

A positive association between population genetic differentiation and speciation rates in New World birds

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Abstract

Although an implicit assumption of speciation biology is that population differentiation is an important stage of evolutionary diversification, its true significance remains largely untested. If population differentiation within a species is related to its speciation rate over evolutionary time, the causes of differentiation could also be driving dynamics of organismal diversity across time and space. Alternatively, geographic variants might be short-lived entities with rates of formation that are unlinked to speciation rates, in which case the causes of differentiation would have only ephemeral impacts. Combining population genetics datasets including 17,746 individuals from 176 New World bird species with speciation rates estimated from phylogenetic data, we show that the population differentiation rates within species predict their speciation rates over long timescales. Although relatively little variance in speciation rate is explained by population differentiation rate, the relationship between the two is robust to diverse strategies of sampling and analyzing both population-level and species-level datasets. Population differentiation occurs at least three to five times faster than speciation, suggesting that most populations are ephemeral. Population differentiation and speciation rates are more tightly linked in tropical species than temperate species, consistent with a history of more stable diversification dynamics through time in the Tropics. Overall, our results suggest investigations into the processes responsible for population differentiation can reveal factors that contribute to broad-scale patterns of diversity.

Significance

The causes of differentiation among populations are well circumscribed, but it remains unclear if they impact the proliferation of organisms over deep time. If, as some recent theory and observations suggest, population differentiation is untethered from species formation, then the causes of population differentiation are unlikely to have long-term evolutionary effects. We provide the first large-scale test of the link between standardized estimates of rates of population differentiation from population genetic data and speciation rates. We find that relative population differentiation rates predict speciation rates across New World birds, confirming the potential macroevolutionary importance of causes of differentiation. We also find that population differentiation and speciation rates are more tightly linked in the Tropics, which may contribute to greater tropical species richness.

Speciation in most organisms is initiated via the geographic isolation and differentiation of populations. The rate that populations differentiate within a species is determined by many extrinsic and intrinsic factors, including the rate of geological and climatic change (1, 2), the dispersal ability of organisms (3), and the availability of ecological opportunities and strength of natural selection (4, 5). An implicit assumption of speciation biology is that these factors have an impact that percolates through to long evolutionary timescales and influences the proliferation of species. This connection, however, is not assured. The factors responsible for population differentiation can only affect species diversification if differentiation acts as a limiting control on diversification - for example, if the rate at which differentiated populations form within a given lineage determines the rate at which species can form in that lineage - or if differentiation and diversification are both responses to the same causal processes. In either case, differentiation and diversification should be associated across evolutionary lineages.

Recent work, however, suggests that differentiation dynamics are untethered from those of diversification. Some macroevolutionary biologists suggest that geographic populations or variants are often short-lived entities and that their rate of formation within a species might have little relation to speciation rates (6, 7, 8). Instead, speciation may be limited by other population-level processes, such as the persistence of differentiated populations (9) or the evolution of sufficient ecological divergence (5, 10) or reproductive isolation (11, 12) for differentiated populations to coexist in sympatry, or speciation may be random with respect to population-level processes. If differentiation is not associated with diversification, the factors responsible for differentiation cannot be expected to have macroevolutionary impacts.

The association between population differentiation and diversification can be tested by comparing present-day population differentiation within species to the speciation rate of their lineages over deeper evolutionary time. An association between differentiation and speciation rate across lineages would support the hypothesis that differentiation is important for speciation. Few studies have attempted to make this comparison (13, 14). Haskell and Adhikari (15) compared the number of taxonomic subspecies within species to the number of species in avian genera and found a correlation, suggesting that levels of geographic differentiation are a predictor of species diversity. Phillimore (16) used species stem ages from phylogenies to calculate the rate that their taxonomic subspecies had formed and found that the rate that subspecies accrued was correlated with phylogenetic speciation rates. Kisel and Barraclough (17), however, found no link between the magnitude of genetic divergence between populations and diversification rates in five sister clades of Costa Rican orchids. This conflicting evidence suggests that resolving the connection between differentiation and speciation is challenging, and will likely require the examination of standardized, quantitative metrics of population differentiation from a large sample of species.

Here, we assess the association between population differentiation and speciation rate using estimates of differentiation from population-level genetic data. We estimate population differentiation based on an application of the coalescent model to gene trees estimated from new and existing population genetic and phylogeographic datasets from 176 species of New World birds. We compare population differentiation to speciation rates estimated for the lineages subtending the same 176 species from phylogenetic trees of all birds. We first test whether population differentiation and speciation rates are associated across all sampled species. Because

the association between population differentiation and speciation rates may vary across geographic contexts, we also test whether the association between differentiation and speciation rates in the Tropics differs from that in the Temperate Zone. Finally, we perform a suite of supplementary tests to assess the robustness of recovered relationships to the approach used for sampling and analysis.

Results

We estimated population differentiation based on genetic data from range wide samples of individuals ($n = 17,746$) in 176 bird species from across the avian tree of life (Fig. 1A; *SI Materials and Methods*) and inhabiting all biogeographic regions of the New World (Fig. 1B). We used a Bayesian implementation of the Generalized Mixed Yule Coalescent model (18, 19) to standardize population differentiation estimates within each species (Fig. 1C). The number of genetically distinguishable geographic populations within species varied from one to 35 with a median of three (Fig. 2). Because species might vary in the number of geographic populations simply due to differences in age, we calculated the rate of population formation since the crown age of each species (age of the most recent common ancestor of extant haplotypes within the species) based on a time-calibrated phylogenetic tree. The rate at which geographic populations arose, hereafter the rate of population differentiation, varied from zero to 6.64 divergences/million years (My) with a median of 0.53 divergences/My (Fig. 2).

We estimated macroevolutionary speciation rates along the ancestral lineage leading to each of the 176 species in the population genetic datasets using two methods applied to an existing phylogenetic tree of all bird species (20). First, we computed a simple summary metric of net speciation rate for each tip based on the weighted number of phylogenetic splits between the tip and the root of the phylogeny. This metric was used by Jetz et al. (20) and referred to as the diversification rate (DR) statistic, although it is more tightly related to speciation rate than diversification rate in many cases (21). Speciation rates based on the DR statistic ranged from 0.03 to 3.35 species/My with a median of 0.18 species/My. Second, we used BAMM v.2.5, a Bayesian implementation of a model that jointly estimates the number of distinct evolutionary rate regimes across a phylogenetic tree and the speciation and extinction rates within each of the regimes (22, 23). Speciation rates for tips on the tree were extracted from the marginal distribution of rates for their terminal branches. Based on BAMM analysis, diversification in birds was characterized by 69 statistically distinguishable rate regimes (Fig. S1), 23 of which included the 176 species in our population genetic dataset. The speciation rate across the 176 species varied from 0.04 to 0.72 species/My, with a median of 0.14 species/My (Figs. 2, S2). Importantly, speciation rates inferred using both methods were slower than population differentiation rates. Across all study species, 3.23 times more population differentiation occurred than speciation using the DR statistic, or 4.80 times more using the BAMM speciation rate. These ratios are likely to be conservative because they do not account for population extinction since the crown age of each species. Although most geographic variants are ephemeral and do not persist to become reproductively isolated species, this does not obviate the possibility that variation among lineages in differentiation rate predicts variation in speciation rates.

We tested whether population differentiation rates within species were associated with speciation rates inferred using both BAMM diversification analyses and the number of split summary statistic. We tested for a relationship between population differentiation and speciation rates estimated in BAMM using STRAPP, a trait-dependent diversification test that avoids phylogenetic pseudoreplication while accounting for autocorrelation in evolutionary rates within evolutionary regimes inferred using BAMM (24). We found BAMM speciation rates were positively correlated with population genetic differentiation rates (Spearman's correlation coefficient [r] = 0.250, P = 0.021, Fig. 3A). We compared population differentiation and speciation rates based on the DR statistic using phylogenetic generalized least squares (PGLS; 25, 26). This test is analogous to that first developed and applied to trait-dependent diversification analyses by Freckleton et al. (27). As with BAMM speciation rate, population differentiation rate predicted speciation rate based on the DR statistic across all study species (PGLS slope = 0.201, P < 0.001; Fig. 3B). Using simulations, we found the false positive rate, which is problematic in many tests of trait-dependent diversification, was minimal for both the STRAPP (0.022) and PGLS (0.056) analyses relative to a Spearman's correlation not accounting for covariance (0.568 using BAMM speciation rates, 0.202 using the DR statistic). We found no correlations between the raw number of population clusters and speciation rate (BAMM r = 0.104, P = 0.313; PGLS slope = -0.077, P = 0.111), suggesting that the rate of population genetic differentiation rather than the level of standing differentiation is associated with the rate of speciation. This result provides quantitative evidence supporting the idea that population differentiation within species predicts macroevolutionary dynamics at a large spatial and taxonomic scale.

