

## LETTER

# Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes

Adam M. Lawson<sup>1</sup> and Jason T. Weir<sup>1,2\*</sup>

<sup>1</sup>*Department of Ecology and Evolutionary Biology University of Toronto Toronto, ON, M1C 1A4, Canada*

<sup>2</sup>*Department of Biological Sciences University of Toronto Scarborough Toronto, ON, M1C 1A4, Canada*

\*Correspondence: E-mail: jason.weir@utoronto.ca

### Abstract

Despite the importance of divergent selection to the speed of evolution, it remains poorly understood if divergent selection is more prevalent in the tropics (where species richness is highest), or at high latitudes (where paleoclimate change has been most intense). We tested whether the rate of climatic-niche evolution – one proxy for divergent selection – varies with latitude for 111 pairs of bird species. Using Brownian motion and Ornstein–Uhlenbeck models, we show that evolutionary rates along two important axes of the climatic-niche – temperature and seasonality – have been faster at higher latitudes. We then tested whether divergence of the climatic-niche was associated with evolution in traits important in ecological differentiation (body mass) and reproductive isolation (song), and found that climatic divergence is associated with faster rates in both measures. These results highlight the importance of climate-mediated divergent selection pressures in driving evolutionary divergence and reproductive isolation at high latitudes.

### Keywords

birds, body mass, climatic-niche, ecological speciation, evolutionary rates, latitudinal gradients, song.

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## INTRODUCTION

Divergent ecological selection is believed to accelerate the speed of trait evolution and speciation (Darwin 1859; Schluter 2000). When divergent selection is absent, populations remain in ecological niches similar to their common ancestor and experience slow rates of divergence in ecologically relevant traits (Sobel *et al.* 2010). Under strong divergent selection, evolution in ecologically relevant traits should be accelerated, leading to both rapid ecological differentiation and ultimately the development of reproductive isolation between incipient species (i.e. ecological speciation; Schluter 2009). Because both reproductive isolation and ecological differentiation are important aspects of species formation, geographical regions which promote strong divergent selection should also induce fast rates of speciation. While strong divergent ecological selection has been shown to drive rapid trait evolution in specific species exposed to rapidly changing environments (e.g. Darwin's finches to El Niño cycles; Grant & Grant 2010), the extent to which divergent selection drives trait evolution more broadly across continental faunas and floras remains poorly studied.

While it is difficult to quantify all components of divergent selection, the climatic conditions a population experiences within its geographical range, referred to as the realised climatic-niche (Hutchinson 1957), is an easily quantifiable component of the environment that may differ between diverging populations. Such climatic differences could drive divergent selection on climate-sensitive traits, leading to ecological differentiation and ultimately reproductive isolation between populations. For example, ecological traits like body size may be greatly influenced by climate, because body size

is believed to be important in thermoregulation (Riesenfeld 1981; Rodríguez *et al.* 2008). Traits important to reproductive isolation, like song and colour, are known to vary in response to habitat density (lower pitched songs in habitats with dense vegetation; Tobias *et al.* 2010) and aridity (paler plumage in more arid environments; Zink & Remsen 1986), and therefore might be expected to diverge in response to climatic-niche divergence. The realised climatic-niche is shaped by both abiotic (e.g. physiological tolerance to climate, geographical barriers, etc.) and biotic interactions (e.g. competitive exclusion, prey availability, etc.). Thus, while climate is abiotic, the selective force exerted by the realised climatic-niche on climate-sensitive traits includes both abiotic and biotic factors.

Geographical heterogeneity in the climatic environment could cause geographically separated populations to diverge in their realised climatic-niches. If climatic conditions vary greatly across a geographical region, then species diverging in allopatry may experience more divergent selection on climate-sensitive traits than species in geographical regions with more uniform climate. Likewise, recent theory linking fluctuating climate change to speciation (Hua & Wiens 2013) suggests that geographical regions which experienced extensive paleoclimatic fluctuations may have also experienced climate-mediated divergent selection pressures. For example, climatic fluctuations may have forced geographically isolated populations to adapt to different climatic conditions within their respective ranges; or some populations may have responded to climate change by local adaptation, whereas others responded through habitat tracking, leading to climatic-niche divergence. Because the Plio–Pleistocene glaciations resulted in more intense temperature fluctuations

towards the poles (Colinvaux *et al.* 1996; Bush & De Oliveira 2006; Sandel *et al.* 2011), we predict that divergent selection on the realised climatic-niche will be strongest at high latitudes and weakest in the tropics. Elevated terrestrial speciation rates at high latitudes over the past several million years (Weir & Schluter 2007), but not during earlier time periods (Rolland *et al.* 2014), are consistent with the role of divergent selection speeding up the speciation cycle during glacial periods.

