No latitudinal gradients in tempo or mode of morphological evolution in birds

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Data accessibility statement: All datasets used will be submitted to a public repository (e.g., Dryad) upon initial acceptance. All scripts for fitting models are currently available at https://github.com/jonathanpdrury/two_regime_models and will be submitted to the R package RPANDA upon acceptance.

Abstract
The latitudinal diversity gradient is one of the most striking patterns in nature yet its implications for morphological evolution are poorly understood. In particular, it has been proposed that an increased intensity of species interactions in tropical biota may either promote or constrain trait evolution, but which of these outcomes predominates remains uncertain. Here, we develop tools for fitting phylogenetic models of phenotypic evolution in which the impact of species interactions can vary across lineages. Deploying these models on a global avian trait dataset to explore differences in trait divergence between tropical and temperate lineages, we find that the effect of latitude on the mode and tempo of morphological evolution is weak and clade- or trait-dependent. Our results indicate that species interactions do not disproportionately impact morphological evolution in tropical bird families and question the validity and universality of previously reported patterns of slower trait evolution in the tropics.

Introduction

In many groups of organisms, species richness increases toward lower latitudes—a pattern known as the latitudinal diversity gradient—inspiring generations of biologists to search for causal explanations (Mittelbach *et al.* 2007). One hypothesis is that species interactions are stronger in the tropics where they play a more important role driving diversification (Darwin 1859; Dobzhansky 1950; Schemske 2002; Schemske *et al.* 2009; but see Moles & Ollerton 2016). Previous tests of this 'biotic interactions hypothesis' have generally focused on latitudinal gradients in the strength of ecological interactions between trophic levels (Roslin *et al.* 2017; Longo *et al.* 2019; Roesti *et al.* 2020). However, to address the impact of biotic interactions on diversification it makes more sense to focus on their effects at relatively shallow timescales, such as between closely related species in the same taxonomic family (Mayr 1942; Lack 1947; Simpson 1953; Schluter 2000b). Interactions among related lineages are often assumed to be strong since their ecological and phenotypic similarity increases the likelihood of competition for access to resources or space (Schluter 2000a). Such interactions could influence trait evolution in different ways, either by promoting divergence between lineages via character displacement (Brown & Wilson 1956; Pfennig & Pfennig 2012) or, alternatively, by imposing constraints on ecological opportunity, reducing trait diversification as niches fill and limit speciation (Mahler *et al.* 2010; Weir & Mursleen 2013).

Whether competition predominantly drives or constrains divergence, the impacts on trait evolution should leave a detectable phylogenetic signature. In addition, this signature should be most prevalent in the tropics, where each lineage interacts with far larger numbers of potential competitors. As such, the biotic interactions hypothesis predicts differences between tropical and temperate taxa in the pace of evolution (the 'tempo', in the parlance of comparative studies) and/or the processes that drive trait diversification (the 'mode'). In comparison with the wealth of studies that have investigated latitudinal gradients in rates of species diversification (Jetz *et al.* 2012; Rolland *et al.* 2014; Schluter & Pennell 2017; Rabosky *et al.* 2018; Igea & Tanentzap 2020), relatively few have tested for latitudinal gradients in the dynamics of phenotypic evolution, mainly focusing on tempo rather than mode. Their results so far suggest a potentially complex relationship between trait diversification and latitude. On the one hand, some studies have found that divergence between sympatric sister taxa in body mass (Bothwell *et al.* 2015) and in plumage coloration (Martin *et al.* 2015) is higher in the tropics, supporting the hypothesis that increased competition at lower latitudes fosters character displacement (Schemske *et al.* 2009). On the other hand, some studies have found that species attain secondary sympatry after speciation more slowly in tropical regions (Weir & Price 2011), or that evolutionary rates are lower in the tropics for climatic niches (Lawson & Weir 2014), body-size (Cooper & Purvis 2010; Lawson & Weir 2014) or social signalling traits (Martin *et al.* 2010; Weir & Wheatcroft 2011; Weir *et al.* 2012; Lawson & Weir 2014; Weir & Price 2019), implying that competition may limit ecological opportunity and therefore constrain trait divergence in tropical regions.

Disentangling these opposing effects is challenging in part because previous macroecological studies have generally been restricted to either relatively few traits or limited samples of species. In addition, progress has been impeded by the lack of suitable methods for detecting the impact of species interactions on trait evolution (Weber *et al.* 2017; Harmon *et al.* 2019). Recent developments make it possible to detect an impact of species interactions on phenotypic evolution in standard comparative analyses (Weir & Mursleen 2013; Nuismer & Harmon 2015; Drury *et al.* 2016; Clarke *et al.* 2017; Manceau *et al.* 2017). However, these developments have yet to be deployed in the context of latitudinal sampling and thus the key prediction of a latitudinal gradient in trait diversification has yet to be tested.

Here, we begin by expanding existing phylogenetic models of phenotypic evolution, including models that incorporate competition between species — namely, diversity-dependent models (Mahler *et al.* 2010; Weir & Mursleen 2013) and the matching competition model (Nuismer & Harmon 2015; Drury *et al.* 2016) — such that the impact of competition can be estimated separately in lineages belonging to different, pre-defined competitive regimes (e.g., tropical and temperate). The models we develop are designed to account for known intraspecific variability and unknown, nuisance measurement error, both of which can strongly bias model support and parameter estimates (Silvestro *et al.* 2015). In particular, it has been suggested that intraspecific variability is lower in the tropics (Read *et al.* 2018), which could inflate estimates of evolutionary rates in the temperate biome. Finally, we conduct a comprehensive test of the biotic interactions hypothesis using these new tools to model the effect of interspecific competition on the tempo and mode of morphological evolution based on seven morphological characters sampled from ~9400 species representing more than 100 avian families worldwide.

Materials and methods

Two-regime phylogenetic models of phenotypic evolution

One approach to analyse gradients in phenotypic evolution is to fit phylogenetic models of phenotypic evolution that allow model parameters (e.g., evolutionary rates) to vary across the phylogeny; such models are already available for the simplest models of trait evolution such as Brownian motion (BM) and Ornstein-Uhlenbeck (OU) models (Hansen 1997; Butler & King 2004). To explore effects of species interactions, we developed further extensions to standard models allowing parameters to be estimated separately in two mutually exclusive groups of lineages in a clade. Generalizing these new models to estimate parameters on more than two groups, or on non-mutually exclusive groups, is straightforward.