A series of tests ensured our results are not dependent on sampling, particular methodological decisions, or statistical artifacts. For brevity, we present results from STRAPP tests of BAMM speciation rates below, but results from PGLS of the DR statistic were similar and are presented in the *SI Materials and Methods*. The positive correlation between the population genetic differentiation rate and the speciation rate was robust to the taxonomy used to circumscribe species for the population-level analysis, with a more finely subdivided taxonomy producing similar results to the primary taxonomy we examined ($r = 0.210$, $P = 0.014$). The correlation was also robust to the use of lower (PP = 0.7; $r = 0.243$, $P = 0.019$) and higher (PP = 0.9; $r = 0.251$, $P = 0.026$) posterior probability thresholds for assigning individuals to population clusters, to whether the population differentiation rate was measured using the stem age rather than crown age of a species ($r = 0.242$, $P = 0.012$), to the random removal of 20% ($r = 0.238$, $P = 0.027$) of samples from the dataset, and to models of population differentiation incorporating moderate ($eps = 0.45$; $r = 0.199$, $P = 0.043$) or high ($eps = 0.9$; $r = 0.227$, $P = 0.046$) extinction rates. Population differentiation rate might be associated with speciation rate if clades with high speciation rates necessarily have shallower crown ages that result in elevated differentiation rates. However, crown age was unrelated to speciation rate ($r = -0.1134$, $P = 0.2816$).

After dividing the species into Tropical ($n = 101$) and Temperate ($n = 75$) groups, we found a strong positive correlation between population differentiation and speciation rates in the tropical species ($r = 0.409$, $P = 0.005$, Fig. 4a), but no correlation in the temperate species ($r = 0.0358$, $P = 0.7456$). The correlation coefficients in tropical and temperate species were more different than expected based on a random permutation test to account for differences in sample sizes between the two groups ($P = 0.001$). Neither population differentiation rate nor speciation rate varied

significantly with latitude (Fig. 4A), nor was the average ratio of population differentiation to speciation rate different between temperate and tropical species. There was, however, a large disparity across species in the ratio of population differentiation to speciation rates at temperate latitudes, compared to a more peaked distribution in the Tropics (F-test of equal variances $F = 2.002$, $P = 0.002$; Fig. 4B,C). These results suggest that population differentiation leads to speciation at a relatively predictable rate in the Tropics, but that this rate is less predictable in the Temperate Zone.

Discussion

We found a robust association between population differentiation rate and speciation rate across New World birds, although considerable variance in speciation rate remained unexplained. Given the potential for estimation error in both population differentiation rates and speciation rates, detecting any association was remarkable. This result suggests that the rate of population differentiation within a species can be used, in part, to predict its speciation rate over longer timescales, and vice versa. Statements of causality between rates of population differentiation and speciation would be misleading, however. Population differentiation may be a rate-limiting step in speciation, or both may be related through an unresolved, underlying causal structure involving shared processes that affect rates at both timescales. In either case, our results support an implicit but largely untested assumption of speciation research, that the often-studied processes leading to population differentiation could also be responsible for elevated diversification rates over deep evolutionary time. Our results accord well with prior evidence that

taxonomic subspecies richness within species is tied to species richness or speciation rate in their higher taxonomic groups (15, 16) and that some traits predict diversity both within and across species (28). Further support for the link between differentiation and diversification comes from the observation that certain traits thought to lead to population differentiation, such as limited dispersal ability or range fragmentation, predict speciation rate in certain clades (29, 30, 31).

Much of the variance we observed in speciation rates is unexplained by population differentiation. This unexplained variance may be partly due to estimation error in speciation or differentiation rates, but it also leaves room for the possibility that population-level processes in addition to differentiation act as controls on speciation rate. For allopatric speciation to be complete, geographically isolated populations must not only differentiate, but persist until the evolution of reproductive isolation and ecological divergence permit the completion of speciation (6, 13). Variation among species in population persistence, time to reproductive isolation, or time to ecological differentiation therefore may explain some of the variance in speciation rate not attributable to differences in population differentiation rate. However, extinction is notoriously difficult to estimate from molecular phylogenies alone (9, 32), and measuring population persistence for exploration of this potential control using empirical data from extant populations may be equally challenging. Associations between rates of reproductive isolation and speciation rate have been investigated in some groups. The rate of intrinsic postzygotic reproductive isolation does not predict speciation rate across birds (33), but other forms of reproductive isolation are potentially more important in birds (34) and may merit further investigation. Elevated ecological opportunities can be associated with increased speciation rates (35) and there is evidence rates of ecological divergence vary regionally (36),

but more data are needed to establish a link between rates of ecological divergence between populations and speciation rate. Regardless, although variation among lineages in rates of population persistence, evolution of reproductive isolation, and ecological divergence may explain some variation in avian speciation rate, they are insufficient to erase the association between population differentiation and speciation observed in our datasets.

Population differentiation predicts speciation rate across all New World birds examined, but the relationship is strongest among tropical species. Tropical species, moreover, show less variability in the rate at which differentiated populations become species compared to temperate species. Because the inverse of the ratio of population differentiation to speciation rates provides an index of population extinction rates, this pattern also indicates that population extinction rates, although not higher in the Temperate Zone, are more variable across temperate species than tropical species. This pattern is consistent with a scenario in which the conversion of population differentiation to new species occurs predictably through time in the Tropics, but is episodic or unpredictable at temperate latitudes. Climatic cycling over the past 420,000 years (37) suggests that major shifts in external environmental conditions may be the dominant driver of speciation rates in those regions, which could dampen the association between population differentiation and speciation at high latitudes. The tighter association between population splitting and speciation rates in the Tropics may be due to the relative environmental stability in that region over recent timescales (38), which might relegate control of speciation rates to the population-level processes occurring constantly within lineages. The latitudinal difference in the correlation between population differentiation and speciation therefore supports hypotheses that invoke greater tropical environmental stability as a cause of the latitudinal diversity gradient (39, 40),

and suggests an underlying mechanism in the form of less episodic diversification dynamics resulting from less dramatic climatic shifts.

In conclusion, we suggest that further research on population differentiation is warranted because it captures responses to the same processes that are responsible for organismal diversification generally. We anticipate more and larger comparative, population-level genetic datasets will allow investigation of additional processes responsible for the diversity of organisms worldwide. Furthermore, we expect traits associated with processes that promote population differentiation will prove promising in searches for the attributes of organisms that predispose them to diversify.

Methods

Sampling. We examined population genetic data from 176 species from across the New World (*SI Appendix*). We limited our analysis to mainland New World taxa to help control for the area available to each species for accruing allopatric divergence (i.e. differentiation via geographic isolation of populations). Five species whose distributions extend into the Old World were included, but samples from Old World populations were not examined. Species were defined as all non-sympatric monophyletic populations for which we had sampling, regardless of their current treatment by taxonomic authorities. Thus, metrics of population differentiation reflect geographic patterns of diversity among allopatric or parapatric groups, whereas metrics of speciation reflect deeper patterns among potentially sympatric and reproductively isolated groups.

Controlling for Taxonomic Bias. Despite our attempt at a standardized taxonomy, differences among geographic regions in taxonomic treatment may result in biased results. We alleviated the possibility of taxonomic bias by focusing on rates of differentiation rather than standing levels of differentiation (see below). We expect differentiation rates to be similar in a species regardless of the taxonomic treatment used, because a more inclusive treatment for a given species will generally result in an older species age in addition to more genetic structure. We also investigated the effect of taxonomic treatment on our results by applying a second taxonomy corresponding to the current taxonomy of the American Ornithologist's Union (AOU) North American (41, 42) and South American (43) checklist committees. In situations where the North and South American committees differed in their treatment, we reverted to the North American committee's treatment. The AOU taxonomy is more subdivided or "split" (206 species) than the primary taxonomy (176 species), so examination of both provides an index of the impact of the level of taxonomic splitting on results.

