The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals

Jason T. Weir* and Dolph Schluter

Although the tropics harbor greater numbers of species than do temperate zones, it is not known whether the rates of speciation and extinction also follow a latitudinal gradient. By sampling birds and mammals, we found that the distribution of the evolutionary ages of sister species—pairs of species in which each is the other's closest relative—adheres to a latitudinal gradient. The time to divergence for sister species is shorter at high latitudes and longer in the tropics. Birth-death models fitting these data estimate that the highest recent speciation and extinction rates occur at high latitudes and decline toward the tropics. These results conflict with the prevailing view that links high tropical diversity to elevated tropical speciation rates. Instead, our findings suggest that faster turnover at high latitudes contributes to the latitudinal diversity gradient.

The tropics possess many more species than temperate regions, yet the underlying causes of this latitudinal gradient in species diversity are poorly understood (*1*–*3*). A number of authors have estimated net diversification rates (speciation minus extinction) across a latitudinal gradient and concluded that more species accumulate per unit time at tropical latitudes [including birds (*4*–*7*), primates (*8*), marine bivalves (*9*), foraminifera (*10*), and butterflies (*4*)]. By examining the age distributions of the youngest species of birds and mammals, and how they change with latitude, we examined the contributions of recent speciation and extinction to the latitudinal gradient in net diversification.

We studied a large data set comprising the ages and midpoint latitudes of breeding range for 309 sister species pairs of New World birds and mammals. We defined sister species as the most closely related pair of extant species descended from an immediate common ancestor. Their ages were estimated from genetic distances of mitochondrial DNA from the cytochrome b gene. The rate of evolution in this gene is approximately constant with time within birds and mammals (*11*–*13*) and has been used widely to date phylogenetic events in these groups. The average of the absolute value of midpoint breeding latitude for a sister-species pair was used to approximate the latitude at which speciation occurred. This approach is reasonable for sister-species pairs that have narrow latitudinal ranges, but greater uncertainty exists when latitudinal ranges are broad. Excluding all species pairs with a combined latitudinal range (defined by the northern and southern limits for the pair) of greater than 40° did not affect the relationship between age and midpoint latitude. Latitudinal ranges of species at high latitudes have shifted in response to glacial cycles. However, using the presumed latitudes of species ranges during past glacial maxima, when many temperate species were forced southward, would only steepen the gradients estimated here.

Near the equator, the ages of sister-species pairs spanned the past 10 million years, with a mean age of 3.4 million years ago (Ma) (Fig. 1A). As distance from the equator increased, the upper limit and mean ages of sister species declined significantly [slope = −0.043 ± 0.007 Ma/degree latitude (± SEM), student's t test = −6.5, $P < 0.0001$, intercept = 3.37, degrees of freedom (df) = 307]. At the highest latitudes, all of the sister species diverged less than 1.0 Ma. This pattern of declining age with latitude is opposite to the pattern that would occur if faster rates of speciation had driven the buildup of Neotropical diversity, because the ages of sister species should be youngest where speciation rates are highest.

The differences in species ages between low and high latitudes is partly the result of a longer lag time in tropical faunas between population splitting, as measured by genetic markers, and species designation (Fig. 1, B and C). The evidence for this lies in the coincident latitudinal gradient in the ages of the oldest haplotype splits within 154 currently defined species of birds and mammals (Fig. 1B) and in the oldest phylogroup splits within 130 species (Fig. 1C). Avise (*14*, *15*) defined a phylogroup as a reciprocally monophyletic geographic subdivision

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within a species. By examining sets of closely linked alleles (haplotypes), we were able to use maximum haplotype divergence as well as the age of the deepest phylogroup splits to compare the lag time to species formation, because species at high latitudes are so young that most lack phylogroups. Both haplotype and phylogroup splits are older in the tropics than in temperate zones, on average, implying that the process of speciation takes longer at low latitudes. This may be in part an artifact of the greater taxonomic uncertainty at lower latitudes, because a higher proportion of tropical species are currently undescribed and thus considered together in our analysis. Nevertheless, taxonomic uncertainty is unlikely to be the sole cause of the gradient. This is because the latitudinal gradient in the ages of sister species is present even within the Nearctic fauna of North America, which is well defined taxonomically north of approximately 30°N (slope = −0.041 ± 0.017, $t = -2.44$, $P = 0.017$, intercept = 3.3, df = 99). Reproductive isolation, marking the completion of the speciation process, usually takes time to evolve after population splitting, and our data suggest that this process might take a longer period of time at lower latitudes, although we are not sure why this is the case.

