The latitudinal gradient in the rate of evolution of a biotic interaction trait

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Abstract

Where is evolution fastest? The biotic interactions hypothesis proposes that greater species richness creates more ecological opportunity, driving faster evolution at low latitudes, whereas the "empty niches" hypothesis proposes that ecological opportunity is greater where diversity is low, spurring faster evolution at high latitudes. Here we test these contrasting predictions by analyzing rates of bird beak evolution for a global dataset of 1141 sister pairs of birds. We find that beak size evolves at similar rates across latitudes, while beak shape evolves faster in the temperate zone, consistent with the empty niches hypothesis. By comparing rates of evolution in sympatric versus allopatric sister lineages, we also find evidence that character displacement is similar between latitudes. Our analyses focusing on recent speciation events finds that drivers of evolutionary diversification are more potent at higher latitudes, thus calling into question multiple hypotheses invoking faster tropical evolution to explain the latitudinal diversity gradient.

Introduction

The biotic interactions hypothesis proposes strong tropical biotic interactions are both a cause and a consequence of the latitudinal diversity gradient (Schemske 2009). Imagine that diversity were equal in the tropics and temperate zone. If so, then stronger biotic interactions in the tropics are proposed to lead to faster adaptation and speciation at low latitudes, generating an excess of tropical species. This is because biotic interactions are thought to be the dominant drivers of selection for tropical organisms, and adaptation to biotic interactions is expected to lead to faster evolutionary change than adaptation to abiotic challenges (Dobzhansky 1950; MacArthur 1972). Now imagine that the latitudinal diversity gradient already exists. A greater number of species in the tropics could provide increased ecological opportunity via an increase in the diversity of possible interactions between species and greater spatial heterogeneity in these interactions, also leading to faster evolution (Schemske 2009). In this conception, diversity begets diversity in a positive feedback loop. Whether biotic interactions are stronger in the tropics has been tested by many studies, with mixed results (Schemske *et al.* 2009; Anstett *et al.* 2016; Moles & Ollerton 2016; Roslin *et al.* 2017; Baskett & Schemske 2018; Hargreaves *et al.* 2019; Freeman *et al.* 2020; Roesti *et al.* 2020). However, the prediction that stronger biotic interactions or higher diversity can drive faster evolution in the tropics remains largely unexplored (but see Benkman 2013).

An alternative is that evolutionary rates are instead greatest where diversity is low. According to standard niche theory, ecological opportunity should be negatively related to diversity (Hutchinson 1959), such that evolutionary rates are fastest where diversity is low (Schluter 2016; Schluter & Pennell 2017; Machac 2020). A geographic

prediction arising from this "empty niches" hypothesis is that evolutionary rates should be faster in the species-poor temperate zone than the species-rich tropics.

Here, we investigate these contrasting predictions by analyzing latitudinal differences in rates of bird beak evolution. Since birds use their beaks to feed on living things, bird beaks can be considered a key trait mediating biotic interactions. Interactions with the animals and plants that form bird's diets are widely thought to drive beak morphological evolution (Smith 1987; Benkman 2003; Lerner *et al.* 2011; Grant & Grant 2014). Diet can also drive beak morphological evolution via interactions between individuals competing for food, leading to character displacement between species (Brown & Wilson 1956; Schluter 2000; Grant & Grant 2006). Bird beak morphology may also be shaped by adaptation to abiotic factors such as thermoregulation (Tattersall *et al.* 2009, 2017). However, beak morphological form is tightly coupled to dietary ecological function across all ~10,000 species of birds, suggesting a pervasive role for diet-related biotic interactions in driving bird beak evolution (Pigot *et al.* 2020).

We tested whether empirical patterns of bird beak evolution better matched predictions of the biotic interactions or empty niche hypotheses, using new measurements of beak size and shape for a previously published global dataset of bird sister pairs (Cooney *et al.* 2017b). First, we tested whether beak size and shape evolution are fastest for tropical sister pairs, as expected under the biotic interactions hypothesis, or fastest for temperate sister pairs, as expected under the empty niches hypothesis. Second, we examined one specific biotic interaction—competition between closely related species in sympatry that results in greater trait divergence. This pattern includes both character displacement, where competition directly drives trait divergence (Stuart & Losos 2013;

Weber & Strauss 2016), and ecological sorting, where competition prevents sympatry between species with similar traits but permits sympatry between species with divergent traits (Pigot & Tobias 2013; Tobias *et al.* 2014; Freeman 2015). If competition between sympatric relatives leads to faster trait divergence in the tropics, as predicted by the biotic interactions hypothesis, then evolutionary rates for sympatric sister pairs (relative to baseline rates for allopatric sister pairs) should be faster in the tropics than the temperate zone. The empty niches hypothesis makes no clear prediction about latitudinal gradients in the strength of competition between close relatives.

Our analysis of global patterns of bird beak evolution sheds light on the more general problem of why species richness is highest in the tropics. Dozens of hypotheses have been proposed to explain the latitudinal diversity gradient. The biotic interactions hypothesis is one of at least seven distinct hypotheses that invoke faster tropical evolution to explain why species richness peaks near the equator (Mittelbach *et al.* 2007). These "fast tropical evolution" hypothesis propose different mechanisms for why evolution is most rapid in the tropics, including stronger biotic interactions (a focus of this manuscript), faster rates of molecular evolution (the evolutionary speed hypothesis (Rohde 1992; Gillman & Wright 2014)), narrower physiological tolerances (Janzen 1967), larger area (Rosenzweig 1995), greater climatic variation (Haffer 1969), greater genetic drift (Fedorov 1966), and greater divergence in the face of gene flow (Moritz *et al.* 2000). Finding faster rates of beak evolution in the tropics would therefore support the biotic interactions hypothesis, but also be consistent with the entire set of fast tropical evolution hypotheses. A result that beak evolution is faster in the temperate zone,

however, would support the empty niches hypothesis while calling into question all hypotheses based on the concept of faster tropical evolution.