Molecular Data. For 146 species, we relied on previously published population-level mitochondrial datasets of New World birds, restricting our sampling to those datasets containing at least 8 samples (mean = 95) and range-wide sampling. We also gathered data from an additional 30 species, again sampling at least 8 individuals (mean = 111) from across the distribution of each species. We extracted total DNA from tissue samples associated with voucher specimens and used polymerase chain reaction to amplify sequence from the mitochondrial genes NADH dehydrogenase 2 (ND2) or Cytochrome b (*cyt b*) using standard primers. We conducted Sanger sequencing on PCR amplicons. We evaluated how robust our

results were to the level of sampling within species by randomly pruning 20% and 40% of the tips of the mitochondrial gene trees estimate from the full dataset, re-estimating the number of bGMYC clusters and rates of population differentiation, and conducting trait-dependent diversification tests.

Population Divergence Estimation. We estimated mitochondrial gene trees for each species using the Bayesian method implemented in BEAST v.1.7.5 (44). All trees were time-calibrated using an uncorrelated relaxed substitution rate based on published avian mitochondrial rates (*SI Materials and Methods*). We included taxa deemed to be sister to study species based on prior phylogenetic work and we extracted stem and crown age estimates for each species from maximum clade credibility (MCC) trees. We quantified phylogeographic structure using a Bayesian implementation of the General Mixed Yule Coalescent model (bGMYC; *SI Materials and Methods*). We used the MCC tree from BEAST for each bGMYC run. bGMYC provides a posterior probability that two sequences belong to the same genetic species which can be used, along with a probability threshold, to determine the number of clusters present. For the primary analysis we used a posterior probability threshold of 0.8 for clustering, but we also examined higher (0.9) and lower (0.7) thresholds.

To account for the fact that species might differ in the number of bGMYC clusters by virtue of differences in their age, we estimated the rate of bGMYC cluster formation, hereafter the phylogeographic splitting rate. We calculated rates using crown age, the time before present of the first intra-specific divergence event. We calculated rates of bGMYC cluster formation under a pure-birth model using formula (6) from Magallón and Sanderson (45). All rates were

calculated using a starting diversity of one despite the use of crown age. Crown age in our study corresponds to the first divergence between mitochondrial haplotypes rather than the first divergence between bGMYC clusters, and thus represents a time point when only one bGMYC cluster was present. We also examined rates of population differentiation using the stem age, although crown age is generally superior to stem age for rate estimation because it is positively correlated with diversity (46), increasing the comparability of rate estimates across species and taxonomic treatments. We did not control for area in our rate estimates, because we expect population differentiation to have equivalent evolutionary importance regardless of the size of the area over which it is distributed.

Because we modeled differentiation at shallow time scales, we might assume that extinction is infrequent and pure-birth (Yule) models provide reasonable estimates of differentiation rate. Jointly estimating speciation and extinction is possible using birth-death models and taking advantage of branch length information in population phylogenies. However, many of our population trees contained so few tips that the likelihood surface for parameter estimation was flat and confidence intervals were very large (T. J. Stadler, pers. comm.). Instead, we examined models that estimated speciation provided different fixed extinction rates. We examined differentiation rates using models with moderate ($\epsilon = 0.45$) and high ($\epsilon = 0.9$) constant rates of extinction, in addition to a pure-birth model.

Speciation Rate Estimation. We used time-calibrated MCC trees from a prior phylogeny of all birds (20) for estimation of speciation rates. Jetz et al. placed species lacking genetic data using taxonomic constraints, but we removed these (leaving 6,670 species) for our analyses to

eliminate potential artifacts due to incorrect placement. All study species were represented in the phylogeny by genetic data, and tips in the phylogeny were collapsed in cases in which one of our study species was represented by multiple species in the Jetz et al. taxonomy. We estimated speciation rates on the tree topology based on the Hackett et al. (47) backbone using the model implemented in the program BAMM v.2.5 (22, 23). BAMM was run assuming 67% sampling across the avian tree to account for species without genetic data (48; *SI Materials and Methods*). Speciation rates for a given terminal branch on the tree were extracted from the marginal distribution of rates, which is based on all processes sampled at that branch. We also estimated speciation rates using a simple summary statistic (the “DR statistic”) that reflects the number of splitting events subtending each tip on a phylogenetic tree (20). For this analysis we were unable to analytically account for incomplete sampling, so we used the full avian phylogeny.

Comparative Analyses. We examined correlations between the population genetic differentiation rate and speciation rates inferred both using the DR statistic and diversification modeling in BAMM. We tested for correlations between log-transformed population differentiation and log-transformed BAMM speciation rates using a semi-parametric trait-dependent diversification test (STRAPP) that detects effects based on replicated associations between trait values and diversification rates estimated using BAMM (24; *SI Materials and Methods*). This test accounts for covariance between species using permutations of trait values amongst species sharing the same evolutionary rate regime. We used PGLS (25, 26) to test for a correlation between log-transformed population differentiation rates and log-transformed DR statistic while accounting for relatedness between species based on phylogenetic distance in the avian tree (20). We tested the rate of false positives (type I error rate) of our STRAPP trait-

dependent diversification analysis by simulating trait evolution on our tree under a Brownian motion model (1000 replicates) and conducting the trait-dependent diversification test on the simulated data. We compared the rate of false positives with STRAPP to that based on PGLS using the DR statistic and that based on a simple Spearman's rank correlation of the population differentiation rates versus BAMM speciation rates.

We conducted comparative analyses on both the full dataset and on datasets containing species from either the Temperate Zone or Tropical Zone. Species were assigned to latitudinal zone based on the latitudinal midpoint of their breeding distribution. We examined partitioning schemes in which south temperate species ($n = 45$) were included either in the tropical partition or the temperate partition. The results were similar in both cases, and we present those with the south temperate species included in the tropical partition, because it resulted in more similar sample sizes between the two partitions (but see *SI Materials and Methods* for results of tests with south temperate species included in the temperate partition).

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Footnotes

Author Contributions: M.G.H., G.F.S., B.T.S., and R.T.B. designed the study. M.G.H., G.F.S., B.T.S., A.M.C., J.T.K., and R.T.B. collected data. M.G.H., G.F.S., and B.T.S. analyzed population-level data. M.G.H. and D.L.R. conducted comparative analyses. All authors contributed to interpretation of the data. M.G.H. wrote the manuscript, and all authors provided comments and revisions.

Genetic data used in this study are available from Genbank (pending acceptance).

Estimates of number of bGMYC clusters, population divergence rates, crown ages, and BAMM speciation rates are available from Dryad (pending acceptance).

Computer scripts used to process data are available from Github (pending acceptance).

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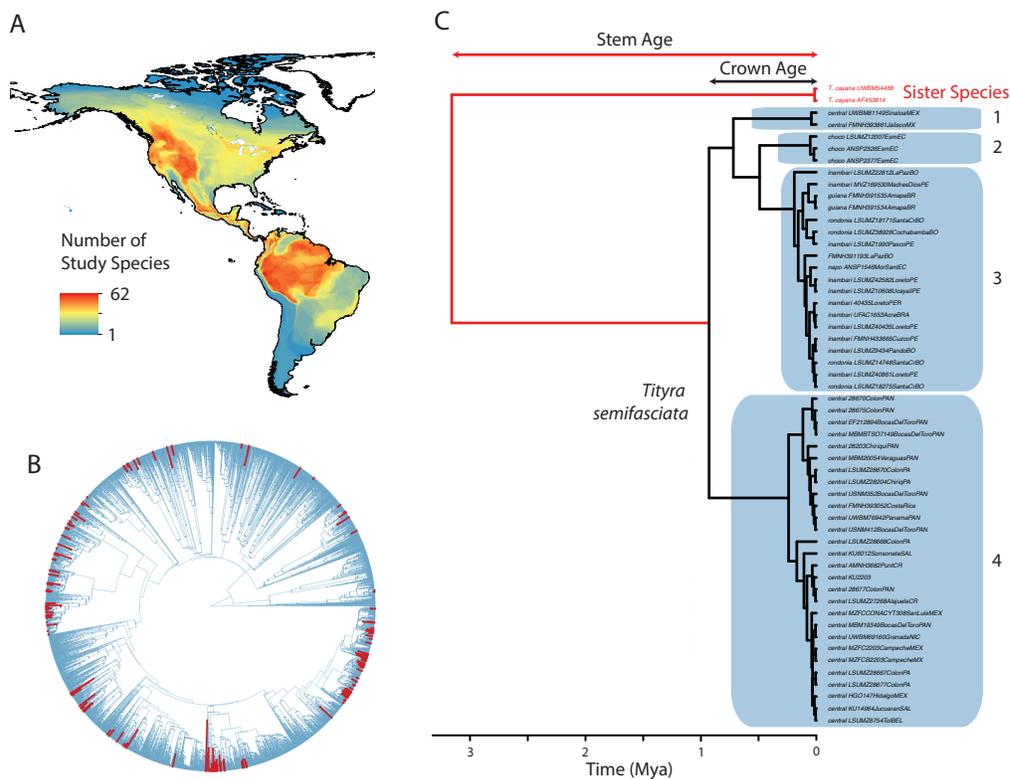