There are differences in the age distributions of sister species across the latitudinal gradient apart from the lag-time difference. Therefore, it may be possible to extract information about speciation (rate of cladogenesis) and extinction rates from the distribution of sister-species ages after correcting for the lag-time, because speciation and extinction can be inferred by the shape of the age distributions of sister species. In phylogenetic simulations using a pure birth model, in which speciation rates are constant through time and no extinction occurs (*16*), ages of sister species approximate an exponential distribution for which the mean is proportional to the speciation rate; adding a lag time shifts the mode in the distribution toward the mean lag time. Extinction changes the shape of these distributions by increasing the breadth of the tails (*17*).

We used maximum likelihood to fit a birth-death (*18*) model in which speciation (λ) and extinction (μ) rates changed linearly across the latitudinal gradient:

$$\lambda = b_{\lambda}L + c_{\lambda} \qquad (1)$$

$$\mu = b_{\mu}L + c_{\mu} \qquad (2)$$

where L is the absolute value of latitude, b is the slope, and c is the rate at 0° latitude. The model estimated the slopes (b_{λ}, b_{μ}) and intercepts (c_{λ}, c_{μ}) for the linear relationships between λ, μ, and L (Fig. 2) by fitting data points at each latitude to simulated probability distributions of sister species ages corresponding to different values of speciation and extinction in a reconstructed birth-death process (*17*). We generated probability distributions of sister-species ages by simulating a large number of phylogenetic trees under a birth-death process and recording the resulting distribution of sister-species ages for a range of parameter values. Simulated trees were corrected for the lag time to species recognition assuming that lag times had an exponential distribution with mean equal either to the average age of the oldest known haplotype splits, or to the average age of phylogroup splits within species at that latitude (*17*).