We also predict that biotic interactions are more likely to hinder climatic-niche divergence in the tropics than at high latitudes. Competitive exclusion limits expansion of a species geographical range, thus reducing the breadth of the realised climatic-niche. High levels of competition resulting from the high species richness in the tropics may greatly constrain a species ability to expand its geographical range (Weir & Price 2011) and realised climatic-niche. In contrast, species in high latitude regions should experience less constraint by competitors in the evolution of their climatic-niche, due to the low species richness towards the poles. Likewise, extinction rates over the past several million years are estimated to be higher at high vs. low latitudes (e.g. Weir & Schluter 2007; Pyron & Wiens 2013; Pyron 2014; Rolland *et al.* 2014). Elevated extinction at high latitudes promotes ecological release, allowing species to expand their geographical ranges and realised climatic-niches.

Previous authors have studied climatic-niche overlap between closely related species at different latitudes. These studies have produced contradictory results (Hua & Wiens 2010) with reduced niche overlap occurring in the tropics (plethodontid salamanders: Kozak & Wiens 2007), at high latitudes (various high elevation vertebrate groups; Cadena *et al.* 2012) or with no latitudinal differences detected (frogs; Hua & Wiens 2010). While niche overlap provides an important measure of niche differentiation, it lacks the time component of divergence, and does not quantify the evolutionary rate at which the niche evolves. Studies that quantify rates of climatic-niche evolution across latitudinal gradients are needed. Rates of climatic-niche evolution have been estimated for specific clades (e.g. Kozak & Wiens 2010; Pyron & Wiens 2013; Quintero & Wiens 2013), but have not previously been quantified across latitude at the species level.

Here, we evaluate the climatic-niche of closely related sister pairs of New World bird species to test the prediction that divergent selection pressures driven by climate are stronger at high latitudes than in the tropics over the past several million years. We used Brownian motion and Ornstein–Uhlenbeck models to quantify rates of climatic-niche evolution, and treat these rates as proxies for the strength of divergent selection pressures acting on climate-sensitive traits (body mass and song). We ask whether the rate of climatic-niche divergence for sister pairs correlates with their evolutionary rates in traits indicative of reproductive isolation (the pitch, length and syllable diversity of bird song) and ecological differentiation (body mass). We expect to find that body mass and song will evolve fastest in sister pairs experiencing the fastest divergence in realised climatic-niche. If climate-induced divergent selection is elevated at high latitudes, then we expect to find that evolutionary rates in body size and song are strongly

influenced by the degree of climatic-niche divergence at high latitudes.

## METHODS

### Data collection

Published molecular phylogenies were used to obtain 111 New World sister pairs from the order Passeriformes. We included only Passeriformes, because this order is the most species diverse and song data are readily available. Sister pairs included both allopatric and parapatric sister species and phylogroup splits within species (sister pairs were never phylogenetically nested within other sister pairs). Phylogroup splits were included because they represent incipient speciation events, with diverging phylogroups generally separated by barriers to gene flow and often having diverged for one to three million years in our data set. To determine the approximate age of each sister pair, a phylogeny was created from mitochondrial cytochrome *b* sequences in BEAST (Drummond *et al.* 2012) (see Appendix S1). Sister pairs with very low sequence divergence may represent cases of mitochondrial introgression and were excluded (see Appendix S1).

Latitudinal values were obtained from range maps located on NatureServe (Ridgely *et al.* 2003). The centroid latitude of a sister pair was calculated as the mean absolute centroid latitude of each sister's breeding range, and was used to quantify their latitudinal position. This position is most meaningful if species in a sister pair do not have very large latitudinal extents and if they have similar centroids. Thus, we excluded sister pairs if their combined latitudinal distribution was  $> 45^\circ$  latitude and if the absolute centroid latitudes of both sisters in a pair exceeded  $25^\circ$ . These threshold values ensure that we excluded species with very different latitudinal centroids, or whose latitudinal extents are so broad that their centroid-based placement along the latitudinal gradient is arbitrary.

We obtained climate data for ca. 275 000 georeferenced occurrences within the breeding range of the species in our data set from ORNIS 2 (<http://ornis2.ornisnet.org/>) and the Global Biodiversity Information Facility (<http://data.gbif.org/welcome.htm>). Occurrences were excluded if they did not occur within a species range, as specified by NatureServe range maps. With the exception of some small range species (i.e. known from less than five localities), species were excluded if  $< 5$  unique locality records were obtained.