Fig. 1. Sampling strategy and approach to measuring population differentiation. (A) Overlaid distribution maps from the New World bird species used to estimate amount of population genetic differentiation ($n = 176$). (B) The phylogenetic distribution of the study species within the tree of life of all birds (20). The red branches, which indicate the species examined in this study, occur throughout the tree and represent replicates with varying levels of phylogenetic independence for the purpose of comparative analysis. (C) An example of a mitochondrial gene tree used to estimate the rate of population genetic differentiation within one of the 176 study species, the Masked Tityra (*Tityra semifasciata*). The blue polygons represent population clusters for this species as inferred using bGMYC (19) based on a posterior probability threshold of shared population membership of 0.8. The stem age and crown age for this species, used to estimate rates of differentiation, are also depicted.

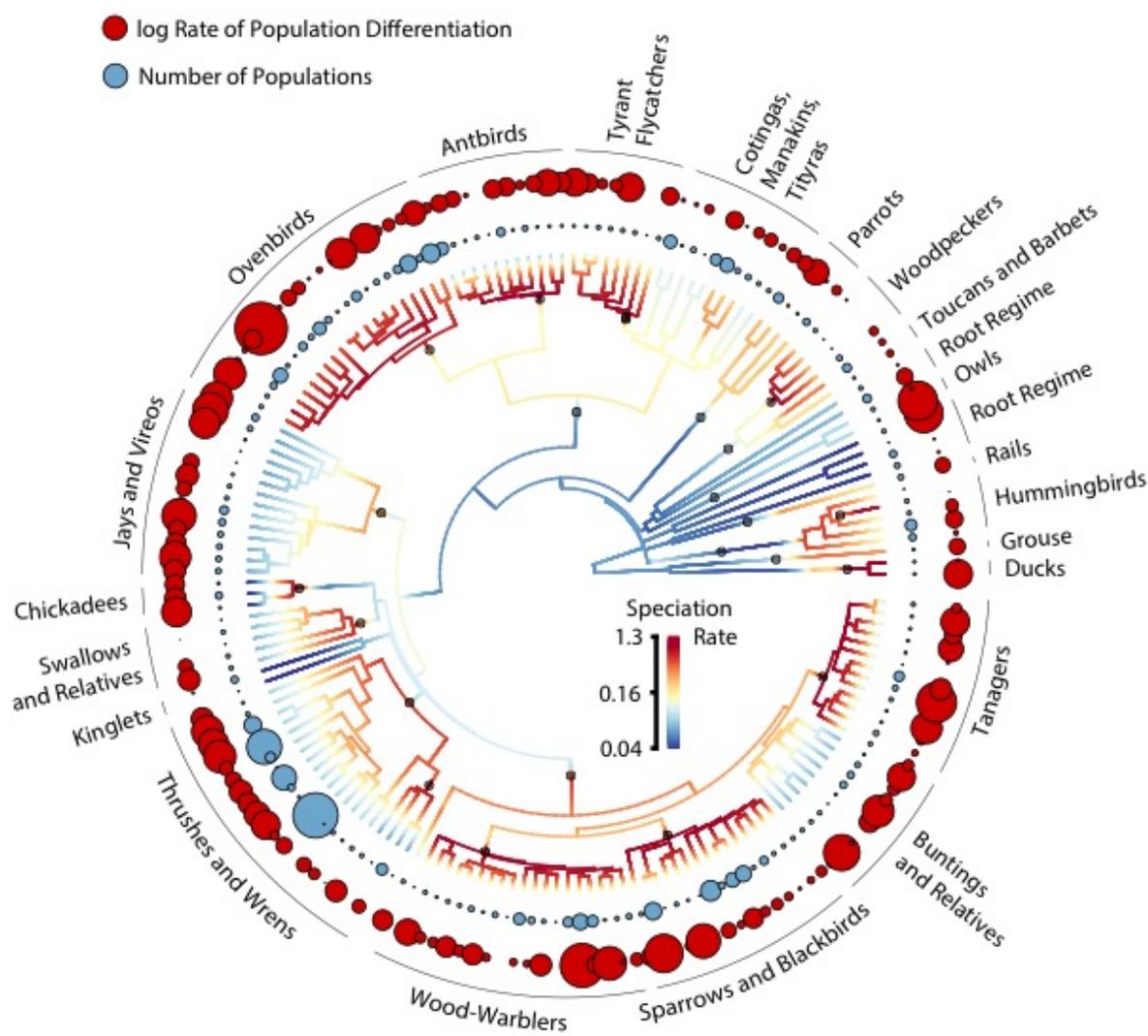


Fig. 2. A circular phylogenetic tree of the 176 study species used to estimate rates of population genetic differentiation, colored with a gradient that depicts speciation rates along each branch. The set of 23 macroevolutionary regime shifts with the maximum *a posteriori* probability is plotted on the phylogeny with black circles. The diameter of the blue circles encircling the tree is proportional to the number of populations based on bGMC analysis within the adjacent terminal species. The diameter of the red circles at the periphery of the plot is proportional to the log-transformed rate of population differentiation since the crown age of each terminal species.

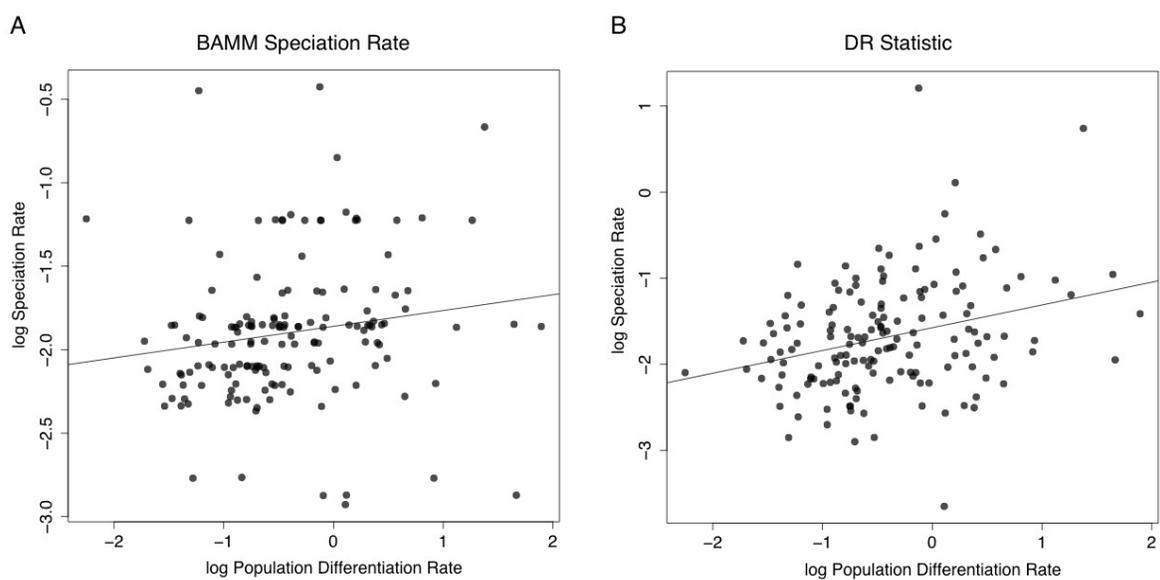


Fig. 3. Plots showing the relative population differentiation and speciation rates across all 176 study species. Plots are presented based on speciation rates from (A) BAMM analysis (BAMM correlation coefficient (r) = 0.250, P = 0.021) and (B) the DR statistic (PGLS slope = 0.201, P < 0.001). The trend line for the plot using BAMM speciation rates is based on OLS regression.

