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

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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).

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**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.
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.

References

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