Materials and methods

Sister pair selection and geographic variables

We analyzed a previously published dataset of 1306 sister pairs of birds with information on median latitude and range overlap for each pair (Cooney *et al.* 2017b). This dataset defined sister pairs from a dated global bird phylogeny of species, subsetted to include only species placed on the tree on the basis of genetic data (6670 species out of 9993) (Jetz *et al.* 2012). Each sister pair in this dataset comprises two species that are each other's closest relatives. Because of incomplete sampling, not all sister pairs are true sister species. Nevertheless, each sister pair is a phylogenetically independent comparison between two closely related species, and is therefore appropriate for our purposes. Because our primary goal is to compare rates of beak evolution between tropical and temperate sister pairs, we excluded 141 sister pairs where one species was classified as tropical (median latitude < 23.4°) and the other as temperate (median latitude > 23.4°). We further excluded the small number (1%) of sister pairs with estimated divergences greater than 20 million years, and 11 sister pairs where morphological data was lacking for one species within the pair. A total of 1141 sister pairs met these criteria.

Three key variables in this dataset are: (1) divergence time; (2) latitude; and (3) range overlap, coded as allopatric vs. sympatric. We used divergence time—the time to most recent common ancestor estimated using the dated phylogeny—as an estimate of evolutionary age. We used the absolute latitude of each sister pair to classify it as tropical

(< 23.4°; N = 800) or temperate (> 23.4°; N = 341). Range overlap is a continuous variable ranging from 0, where the two species in the pair do not overlap in range, to 1, where the range of the smaller-ranged species is completely subsumed within the range of the larger-ranged species. Following previous studies (Tobias *et al.* 2014; Cooney *et al.* 2017b), we used a threshold of 20% range overlap to define whether sister pairs were sympatric or allopatric (< 20% range overlap; N = 746) or sympatric (> 20% range overlap; N = 395). We chose this threshold so that sister pairs were coded as sympatric only when they had substantial range overlap (such that the two species likely interact). To examine sensitivity of results, we conducted further tests using thresholds of > 0% and > 50% range overlap to define sympatry/allopatry.

Morphological divergence

We extracted morphological data for each species in each species pair from a global dataset of bird morphology (Pigot *et al.* 2020). We analyzed four traits, all measured in mm: (1) bill length of the culmen; (2) bill length measured from the nares; (3) bill depth; and (4) bill width. We excluded individuals that had missing values for any beak traits. Our final morphological dataset contained 9,966 individuals (mean 4.4 individuals per species; range = 1 – 89; 94% of species had four or more individuals measured).

We used a principal components analysis to place each of the 9,966 measured individuals within a single multidimensional beak morphospace. To generate independent axes of variation in beak morphology, we ran a principal component analysis (PCA) on logged values of each of the four beak traits. The resulting morphospace is essentially two dimensional: PC1, related to overall beak size, explained 82.1% of variation, while

PC2, a metric of beak shape, explained a further 14.3% of variation (Table S1, Figure S1). We quantified the volume of beak morphospace for tropical and temperate zone species by constructing a hypervolume using Gaussian kernel density estimation and calculating its volume using the "hypervolume" package (Blonder *et al.* 2014; Blonder & Harris 2019). Tropical species outnumber temperate species by ~ 3 to 1 in this dataset, as in reality. However, the volumes of beak morphospace occupied by tropical and temperate species in this dataset are nearly identical (four-dimensional volumes of 4.94 versus 4.86 and two-dimensional volumes of 1.00 versus 1.01, see Figure S2 for a two-dimensional representation). This implies that tropical species in this dataset are more densely packed within beak morphospace than temperate species, a feature found in other avian diversity gradients (Pigot *et al.* 2016). We calculated divergence in beak size (PC1) and shape (PC2) for each taxon pair as the absolute value of the difference in species means along these axes. Sampling error will cause the raw difference in species' means to be larger than the true difference in species means. We therefore estimated bias-corrected divergence in beak size and shape for each sister pair using pooled sample variance, calculated for all species (see demonstration of bias, as well as code to calculate bias-corrected divergence, in a R script provided in the Supporting Information). Following bias correction, some values of beak size and shape divergence between sister pairs are negative.

Statistical analysis

We tested the hypothesis that evolutionary rates of beak divergence differ between latitudes by fitting evolutionary and empirical models to our trait data in R version 3.9 (R

Development Core Team 2020). We fit distinct models to beak size (PC1) and beak shape (PC2). For all beak size models, we removed two outlier sister pairs (the temperate pair *Numenius minutus* and *N. arquata* (curlews) and the tropical pair *Geospiza magnirostris* and *G. fuliginosa* (Darwin's finches from the Galápagos) with very low estimated divergence dates and extremely high beak size divergence. These cases are likely to represent phylogenetic error or instances where repeated introgression at target loci generates spuriously short branch lengths among interacting lineages (Tobias et al. 2020). We first fit Brownian motion (BM) and Ornstein Uhlenbeck (OU) models. These common models of trait evolution pass through the origin. In our dataset, however, both beak size and beak shape divergence are relatively high even at very young evolutionary ages (Figure 1a and 1b).