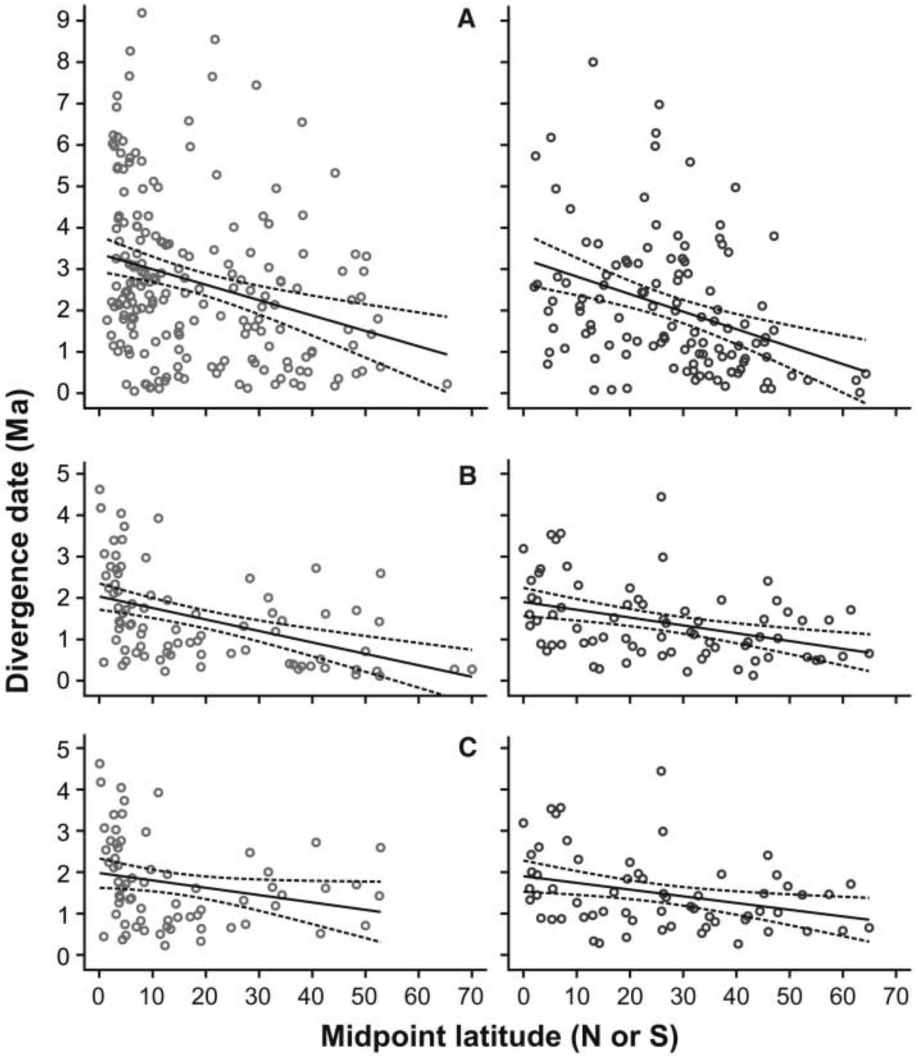

Fig. 1. Relationship between time since splitting and average absolute midpoint latitude for sister taxa of New World birds and mammals. (**A**) Ages of 309 sister-species pairs of New World birds (left; $n = 191$) and mammals (right; $n = 118$). Linear regression lines are shown for birds (slope = –0.040, $t = -4.368$, $P < 0.0001$, intercept = 3.38 Ma) and mammals (slope = –0.042, $t = -4.258$, $P < 0.0001$, intercept = 3.26 Ma). (**B**) Ages of 154 maximum coalescent dates for intraspecific haplotype variation within bird ($n = 81$) and mammal ($n = 73$) species. Linear regression lines are shown for birds (slope = –0.028, $t = -4.58$, $P < 0.0001$, intercept = 2.03 Ma) and mammals (slope = –0.019, $t = -3.62$, $P < 0.0006$, intercept = 1.91 Ma). (**C**) 130 phylogroup splits for birds ($n = 68$) and mammals ($n = 62$). Linear regression lines are shown for birds (slope = –0.018, $t = -2.00$, $P = 0.049$, intercept = 1.98 Ma) and mammals (slope = –0.016, $t = -2.67$, $P < 0.01$, intercept = 1.91 Ma).

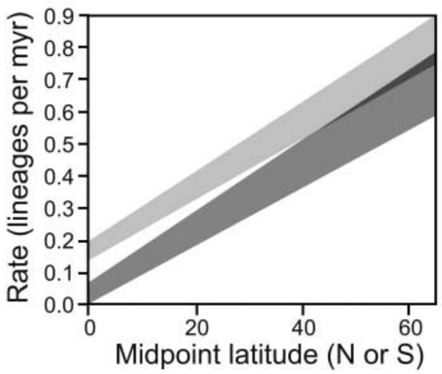

Fig. 2. Estimates of speciation (light gray) and extinction (medium gray) rates in millions of years (myr) across latitude (L) for New World birds and mammals. All rate estimates within 1 log likelihood unit of the maximum likelihood estimate are shown. Region of overlap shown in dark gray.

The maximum likelihood model estimated significantly positive slopes for the relationship between λ (support interval, 0.0076 to 0.0117), μ (support interval, 0.0046 to 0.0135), and latitude for the combined data set of bird and mammal sister species (Fig. 2). Results were similar when maximum haplotype or oldest phylogroup splits were used to correct for lag times, and only the correction with haplotypes is reported here. Estimated speciation and extinction rates were lowest at the equator and increased significantly toward the poles (Fig. 2). The same trends were obtained when excluding sister-species pairs with combined latitudinal ranges greater than 40° and when bird and mammal data sets were fit separately, but results were not significant in the mammal data set. These results hold true even when correcting for the latitudinal gradient in lag time to speciation. We expect that better knowledge of species-level taxonomy in the tropics will revise the lag time and sister-species age gradients. This revision should have minimal influence on the estimates of speciation and extinction, given that they are adjusted for lag time.