We began by developing a two-regime version of the early burst (EB) model in which rates of trait evolution decline according to an exponential function of time passed since the root of the tree (Harmon *et al.* 2010). We used this model here to ensure that the diversity-dependent models, which incorporate changes in the number of reconstructed lineages through time, are not erroneously favoured because they accommodate an overall pattern of declining rates through time. To estimate rates of decline separately for mutually exclusive groups, we formulated a two-regime EB model with four parameters (Table 1): z_0 (the state at the root), σ_{02} (the evolutionary rate parameter at the root of the tree), r_A (controlling the time dependence on the rate of trait evolution in regime "A"), and r_B (time dependence in regime "B"). This model can be written as:

$$dX_t^{(j)} = \begin{cases} \sigma_0 e^{r_A t} dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ \sigma_0 e^{r_B t} dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \qquad \text{(Eq. 1)}$$

where $X_t^{(j)}$ is the trait value of lineage *j* at time *t*, and dW_t represents the Brownian motion process (Fig. S1 in Supporting Information).

Diversity-dependent (DD) models represent a process where rates of trait evolution respond to changes in ecological opportunity that result from the emergence of related lineages (Mahler *et al.* 2010; Weir & Mursleen 2013). When the slope of these models is negative, this is interpreted as a niche-filling process where rates of trait evolution slow down with the accumulation of lineages. We considered two versions of DD models, with either exponential (DD_{exp}) or linear (DD_{lin}) dependencies of rates to the number of extant lineages.

The two-regime model has four free parameters (Table 1): z_0 (the state at the root), σ_2 (the evolutionary rate parameter), r_A (the dependence of the rate of trait evolution on lineage diversity in regime "A"), and r_B (diversity dependence in regime "B"). This model can be written as:

$$dX_t^{(j)} = \begin{cases} \sigma_0 e^{r_A n_t^{(A)}} dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ \sigma_0 e^{r_B n_t^{(B)}} dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \qquad \text{(Eq. 2)}$$

for the exponential case, where $n_t^{(A)}$ and $n_t^{(B)}$ are the number of lineages in regime *A* and *B* at time *t* and *r* denotes the slope in the exponential model), and:

$$dX_t^{(j)} = \begin{cases} (\sigma_0 + b_A n_t^{(A)}) dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ (\sigma_0 + b_B n_t^{(B)}) dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \qquad \text{(Eq. 3)}$$

for the linear case (where *b* denotes the slope in the linear model). Standard DD models ignore whether lineages coexist, yet only those lineages likely to encounter one another in sympatry are able to compete with one another. Thus, we extended our model to incorporate ancestral biogeographic reconstructions to identify which species interactions are possible at any given point in time (i.e., which species co-occur; Drury *et al.* 2016). With biogeography, these become:

$$dX_t^{(j)} = \begin{cases} \sigma_0 e^{r_A \sum_{l=1}^{n_t^{(A)}} \mathbf{A}_{j,l}} dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ \sigma_0 e^{r_A \sum_{l=1}^{n_t^{(B)}} \mathbf{A}_{j,l}} dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \text{(Eq. 4)}$$

for the exponential case, and:

$$dX_t^{(j)} = \begin{cases} (\sigma_0 + b_A \sum_{l=1}^{n_t^{(A)}} \mathbf{A}_{j,l}) dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ (\sigma_0 + b_B \sum_{l=1}^{n_t^{(B)}} \mathbf{A}_{j,l}) dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \quad \text{(Eq. 5)}$$

for the linear case, where **A** is a matrix denoting biogeographical overlap, such that $\mathbf{A}_{j,l} = 1$ if lineages *j* and *l* coexist in sympatry at time *t*, and 0 otherwise (Fig. S1).

The matching competition (MC) model is a model of competitive divergence (Nuismer & Harmon 2015; Drury *et al.* 2016), wherein sympatric lineages are repelled away from one another in trait space. We formulated the two-regime matching competition model, which has four parameters (Table 1): z_0 (the state at the root), σ_2 (the evolutionary rate parameter), S_A (the strength of competition in regime "A"), and S_B (the strength of competition in regime "B"). This model can be written:

$$dX_t^{(j)} = \begin{cases} S_A \left(\frac{\sum_{l=1}^{n_t^{(A)}} X_t^{(l)}}{n_t^{(A)}} - X_t^{(j)} \right) + \sigma dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ S_B \left(\frac{\sum_{l=1}^{n_t^{(B)}} X_t^{(l)}}{n_t^{(B)}} - X_t^{(j)} \right) + \sigma dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \qquad \text{(Eq. 6)}$$

Incorporating biogeography, this becomes:

$$dX_t^{(j)} = \begin{cases} S_A\left(\frac{\sum_{l=1}^{n_t^{(A)}} \mathbf{A}_{j,l} X_t^{(l)}}{\sum_{l=1}^{n_t^{(A)}} \mathbf{A}_{j,l}} - X_t^{(j)}\right) + \sigma dW_t & \text{if } j \text{ is in } A \text{ at time } t \\ S_B\left(\frac{\sum_{l=1}^{n_t^{(B)}} \mathbf{A}_{j,l} X_t^{(l)}}{\sum_{l=1}^{n_t^{(B)}} \mathbf{A}_{j,l}} - X_t^{(j)}\right) + \sigma dW_t & \text{if } j \text{ is in } B \text{ at time } t \end{cases}, \quad \text{(Eq. 7)}$$

We developed inference tools for fitting the two-regime MC and DD models to comparative trait data, following the numerical integration approach used previously (Manceau *et al.* 2017; Drury *et al.* 2018b). For the EB model, we developed a branch transformation approach similar to the one used in mvMORPH (Clavel *et al.* 2015). In all model fits, we incorporated the possibility to account for deviations between measured and modelled mean trait values for each species (Housworth *et al.* 2004; Ives *et al.* 2007; Felsenstein 2008; see Appendix S1 for details). These deviations are of two types: the 'known' deviation associated with estimating species means from a finite sample, and the 'unknown' deviation linked to intraspecific variability unrelated to the trait model (e.g. instrument errors and phenotypic plasticity). We follow the common practice of lumping these two sources of deviations (often called 'measurement error') and referring to them as 'observational error'. A simulation study demonstrated the reliability of estimates using these tools (Appendix S1). Functions to simulate and fit these phenotypic models are available in the R package RPANDA (Morlon *et al.* 2016) (note to reviewers: these tools are at https://github.com/jonathanpdrury/two_regime_models and will be submitted to CRAN upon acceptance).

Phylogeny and trait data

We obtained phylogenies of all available species from birdtree.org (Jetz *et al.* 2012) and created a maximum clade credibility tree in TreeAnnotator (Drummond *et al.* 2012) based on 1000 samples from the posterior distribution. Since the MC and DD models require highly sampled clades (Drury *et al.* 2016), we used the complete phylogeny including species placed based on taxonomic data (Jetz *et al.* 2012) and the backbone provided by Hackett *et al.* (2008). We then extracted trees for each terrestrial (i.e., non-pelagic) family with at least 10 members (n = 108). As island species are generally not sympatric with many other members of their families (median latitudinal range of insular taxa = 1.28º, non-insular taxa = 15.27º), we further restricted our analyses to continental taxa, excluding island endemics and species with ranges that are remote from continental land masses. We gathered data on the contemporary ranges of each species from shapefiles (NatureServe & BirdLife International 2015).