There are two likely explanations for this seemingly impossible initial rate of evolution. The first is statistical: evolutionary age is estimated with error, and any species pairs whose ages are underestimated will lead to models having an intercept fitting better than models fit through the origin. The second explanation is biological: rapid evolution (or phenotypic plasticity) can lead to trait differences that arise before any divergence at the putatively neutral loci that are used to estimate evolutionary age. We therefore explored fitting simple models with intercepts that better captured the patterns in our data than formal evolutionary models. We interpret a high intercept as equivalent to a high rate of evolution in the early stages of divergence, and hence we compare intercepts as well as slopes of fitted models. We included simple power functions in the set of models because they are more flexible than the evolutionary models, and can fit relationships suggested by the loess regressions in Figure 1. In sum we fit BM and OU models, a BM

model with an intercept, a power function forced through the origin, and a power function with an intercept, and compared model fit using AIC.

The response variable in our models (either beak size divergence or beak shape divergence) was the signed square root of squared differences between bias-corrected species means divided by two. BM and OU models estimate the variance between species times two on the squared differences scale; we correct for this by dividing by two. We used the signed square root of squared differences—the visual scale for analyzing trait differences—because residuals are more normally distributed and had more homogenous variance on this scale. All results from models fit to squared differences data, weighting by the variance of residuals, were similar, but the highly skewed distributions of residuals on the squared difference scale led us to be cautious in interpretation of AIC scores and p-values (Figures S3 and S4, Tables S2 and S3).

We tested whether rates of trait evolution differed between the tropics and temperate zone by fitting models with and without a latitudinal zone term (temperate or tropical), and conducting *F* tests using the "anova" command in R. For the BM intercept and power function with intercept, we fit three models in which (1) neither the intercept nor the slope varied between tropical and temperate zone sister pairs; (2) the intercept varied between tropical and temperate zone sister pairs; and (3) both slope and intercept varied between tropical and temperate zone sister pairs.

Last, we analyzed the relationship between trait evolution and range overlap of sister pairs in our dataset (Figure 1c). For both beak size and beak shape, we tested whether rates of trait evolution differed between sympatric and allopatric sister pairs by fitting three models using the power function with intercept (the best-fit model for both

beak size and beak shape) in which (1) neither the intercept nor the slope varied between allopatric and sympatric sister pairs; (2) the intercept varied between allopatric and sympatric sister pairs; and (3) both slope and intercept varied between allopatric and sympatric sister pairs. We compared these models by conducting *F* tests using the "anova" command in R. The key range overlap prediction arising from the biotic interactions hypothesis is that evolutionary rates in sympatry are particularly fast in the tropics. We tested this hypothesis by fitting three models of the best-fit power function with intercept that included a sympatric/allopatric term in which (1) neither the intercept nor the slope varied between tropical and temperate zone sister pairs; (2) the intercept varied between tropical and temperate zone sister pairs; and (3) both slope and intercept varied between tropical and temperate zone sister pairs with and without a tropical/temperate term. We compared these models by conducting *F* tests using the "anova" command in R.

Literature review

Last, we placed the results of our study in the broader context of latitudinal gradients in rates of evolution. To do so, we reviewed the peer-reviewed published literature to find previous studies of latitudinal gradients in evolutionary rates. BGF conducted Google Scholar searches on 30 June 2020 for "molecular evolution AND latitudinal gradient", "trait evolution AND latitudinal gradient", "speciation AND latitudinal gradient", and "evolution AND latitudinal gradient", and examined the first 100 results for each search, as well as additional studies cited within the papers uncovered via these searches.

Results

We found evolutionary rates were faster in the temperate zone for beak shape and similar between tropical and temperate zone birds for beak size (Figures 2 and S5). For both beak size and beak shape, the best-fit model was a power function with an intercept, and standard evolutionary models (Brownian motion and Ornstein Uhlenbeck) were poor fits (Δ AIC > 40; Table 1). For beak shape but not beak size, models that included a latitudinal zone term (tropical/temperate) improved model fit (e.g., for the best-fit power function with intercept, $p = 0.0034$; Table 2), with higher intercepts for beak shape divergence in the temperate zone. We further found evidence that the slope of beak shape divergence is steeper in the temperate zone ($p = 0.039$, model where both intercept and slope differ between tropics and temperate zone plotted in Figure 2b): young lineages in the temperate zone have greater beak shape divergence than equivalently aged lineages in the tropics (higher intercept), but successively older lineages in the temperate zone have even greater beak shape divergence than equivalently aged lineages in the tropics (steeper slope).

Sympatric sister pairs have greater trait divergence than allopatric sister pairs for beak size (Figure 3a, t-test $p = 0.020$, means = 0.17 and 0.14, respectively) and beak shape (Figure 3b, t-test $p < 0.001$, means = 0.077 and 0.061, respectively). This pattern of greater divergence in sympatry is consistent with a role for character displacement. However, beak size and beak shape divergence also increase with evolutionary age (Figure 1 a,b), and sympatric sister pairs are older than allopatric sister pairs. In this dataset, median sister pair ages are 2.90 and 4.54 million years for tropical allopatric and sympatric sister pairs, respectively (t-test on mean age; $p < 0.001$), and 2.30 and 3.60