These results are surprising because the latitudinal gradient in estimated speciation rate is opposite to the gradient in net rate of diversification estimated by many studies to be highest in tropical taxa (*4–10*). For our data on sister species, the gradient in net diversification is not significantly different from zero ($b_\lambda = b_\mu$). Still, the range of estimates for the net diversification gradient supported by this study is consistent with estimates obtained elsewhere for birds (*5*). If the gradient is real, as other studies encompassing longer time periods indicate (*4–10*), our findings would support the classic views of Wallace (*19*), Fisher (*20*), and others (*12*, *21*, *22*), who reported that reduced extinction risks at tropical latitudes promoted the gradual buildup of high species diversity there.

These quantitative estimates are based on the assumption that speciation and extinction can be approximated by a continuous birth-death process as latitude becomes higher or lower. Yet, we know that there have been fluctuations in the opportunities for speciation and extinction over the past few million years (*12*, *23*). For example, extensive climatic fluctuations that occurred at high latitudes during the late Pliocene and Pleistocene (2.5 Ma to present) may have concentrated speciation and extinction events in time, resulting in episodic species turnover. In contrast, the bursts of diversification in tropical faunas may predate the late Pliocene and Pleistocene, and the patterns observed today may be the result of a subsequent decline in diversification either because the geological processes that promoted diversification (e.g., formation of Isthmus of Panama, marine incursions, orogeny, and river formation) have slowed or because diversification rates declined as the number of tropical species approached a "carrying capacity" (*7*, *12*).

Given such variability, our estimates are best regarded as averages over the periods studied. Despite these uncertainties, our results suggest that elevated speciation and extinction rates in the temperate zone can drive high turnover of species, whereas rates of species turnover at tropical latitudes are reduced. A recent study of fossil marine bivalves also showed higher per capita rates of genus extinction at high latitudes, suggesting higher species extinction rates as well (*24*) (estimates of per capita speciation rates are still lacking). Together, these results suggest that extinction rates are greatest where species diversity is lowest. Whereas most efforts have aimed at identifying the geological, climatic, and ecological factors that might have elevated tropical speciation rates, our results suggest that both speciation and extinction vary with latitude and contributed importantly to the latitudinal diversity gradient.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/315/5818/1574/DC1
Materials and Methods
Fig. S1
Tables S1 and S2
References
Database S1

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Comment on "The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals"

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Weir and Schluter (Reports, 16 March 2007, p. 1574) used variation in the age distribution of sister species to estimate that recent rates of speciation decline toward the tropics. However, this conclusion may be undermined by taxonomic biases, sampling artifacts, and the sister-species method, all of which tend to underestimate diversification rates at low latitudes.

Weir and Schluter (*1*) examined the relationship between time to divergence and latitude in sister species of New World birds and mammals. They concluded that the slowest recent rates of speciation occur at low latitudes, thus contradicting the widespread view that rapid diversification plays a role in generating tropical diversity (*2*, *3*). However, their findings rest heavily on current taxonomy and phylogenetics, which are subject to latitudinal gradients of their own. Using examples from birds, we show that the apparent slope in rates of speciation can be attributed to biases in data and methods.

Weir and Schluter (*1*) demonstrated that sister species, haplotype splits, and phylogroup splits are older in the tropics, but these uncorrected age distributions are uninformative. Rather than being "opposite to the pattern that would occur if faster rates of speciation had driven the buildup of Neotropical diversity" (*1*), we interpret the raw gradients as the signature of extinction, or reduced historical speciation, at high latitudes. In other words, even if species are generated at a faster rate near the equator, the gradients persist because old sisters are absent near the poles.

Raw gradients cannot disentangle speciation and extinction, and therefore the key result is the estimated diversification rates extracted from the distribution of sister-species ages. Leaving aside the controversies surrounding species definitions and molecular clocks, to what extent are these rates influenced by taxonomic uncertainty? Although Weir and Schluter accept that "a higher proportion of tropical species are currently undescribed," they argue that their estimated rates of diversification are robust because they are corrected for the lag time to speciation, as measured by genetic markers. We disagree with this and suggest instead that an adjustment based on maximum intraspecific divergence of haplotypes or phylogroups will not adequately correct for latitudinal bias in taxonomic treatment. The most obvious reason is that genetic sampling is correlated with latitude, a relationship detected in Weir and Schluter's data set (sequences per species/latitude: Spearman's rho = 0.301, $P = 0.006$, $N = 81$). As tropical taxa tend to have more complex genetic structure (*4*), undersampling may lead to multiple missing lineages.