Mass data were compiled from EltonTraits (Wilman *et al.* 2014) (n = 9442). In addition, we used a global dataset based on measurements of live birds and museum specimens (Pigot *et al.* 2020) to compile six linear morphological measurements: bill length (culmen length), width, and depth (n = 9388, mean = 4.5 individuals per species), as well as wing, tarsus, and tail length (n = 9393, mean = 5.0 individuals per species). These linear measurements were transformed into phylogenetic principal component (pPC) axes describing functionally relevant variation in bill shape and locomotory strategies (Appendix S1 & Table S2)

Latitudinal variation in mode of phenotypic evolution

We tested whether modes of phenotypic evolution varied with latitude in several ways. First, we used 'single-regime' models (Table 1), that is, models that estimate a single set of parameters on the entire phylogeny regardless of whether lineages are tropical or temperate. We tested whether support for each of these single-regime models varied according to a clade-level index of tropicality (i.e., the proportion of species in each clade with exclusively tropical breeding ranges). Second, we used our newly developed 'two-regime' models (Table 1) with distinct sets of parameters for tropical and temperate species and tested whether these latitudinal models were better supported than models without latitude.

We used maximum likelihood optimization to fit several 'single-regime' models of trait evolution to the seven morphological trait values described above. For all families, we fitted a set of six previously described models (Drury *et al.* 2016) that include three models (BM, OU, and EB) of independent evolution across lineages, implemented in the R-package mvMORPH (Clavel *et al.* 2015), and three further models (DD_{exp}, DD_{lin}, and MC) that incorporate competition and biogeography, implemented in the R-package RPANDA (Morlon *et al.* 2016). For details of reconstruction of ancestral biogeography, see Appendix S1. In the diversity-dependent models, the slope parameters can be either positive or negative, meaning that species diversity could itself accelerate trait evolution (positive diversity-dependence), with increasing species richness driving an ever-changing adaptive landscape (Schemske 2002; Drury *et al.* 2018a); or, alternatively, increasing species diversity could drive a concomitant decrease in evolutionary rates (negative diversity-dependence), as might be expected if increases in species richness correspond to a decrease in ecological opportunity (Price *et al.* 2014).

In cases where families were too large to fit because of computational limits for the matching competition model (>200 spp., n = 13), we identified subclades to which we could fit the full set of models using a slicing algorithm to isolate smaller subtrees within large families. To generate subtrees, we slid from the root of the tree toward the tips, cutting at each small interval (0.1 Myr) until all resulting clades had fewer than 200 tips. We then collected all resulting subclades and fitted the models separately for each subclade with 10 or more species separately, resulting in an additional 28 clades (n = 136 total).

In addition to this set of models, we fitted a second version of each of these models where the parameters were estimated separately for lineages with exclusively tropical distributions and lineages with ranges that include the temperate region (i.e., 'two-regime' models, Appendix S1, Fig. S2), limiting our analyses to clades with trait data for more than 10 lineages in each of temperate and tropical regions (Fig. S1, for details of ancestral reconstruction of tropical and temperate habitats, see Appendix S1 & Fig. S3). The BM and OU versions of these latitudinal models were fit using the functions mvBM and mvOU in the R package mvMORPH (Clavel *et al.* 2015), and the latitudinal EB, MC, and DD models were fitted with the newly-developed functions available in RPANDA (Morlon *et al.* 2016) (note to reviewers: these tools are at https://github.com/jonathanpdrury/two_regime_models and will be submitted to CRAN upon acceptance).

We examined model support in several ways. First, we calculated the Akaike weights of individual models (Burnham & Anderson 2002), as well as the overall support for any model incorporating species interactions and overall support for any two-regime model. Second, we identified the best-fit model as the model with the lowest small-sample corrected AIC (AICc) value, unless a model with fewer parameters had a ΔAICc value < 2 (Burnham

& Anderson 2002), in which case we considered the simpler model with the next-lowest AICc value to be the best-fitting model.

Latitudinal variation in strength of interactions and tempo of phenotypic evolution

We tested for latitudinal variation in the effect of species interactions on trait evolution using both our single- and two-regime model fits. With the first class of model, we tested whether parameters that estimate the impact of competition on trait evolution (i.e., the slope parameters of the DD models and the *S* parameter from the MC model) estimated from our single-regime models varied according to the proportion of lineages in each clade that breed exclusively in the tropics. With the second class of models, we tested whether two-regime models estimated a larger impact of competition on trait evolution in tropical than in temperate lineages.

Similarly, we tested whether lineages breeding at low latitudes experience lower or higher rates of morphological evolution compared to temperate lineages using our two types of models. First, we tested whether rates of morphological evolution varied according to the proportion of lineages in each clade that breed exclusively in the tropics. We estimated this rate directly as the $\sigma 2$ parameter from the single-regime BM model. For the single-regime EB and DD models, we calculated estimates of evolutionary rates at the present from estimates of the rate at the root and the slope parameters. Second, we compared rates estimated separately for tropical and temperate lineages from the two-regime implementations of the BM, EB, and DD models. We also examined the impact of observational error on rate estimates by fitting single-regime and two-regime BM models without accounting for observational error.

Predictors of support for models with competition

To identify factors other than latitude which influence whether models with competition were favoured by model selection, we examined the impact of habitat (the proportion of species in single-strata habitats), territoriality (the proportion of species with strong territoriality), diet specialization (calculated as the Shannon diversity of diets among species in a clade), clade age, clade richness, and the maximum proportion of species co-occurring on a continent.

Statistical approach

We tested for an impact of the proportion of species in a clade that breed exclusively in the tropics on model support and parameter estimates in single-regime models by conducting phylogenetic generalised least squares using the pgls function in the R package caper (Orme *et al.* 2018), estimating phylogenetic signal (λ) using maximum likelihood optimization, constraining values to $0 \leq \lambda \leq 1$. We tested support for the two-regime versions of each model type (BM, OU, EB, DD and MC) across families for a given trait by fitting intercept-only PGLS models with support for latitudinal models as the response variable. We conducted similar analyses to test overall support for latitudinal models across families for each trait and for differences in parameter estimates for tropical and temperate taxa. We found that statistical support for models incorporating competition was relatively rare in small clades (Fig. S4). As this pattern could be related to lower statistical power in smaller datasets (Drury *et al.* 2016), we focused all analyses of evolutionary mode (i.e., model support and parameter estimates from models incorporating competition) on clades with at least 50 species (n = 66 for single-regime fits, and n = 59 for two-regime fits).

For analyses of predictors of support for models with competition, we used the R package MCMCglmm (Hadfield 2010) to fit phylogenetic generalised linear mixed models

with categorical response variables indicating whether MC or DD_{exp} models were chosen as the best-fit model.