252 million years for temperate zone allopatric and sympatric sister pairs (t-test on mean age;
253 $p = 0.0083$; Figure 3). For beak shape, including a range overlap term
254 (sympatry/allopatry) improved model fit ($p = 0.0022$, Figure 4b), consistent with a role
255 for character displacement in driving beak shape evolution. In contrast, models that
256 included a range overlap term did not improve model fit for beak size ($p = 0.20$, Figure
257 4a), indicating that greater divergence in beak size for sympatric sister pairs is primarily
258 due to their older age rather than character displacement. Models that included a
259 temperate/tropical term in addition to a sympatry/allopatry term further improved fit for
260 beak shape ($p = 0.0032$, Figure 4d) but not for beak size ($p = 0.69$, Figure 4c). However,
261 excess rates of divergence in sympatry compared to allopatry for beak shape were similar
262 between the tropics and temperate zone (Figure 4d). Results were similar when using
263 alternative thresholds to define sympatric versus allopatric sister pairs (Figures S6 and
264 S7, Tables S4 and S5).
265 Most studies measuring latitudinal variation in recent evolutionary rates,
266 particularly studies with large sample sizes, have found that rates are either fastest in the
267 temperate zone or similar between the temperate zone and tropics (Table 4).
268
269 Discussion
270 Our analyses of evolutionary rates across 1141 pairs of sister species reveal that bird beak
271 shape evolution is faster in the temperate zone whereas bird beak size evolution is similar
272 in rate across latitudes. In addition, sympatric tropical sister pairs do not have particularly
273 fast evolutionary rates, as predicted if one specific biotic interaction—competition
274 between closely related species that leads to character displacement—were stronger in

the species-rich tropics. These results contradict both aspects of the biotic interaction hypothesis: that stronger biotic interactions in the tropics lead to faster evolution in biotic interaction traits, and that greater species richness leads to faster evolution in the tropics. Diversity does not beget diversity, at least for beak morphology. Instead, they are more consistent with the empty niches hypothesis that proposes ecological opportunity is greatest in the temperate zone where species richness is low.

It is perhaps unsurprising that ecological opportunity for bird beaks appears to be greater in species-poor temperate regions. Bird beaks are well described by a two dimensional morphospace, and there is little a priori reason to suspect the size of this morphospace expands in response to increasing bird species richness. It is more likely that a greater variety of resources in the tropics permits a larger beak morphospace volume in tropical birds. However, beak morphospace is only slightly larger in the tropics in this dataset. This implies that greater diversity is primarily associated with greater niche packing rather than with niche expansion (Pigot *et al.* 2016), with this increased saturation of available niche space offering fewer opportunities for rapid trait evolution (Tobias *et al.* 2020). Diversity may beget diversity in other situations. For example, greater diversity could spur rapid evolution (and coevolution) in biotic interaction traits that are more multidimensional, such as behavioral traits or chemical traits associated with defense or attraction. Studies that measured rates of evolution along the latitudinal gradient for traits that differ in their dimensionality would test this idea.

It could also be argued that investigating rates of evolution among avian sister species, in which both lineages universally share the same trophic level, runs counter to some of the theoretical underpinnings of the biotic interactions hypothesis. For example,

earlier conceptualizations of this idea point towards diversity in lower trophic levels, i.e. producers, having a knock-on effect on lineage diversification in consumers (Schemske et al. 2009). Our results suggest that further studies of diversity-begets-diversity mechanisms should not focus on within trophic levels, but across levels, to assess whether the higher overall volume of tropical diversification (Schluter 2016) sends ecological opportunities cascading through networks of interactions across the structure of biodiversity as a whole.

A further caveat relates to the precision of our beak shape quantification. Our data are based on a set of linear beak measurements and thus provide only a partial estimate of aspects such as curvature. The beaks of two interacting hummingbird species may potentially diverge in the extent of curvature linked to different floral niches while appearing identical from the perspective of our measurements. It is clear that the linear measurements we use nonetheless explain most of the ecological variation among species, including relatively subtle behavioral differences (Pigot et al. 2020), but further studies could revisit latitudinal effects on beak evolution using methods that account for curvature, bill tip differences and other details of beak structure (Cooney *et al.* 2017a).

Sympatry is weakly associated with bird beak evolution

Based on linear measurements, we find that beak shape evolution is faster in sympatry than allopatry across latitudes, while rates of beak size evolution are similar between sympatric and allopatric sister pairs. We interpret faster evolution of beak shape in sympatry to indicate a role for competition in driving divergence, either via character displacement or ecological sorting (Tobias *et al.* 2020). Discriminating between these

alternative pathways is complicated by the fact they leave very similar signatures on spatial patterns of trait divergence, but further sampling of sister pairs in allopatry vs. sympatry across a range of latitudes may help to tease them apart. Beak size divergence is greater for sympatric sister pairs than for allopatric sister pairs, but this appears to be explained by the older age of sympatric sister pairs (Tobias *et al.* 2014). Given the lack of differences in beak size evolution between sympatric and allopatric sister pairs, and the relatively minor differences in beak shape evolution, our results provide further evidence that character displacement (and ecological sorting) play a relatively minor role in bird beak evolution (Tobias *et al.* 2020)

Comparison with previous studies of evolutionary rates across latitudes

Our study adds to a growing body of evidence documenting that recent evolutionary rates are often faster in the temperate zone than in the tropics (see Table 4). While early empirical tests reported faster molecular evolution in the tropics (e.g., Gillooly *et al.* 2005; Wright *et al.* 2006), a recent comprehensive analysis of ~8,000 taxon pairs from six phyla of animals found that latitudinal differences in the rate of molecular evolution are minimal (faster in the tropics in 51.6% of comparisons vs. faster in the temperate zone in 48.4% of comparisons) (Orton *et al.* 2019). Consequently, the evolutionary speed hypothesis, which proposes that higher temperatures lead to faster molecular evolution via faster chemical reactions and faster generation times, appears unlikely to be generally true. For trait evolution and speciation, a majority of studies report faster evolution in the temperate zone. Song, plumage and body mass evolution in New World birds are fastest in the temperate zone (Martin *et al.* 2010; Weir & Wheatcroft 2011; Lawson & Weir

2014), and speciation rates are fastest at high latitudes in marine fishes (Rabosky *et al.* 2018) and in New World birds and mammals (Weir & Schluter 2007) (but see (Rolland *et al.* 2014). While evidence remains mixed—indeed, we find no latitudinal patterns for beak size evolution and a fairly small difference for beak shape—the growing body of available evidence suggests that rates of recent evolution are often faster in the temperate zone, and seldom faster in the tropics (Table 4).

