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

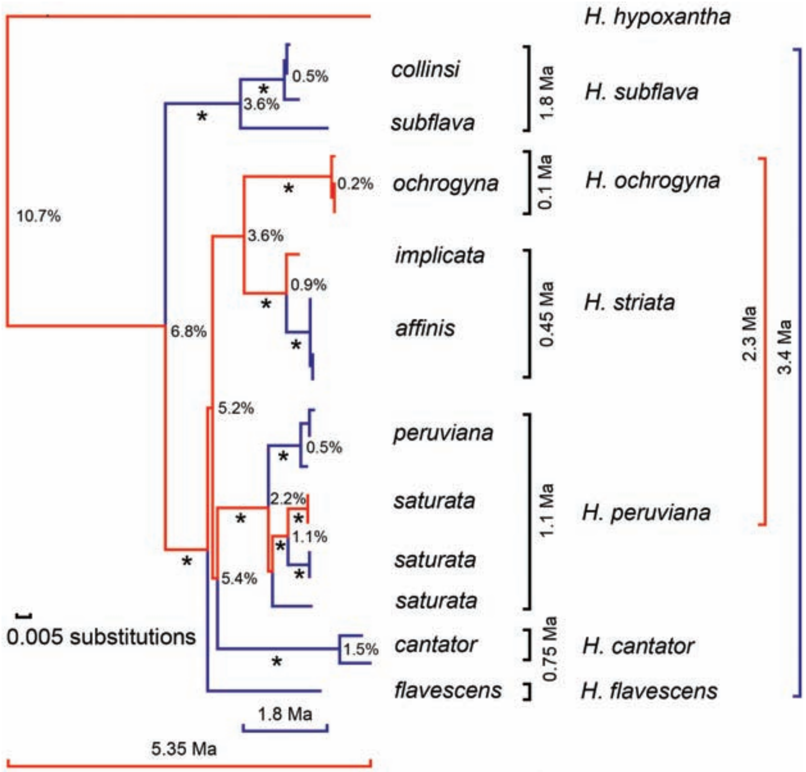

Fig. 1. Maximum likelihood phylogenetic tree summarizing relationships among members of the genus *Hypocnemis* (Aves: Thamnophilidae). All nodes have bootstrap values greater than 70%; nodes with bootstrap support ≥90% are indicated with an asterisk. Red branches show sampling by Weir and Schluter (*1*) 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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6. Materials and methods are available as supporting materials on *Science* Online.
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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).

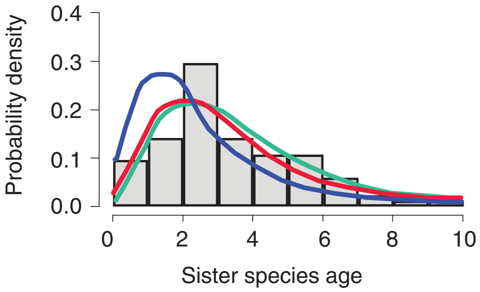

Fig. 1. Histogram of avian sister-species ages near the equator (those with range midpoints between 0° and 10° latitude). The red curve is the corresponding frequency distribution of sister-species ages under the maximum likelihood estimates of speciation (0.2 species per lineage per million years) and 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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