Results

Latitudinal variation in mode of phenotypic evolution

Across single-regime fits, we found no evidence for a latitudinal trend in the overall support for any model of phenotypic evolution (Fig. 1a-f, Tables S3), with one exception: there was an increase in model support for the matching competition model in tropical lineages for the locomotion pPC3 (Fig. 1f, Table S3). Similarly, there was no evidence that the overall support for models incorporating competition is higher in tropical clades (Fig. 1g, Table S3). Models with latitude (i.e., two-regime models) were not consistently better supported than models without latitude, for any model or trait (Table S4). Indeed single-regime models were the best fit models across 86% of individual clade-by-trait fits (Fig. S5).

Latitudinal variation in strength of interactions and tempo of phenotypic evolution

We found no evidence for a latitudinal trend in the strength of competition estimated from slopes of single-regime diversity-dependent models (Fig. 2c,d, Table S5). However, the strength of competition estimated from single-regime matching competition models increased in more tropical families for locomotion pPC3 (Fig. 2b, Table S5). Parameter estimates from two-regime models with competition do not support the biotic interactions hypothesis (Fig. 3b-d)—in most traits, there is no consistent difference between estimates of the impact of competition on tropical and temperate lineages, and in one case (bill pPC2), there is evidence that competition impacts temperate lineages to a larger degree than tropical lineages (Fig. 3b-d, Table S6). In all cases, there was substantial variation in the fits, and the overall magnitude of differences between tropical and temperate regions was rather small (Fig. 3b-d).

Evolutionary rates estimated from single-rate models did not vary according to clade-level index of tropicality (Fig. 2, Fig. S6, Table S7). Similarly, estimates of rates from latitudinal models were neither consistently lower nor higher in tropical regions (Fig. 3d, Fig S7, Table S8). We did find lower rates of locomotion pPC3 (Fig. 3d, Fig. S7, Table S8) and bill pPC2 evolution in tropical lineages (Fig. S7, Table S8), but the difference between regions was small and the overall strength of this relationship was weak. Observational error contributed to these patterns: we found a significant negative correlation between observational error and the clade-level index of tropicality for body mass (Fig. S8, Table S9); we also found that there was a correlation between rates of body mass and locomotion pPC3 evolution in standard single-regime BM models excluding error (Fig. S9, Table S10), and that the magnitude of the difference between tropical and temperate rates of trait evolution was higher in analyses of two-regime fits excluding error (Fig. S9, Table S11).

Predictors of support for models with competition

We found no evidence that territoriality or diet specialization are useful predictors of support for a model with competition (Table S12). We did, however, find that the maximum proportion of species co-occurring on a continent (i.e., the maximum number of extant lineages on a single continent divided by the total clade size) had a pronounced impact on model selection—clades with a high proportion of co-occurring lineages were more likely to be best-fit by the MC model, whereas clades with a low proportion of co-occurring lineages were more likely to be best-fit by the DD_{exp} model (Figs. S10, S11, Table S12). In addition, we found that the matching competition model was less likely to be favoured in clades with many members living in single-strata habitats (Table S12).

Discussion

Contrary to the prediction of the biotic interactions hypothesis, we did not find a consistent latitudinal gradient in the dynamics of phenotypic evolution across the entire avian radiation. This lack of consistent latitudinal effect was true for both the support for specific models of phenotypic evolution and the parameters of these models. Our results contrast with several previous studies have found a consistent signature of faster rates in the temperate biome (Martin *et al.* 2010; Weir & Wheatcroft 2011; Weir *et al.* 2012; Lawson & Weir 2014; Weir & Price 2019).

One plausible explanation for discrepancies between our results and other studies that examine gradients in the tempo of morphological trait evolution is that our study accounted for observational error. Indeed, we found that overall observational error for body mass increased with latitude; and when we intentionally ignored observational error, Brownian motion models were more likely to pick up faster rates of trait evolution at high latitudes. This result makes sense in the light of previously reported higher trait variance for temperate taxa (Read *et al.* 2018) and a positive correlation between such variance and rate estimates (Chira *et al.* 2018). Our analyses demonstrate that accounting for observational error when testing for latitudinal trends in evolutionary rates is crucial and also suggest that previous analyses overlooking error may have detected spurious latitudinal gradients in trait evolution.

Another potential explanation for the discrepancy between this and previous studies is that many previous studies examined gradients in rapidly evolving plumage and song traits, which may vary latitudinally if sexual or social selection is more pronounced in temperate regions (Badyaev & Hill 2003). In contrast, divergence in ecological traits is likely more constrained, as they tend to evolve relatively slowly (Blomberg *et al.* 2003; Drury *et al.* 2018b).

The virtual absence of latitudinal patterns in support for competition models and estimates of competition strength did not arise from overall weak support for competition models. Instead, models incorporating species interactions were the best fit models in 25% of clade-by-trait combinations for single-regime fits. In sunbirds (Nectariniidae), for instance, the matching competition model was the best fit model for body mass and two pPC axes describing variation in bill shape, suggesting that competition has driven trait divergence in this diverse clade. In owls (Strigidae), the exponential diversity-dependent model was the best fit model for body mass and several pPC axes describing bill shape and locomotory traits, suggesting that the rate of evolution in owls responds to changing ecological opportunity.

Within these models, the matching competition model was more likely to be chosen as the best-fit model than diversity-dependent models, which is consistent with the notion that competition promotes divergence (e.g., via character displacement, Brown & Wilson 1956; Pfennig & Pfennig 2012) more often than it constrains divergence (e.g., via niche saturation, Mahler *et al.* 2010) at relatively shallow taxonomic scales (Schluter 2000b; Aristide & Morlon 2019). However, although recent evidence suggests that the effects of competitive exclusion on community assembly is distinguishable from the action of character displacement in comparative datasets (Quintero & Landis 2020), the possibility remains that the matching competition model may detect a signal of ecological sorting of morphologically distinct lineages (Pigot *et al.* 2018) in addition to or instead of evolutionary divergence. Moreover, by focusing on clade members, we excluded other competitors (e.g., non-family members with similar diets) that impose constraints on niche divergence. Such competitors have been shown to impact rates of trait evolution across clades of birds (Chira *et al.* 2018). Future research could extend our approach by examining the impact of interactions between competitors from a wider diversity of clades.

We further found evidence that support for the matching competition model was greater in clades with a higher proportion of coexisting taxa, suggesting that trait divergence may make coexistence possible (Schluter 2000b; Pfennig & Pfennig 2012). The exponential diversity-dependent model, on the other hand, was more likely to be the best-fit model in clades with relatively low levels of continental overlap, which may indicate that in these clades, niche saturation negatively impacts coexistence (Price & Kirkpatrick 2009; Rabosky & Hurlbert 2015). In addition, we found that model fits on clades with a high proportion of species living in single-strata habitats were less likely to favour the matching competition model, suggesting that divergence may be limited in such habitats (Orians & Willson 1964). These relationships between ecological opportunity, trait evolution, and coexistence highlight the need for models that can jointly estimate the effects of diversification, range dynamics, and trait evolution (Aristide & Morlon 2019; Quintero & Landis 2020). Such models may identify an impact of competition on processes other than trait evolution, such as competitive exclusion, which may themselves vary latitudinally (Weir & Price 2011).