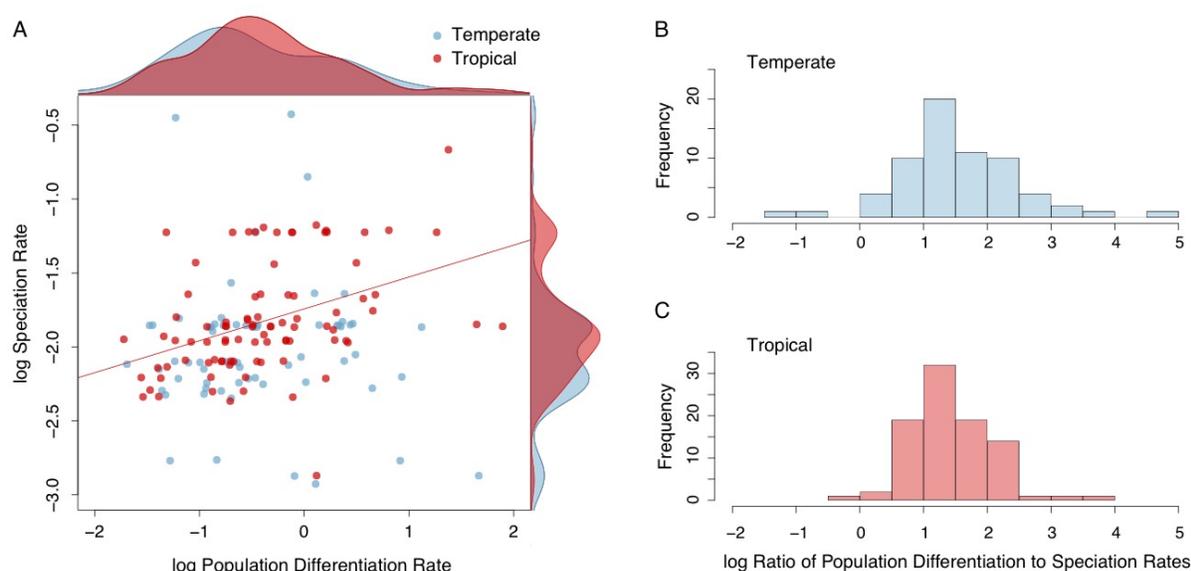


Fig. 4. Plots showing differences in relative population differentiation and speciation rates between temperate ($n = 75$) and tropical ($n = 101$) species. (A) Tropical species show a relationship between population differentiation rates and speciation rates ($r = 0.409$, $P = 0.005$), whereas temperate species do not ($r = 0.0358$, $P = 0.7456$). Kernel density plots showing the relative distributions of rates between tropical and temperate species are plotted opposite the axis of the rate to which they correspond and show that neither differentiation or speciation rates differ noticeably between temperate and tropical species. The ratio of population differentiation rate to speciation rate, however, is more variable in temperate species (B) than tropical species (C). Plots reflect values based on speciation rates estimated using the BAMM speciation rates (see Fig. S3 for plots using the DR statistic).

Supporting Information

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SI Materials and Methods

Sampling and Taxonomy. Our species sampling was determined by the species for which datasets were currently available or under construction in our labs. We restricted sampling to the mainland New World because New World birds are much better represented in existing genetic resources collections and genetic datasets than Old World species, which are particularly poorly sampled in tropical areas (1). In only a few cases (*Anas strepera*, *Calidris ptilocnemis*, *Corvus corax*, *Hirundo rustica*, and *Pinicola enucleator*) do study species contain Old World populations, which were not sampled for our analyses. Several of these species (the *Anas*, *Calidris*, and *Pinicola*) are important as the only or one of few representatives of their clade with phylogeographic data available. The phylogenetic dataset used to estimate speciation rates was worldwide in coverage. This strategy allowed us to maintain consistency between datasets – both the population genetic datasets (with the five exceptions above) and the phylogenetic dataset included all subtending lineages rather than a potentially biased subsample. Including all species in the phylogeny, combined with an analytical correction for taxa lacking genetic data, allowed us to estimate absolute speciation rates from each lineage for direct comparison with population differentiation rates.

Population Differentiation Rate Estimation. Mitochondrial gene trees were time-calibrated using an uncorrelated relaxed substitution rate based on published avian mitochondrial rates of 0.0125 substitutions/site/My for ND2 and ATPASE6, 7, & 8 (2) and 0.0105s s/s/My for *cyt b* (3). For the gene COI we used the same rate as *cyt b* because the loci mutate at similar rates (2). For the clock rate parameter we specified a lognormal distribution on the prior with the mean set to the above-mentioned mutation rates and a standard deviation of 0.1. We note that these substitution rates may differ from the rates represented in the phylogenetic data. Because substitution rates differ between short and long timescales (4), however, using rates that have been widely applied and tested on intraspecific timescales is the best option in this case. We expect any bias in crown and stem ages from the population-level data relative to branching times from the phylogenetic data to be minimal and have minimal impact on population differentiation rate estimates. Moreover, because we apply the same calibrations for all study species, this bias would be equivalent across species and therefore would not impact correlations between population differentiation and speciation rates.

We estimated time-calibrated gene trees in BEAST using a coalescent-constant-size tree prior and the best-fit nucleotide substitution model as determined in MEGA6 (5). We ran each analysis for 50 million generations sampling every 2,500 generations, performed multiple independent runs for validation, and assessed Markov chain Monte Carlo (MCMC) convergence and determined burn-in by examining ESS values and likelihood plots in Tracer v.1.5 (6). For some datasets that did not achieve high ESS values after 50 million generations, we included additional generations until the results were stable. Maximum clade credibility (MCC) trees were estimated from the posterior distribution of trees for each species using TreeAnnotator (7).

Units delimited using the GMYC model are typically regarded as species. In birds, however, more stringent criteria, involving metrics of reproductive isolation or phenotypic divergence, are typically applied for species delimitation (8, 9). Non-interbreeding populations failing to meet this criteria, such as many of the units delimited in this study, are often assigned subspecies status. Many of the units in this study may even fail to meet some researchers' criteria for subspecies status, indeed many have not been elevated to subspecies despite prior publications based on the same genetic data examined here. As a result, GMYC units in birds are perhaps better treated as genetically differentiated populations, and we follow this philosophy here. Regardless of their taxonomic status, however, GMYC clusters represent more finely resolved and more recently diverged groups relative to the terminal taxa in the avian phylogeny we examined, and thus are appropriate for comparing divergence rates between recent and deep timescales, the fundamental goal of this study. An alternate method for identifying geographic variants would have been to use named subspecies, but naming practices are far from standardized and many cryptic taxa in poorly studied groups would be missed (10).

bGMYC determines the number of genetic species by estimating the number of clusters within which splits in the gene tree fit a coalescent model rather than a model of interspecific diversification (Yule model). We ran the program for 250,000 generations using the `single.phy` function and discarded the first 15,000 generations as burn-in. We ran each analysis multiple times for validation, and assessed MCMC diagnostics by examining likelihood plots in Tracer.

We corrected for differences in the age of species by calculating the rate at which bGMYC clusters formed since the species' crown age. The area across which a species is distributed might also predict its level of differentiation, but we found area was not strongly correlated with the number of differentiated populations ($R^2 = 0.014$, $P = 0.065$), certainly much less so than age ($R^2 = 0.298$, $P \ll 0.001$). This suggests that population differentiation has similar evolutionary potential regardless of the size of the area across which it occurs, and we therefore do not control for area in any subsequent analyses.