The climatic-niche was calculated for only allopatric and parapatric sister pairs, because sympatric sister pairs occupy the same geographical range and experience similar climates. Our goal was to estimate the strength of divergent selection pressures as mediated by the climatic-niche during the allopatric phase of diversification when differences in climatic-niche are most relevant to ecological speciation. Here, we assumed that our allopatric and parapatric sister pairs have never been sympatric in the past (an assumption likely to be generally true given most sister pairs belong to super-species complexes comprised of ecologically similar taxa that exclude each other geographically due to ecological incom-

patibility, presence of hybrid zones or geographical barriers; see Weir & Price 2011).

Climatic information for each coordinate was obtained from WorldClim (<http://www.worldclim.org/>) using a global resolution of 30 arc seconds (~1 km<sup>2</sup>). 48 climatic variables were analysed, including 36 temperature variables (maximum, minimum and mean for each month of the year) and 12 precipitation variables (mean for each month of the year). Monthly values for each climatic measure were sorted from highest to lowest for each locality within a species range, and analysis were performed on sorted values (details in Appendix S1).

To quantify climatic-niche, a principal component analysis (PCA) was performed on log-transformed climatic variables across all species. For each of the first three principal components (PCs), the range and midpoint value along that PC were calculated for each species. Climatic ranges were used to explore niche breadth and overlap (see next section). Midpoint climatic values were used to model evolution of the climatic-niche (see below). We followed Fisher-Reid *et al.* (2012) by using midpoint climatic values to model niche evolution. This method was chosen because means are more heavily skewed by densely surveyed regions within a species range than midpoints. Euclidean distance between the midpoints of species within a sister pair were used as a measure of climatic divergence between sister pairs. Separate Euclidean distances were calculated for each of the first three PCs.

We quantify climatic-niche from the breeding range for all months of the year, but note that Neotropical migrants overwinter in areas far from their breeding range. Many previous authors have simply ignored the issue. To address the issue, Botero *et al.* (2014) analysed their global avian data set both with and without migrants included. To determine if Neotropical migrants (which breed in the Nearctic and overwinter in the Neotropics) were influencing our results, we likewise applied our models of climatic-niche evolution with Neotropical migrants included and excluded.

Body mass for each species is taken from Dunning (2008), and distances were measured as the absolute difference in the log-transformed mean body masses (adult males and females combined) for each sister in a pair. For bird song, we used principal components 1 (a measure of song length) and 2 (the number of distinct syllable types within a species song) from Weir & Wheatcroft (2011) and a Euclidean distance of PC1 and PC2 from Weir *et al.* (2012) as a measure of song pitch.

### Patterns across the latitudinal gradient

Geography could play a role in accelerating climatic-niche evolution. Sister pairs separated further geographically might experience more dissimilar climates. Phylogenetically corrected regressions were used to determine if geographical distances between the centroids of species (measured in kilometres) within each sister pair varied with latitude (using the centroid latitude of each sister pair). These were performed in the R package Caper v0.5 using generalised least-squares regression (Freckleton *et al.* 2002) with branch lengths transformed using Pagel's  $\lambda$  (with  $\lambda$  optimised using maximum likelihood). We

also used the same methods to test whether the climatic Euclidean distances (between climatic midpoints for each of the first three climatic PCs) were correlated with geographical distances, as expected if climate changes as a function of geographical distance. Even if geographical distances do not vary latitudinally, increased geographical heterogeneity of climate at high latitudes could accelerate climatic-niche divergence there. To explore this, we calculated variance in climate across the latitudinal gradient for each PC (we estimated variance in midpoint climatic values across all species whose centroid latitudes fell within a 20° latitude sliding window). Variance should be highest at high latitudes if climate is more geographically heterogeneous there.

In addition to geography, climatic specialisation may influence a species' ability to diverge in climate (see Fisher-Reid *et al.* 2012). We used niche breadth (e.g. climatic range estimated separately for each of the first three climatic PC's) as a measure of specialisation, with narrow breadth indicating specialisation, and broad breadth, generalisation. Phylogenetically corrected regressions were used to determine if climatic-niche breadth increased with latitude, as previously suggested (e.g. Janzen 1967).