By including a suite of traits that capture functional variation in niches (Pigot *et al.* 2020), we were able to identify patterns that would have been highly biased, or that we would have missed, by focusing on one specific trait, in particular body mass. Model support was distributed evenly across different traits, suggesting that the impact of competition varies both across clades and across different functionalities. For instance, while 31% (42/135) of clades exhibit some signature of competition acting on body size evolution in single-regime fits, 68% (92/135) of them exhibit some signature of competition acting on at least one of the seven functional traits (body-size, bill pPC axes and locomotion pPC axes). These results further strengthen the notion that multiple trait axes are necessary to robustly test hypotheses about ecological variation (Slater & Friscia 2019; Pigot *et al.* 2020).

We have extended various phylogenetic models of phenotypic evolution, including models with competition, to allow model parameters to vary across lineages and to account for biogeography and sources of observational error. We then applied them to the case of latitudinal gradients, but they could be used to study other types of geographic (e.g. elevation), ecological (e.g. habitat, diet), behavioural (e.g. migratory strategy) or morphological (e.g. body size) gradients. Studies of gradients in evolutionary rates are often performed using sister-taxa analyses, assuming BM or OU processes (Weir & Lawson 2015). These analyses are useful because they enable quantitative estimates of the impact of continuous gradients on rate parameters. However, by limiting analyses to sister taxa datasets, they are unable to reliably detect signatures of species interactions (Drury *et al.* 2018a). In addition, these approaches are not well-suited to differentiating between different evolutionary modes. Applying process-based models of phenotypic evolution that incorporate interspecific competition and biogeography allow for such tests of evolutionary hypotheses about the mode of trait evolution across entire clades.

Species interactions are multifarious; individuals face selective pressures arising from interactions with many biotic factors both within and between trophic levels. Perhaps as a result of this complexity, pinning down clear empirical relationships between latitude and biotic interactions has yielded a complex and often inconsistent set of results (Moles & Ollerton 2016), with empirical evidence ranging from stronger interactions in the tropics (Roslin *et al.* 2017; Longo *et al.* 2019) to stronger interactions in temperate regions (Roesti *et al.* 2020). Overall, using novel methods for examining macroevolutionary signatures of competition, we show that even though species interactions are important drivers of trait evolution, we found no evidence that competition at shallow taxonomic scales has impacted the dynamics of trait diversification more in the tropics than in the temperate regions.

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References

1.Aristide, L. & Morlon, H. (2019). Understanding the effect of competition during evolutionary radiations: an integrated model of phenotypic and species diversification. *Ecol. Lett.*, 22, 2006–2017

2.Badyaev, A. V & Hill, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Evol. Syst.*, 34, 27–49

3.Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745

4.Bothwell, E., Montgomerie, R., Lougheed, S.C. & Martin, P.R. (2015). Closely related species of birds differ more in body size when their ranges overlap — in warm, but not cool, climates. *Evolution*, 69, 1701–1712

5.Brown, W.L. & Wilson, E.O. (1956). Character displacement. *Syst. Zool.*, 5, 49–64

6.Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer, New York, NY

7.Butler, M.A. & King, A.A. (2004). Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. *Am. Nat.*, 164, 683–695

8.Chira, A.M., Cooney, C.R., Bright, J.A., Capp, E.J.R., Hughes, E.C., Moody, C.J.A., *et al.* (2018). Correlates of rate heterogeneity in avian ecomorphological traits. *Ecol. Lett.*, 21, 1505–1514

9.Clarke, M., Thomas, G.H. & Freckleton, R.P. (2017). Trait evolution in adaptive radiations: modelling and measuring interspecific competition on phylogenies. *Am. Nat.*, 189, 121–137

10.Clavel, J., Escarguel, G. & Merceron, G. (2015). mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol. Evol.*, 6, 1311–1319

11.Cooper, N. & Purvis, A. (2010). Body size evolution in mammals: complexity in tempo and mode. *Am. Nat.*, 175, 727–738

12.Darwin, C. (1859). On the origin of the species by natural selection

13.Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.*, 38, 209–221

14.Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.*, 29, 1969–1973

15.Drury, J., Clavel, J., Manceau, M. & Morlon, H. (2016). Estimating the effect of competition on trait evolution using maximum likelihood inference. *Syst. Biol.*, 65, 700–710

16.Drury, J.P., Grether, G.F., Garland Jr, T. & Morlon, H. (2018a). An assessment of phylogenetic tools for analyzing the interplay between interspecific interactions and

phenotypic evolution. *Syst. Biol.*, 67, 413–427

17.Drury, J.P., Tobias, J.A., Burns, K.J., Mason, N.A., Shultz, A.J. & Morlon, H. (2018b). Contrasting impacts of competition on ecological and social trait evolution in songbirds. *PLoS Biol.*, 16, e2003563

18.Felsenstein, J. (2008). Comparative methods with sampling error and within-species variation: contrasts revisited and revised. *Am. Nat.*, 171, 713–725

19.Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., *et al.* (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768

20.Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.*, 33, 1–22

21.Hansen, T.F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, 51, 1341–1351

22.Harmon, L.J., Andreazzi, C.S., Débarre, F., Drury, J., Goldberg, E.E., Martins, A.B., *et al.* (2019). Detecting the macroevolutionary signal of species interactions. *J. Evol. Biol.*, 32, 769–782

23.Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W., *et al.* (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, 64, 2385–2396

24.Housworth, E.A., Martins, E.P. & Lynch, M. (2004). The phylogenetic mixed model. *Am. Nat.*, 163, 84–96

25.Igea, J. & Tanentzap, A.J. (2020). Angiosperm speciation cools down in the tropics. *Ecol. Lett.*, 23, 692-700.

26.Ives, A.R., Midford, P.E. & Garland, T. (2007). Within-species variation and measurement error in phylogenetic comparative methods. *Syst. Biol.*, 56, 252–270

27.Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444

28.Lack, D. (1947). *Darwin's Finches*. Cambridge University Press, Cambridge, UK

29.Lawson, A.M. & Weir, J.T. (2014). Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecol. Lett.*, 17, 1427–1436

30.Longo, G.O., Hay, M.E., Ferreira, C.E.L. & Floeter, S.R. (2019). Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Glob. Ecol. Biogeogr.*, 28, 107–117

31.Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. (2010). Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles.