The implications are demonstrated by *Hypocnemis cantator*, an Amazonian taxon recently shown to comprise six biological species (*5*), thereby disrupting a sisterhood in Weir and Schluter's data set. We explored the effect of revised species limits in conjunction with improved genetic sampling (Fig. 1). Our data estimate coalescence of the youngest sisters at 1.8 million years ago (Ma) (*6*) rather than 4.5 Ma (*1*). They also reveal that Weir and Schluter's analysis failed to sample 50% of species, and ~75% of phylogroups, in the *H. cantator* clade. If this scenario is repeated in many tropical species analyzed by Weir and Schluter, as seems

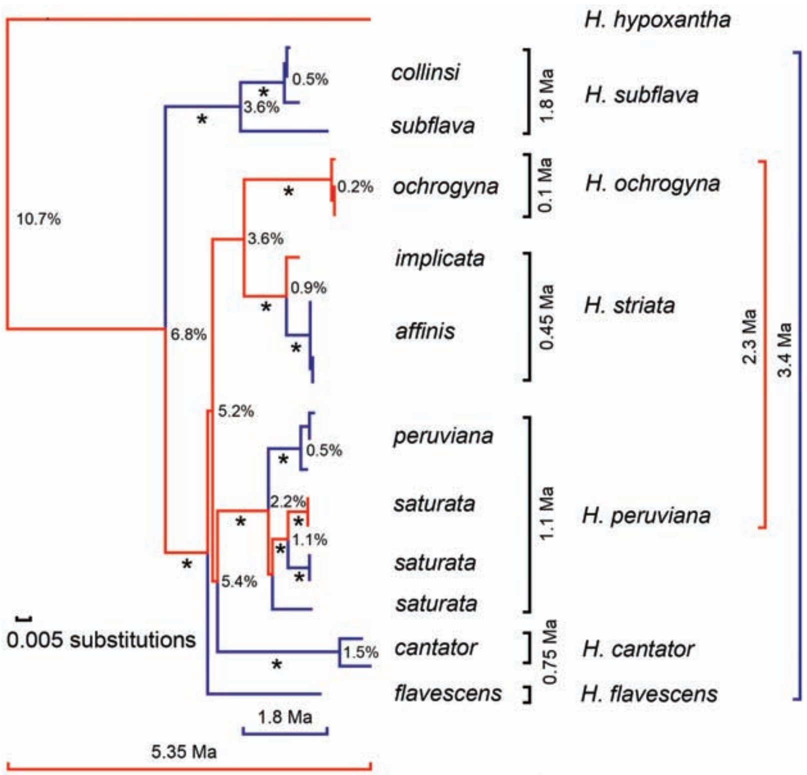

Fig. 1. Maximum likelihood phylogenetic tree summarizing relationships among members of the genus *Hypocnemis* (Aves: Thamnophilidae). All nodes have bootstrap values greater than 70%; nodes with bootstrap support ≥90% are indicated with an asterisk. Red branches show sampling by Weir and Schluter (*1*) for the *H. hypoxantha*/*H.* "*cantator*" sister-species pair; blue branches reflect structure uncovered by additional sampling. Labels at tips of the tree are traditional subspecies; bracketed taxa represent species limits according to Isler *et al.* (*5*). Following Weir and Schluter (*1*, *6*), approximate timing of divergence events is estimated by dividing sequence divergence by two. Thus, *H. hypoxantha* diverged over 5 Ma; main clades diverged 2.5 to 3.5 Ma; divergence within named species occurred during the past 2 million years. For traditional species limits (*H. hypoxantha*/*H.* "*cantator*"), colored scale bars show estimated age of youngest sisterhood (*x* axis) and maximum haplotype divergence (*y* axis), according to the sample used by Weir and Schluter (red) and deeper sampling (blue). For revised species limits, brackets are labeled with estimates of maximum intraspecific haplotype divergence where possible (*6*). *H. cantator* was more deeply sampled (six sequences) than 57% of the tropical species (midpoint latitude <30°N) included in Weir and Schluter's data set (*1*).

