. $= 1$, $p = 0.006$).)

	Nearctic	Neotropical	Palaearctic	African	Oriental	Australasian
total tribes	28	28	27	36	40	40
endemic tribes	5	12	3	6	5	27
with fewer than five species	5	2	3	5	3	14

of the Andes in South America (family Tyrannidae, six tribes).

(b) *Small clades*

Except for an unusually high number of tribes in a small number of phylogenetically unrelated families, the most conspicuous lack of homogeneity in the distribution of species richness is the large proportion of small clades. Most of these phylogenetically unrelated small tribes are marginal either geographically or ecologically, in the sense that they are isolated from the major continental landmasses of the Earth, occur in habitats with relatively low avian diversity, or have unusual diets (figure 4; table 1). Only four out of 30 tribe-level clades with fewer than five species lack these special features. Retaining only these four, the resulting distribution of species richness among 80 tribe-level clades matches a geometric distribution closely ($u = 0.9883$, $N = 70.6$, s.d.$(n) = 76.9$), with 3.6 tribes expected to have fewer than five species and the largest tribe expected to have 361 species (observed $= 413$).

(c) *Key innovations*

Most passerine clades distributed on the major continents appear to share a common net rate of diversification. Thus, the variation in species richness among family-level lineages (1–993 species) and, especially, tribe-level lineages (1–413 species) is largely consistent with the effects of random chance. Over a wide range of body size, ecological relationship, global geographical distribution and climate region, lineages of passerine birds have had similar probabilities of splitting or dying out, regardless of their lineage-specific characteristics (Owens *et al.* 1999), at least since the origin of modern tribes. It is not necessary to invoke key innovations to explain variation in lineage diversity (Gage *et al.* 2002; Morrow *et al.* 2003). The apparent relationship between species richness and mating system observed in several analyses (Barraclough *et al.* 1995; Mitra *et al.* 1996; Møller & Cuervo 1998; Owens *et al.* 1999) is either restricted to a higher taxonomic level of analysis than families or tribes within Passeriformes, or reflects reversed causation. Accordingly, high species richness attained within clades by chance might select

Table 2. Parameters of a random speciation and extinction process that provide reasonable approximations to the observed distribution of species per family when extinction rate is a specified fraction of the speciation rate ($d \leqslant b$).
(Families of passerine birds are assumed to have descended from lineages established 24 Myr ago; initial number of clades calculated according to $N_o = N_t \exp[-(b-d)t]$, where $N_t = 5712$ and $t = 24$ Myr. NA, not applicable.)

	extinction rate (d) as a percentage of the speciation rate (b)			
	0	50	90	100
speciation interval (Myr)	5.00	2.90	0.93	0.16
extinction interval (Myr)	NA	5.80	1.03	0.16
speciation rate × time (bt)	4.80	8.3	25.8	150
initial number of clades	1	90	430	5712

enhanced sexual dichromatism and strong female mate choice to the extent that these traits minimized hybridization and allowed coexistence of species. Because diversification within passerine families and tribes apparently is unrelated to intrinsic attributes, excessive species richness in some taxonomic groups at a higher level (Dial & Marzluff 1989; Nee *et al.* 1992; Owens *et al.* 1999) might similarly be explained by extrinsic circumstances and events that drive diversification.

(d) *Rates of speciation and extinction*

The net rate of lineage proliferation reflects a balance between speciation and extinction. In a homogeneous birth–death process, the distribution of clade sizes provides no information concerning the relative rates of speciation and extinction. However, for a given distribution of clade sizes, different rates of speciation and extinction are paralleled by different intervals between speciation or extinction events, which may be compared with information from time-calibrated molecular phylogenetic analyses.