Evolution, 64, 2731–2745

32.Manceau, M., Lambert, A. & Morlon, H. (2017). A unifying comparative phylogenetic framework including traits coevolving across interacting lineages. *Syst. Biol.*, https://doi.org/10.1093/sysbio/syw115

33.Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2010). Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution*, 64, 336–347

34.Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.*, 185, 443–451

35.Mayr. (1942). *Systematics and the Origin of Species*. Harvard University Press, Cambridge, MA

36.Mittelbach, G.G., Schemske, D.W., Cornell, H. V, Allen, A.P., Brown, J.M., Bush, M.B., *et al.* (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.*, 10, 315–331

37.Moles, A.T. & Ollerton, J. (2016). Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, 48, 141–145

38.Morlon, H., Lewitus, E., Condamine, F.L., Manceau, M., Clavel, J. & Drury, J. (2016). RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods Ecol. Evol.*, 7, 589–597

39.NatureServe & BirdLife International. (2015). *Bird species distribution maps of the world.*

40.Nuismer, S.L. & Harmon, L.J. (2015). Predicting rates of interspecific interaction from phylogenetic trees. *Ecol. Lett.*, 18, 17–27

41.Orians, G.H. & Willson, M.F. (1964). Interspecific territories of birds. *Ecology*, 45, 736–745

42.Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., *et al.* (2018). caper: Comparative Analyses of Phylogenetics and Evolution in R

43.Pfennig, D.W. & Pfennig, K.S. (2012). *Evolution's Wedge: Competition and the Origins of Diversity*. Univ of California Press, Los Angeles, CA

44.Pigot, A.L., Jetz, W., Sheard, C. & Tobias, J.A. (2018). The macroecological dynamics of species coexistence in birds. *Nat. Ecol. Evol.*, 2, 1112–1119

45.Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T.P., Freeman, B.G., Roll, U., *et al.* (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.*

46.Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., *et*

al. (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509, 222–225

47.Price, T.D. & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proc. R. Soc. B Biol. Sci.*, 276, 1429–1434

48.Quintero, I. & Landis, M.J. (2020). Interdependent phenotypic and biogeographic evolution driven by biotic interactions. *Syst. Biol.*, 69, 739–755

49.Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, M., *et al.* (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392

50.Rabosky, D.L. & Hurlbert, A.H. (2015). Species richness at continental Scales is dominated by ecological limits. *Am. Nat.*, 185, 572–583

51.Read, Q.D., Baiser, B., Grady, J.M., Zarnetske, P.L., Record, S. & Belmaker, J. (2018). Tropical bird species have less variable body sizes. *Biol. Lett.*, 14

52.Roesti, M., Anstett, D.N., Freeman, B.G., Lee-Yaw, J.A., Schluter, D., Chavarie, L., *et al.* (2020). Pelagic fish predation is stronger at temperate latitudes than near the equator. *Nat. Commun.*, 11, 1–7

53.Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.*, 12

54.Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., *et al.* (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356, 742–744

55.Schemske, D.W. (2002). Ecological and evolutionary perspectives on the origins of tropical diversity. *Found. Trop. For. Biol.*, 163–173

56.Schemske, D.W., Mittelbach, G.G., Cornell, H. V, Sobel, J.M. & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.*, 40, 245–269

57.Schluter, D. (2000a). Ecological character displacement in adaptive radiation. *Am. Nat.*, 156, S4–S16

58.Schluter, D. (2000b). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK

59.Schluter, D. & Pennell, M.W. (2017). Speciation gradients and the distribution of biodiversity. *Nature*, 546, 48–55

60.Silvestro, D., Kostikova, A., Litsios, G., Pearman, P.B. & Salamin, N. (2015). Measurement errors should always be incorporated in phylogenetic comparative analysis. *Methods Ecol. Evol.*, 6, 340–346

61.Simpson, G.G. (1953). *The Major Features of Evolution*. Columbia University Press, New York, NY

62.Slater, G.J. & Friscia, A.R. (2019). Hierarchy in adaptive radiation: a case study using the Carnivora (Mammalia). *Evolution*, 73, 524–539

63.Weber, M.G., Wagner, C.E., Best, R.J., Harmon, L.J. & Matthews, B. (2017). Evolution in a community context: On integrating ecological interactions and macroevolution. *Trends Ecol. Evol.*, 32, 291–304

64.Weir, J.T. & Lawson, A. (2015). Evolutionary rates across gradients. *Methods Ecol. Evol.*, 6, 1278–1286

65.Weir, J.T. & Mursleen, S. (2013). Diversity-dependent cladogenesis and trait evolution in the adaptive radiation of the auks (Aves: Alcidae). *Evolution*, 67, 403–416

66.Weir, J.T. & Price, T.D. (2011). Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Am. Nat.*, 177, 462–469

67.Weir, J.T. & Price, T.D. (2019). Song playbacks demonstrate slower evolution of song discrimination in birds from Amazonia than from temperate North America. *PLoS Biol.*, 17

68.Weir, J.T. & Wheatcroft, D. (2011). A latitudinal gradient in rates of evolution of avian syllable diversity and song length. *Proc. R. Soc. B Biol. Sci.*, 278, 1713–20

69.Weir, J.T., Wheatcroft, D.J. & Price, T.D. (2012). The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evol. Int. J. Org. Evol.*, 66, 2773–2783

70.Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027

Table 1. Parameters of models used in analyses. The subscripts 'trop' and 'temp' in the two-regime versions of each model refer to parameters estimated separately for lineages with exclusively tropical breeding ranges and lineages with breeding ranges that include the temperate region. k indicates the number of free parameters estimated in each model, σ^2 indicates the rate parameter describing the tempo of trait evolution, z_0 indicates the trait value at the root of the clade, and α describes the strength of the pull toward a stable optimum in the Ornstein-Uhlenbeck model. For descriptions of other parameters, see the main text.

model	***k***	σ^2	z_0	**other**
BM_single	2	σ^2	z_0	—
BM_two	3	σ^2_{trop}; σ^2_{temp}	z_0	—
OU_single	3	σ^2	z_0	α
OU_two	4	σ^2	z_{0trop}; z_{0temp}	α
EB_single	3	σ^2	z_0	r (slope)
EB_two	4	σ^2	z_0	r_{trop}; r_{temp}
DDexp_single	3	σ^2	z_0	r (slope)
DDexp_two	4	σ^2	z_0	r_{trop}; r_{temp}
DDlin_single	3	σ^2	z_0	b (slope)
DDlin_two	4	σ^2	z_0	b_{trop}; b_{temp}
MC_single	3	σ^2	z_0	S
MC_two	4	σ^2	z_0	S_{trop}; S_{temp}

Figure legends

Figure 1. Model support for single-regime models reveal little impact of latitude on the mode of phenotypic evolution. There is no relationship between the proportion of taxa in a clade that breed in the tropics and statistical support (measured as the Akaike weight) for **(a)** Brownian motion, **(b)** Ornstein-Uhlenbeck, **(c)** early burst models, **(d)** exponential diversity-dependent models or **(e)** linear diversity-dependent models. In matching competition models **(f)**, there is an increase in model support for locomotion pPC3 (solid line). The relative support for a model incorporating competition does not vary latitudinally for any trait (Table S3). Each point represents the mean Akaike weight across clade-by-trait fits to stochastic maps of biogeography (for all families with at least 50 species) (i.e., each clade contributes a point for each of seven traits).