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likely to be the case (*4*), their methods will consistently overestimate evolutionary ages, and misjudge haplotype and phylogroup divergence, at low latitudes (Fig. 1).

A second key issue raised by our data is that tropical lineages tend not to bifurcate but to proliferate. This makes sense because, as noted elsewhere (*7*), populations at low latitudes are typically sedentary and susceptible to subdivision by multiple barriers. By diverging concurrently, an ancestral *Hypocnemis* population (*5*) generated six daughter species at a rate of 1.8 lineages per million years (Fig. 1). The sister-species method produced a low rate estimate of 0.2 lineages per million years for equatorial species (*1*), perhaps because it assumes that lineage splitting is sequential. Sequential splitting may approximate the situation at high latitudes, but it ignores the contribution of parallel speciation events in the tropics. Thus, methodological biases may in part explain why Weir and Schluter found lower diversification rates in tropical taxa, whereas analyses of net diversification rate produce the opposite result (*2*, *3*).

Other biases may lead to younger sisterhoods being sampled at high latitudes but overlooked nearer the tropics. For example, the most speciation-prone tropical families contribute few data because they have yet to be studied by phylogeneticists, who have focused on more manageable groups. Thus, Trochilidae, Furnariidae, Thamnophilidae, and Tyrannidae account for ~40% of the Neotropical avifauna, and many recent splits, but they lack species-level phylogenies. This contrasts with the Nearctic, where sampling is more comprehensive and contentious taxa have been sequenced precisely because they are narrowly divergent (*8*). Finally, latitudinal gradients in familiarity and sampling depth may explain a preponderance of errors or weak sisterhoods in tropical taxa (*9*).

We have illustrated some potential problems for Weir and Schluter's analysis, but our examples cannot settle the broader issue. This will have to wait until knowledge of species limits in tropical biota is much improved. At present, we can only predict that, if Neotropical taxa were studied as intensively as Nearctic taxa, numerous intraspecific phylogroups would require classification as species, and within those species, new phylogroups would emerge. From this perspective, the older haplotype and phylogroup splits of tropical taxa suggest, not that "the process of speciation takes longer at low latitudes" (*1*), but that many intraspecific lineages await description as species-level taxa (*10*). Moreover, if phylogroups are indicators of incipient speciation (*11*), the potential for generating multiple species is clearly greater in the tropics.

Weir and Schluter used a novel and elegant analysis to explore latitudinal patterns in rates of speciation and extinction. Their conclusion that a gradient in extinction rates facilitates the build-up of tropical diversity supports an old, intuitive idea (*12*). However, their most eye-catching claim—that speciation rates decline toward the tropics—may be explained by cumulative artifacts in taxonomy and phylogenetics, compounded by the sister-species method. Overall, the message emerging from studies of Neotropical birds, and other taxa, is that diversity gradients are steeper than expected (*10*) and that diversification rates are likely faster in the tropics (*13*).

Distinguishing the roles of history, speciation, and extinction in shaping the latitudinal diversity gradient remains a major challenge (*13*). It will not be met until the diversity and evolutionary history of tropical taxa is more accurately described by empirical data and systematic revisions. The priority, as we see it, is to improve the data set, rather than subject it to ever more refined analysis. This brings us back to the critical importance of detailed field studies, taxonomy, and phylogenetics as foundations of theoretical biology.