Conclusion

Explaining the latitudinal diversity gradient is a longstanding goal of evolutionary ecology. The generality of the latitudinal diversity gradient across taxa, space and time suggests the tantalizing possibility of a common explanation. Since Darwin and Wallace, generations of biologists have added new hypotheses to a growing list of contenders (reviewed by Pianka 1966; Rohde 1992; Mittelbach *et al.* 2007). We argue that, on the strength of current evidence, hypotheses that invoke faster evolution in the tropics to explain the latitudinal diversity gradient should be rejected. Not only do bird beaks evolve either faster in the temperate zone or at similar rates across latitudes (this study), but rates of molecular evolution are similar in animals across latitudes (Orton *et al.* 2019), and trait evolution and speciation are faster in the temperate zone for several animal taxa (see Table 4). Evolutionary hypotheses that invoke slower extinction in the tropics (rather than faster evolution) remain viable, though difficult to test. For example, strong biotic interactions in the tropics may help explain the maintenance of high tropical diversity (lower extinction in the tropics) rather than the origin of high tropical diversity

(faster evolution in the tropics). Last, we call attention to the repercussions of faster evolution at high latitudes for the shape of the latitudinal diversity gradient. We might expect that, all else equal, faster evolution and speciation at high latitudes would gradually flatten of the latitudinal diversity gradient, all else equal. However, the large majority of species currently inhabit the tropics. If per-capita speciation rates are only somewhat faster in the temperate zone than in the tropics, then the latitudinal diversity gradient may actually become steeper over time despite faster evolution and speciation in the temperate zone.

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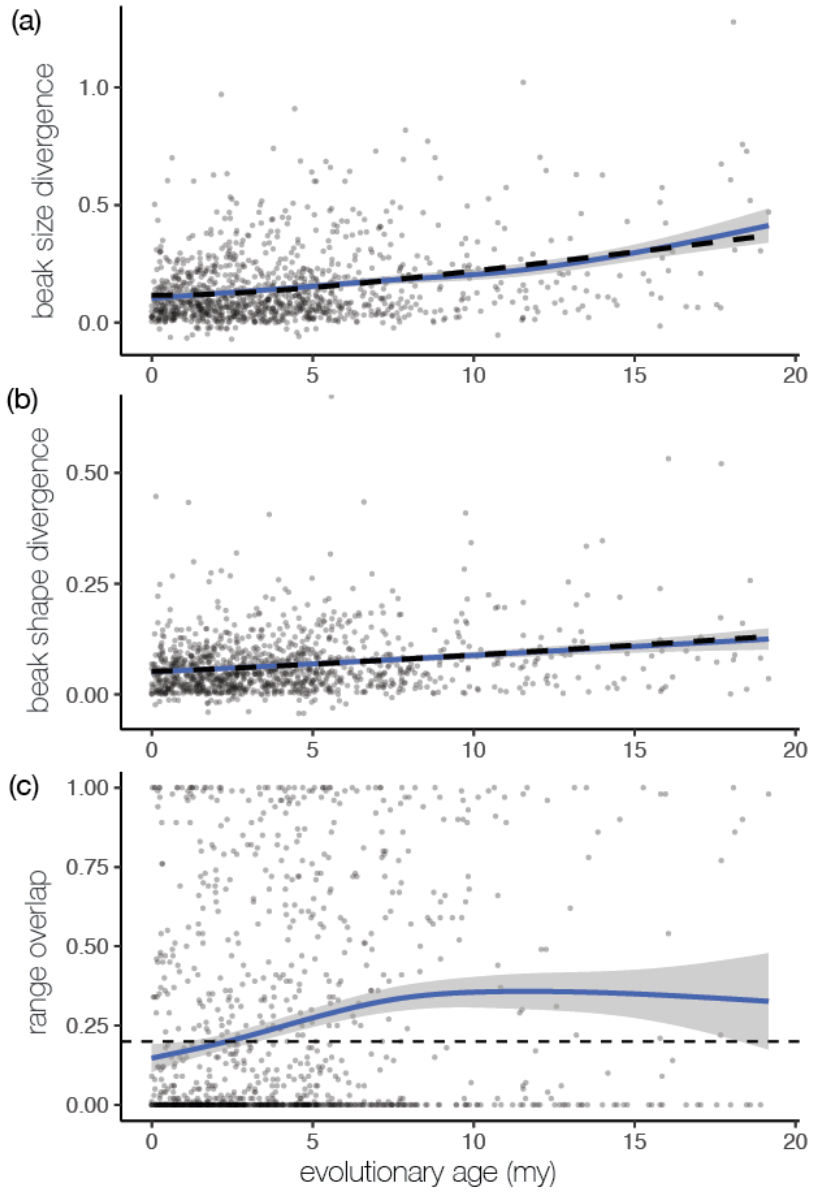

Figure 1. Patterns of divergence in beak size (a), beak shape (b) and range overlap (c) in 1141 sister pairs of birds. Raw data are plotted. Loess regressions are shown in blue; predictions from the best-fit models (power functions with intercepts) are shown as dashed black lines. Beak size and shape divergence values are corrected for bias arising from sampling error. Range overlap is the proportion of the smaller-ranged species that falls within the range of the larger-ranged species. Sister pairs were coded as sympatric if they had range overlaps > 0.20 (the dashed line).