I have estimated rates for the cases in which extinction rate (d) equals either 0 or various proportions, up to 100%, of the speciation rate (b) (table 2). When $d = 0$, $N = e^{bt}$, and the product $bt = 4.80$ for families and 3.99 for all tribes. When $d = b$, the total number of lineages remains constant over time. Accordingly, for passerine birds, the 5712 species extant at the time of origin of modern family-level clades would leave as descendants 47 clades comprising a current total of 5712 species. In simulations of lineage diversification beginning with 5712 clades of one lineage each, speciation and extinction rates of $bt = dt = 150$ approximated the observed species richness of modern family-level clades reasonably well (43.3 ± 8.7 clades, $N = 130.6 \pm 14.0$, s.d.$(N) = 120.1 \pm 17.8$, $n_{\max} = 539.6 \pm 107.0$, 10 trials). The same simulation run for $t = 575$ steps to approximate the relative diversification of tribes resulted in $n = 75.1 \pm 8.2$ clades with an average of $N = 76.9 \pm 10.5$ species (s.d.$(n) = 79.2 \pm 11.7$; total species $= 75.1 \times 76.9 = 5775.2$) and a maximum of 442.5 ± 87.1 (10 trials). Except for the excess of 25 or so small clades, which might represent relicts that have avoided extinction, this also matches the observed distribution very closely. Indeed, the actual number of species in 76 tribe-level clades with five or more species averages 74.2 ± 77.3 s.d.(n).

If family-level clades arose at an average of 24 Myr, the speciation and extinction rates of lineages for the case $b = d$ would each be 6.25 per million years ($bt = 150$ divided by 24 Myr). Accordingly, the average duration of a lineage before either splitting or dying out would be 0.16 Myr or 160 000 years. Over all 5712 species of passerine bird, this would amount to speciation and extinction rates of 0.036 per year, or a speciation and extinction event every 28 years, which appears short. Only one continental species—the slender billed grackle (*Quiscalus palustris*) of the state of Mexico—is known to have died out in the past century, probably the result of extensive drainage of wetlands (BirdLife International 2000).

Such a rapid turnover of species also is inconsistent with current understanding of the time required for species formation. The average divergence time between geographically separate clades within passerine species (incipient species) in several studies is 1.1×10^6 years (± 1.1 s.d., $n = 21$) (Avise & Walker 1998), and this provides a reasonable estimate of the minimum average time to the separation of populations that will become evolutionarily independent lineages. When the extinction rate is set at 50% of the speciation rate in simulations, a value of $bt = 8.3$, corresponding to an average time between speciation events of 2.90×10^6 years, fits the observed average number of species per family closely. When the extinction rate is set at 90% of the speciation rate, a reasonable fit to the data is provided by $bt = 25.8$, with corresponding intervals before speciation and extinction of 0.93 and 1.03×10^6 years, respectively. Over all 5712 species of passerine bird, this would produce an extinction event every 180 years. Thus, speciation and extinction rates of 1.08 and 0.97 per 10^6 years, and an increase in passerine species diversity from 430 to 5712 over 24 Myr, seem to be reasonable provisional estimates (table 2). They are also similar to the relative rates estimated by Magallón & Sanderson (2001) for flowering plants with $d = 0.9b$. For passerine birds, adopting $d = 0.9b$ and 13.8×10^6 years for the age of tribe-level clades, a slightly higher speciation rate (e.g. 1.5 per 10^6 years, or $bt = 20.7$) is required to approximate the observed data (e.g. 721 initial lineages produce 82 clades averaging 64.6 ± 6.1 species and a maximum clade size of 319 ± 120, $n = 10$).

Long-term persistence of small, relict clades implies very low rates of extinction and speciation. For example, with $bt = dt = 1.5$, which is two orders of magnitude less than the postulated continental rates when $d = b$ and more than one order of magnitude less than when $d = 0.9b$, 100 lineages leave 39.1 ± 5.1 clades with 2.5 ± 1.9 species ($n_{\max} = 8.8 \pm 2.1$), which approximates the distribution of species number among small, tribe-level clades. These results imply that if speciation and extinction rates have been constant over time, relict tribes of passerine birds have experienced extremely low lineage turnover (e.g. average lineage duration, 16×10^6 years), suggesting that low speciation and extinction rates may be correlated outcomes of the special environments or ecological relationships of relict lineages. The extremely long persistence of isolated clades and species (Ricklefs & Bermingham 1999, 2001; Lovette *et al.* 2002) highlights the impact of human activities as a cause of the current rapid rate of extinction of island taxa (Steadman 1995). The rare clades have persisted by their isolation, not their resistance to change.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.