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4. Complex phylogeographic structure has been reported in several Neotropical "species," including *Glyphorhynchus spirurus* (*14*), *Lepidothrix coronata* (*15*), and *Buarremon torquatus* (*16*). Numerous tropical "species," including many in Weir and Schluter's data set (e.g., *Cnemotriccus fuscatus*, *Grallaria rufula*, *Xiphorhynchus ocellatus*, and *Sittasomus griseicapillus*), are thought to represent 2 to 10 species-level taxa.
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8. For example, *Catharus bicknelli* (*17*), *Carduelis hornemanni* (*18*), and *Loxia* spp. (*19*). Species status is disputed for these forms and several other temperate zone sisters in Weir and Schluter's data set (*1*).
9. This is an example of an error unlikely in the temperate sample: On the basis of inaccurate GenBank sequences, Weir and Schluter calculated a divergence time of 8.55 Ma for *Poospiza garleppi* and *P. baeri*, two relatively young tropical taxa (divergence <2 Ma) (*20*). Similarly, a divergence time of 5.47 Ma is given for *Daptrius* (*Ibycter*) *americanus* and *D. ater*, two nonsisters misplaced in the sample (*21*). The tropical sample also appears to contain more sister species (e.g., *Catharus* spp. and *Hypopyrrhus*/*Lamproposar*) with poorly supported nodes (*22*, *23*).
10. Taxonomic revision is a slow process, but it will almost certainly result in the description of many more tropical species than temperate species. Overall, most cryptic species likely occur at low latitudes, not only because the tropics are more diverse in the first place (*24*) but also because tropical taxa have been "overlumped" by taxonomists. For example, detailed revisions suggest that numerous Neotropical passerine bird "species" are complexes of multiple cryptic species or allospecies (*25*–*27*).
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Response to Comment on "The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals"

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Tobias *et al*. suggest that taxonomic uncertainty, an underestimated correction for the lag-time to speciation, and the sister-species method undermine our estimates of speciation rates at tropical latitudes. However, our estimates incorporated a correction for taxonomic uncertainty and are robust to small increases in the lag-time correction. Contrary to the claim of Tobias *et al*., we find no indication that the sister-species method underestimates tropical diversification rates.

It is clear that taxonomic uncertainty affects the ages of sister species at different latitudes, as stated in (*1*). Tobias *et al*. (*2*) give a concrete instance from their own work and additionally plead for further systematic revision, which we cheer. It is far less certain that estimates of speciation and extinction rates are greatly affected by taxonomic uncertainty, because our estimates employ a correction for the problem. Quantitative analysis of comprehensive data are crucial to revising estimates, but it is not yet available.

Recent work by Tobias and others on tropical species [e.g., *Hypocnemis* (*2*), *Glaucidium* (*3*), *Micrastur* (*4*), *Scytalopus* (*5*), and *Myrmotherula* (*6*)], as well as by others on species complexes at temperate latitudes [e.g., *Empidonax* (*7*), *Catharus* (*8*), *Vireo* (*9*), *Sphyrapicus* (*10*), and *Baeolophus* (*11*)], continue to fill gaps in taxonomy that will revise the latitudinal gradient in sister-species ages. These revisions are likely to shorten average sister-species ages in the tropics more than in the temperate zone. Tobias *et al*. illustrate this point with a molecular phylogeny for the *Hypocnemis cantator* complex, which was considered a single species in our analysis. Recent demonstrations of range overlap between the two most deeply diverged clades within this group (~3.4 million years) suggest that the number of biological species present is at least two and might be as high as six if allopatric lineages differing in song are considered distinct species (*12*). At the same time, taxonomic gaps probably do not account for the whole latitudinal gradient in sister-species ages because the gradient holds above 30° latitude, where relatively few species remain to be discovered (*1*).

Our analysis used a method to estimate speciation and extinction rates that takes into account differences in taxonomic practice as well as factors that cause real differences in the lag time to speciation at different latitudes (*1*). The method prunes entire bushy tips from trees simulated from a birth-death process according to a stochastic lag-time distribution. Mean lag time at each latitude is based on the maximum known haplotype ages within each species there. Speciation and extinction rates were then estimated by fitting simulated distributions to observed distributions of sister-species ages of birds and mammals at each latitude. By comparing the observed sister-species ages to the simulated distributions, we estimated speciation and extinction rates conditional on mean lag time. Under the constant-rate birth-death process we modeled, a shorter mean lag time caused by improvements in taxonomy would reduce the number of taxa pruned from simulated trees and shift the simulated distribution of sister-species ages toward the present, without necessarily changing the estimates of speciation and extinction rates (Fig. 1). Thus, it is not apparent that the speciation rate gradient would be reversed by taxonomic revision, as Tobias *et al*. suppose.