Finally, while we modelled evolutionary rates of niche using the Euclidean distances separating midpoint climatic variables for species within each sister pair, an alternative measure of niche differentiation is the degree to which they overlap in climate, with low overlap indicating more differentiation. Climatic overlap for a sister pair was measured as the climatic range of each of the two species within the sister pair that overlapped along a climatic PC. To obtain proportional overlap, these overlap values were divided by the entire climatic range for the species pair. Phylogenetically corrected regressions were used to determine if proportional climatic-niche overlap varied with latitude for each PC.

### Data analysis: climatic-niche evolution

We used both Brownian motion (BM) and Ornstein–Uhlenbeck (OU) models, as implemented in the R package EvoRAG 2.0 (Weir 2014), to compare evolutionary rates of climatic-niche across the latitudinal gradient for sister pairs for each of the first three climatic PC's. BM estimates a single parameter, the evolutionary rate,  $\beta$ , and assumes no limit on trait divergence. The OU model adds an additional parameter,  $\alpha$ , which acts as a constraint on trait divergence so that trait divergence cannot increase indefinitely through time. Under the OU model,  $\alpha$  represents a 'pull' towards an intermediate trait value between each sister pair. This prevents strong trait divergence away from the ancestral trait value and acts as an evolutionary constraint. At high values of  $\alpha$ , evolutionary divergence becomes difficult. As  $\alpha$  approaches 0, the OU model collapses to the simpler BM model in which evolution is not constrained.

To determine if latitude drives rates of climatic-niche evolution, we used maximum likelihood to fit BM and OU models in which a single  $\beta$  (and  $\alpha$  for OU) was estimated for all sister pairs (BM<sub>null</sub> and OU<sub>null</sub>) and to models in which  $\beta$  (but not  $\alpha$ ) were allowed to vary linearly with latitude (BM<sub>linear</sub> and OU <sub>$\beta$ -linear</sub>). Some implementations of the OU model (e.g.

applied to whole tree approaches) are reported to provide biased estimates of the  $\alpha$  parameter, which could affect model selection (Thomas *et al.* 2014). We obtained no appreciable bias in our  $\alpha$  estimates (Appendix S1). Model fit was determined using the Akaike Information Criterion corrected for sample size (AICc) and Akaike weights. We used simulation to determine that our null models without a latitudinal effect on trait evolution ( $BM_{\text{null}}$  and  $OU_{\text{null}}$ ) can be rejected with a Type I error rate  $\leq 0.05$  if the difference between the AICc scores for the best fit null model and the best fit model with latitudinal effect is  $> 1.9$  (Appendix S1).

#### Data analysis: song and mass evolution

We used the same BM and OU modelling framework to determine if climatic-niche divergence is associated with faster evolution in traits important to ecology (body mass) or reproductive isolation (song). Past studies have identified faster evolutionary rates in bird song evolution at high latitudes (Weir & Wheatcroft 2011; Weir *et al.* 2012). Therefore, we tested  $BM_{\text{linear}}$  and  $OU_{\beta\text{-linear}}$  models in which rates of mass and song evolution vary as a linear function of latitude, as a linear function of the degree of climatic divergence for each sister (these were standardised by dividing by the expected standard deviation under the best fit climatic model for PC1, PC2 and PC3. Details in Appendix S1), and as a linear function of both latitude and climatic divergence simultaneously as follows:

$$\beta = b_0 + b_1 L_{1i} + b_2 L_{2i} + b_3 L_{1i} L_{2i} \quad 1$$

where  $L_{1i}$  is the absolute midpoint latitude,  $L_{2i}$  is the standardised climatic difference for sister pair  $i$ ,  $b_0$  is a constant,  $b_1$  and  $b_2$  are regression coefficients and  $b_3$  is the coefficient for an interaction term between latitude and climate. Models with or without the interaction term were tested for BM, but to keep the maximum number of model parameters at 4, OU models were tested only without the interaction term. These models will be included in the next release of the EvoRAG package (Weir 2014). Latitude and climatic divergence in each of the PC's were only weakly to moderately correlated (PC1:  $R^2 = 0.227$ ; PC2:  $R^2 = 0.0023$ ; PC3:  $R^2 = 0.242$ ) indicating a lack of strong colinearity in these explanatory variables. All models were compared to null models without a latitudinal and climatic effect on mass or song evolution.