Speciation Rate Estimation. The software program BAMM uses reversible-jump MCMC to examine models differing in the number of time-varying diversification processes present across the phylogeny. Each process includes a time-varying speciation term and a time-invariant extinction rate. In the BAMM run using the primary taxonomy, multiple tips from within the same species were collapsed so as to avoid overlap in the data used for estimation of speciation and population differentiation rates. We ran BAMM using a model allowing for variable rates for at least 350 million generations in both the split and primary analyses, completing multiple runs with the same settings for validation. We sampled every 200,000 generations and discarded 10% of the sample as burn-in. Marginal distributions of speciation rates at the tips of the tree represent estimates of present-day speciation rates for those taxa.

Comparative Analyses. We first used STRAPP, which computes the correlation between character states at the tips of the tree and their corresponding diversification rates, and assesses significance by permuting speciation rates among regimes estimated in BAMM. Parametric uncertainty in diversification rates is accommodated by conducting tests across the posterior

distribution of rates inferred using BAMM. The permutation test is used to control for the covariance among species from the same macroevolutionary rate regime, thereby explicitly incorporating covariance among replicates with shared history and macroevolutionary dynamics. All tests presented are two-tailed tests, examining the alternative hypothesis that there is a correlation between population differentiation and speciation rates. One-tailed tests, in which the alternative hypothesis is the presence of a positive correlation between population differentiation and speciation rates, resulted in greater significance values than the two-tailed tests presented. The primary two-tailed test presented in the main text, for example, resulted in a significance level of $P = 0.021$, whereas the equivalent one-tailed test resulted in a level of $P = 0.007$. We used the two-tailed test as a more conservative index of trait-dependent diversification.

We also conducted comparative analyses of the number of splits summary statistic of speciation rate using phylogenetic generalized least squares (PGLS) in the caper package (11) in R. PGLS analysis using the number of splits summary statistic produced similar results to STRAPP overall. In addition to the results presented in the main text, PGLS analysis using the split taxonomy resulted in a correlation similar to that using the primary taxonomy (PGLS slope = 0.182, $P = 0.003$), as did the use of lower (0.7; ; PGLS slope = 0.215, $P < 0.001$) and higher (0.9; PGLS slope = 0.236, $P < 0.001$) posterior probability thresholds for assigning individuals to population clusters, to whether the population differentiation rate was measured using the stem age rather than crown age of a species (PGLS slope = 0.342, $P < 0.001$), to the random removal of 20% (PGLS slope = 0.202, $P < 0.001$) and 40% (PGLS slope = 0.189, $P < 0.001$) of samples from the dataset, and to models of population differentiation incorporating moderate ($eps = 0.45$; PGLS slope = 0.183, $P < 0.001$) or high ($eps = 0.9$; PGLS slope = 0.142, $P = 0.002$) extinction

rates. PGLS revealed a correlation between differentiation and speciation rates in the partition containing only tropical species (PGLS slope = 0.215, $P = 0.002$), but no correlation in temperate species (PGLS slope = 0.150, $P = 0.087$). The correlation coefficients in tropical and temperate species were more different than expected based on a random permutation test to account for differences in sample sizes between the two groups ($P = 0.012$). The disparity in the species-specific ratios of population differentiation to speciation rates at temperate latitudes was greater than in the Tropics (F-test of equal variances $F = 2.094$, $P = 0.001$).

When species were partitioned into temperate and tropical for the main analysis, south temperate species were included in the tropical partition because most are members of largely tropical groups and we therefore expect them to exhibit long-term evolutionary dynamics similar to the tropical species, and because it resulted in more equivalent sample sizes between partitions. Including these species in the temperate partition, however, produced similar results, with no or a weak correlation observed between population differentiation in the temperate zone (BAMM $r = 0.149$, $P = 0.179$; PGLS slope = 0.214, $P = 0.001$) and a strong correlation in the Tropics (BAMM $r = 0.458$, $P = 0.007$; PGLS slope = 0.332, $P = 0.002$).

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SI Figures

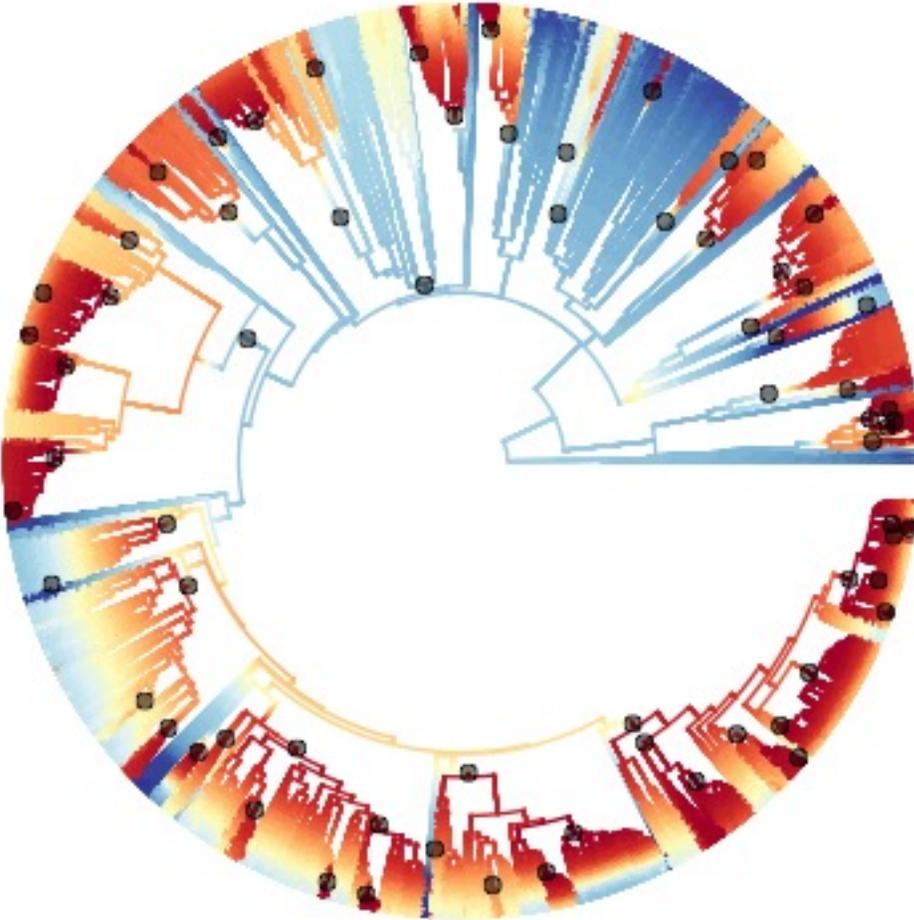


Fig. S1. A phylorate plot showing speciation rates and all 69 macroevolutionary regime shifts across the tree of all 6,670 birds with genetic data based on the Jetz et al. phylogeny.

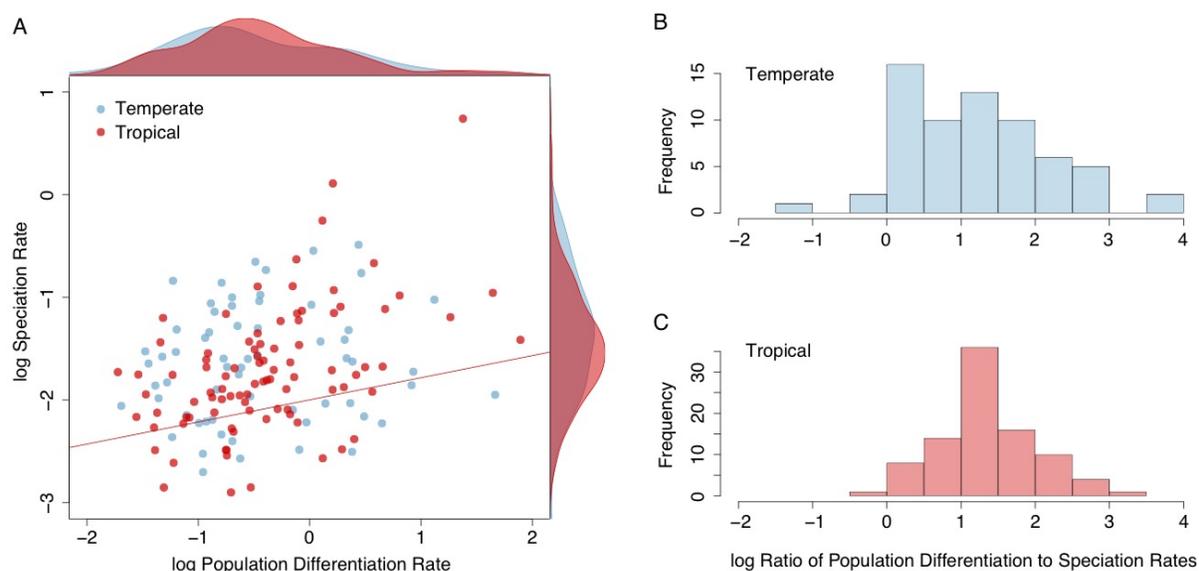


Fig. S3. Plots showing differences in relative population differentiation and speciation rates between temperate and tropical species using the DR statistic. (A) Tropical species show a relationship between population differentiation rates and speciation rates (0.215 , $p = 0.002$), whereas temperate species do not. Kernel density plots showing the relative distributions of rates between tropical and temperate species are plotted opposite the axis of the rate to which they correspond and show that neither differentiation or speciation rates differ noticeably between temperate and tropical species. The ratio of population differentiation rate to speciation rate, however, is more variable in temperate species (B) than tropical species (C).