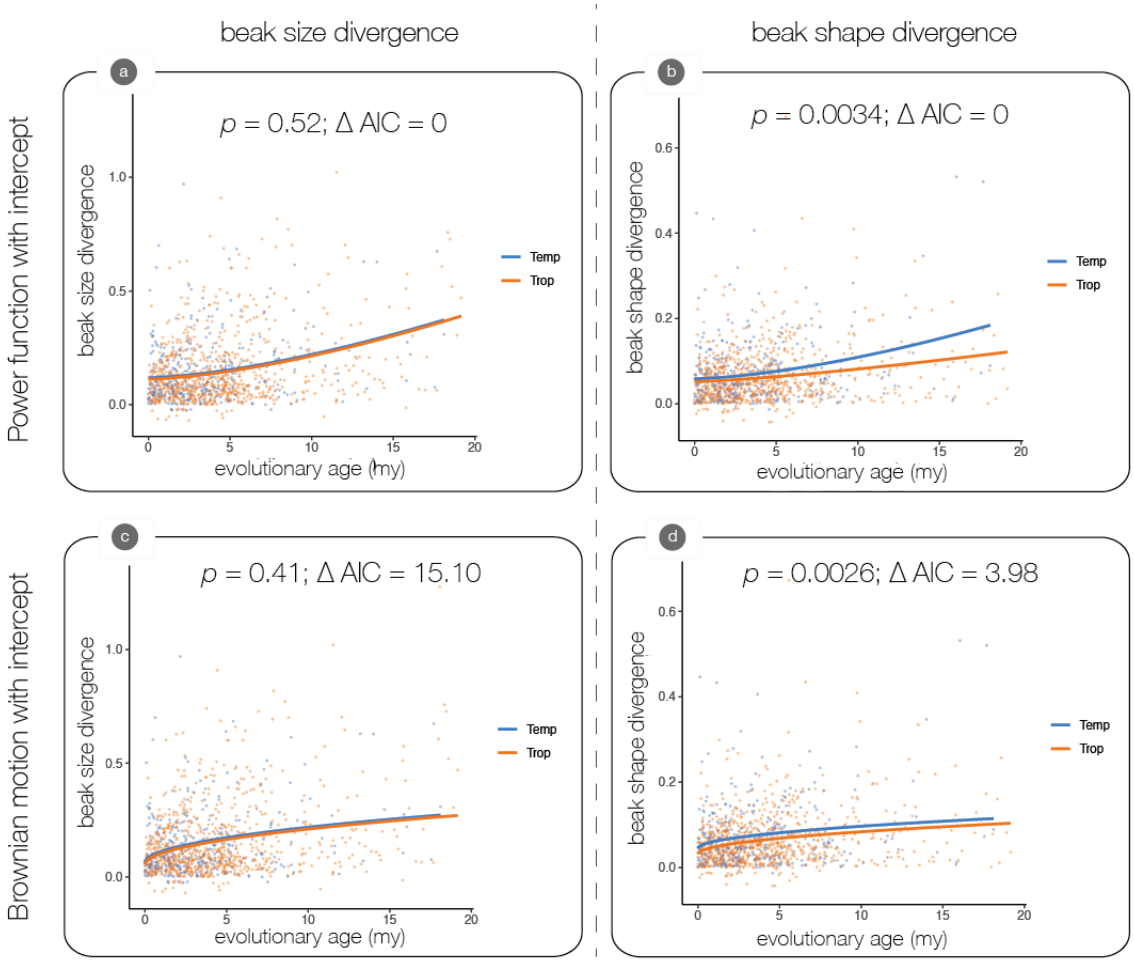

Figure 2. Rates of beak size evolution are similar between tropics and temperate zone (left panels), but beak shape evolution is faster in the temperate zone (right panels). Model predictions are plotted for the two best models: power functions with an intercept (a, b) and Brownian motion models with an intercept (c, d). *P*-values are from *F* tests testing whether the inclusion of a tropical/temperate term improved model fit. Δ AIC values compare different model fits separately for beak size and beak shape.