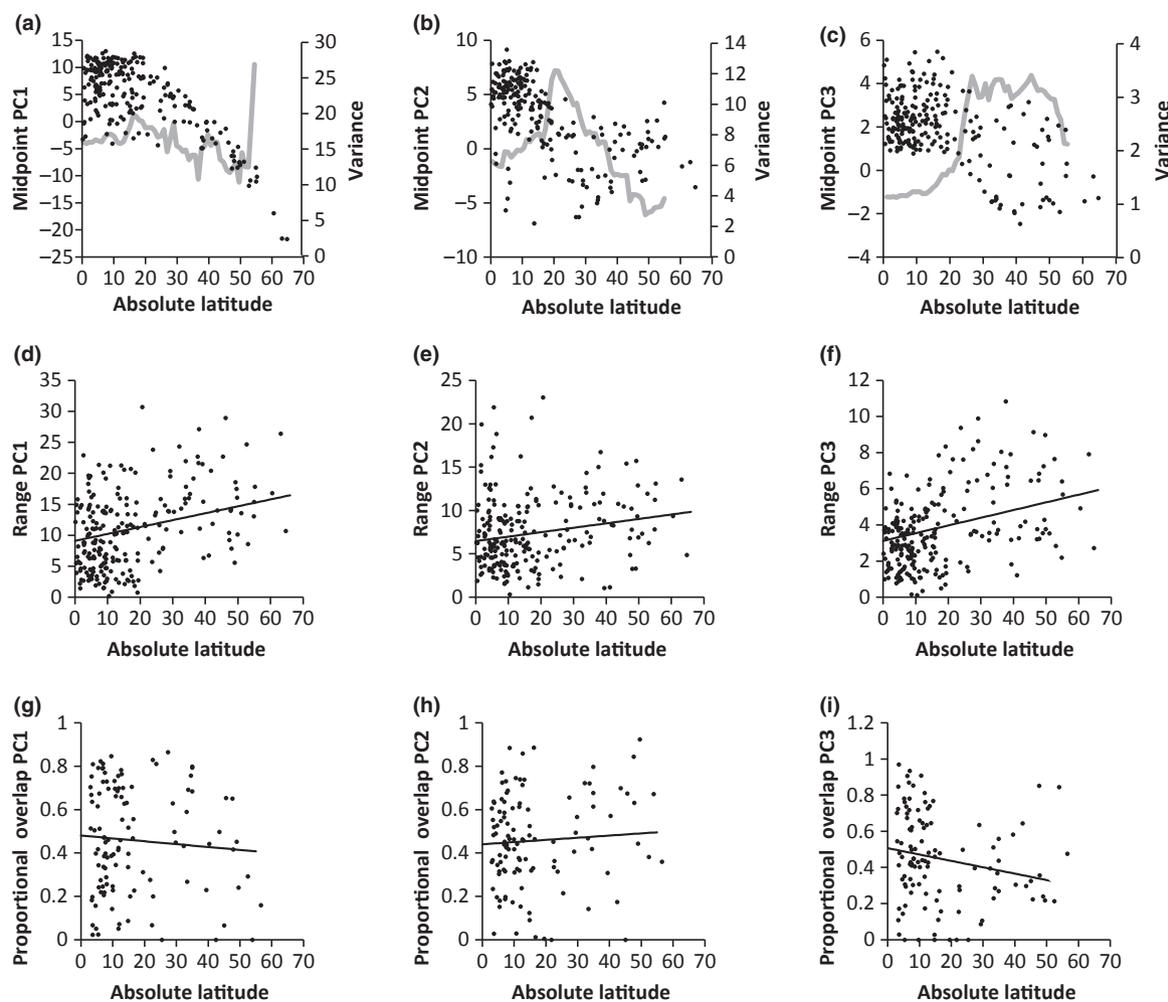
## RESULTS

All analysis used data from the first three PCs, as they explained over 90% of the variance in the climatic variables (PC1 = 61%, PC2 = 20%, PC3 = 13%). PC1 represents a temperature axis with all temperature measures loading positively, PC2 represents precipitation with all precipitation measures loading positively, and PC3 represents seasonality of both temperature and precipitation (Appendix S2). Midpoint climatic values for these PCs (Fig. 1a–c) showed increased variance (calculated using a 20° latitude sliding window) at high latitudes for PC3, no clear latitudinal patterns for PC1 and a peak in variance at 20° for PC2. Though there is considerable scatter (low  $R^2$  values), phylogenetic generalised least-squares