Figure 2. Parameter estimates from single-regime models reveal varying impacts of latitude. There is no latitudinal effect on the effect of competition as measured by the slope of **(a)** exponential diversity-dependent models, or **(b)** linear diversity-dependent models. **(c)** The strength of competition as measured by the S parameter from the matching competition models increases with the index of tropicality (the proportion of species in the clade with exclusively tropical breeding distributions) for locomotion pPC3 but not for other traits. **(d)** There is no relationship between the proportion of taxa in a clade that breed in the tropics and the estimated rate of trait evolution from Brownian motion models. Solid lines represent statistically significant relationships (Tables S5, S7). For (a-c), each point represents the mean across clade-by-trait fits to stochastic maps of biogeography (for all families with at least 50 species), and for (d), each point represents the maximum likelihood estimate for each clade-by-trait fit.

Figure 3. Parameter estimates from two-regime models reveal varying impacts of latitude. Estimates of slopes from **(a)** exponential diversity-dependent models and **(b)** linear diversity dependent models are not consistently different in tropical regions in any trait. **(c)** Matching competition models estimated a decreased strength of competition in the tropics on bill pPC2. **(d)** Estimates of evolutionary rates from Brownian motion models show accelerated rates of locomotion pPC3, but not other functional traits, in temperate regions. Asterisks indicate statistical significance (Tables S6, S8). For **(a-c)**, each point represents the mean across clade-by-trait fits to stochastic maps of biogeography and of tropical/temperate membership (for all families with at least 50 species), and for **(d)**, each point represents the mean across stochastic maps of tropical/temperate membership maximum.

Figure 1

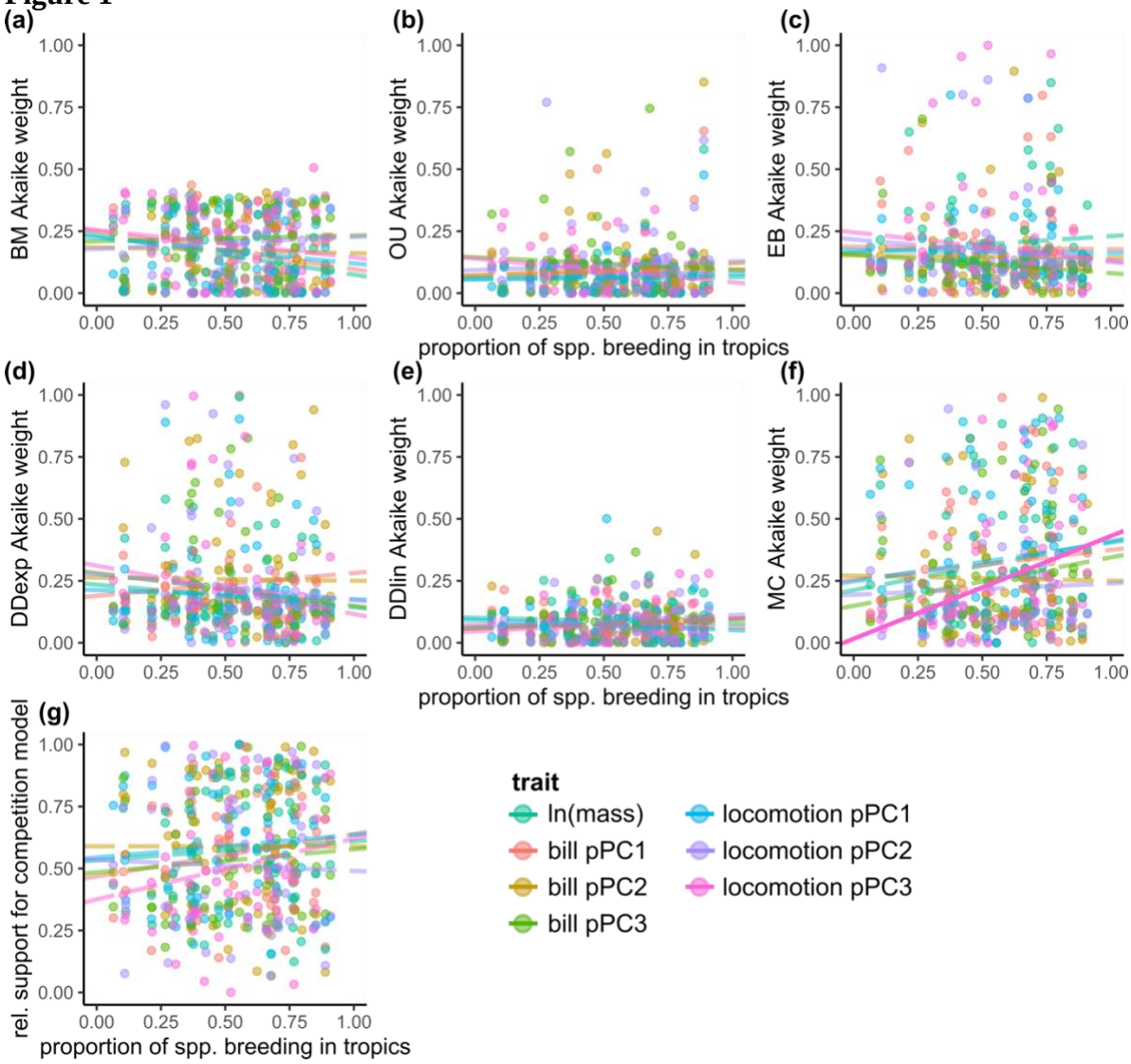

(a)
BM Akaike weight
(b)
OU Akaike weight
(c)
EB Akaike weight
proportion of spp. breeding in tropics
(d)
DDexp Akaike weight
(e)
DDlin Akaike weight
(f)
MC Akaike weight
proportion of spp. breeding in tropics
(g)
rel. support for competition model
proportion of spp. breeding in tropics
trait
ln(mass)
bill pPC1
bill pPC2
bill pPC3
locomotion pPC1
locomotion pPC2
locomotion pPC3