SI Appendix

Species	AOU Species	Locus	References
1	<i>Adelomyia melanogenys</i>	CR-ATP8-ATP6	12, 13
2	<i>Agelaius phoeniceus</i>	ND2	14
	<i>Agelaius tricolor</i>		
3	<i>Amazilia tzacatl</i>	ND2	15
4	<i>Amazona farinosa</i>	cyt	16
5	<i>Amazona ochrocephala</i>	ND2	17, 18
	<i>Amazona aestiva</i>		
6	<i>Anabacerthia striaticollis</i>	ND2	19
7	<i>Anas fulvigula</i>	CR	20
8	<i>Anas strepera</i>	CR	21
9	<i>Aphelocoma caeruleascens</i>	ND2	22
	<i>Aphelocoma californica</i>		
	<i>Aphelocoma insularis</i>		
10	<i>Aphelocoma ultramarina</i>	ND2	22, 23
	<i>Aphelocoma wollweberi</i>		
11	<i>Aphelocoma unicolor</i>	ND2	22, 23
12	<i>Aratinga solstitialis</i>	CytB	24
	<i>Aratinga jandaya</i>		
	<i>Aratinga auricapillus</i>		
13	<i>Arremon brunneinucha</i>	COII	25
14	<i>Arremon torquatus</i>	ND2	19, 26
	<i>Arremon assimilis</i>		
	<i>Arremon atricapillus</i>		
	<i>Arremon basilicus</i>		
	<i>Arremon costaricensis</i>		
	<i>Arremon perijanus</i>		
	<i>Arremon phaeopleurus</i>		
<i>Arremon phygas</i>			
15	<i>Artemisiospiza belli</i>	CytB	27
	<i>Artemisiospiza nevadensis</i>		
16	<i>Attila spadiceus</i>	CytB	28
17	<i>Aulacorhynchus prasinus</i>	ND2	29
18	<i>Automolus ochrolaemus</i>	CytB	28
19	<i>Baeolophus inornatus</i>	CytB	30
	<i>Baeolophus ridgwayi</i>		

20	<i>Basileuterus belli</i>	ND2	31
21	<i>Basileuterus culicivorus</i>	CytB	32
22	<i>Basileuterus tristriatus</i>	ND2	33
	<i>Basileuterus trifasciatus</i>		
23	<i>Calidris ptilocnemis</i>	CytB	34
24	<i>Campylorhynchus brunneicapillus</i>	ND2	35
25	<i>Campylorhynchus rufinucha</i>	ND2	36
26	<i>Cantorchilus nigricapillus</i>	ATP8-ATP6	37
27	<i>Capito wallacei</i>	CytB	38
28	<i>Cardellina pusilla</i>	CytB	39
29	<i>Cardellina rubra</i>	ND2	40
	<i>Cardellina versicolor</i>		
30	<i>Cardinalis cardinalis</i>	ND2	41
31	<i>Catharus fuscater</i>	ND2	19
32	<i>Catharus occidentalis</i>	ND2	Current study
33	<i>Ceratopipra chloromeros</i>	ND2	Current study
	<i>Ceratopipra mentalis</i>		
	<i>Ceratopipra erythrocephala</i>		
	<i>Ceratopipra rubrocapilla</i>		
34	<i>Certhia americana</i>	ND2	42
35	<i>Chamaea fasciata</i>	CytB	43
36	<i>Charadrius montanus</i>	CR	44, 45
37	<i>Charadrius nivosus</i>	CR	45
38	<i>Chlorophanes spiza</i>	CytB	28
39	<i>Chlorospingus flavopectus</i>	ATP8-ATP6	46, 47, 48
	<i>Chlorospingus semifuscus</i>		
	<i>Chlorospingus inornatus</i>		
	<i>Chlorospingus tacarcunae</i>		
40	<i>Chrysomus icterocephalus</i>	ND2	49
41	<i>Cinclodes fuscus</i>	ND3	50, 51
	<i>Cinclodes olrogi</i>		
	<i>Cinclodes oustaleti</i>		
	<i>Cinclodes comechingonus</i>		
	<i>Cinclodes antarcticus</i>		
	<i>Cinclodes albiventris</i>		
42	<i>Colonia colonus</i>	CytB	28
43	<i>Corvus corax</i>	CytB	52
	<i>Corvus cryptoleucus</i>		

44	<i>Cranioleuca antisiensis</i>	ND2	Current study
	<i>Cranioleuca baroni</i>		
45	<i>Cyanerpes caeruleus</i>	CytB	28
46	<i>Cyanocitta stelleri</i>	ND2	Current study
47	<i>Cyanocompsa cyanoides</i>	CytB	53
48	<i>Cyanolyca viridicyanus</i>	ND2	19
	<i>Cyanolyca turcosa</i>		
	<i>Cyanolyca armillata</i>		
49	<i>Cyclarhis gujanensis</i>	ND2	54, Current study
	<i>Cyclarhis nigrirostris</i>		
50	<i>Cymbilaimus lineatus</i>	CytB	28
51	<i>Dendragapus fuliginosus</i>	CR	55
	<i>Dendragapus obscurus</i>		
52	<i>Dendrocincla fuliginosa</i>	CytB	28
	<i>Dendrocincla anabatina</i>		
53	<i>Dendrocolaptes platyrostris</i>	CytB	56
54	<i>Diglossa caerulescens</i>	ND2	19
55	<i>Diglossa cyanea</i>	ND2	19
56	<i>Drymophila caudata</i>	ND2	19, 57
	<i>Drymophila klagesi</i>		
	<i>Drymophila hellmayri</i>		
	<i>Drymophila striaticeps</i>		
57	<i>Drymophila devillei</i>	ND2	58
58	<i>Dubusia taeniata</i>	ND2	19
59	<i>Empidonax difficilis</i>	ND2	Current study
	<i>Empidonax occidentalis</i>		
60	<i>Empidonax flavescens</i>	ND2	Current study
61	<i>Empidonax traillii</i>	CytB	59
62	<i>Forpus coelestis</i>	ND2-CytB	60
	<i>Forpus conspicillatus</i>		
	<i>Forpus xanthops</i>		
	<i>Forpus passerinus</i>		
	<i>Forpus xanthopterygius</i>		
63	<i>Geothlypis tolmiei</i>	ND2	Current study
64	<i>Geothlypis trichas</i>	ND2	Current study
	<i>Geothlypis beldingi</i>		
	<i>Geothlypis nelsoni</i>		
	<i>Geothlypis flavovellata</i>		
65	<i>Glyphorynchus spirurus</i>	CytB	28