model fits (Fig. 1) indicate a significant increase in climatic ranges with latitude for each of the three climatic PCs (PC1: slope = 0.1107/degree latitude,  $R^2 = 0.075$ ,  $P < 0.0021$ ; PC2: slope = 0.0524,  $R^2 = 0.040$ ,  $P = 0.019$ ; PC3: slope = 0.0430,  $R^2 = 0.116$ ,  $P < 0.00016$ ), but that proportional climatic overlaps did not vary significantly with latitude except for PC3, in which overlap declined with increasing latitude (PC1: slope =  $-0.0014$ /degree latitude,  $R^2 = 0.007$ ,  $P = 0.37$ ; PC2: slope = 0.0010,  $R^2 = 0.005$ ,  $P = 0.45$ ; PC3: slope =  $-0.0033$ ,  $R^2 = 0.037$ ,  $P = 0.025$ ). Likewise, geographical distances separating the geographical centroids of species within a pair did not vary significantly with latitude (slope = 5.00 km/degree latitude;  $R^2 = 0.005$ ,  $P = 0.48$ ), and climatic divergence in PC1 to PC3 did not vary significantly with geographical distance separating sisters (PC1: slope = 0.00038 latitudinal units/km,  $R = 0.012$ ,  $P = 0.13$ ; PC2: slope = 0.00004,  $R^2 = 0.0006$ ,  $P = 0.80$ ; PC3: slope =  $-0.00004$ ,  $R^2 = 0.002$ ,  $P = 0.60$ ).

AICc and Akaike weights provided overwhelming support for the OU model of climatic-niche divergence that included a latitudinal effect on evolutionary rate for PC1 and PC3 (Table 1). All other models accounted for less than one percent of the Akaike weight for these PC's. PC1 and PC3 best supported the  $OU_{\beta\text{-linear}}$  model where  $\beta$  increased significantly across latitude (Table 1, Fig. 2), indicating faster evolution of the temperature niche towards the poles. In contrast, PC2 best fit a model ( $OU_{\text{null}}$ ) without a latitudinal effect, but this model was not as strongly supported, and the next best fit model ( $OU_{\beta\text{-linear}}$ ) showed a positive, but non-significant, effect of latitude on evolutionary rate (Table 1). Almost identical results were obtained when Neotropical migrants (which migrate out of their breeding range to winter at tropical latitudes) were excluded from the data set (Appendix S1), suggesting that these results are not biased by inclusion of Neotropical migrants.

Analysis of song and body mass supported models in which climatic divergence was associated with rates of trait evolution (Fig. 3, Appendix S2). With five exceptions (mass and precipitation (PC2); mass and seasonality (PC3); syllable diversity and temperature (PC1); syllable diversity and seasonality, song pitch and temperature), the best fit models included the effect of climatic divergence on evolutionary rates of body mass, song pitch, song length and syllable diversity. Excluding these exceptions, models which supported a climatic effect typically had much higher Akaike weights than models without (Appendix S2), indicating moderate to strong support for the effect of climatic divergence on trait evolution, even while simultaneously correcting for latitudinal effects. For data sets that supported a climatic effect, the best fit models tended to show a positive relationship between rates of mass or song divergence and degree of climatic divergence (Fig. 3). With only one exception (song pitch and seasonality), song and body mass also supported models that included a latitudinal effect, with evolutionary rates generally increasing with latitude. The best fit model for four of these comparisons included an interaction term between climatic divergence and latitude, suggesting that strength of the relationship between mass or song evolution and climatic divergence changes across the latitudinal gradient.



**Figure 1** Relationships between climatic variables and latitude. Midpoint climatic values (a–c) and their associated variances (gray line: calculated using a 20° latitude sliding window) and climatic ranges (d–f) of PC1 to PC3 for each species in our data set. Temperature and precipitation increase with increasing values of PC1 and PC2, respectively, but seasonality decreases with increase value of PC3. Proportional overlap (g–i) shows the climatic overlap for each PC divided by the combined climatic range for the each sister pair. Lines indicate phylogenetically corrected regressions.