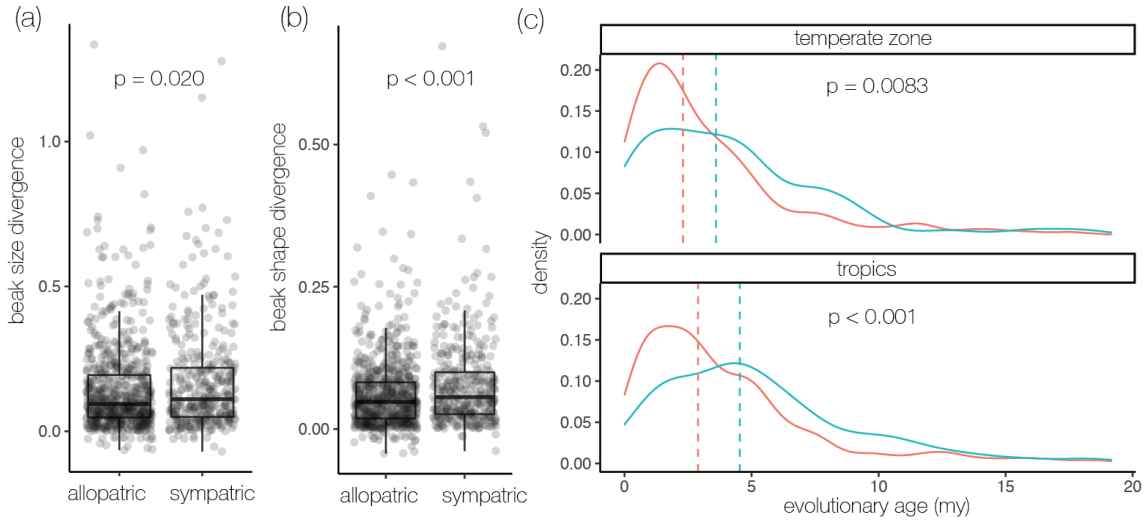

Figure 3. Sympatric sister pairs have greater beak size divergence (a), beak shape divergence (b), and are older (c) than allopatric sister pairs. *P*-values are from t-tests of trait divergence or ages between allopatric and sympatric sister pairs; separate t-tests for age for temperate and tropical zones in panel (c). Median values of ages for temperate and tropical sister pairs are plotted as vertical dashed lines.

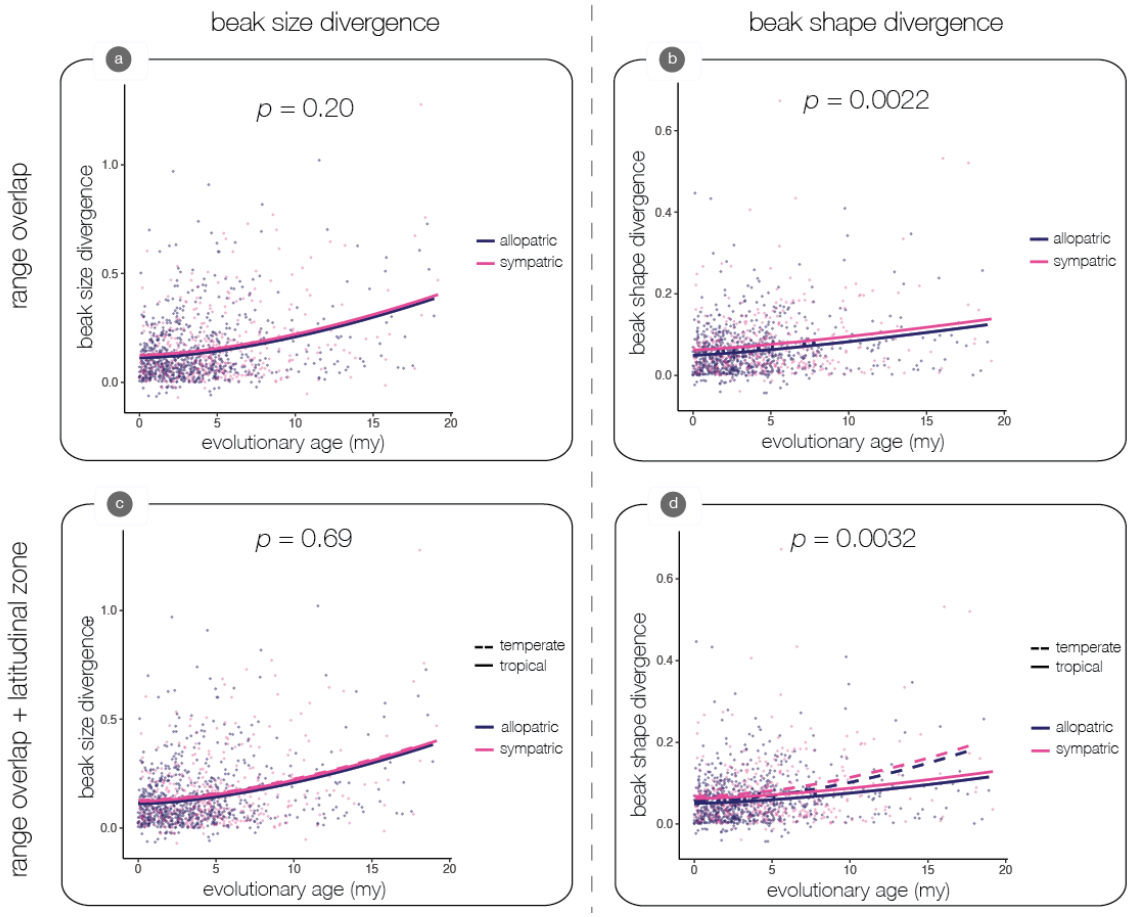

Figure 4. Rates of beak size evolution are similar between allopatric (n = 746) and sympatric (n = 395) sister pairs (left panels), but beak shape evolution is faster in sympatry (right panels). *P*-values are from *F* tests testing whether the inclusion of an allopatric/sympatric term to a power function with an intercept improved model fit (a, b), or whether the inclusion of a tropical/temperate term to a power function with an intercept and an allopatric/sympatric term improved model fit (c, d). The *p*-value for beak shape (d) is from a *F* test comparing a reduced model with an allopatric/sympatric term to a full model with terms allowing both the intercept and slope to differ between tropics and temperate zone. Beak shape evolution is faster in the temperate zone in both allopatry and sympatry compared to the tropics.