66	<i>Habia fuscicauda</i>	ND2	Current study
67	<i>Habia rubica</i>	ND2	Current study
68	<i>Hellmayrea gularis</i>	ND2	19
69	<i>Henicorhina leucophrys</i>	ATP8-ATP6	Current study
	<i>Henicorhina negreti</i>		
70	<i>Henicorhina leucoptera</i>	ATP8-ATP6	Current study
71	<i>Henicorhina leucosticta</i>	CytB	28
72	<i>Hirundo rustica</i>	ND2	61
73	<i>Hylophilus ochraceiceps</i>	ND2	54
74	<i>Hylophylax naevioides</i>	ND2	62
	<i>Hylophylax naevius</i>		
75	<i>Hypocnemis cantator</i>	ND2	58, 63, 64
	<i>Hypocnemis flavescens</i>		
	<i>Hypocnemis peruviana</i>		
	<i>Hypocnemis subflava</i>		
	<i>Hypocnemis ochrogyna</i>		
	<i>Hypocnemis striata</i>		
76	<i>Icterus galbula</i>	CytB	65
	<i>Icterus abeillei</i>		
77	<i>Icterus pustulatus</i>	CytB	66
78	<i>Lampornis amethystinus</i>	CR	67
79	<i>Lepidocolaptes affinis</i>	ND2	68
80	<i>Lepidocolaptes lacrymiger</i>	ND2	19
81	<i>Lepidothrix coronata</i>	CytB	28
82	<i>Margarornis squamiger</i>	ND2	19
83	<i>Mecocerculus leucophrys</i>	ND2	19
84	<i>Melanerpes formicivorus</i>	CytB	69
85	<i>Melozona fusca</i>	CR	35
86	<i>Microbates cinereiventris</i>	ND2	54, 64, Current study
	<i>Microbates collaris</i>		
87	<i>Microcerculus marginatus</i>	CytB	28
88	<i>Mionectes oleagineus</i>	ND2	70
	<i>Mionectes rufiventris</i>		
	<i>Mionectes macconnelli</i>		
89	<i>Mionectes striaticollis</i>	ND2	19
90	<i>Momotus mexicanus</i>	ND2	71
91	<i>Myadestes occidentalis</i>	ND2	31
92	<i>Myioborus miniatus</i>	ND2	72, 73, Current

			study
93	<i>Myiothlypis coronata</i>	ND2	19
94	<i>Myiothlypis fulvicauda</i>	ATP8-ATP7	74
	<i>Myiothlypis rivularis</i>		
95	<i>Myiothlypis leucoblephara</i>	CytB	75
96	<i>Myiothlypis luteoviridis</i>	ND2	19
97	<i>Myrmeciza exsul</i>	ND2	76
98	<i>Myrmeciza hemimelaena</i>	CytB	77
99	<i>Myrmeciza loricata</i>	ND2	78
	<i>Myrmeciza squamosa</i>		
100	<i>Myrmotherula axillaris</i>	CytB	28
101	<i>Myrmotherula schisticolor</i>	ND2	19
102	<i>Nucifraga columbiana</i>	ND2	79
103	<i>Ochthoeca cinnamomeiventris</i>	ND2	19
104	<i>Passerculus sandwichensis</i>	ND2	80
105	<i>Passerina ciris</i>	ND2	81
106	<i>Passerina leclancherii</i>	ND2	71
107	<i>Perisoreus canadensis</i>	ND2	82
108	<i>Petrochelidon fulva</i>	CytB	83
119	<i>Phaethornis guy</i>	ND2	19
110	<i>Pheucticus melanocephalus</i>	ND2	84
111	<i>Phrygilus fruticeti</i>	COI	85
112	<i>Piaya cayana</i>	CytB	28
113	<i>Picoides dorsalis</i>	CytB	86
114	<i>Picoides pubescens</i>	CR-ATP8-ATP6	87
115	<i>Picoides villosus</i>	ND2	88
116	<i>Pinicola enucleator</i>	ND2	89
117	<i>Pipilo erythrophthalmus</i>	ND2	Current study
	<i>Pipilo maculatus</i>		
118	<i>Pipreola riefferii</i>	ND2	19
	<i>Pipreola intermedia</i>		
119	<i>Piranga flava</i>	ND2	Current study
120	<i>Piranga ludoviciana</i>	CytB	Current study
121	<i>Poecile atricapillus</i>	ND6	90
122	<i>Poecile gambeli</i>	ND2	91
123	<i>Polioptila albiloris</i>	ND2	54, 92, Current study
	<i>Polioptila nigriceps</i>		
	<i>Polioptila melanura</i>		

	<i>Polioptila californica</i>		
	<i>Polioptila plumbea</i>		
	<i>Polioptila caerulea</i>		
	<i>Polioptila dumicola</i>		
	<i>Polioptila lactea</i>		
124	<i>Premnoplex tatei</i>	ND2	93
	<i>Premnoplex brunnescens</i>		
125	<i>Psaltriparus minimus</i>	ND2	Current study
126	<i>Pyriglena leucoptera</i>	ND2	94
	<i>Pyriglena atra</i>		
127	<i>Pyrrhomyias cinnamomeus</i>	ND2	19
128	<i>Querula purpurata</i>	CytB	28
129	<i>Quiscalus mexicanus</i>	ND2	95
	<i>Quiscalus major</i>		
130	<i>Rallus longirostris</i>	ND2	96
	<i>Rallus elegans</i>		
131	<i>Ramphocaenus melanurus</i>	ND2	54, Current study
132	<i>Regulus calendula</i>	ATP8-ATP6	Current study
133	<i>Regulus satrapa</i>	ATP8-ATP6	Current study
134	<i>Saltator coerulescens</i>	ND2	97
	<i>Saltator similis</i>		
	<i>Saltator striatipectus</i>		
135	<i>Saltator grossus</i>	ND2	97
	<i>Saltator cinctus</i>		
	<i>Saltator aurantirostris</i>		
136	<i>Saltator maximus</i>	ND2	97
137	<i>Schiffornis turdina</i>	CytB	28
138	<i>Schiffornis virescens</i>	CR	98
139	<i>Sclerurus mexicanus</i>	CytB	28
	<i>Sclerurus rufigularis</i>		
140	<i>Sclerurus scansor</i>	ND2	99
141	<i>Selasphorus platycercus</i>	CR	100
142	<i>Setophaga coronata</i>	ATP8-ATP6	Current study
143	<i>Setophaga dominica</i>	CR	101
144	<i>Setophaga graciae</i>	ND2	Current study
145	<i>Setophaga petechia</i>	CR	102
146	<i>Setophaga ruticilla</i>	CR	103
147	<i>Setophaga striata</i>	CR	104
148	<i>Sialia mexicana</i>	ATP8-ATP6	Current study

	<i>Sialia currucoides</i>		
	<i>Sialia sialis</i>		
149	<i>Sitta carolinensis</i>	ND2	105
150	<i>Spizella passerina</i>	CR	106
151	<i>Strix occidentalis</i>	CR	107
152	<i>Strix varia</i>	CR	107
153	<i>Sturnella magna</i>	ND2	108
	<i>Sturnella neglecta</i>		
154	<i>Synallaxis azarae</i>	ND2	19
	<i>Synallaxis courseni</i>		
155	<i>Tachycineta bicolor</i>	ND2	109
156	<i>Tangara cyanicollis</i>	CytB	28
157	<i>Tangara gyrola</i>	CytB	28
158	<i>Tangara vassorii</i>	ND2	19
159	<i>Tersina viridis</i>	CytB	28
160	<i>Tityra semifasciata</i>	CytB	28
161	<i>Toxostoma curvirostre</i>	ND2	110
162	<i>Toxostoma redivivum</i>	CytB	111
163	<i>Troglodytes aedon</i>	ND2	Current study
164	<i>Troglodytes hiemalis</i>	ND2	112
	<i>Troglodytes pacificus</i>		
165	<i>Trogon rufus</i>	CytB	28
166	<i>Vireo atricapilla</i>	ND2	113
167	<i>Vireo gilvus</i>	ND2	Current study
168	<i>Vireo huttoni</i>	ND2	Current study
169	<i>Vireo solitarius</i>	ND2	Current study
	<i>Vireo plumbeous</i>		
	<i>Vireo cassinii</i>		
170	<i>Xenopipo atronitens</i>	ND2	114
171	<i>Xenops minutus</i>	CytB	28
172	<i>Xiphorhynchus elegans</i>	CytB	115
	<i>Xiphorhynchus spixii</i>		
173	<i>Xiphorhynchus fuscus</i>	ND2	116
174	<i>Xiphorhynchus ocellatus</i>	ND2	117
	<i>Xiphorhynchus pardalotus</i>		
175	<i>Xiphorhynchus triangularis</i>	ND2	19
176	<i>Zonotrichia capensis</i>	CR	118