**Table 1** Support for Brownian Motion and Ornstein–Uhlenbeck models of climatic-niche evolution

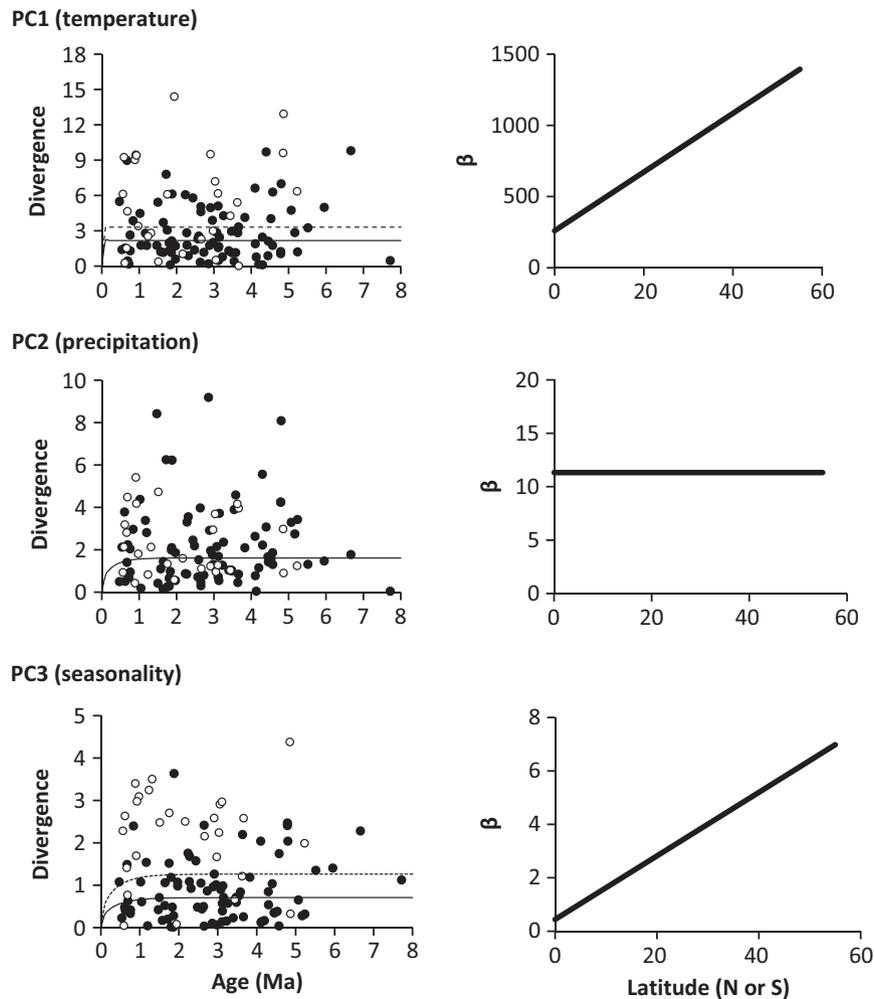
Model	N	PC1			PC2			PC3		
		$\Delta$ AICc	wAICc	$\beta$ slope ( $\pm$ 95% CI)	$\Delta$ AICc	wAICc	$\beta$ slope ( $\pm$ 95% CI)	$\Delta$ AICc	wAICc	$\beta$ slope ( $\pm$ 95% CI)
BM <sub>null</sub>	1	48.07	0.000	NA	22.25	0.000	NA	59.70	0.000	NA
BM <sub>linear</sub>	2	22.34	0.000	0.207 (0.119–0.331)	20.05	0.000	0.104 (0.003–0.15)	14.63	0.001	0.076 (0.022–0.043)
OU <sub>null</sub>	2	17.01	0.000	NA	<b>0</b>	<b>0.737</b>	NA	28.91	0.000	NA
OU <sub><math>\beta</math>-linear</sub>	4	<b>0</b>	<b>1.000</b>	<b>20.6 (0.4–*)</b>	2.06	0.263	0.072 (–1.8 to *)	<b>0</b>	<b>0.999</b>	<b>0.240 (0.05–*)</b>

\*The maximum likelihood estimate occurs along a ridge in the likelihood surface, and the upper end of the confidence interval could not be determined.  $\Delta$ AICc scores (AICc for each model – smallest AICc score) and Akaike Weights (wAICc) are used as metrics of model support. The best-fit model has the smallest  $\Delta$ AICc value of 0 (bold). Akaike weights indicate the probability of fit for each model. N indicates the number of parameters in each model.  $\beta$  slope describes how the evolutionary rates changes with latitude. Confidence intervals were calculated using profile likelihood.

## DISCUSSION

Our results indicate faster divergence in climatic-niche at higher latitudes for temperature (PC1) and seasonality (PC3), and suggest that increased divergence in key aspects of cli-

matic-niche accelerates rates of evolution in body mass and song, even after latitude is taken into account. These results contrast with rates of climatic-niche evolution estimated for 66 families of amphibians (a single rate was estimated for each