Tobias *et al*. point out that genetic undersampling might lead us to underestimate maximum haplotype ages, and thereby mean lag times, within tropical species. Large sample size per se is actually more crucial in the temperate zone because so many high-latitude species lack strong phylogenetic structure, with the result that maximum haplotype divergence is sample-size dependent. In contrast, the deeper phylogenetic structure of most tropical species implies that only a few samples are needed scattered throughout a species range. Thus, where possible we selected a few sequences for the most divergent known phylogroups (and often did not include redundant samples from the same phylogroup), explaining our smaller sample sizes at tropical latitudes. Nevertheless, we agree that if geographic coverage is incomplete, some phylogroup splits may go unrecognized, potentially creating a bias. Tobias *et al*. gave an example from the tropical group *Hypocnemis* in which further geographic sampling extended maximum haplotype age by an additional 30% (6.8% rather than 5.2%). This magnitude of discrepancy in tropical species generates only a slight difference between the simulated sister species age distribution we used in (*1*) and those that incorporate the discrepancy (see Fig. 1) and is unlikely to affect our estimates of speciation and extinction rates.

Contrary to the claim of Tobias *et al*., a large proportion of our species-level data set was indeed derived from the five largest Neotropical families. Forty-three percent of avian sister species pairs are from the families Furnariidae (including Dendrocolaptidae), Thamnophilidae, Thraupidae, Trochilidae, and Tyrannidae—families that, based on their species diversity, might be expected to have experienced the fastest speciation rates and the youngest sister species in the tropics.

Tobias *et al*. also suggest that using only sister species underestimates diversification rates when lineages undergo rapid bursts. However, their calculations based on the *H. cantator* data were not calibrated per lineage and are incorrect. We recalculated per lineage net diversification rates using standard methods (*13*) and obtained almost identical results when analyzing the whole *H. cantator* tree (0.25 species per lineage per million years) and using only the sister species (0.21).

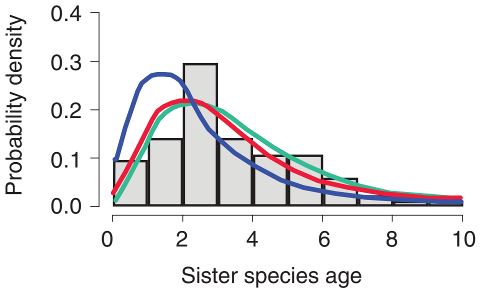

Fig. 1. Histogram of avian sister-species ages near the equator (those with range midpoints between 0° and 10° latitude). The red curve is the corresponding frequency distribution of sister-species ages under the maximum likelihood estimates of speciation (0.2 species per lineage per million years) and extinction rates (0.08 species per lineage per million years), conditional upon a mean lag time to speciation of 2 million years. The blue curve illustrates the effect on the expected distribution of sister-species ages of reducing the mean lag time to 1 million years without altering the speciation and extinction rates, as might occur after substantial taxonomic revision. The reduction elevates the expected proportion of young sister species and diminishes the expected proportion of older sister species, compared with the older mean lag time. The green curve shows the fit of the model to the data when the mean lag time is increased from 2 to 2.6 million years (an increase of 130%), as might occur with wider geographic sampling.

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Our method is most vulnerable to the assumption of a constant-rate birth-death process (*14*). Tobias *et al.*'s point that "tropical lineages tend not to bifurcate but to proliferate" is a special case of this more general rate problem. As we stated in (*1*), geological and climatic events likely concentrated speciation and extinction events in episodes (*13*, *15*). However, we find little evidence to support that tropical lineages are more prone to such bursts than temperate lineages. Indeed, it might be the case that the temperate zone has experienced the most recent series of bursts, namely in the Pleistocene (*15*). We also emphasized that our rate estimates apply only to recent time periods—that covered by the ages of most sister species. More even coverage of a longer temporal record (extending before 10 million years) would be needed to determine by how much our estimates based only on sister species would need to be revised.

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