Table 1. Models that included intercepts (power function with an intercept and Brownian motion model with an intercept) were better fits than models forced through the origin (power function, Ornstein Uhlenbeck and Brownian motion models).

response variable	model	Δ AIC
beak size	power function intercept	0
	Brownian motion intercept	-15.11
	power function	-25.04
	Ornstein Uhlenbeck	-42.36
	Brownian motion	-42.38
beak shape	power function intercept	0
	Brownian motion intercept	-3.98
	power function	-12.99
	Ornstein Uhlenbeck	-40.15
	Brownian motion	-62.01

Table 2. Latitudinal zone is a predictor of beak shape evolution but not beak size evolution. *P*-values are from *F* tests comparing model fit between full and reduced models.

response variable	reduced model	full model	*p*-value
beak size	power intercept	power intercept + latzone (intercept)	0.52
	power intercept + latzone (intercept)	power intercept + latzone (intercept and slope)	0.70
	Brownian motion intercept	Brownian motion intercept + latzone (intercept)	0.41
	Brownian motion intercept + latzone (intercept)	Brownian motion intercept + latzone (intercept and slope)	0.25
	power	power + latzone	0.74
	Ornstein Uhlenbeck	Ornstein Uhlenbeck + latzone	0.58
	Brownian motion	Brownian motion + latzone	0.54
beak shape	power intercept	power intercept + latzone (intercept)	0.0034
	power intercept + latzone (intercept)	power intercept + latzone (intercept and slope)	0.039
	Brownian motion intercept	Brownian motion intercept + latzone (intercept)	0.0026
	Brownian motion intercept + latzone	Brownian motion intercept + latzone (intercept and slope)	0.91
	power	power + latzone	0.052
	Ornstein Uhlenbeck	Ornstein Uhlenbeck + latzone	0.0072
	Brownian motion	Brownian motion + latzone	0.0013

592 Table 3. Range overlap ("patry") is a predictor of beak shape evolution but not beak size

593 evolution. *P*-values are from *F* tests comparing model fit between full and reduced

594 models.

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response variable	reduced model	full model	*p*-value
beak size	power intercept	power intercept + patry (intercept)	0.20
	power intercept + patry (intercept)	power intercept + patry (intercept and slope)	0.11
	power intercept + patry (intercept)	power intercept + patry (intercept) + lat zone (intercept)	0.64
	power intercept + patry (intercept) + lat zone (intercept)	power intercept + patry (intercept) + lat zone (intercept and slope)	0.59
beak shape	power intercept	power intercept + patry (intercept)	0.0022
	power intercept + patry (intercept)	power intercept + patry (intercept and slope)	0.10
	power intercept + patry (intercept)	power intercept + patry (intercept) + lat zone (intercept)	0.011
	power intercept + patry (intercept) + lat zone (slope & intercept)	power intercept + patry (intercept) + lat zone (intercept intercept and slope)	0.026

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605 Table 4. Studies of latitudinal variation in rates of molecular evolution, trait evolution
606 and recent speciation compiled from a survey of the peer-reviewed literature. The key
607 information is whether the fastest evolutionary rate was found to occur in the tropics, the
608 temperate zone, or if was no latitudinal gradient in evolutionary rates. Most studies,
609 particularly those with large sample sizes, find either faster evolutionary rates in the
610 temperate zone or no latitudinal gradient in evolutionary rates.

study	taxa	fastest rate	citation
molecular evolution (mtDNA)	45 lineage pairs of birds	no gradient	(Bromham & Cardillo
molecular evolution (ITS)	45 lineage pairs of plants	tropics	(Wright *et al.* 2006)
molecular evolution (mtDNA)	130 lineage pairs of mammals	tropics	(Gillman *et al.* 2009)
molecular evolution (mtDNA)	94 lineage pairs of amphibians	tropics	(Wright *et al.* 2010)
molecular evolution (mtDNA)	30 lineage pairs of birds	tropics	(Gillman *et al.* 2012)
molecular evolution (mtDNA and nuclear DNA)	224 species of turtles	tropics	(Lourenço *et al.* 2013)
molecular evolution (branch lengths)	1651 species of squamates	no gradient	(Rolland *et al.* 2016)
molecular evolution (mtDNA)	8037 lineage pairs from six animal phyla (Arthropoda, Chordata, Mollusca, Annelida, Echinodermata, and Cnidaria)	tropics, but very small effect size (51.6% vs. 48.4%)	(Orton *et al.* 2019)
trait evolution (color)	78 sister pairs of New World songbirds	temperate zone	(Martin *et al.* 2010)
trait evolution (song)	116 sister pairs of New World	temperate	(Weir & Wheatcroft 2(

	songbirds	zone	
trait evolution (song perception)	109 pairs of songbirds in temperate North America vs. Amazon	temperate zone	(Weir & Price 2019)
trait evolution (climatic niche, body mass)	111 sister pairs of New World songbirds	temperate zone	(Lawson & Weir 2014
trait evolution (beak size)	1141 sister pairs of birds (global)	no gradient	this study
trait evolution (beak shape)	1141 sister pairs of birds (global)	temperate zone	this study
speciation rate	118 sister pairs of New World mammals	temperate zone	(Weir & Schluter 2007
speciation rate	191 sister pairs of New World birds	temperate zone	(Weir & Schluter 2007
speciation rate	all mammals (N = 5,020)	tropics	(Rolland *et al.* 2014)
speciation rate	all New World songbirds (N = 2,571)	no gradient	(Rabosky *et al.* 2015)
speciation rate	all ray-finned fishes (global; N = 31,526)	temperate zone	(Rabosky *et al.* 2018)

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