Figure 2

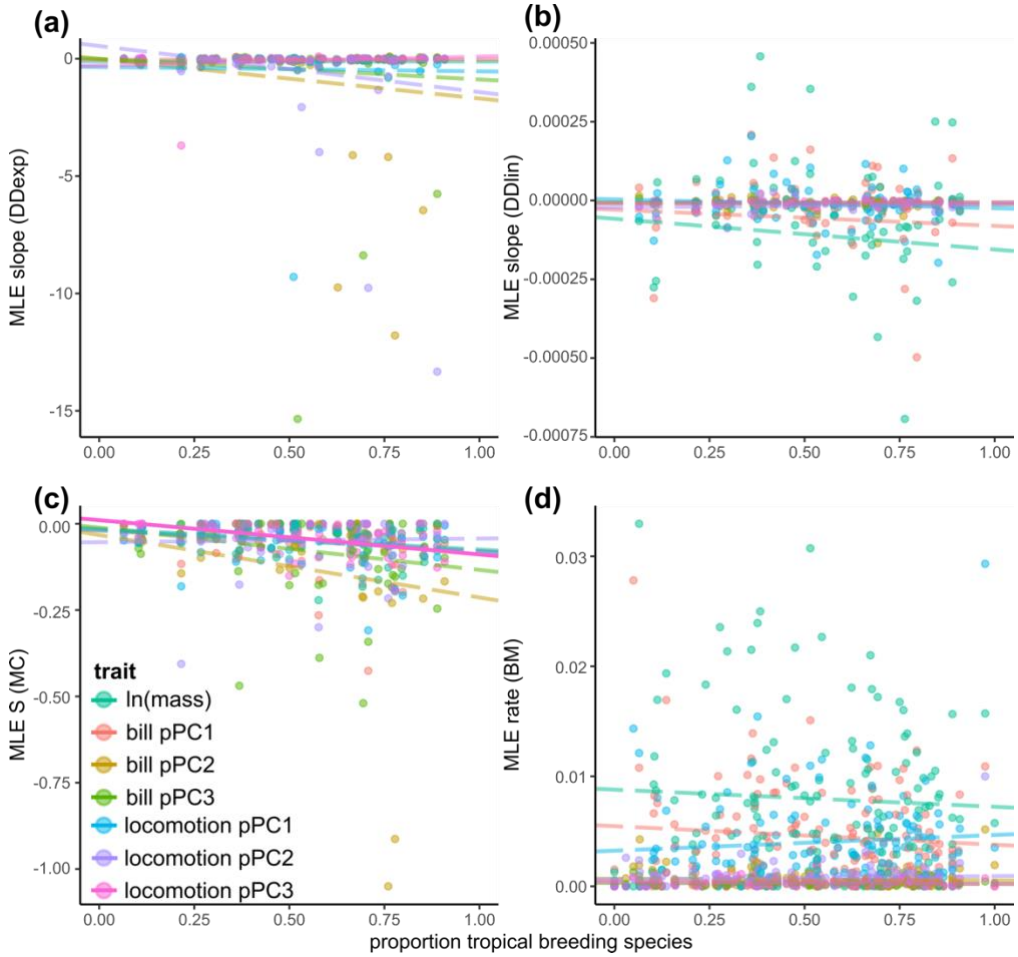
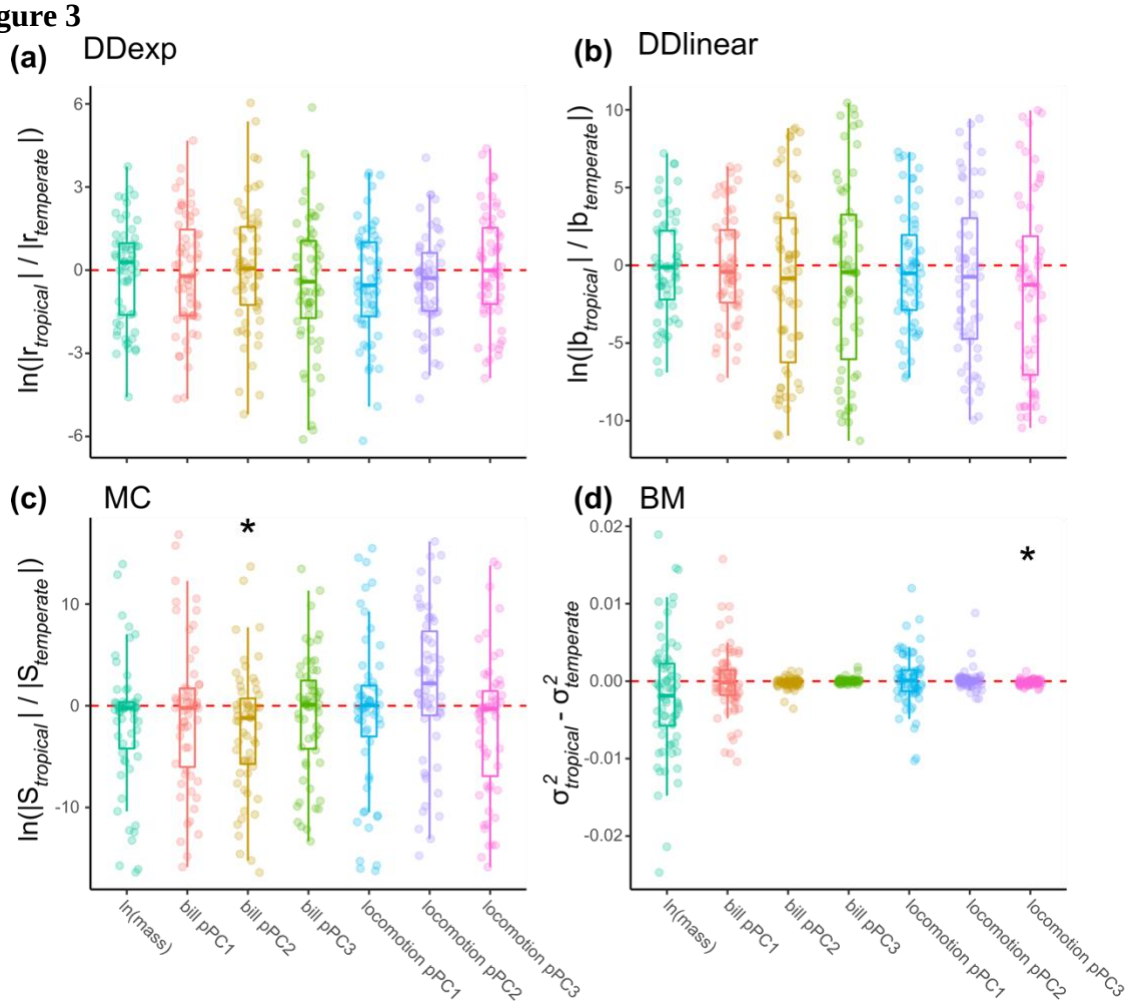

(a)
(b)
(c)
(d)
MLE slope (DDexp)
MLE slope (DDlin)
MLE S (MC)
MLE rate (BM)
trait
ln(mass)
bill pPC1
bill pPC2
bill pPC3
locomotion pPC1
locomotion pPC2
locomotion pPC3
proportion tropical breeding species

Figure 3


(a) DDexp
(b) DDlinear
(c) MC
(d) BM
ln(|r_tropical| / |r_temperate|)
ln(|b_tropical| / |b_temperate|)
ln(|S_tropical| / |S_temperate|)
σ²_tropical - σ²_temperate
*
*
ln(mass)
bill pPC1
bill pPC2
bill pPC3
locomotion pPC1
locomotion pPC2
locomotion pPC3