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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

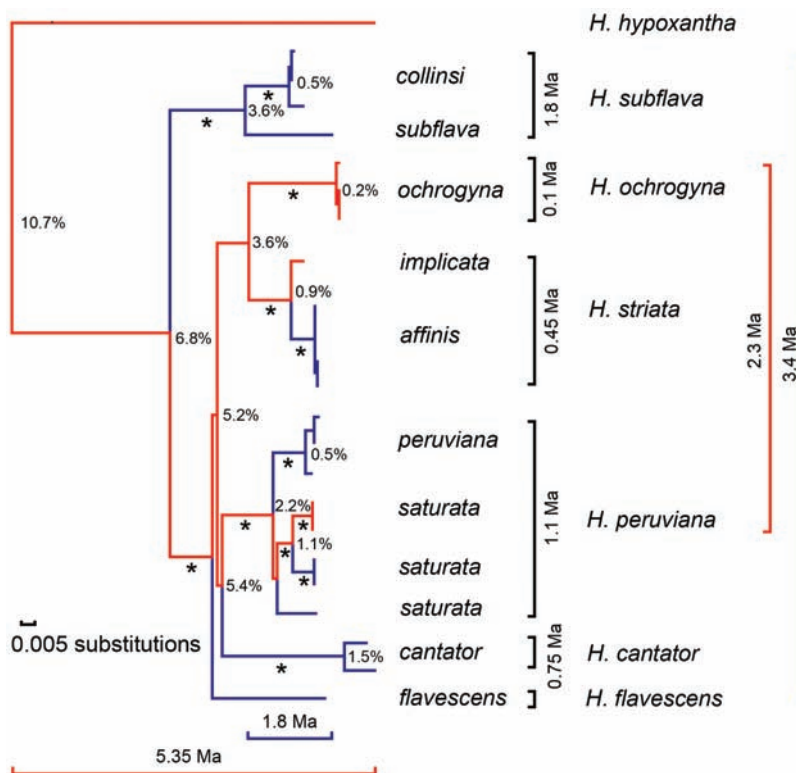


Fig. 1. Maximum likelihood phylogenetic tree summarizing relationships among members of the genus *Hypocnemis* (Aves: Thamnophilidae). All nodes have bootstrap values greater than 70%; nodes with bootstrap support $\geq 90\%$ are indicated with an asterisk. Red branches show sampling by Weir and Schluter (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 Iser *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 $<30^\circ\text{N}$) 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, Fumariidae, 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 per-

spective, 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.

References and Notes

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- 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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- Materials and methods are available as supporting materials on *Science* Online.
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- 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 (2).
- 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/Lampprosar*) with poorly supported nodes (22, 23).
- 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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