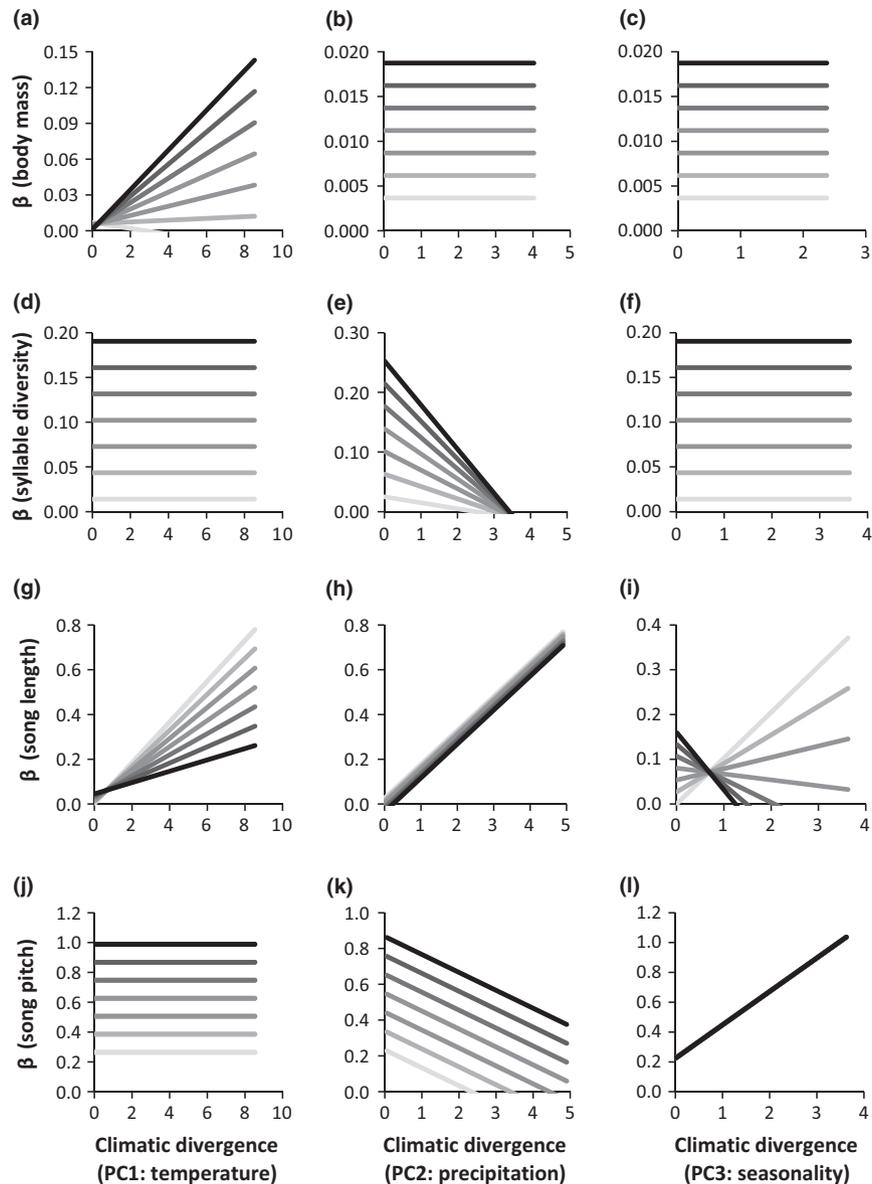
**Figure 2** Latitudinal gradients in climatic-niche evolution. Euclidean distances in climatic-niche divergence are displayed in the first column along with the average expected amount of divergence through time under the best fit evolutionary model. For PC1, sister pairs are divided into tropical ( $< 23^\circ$ ; closed circles, solid line) and temperate ( $> 23^\circ$ ; open circles, dashed line) subsets for illustrative purposes, though the evolutionary rates analysis treats latitude as a continuous variable. The second column displays latitudinal change in evolutionary rates ( $\beta$ ; solid lines) estimated from the best supported model for each PC (see Table 1).

family) in which evolutionary rates did not vary as a function of the midpoint latitude of each family (Pyron & Wiens 2013). While the differences between birds and amphibians may be genuine, they could also arise from the different taxonomic scales used to address whether rates of climatic-niche evolution vary with latitude. The family-level scale of the amphibian study estimated a single evolutionary rate for each family despite the considerable variability of species within families in their latitudinal positions. In contrast, our methodology allows rates of climatic-niche evolution to vary across closely related pairs of species as a function of their individual latitudes, and should be more sensitive at detecting latitudinal variation in climatic-niche.

A number of factors could drive faster climatic-niche evolution at high latitudes. Geography could play a key role in several ways. Geographical distance may drive climatic divergence, with closely related species at high latitudes occurring further apart in geographical space than in the tropics, and thus experiencing less similar climates. However, geographical

distance and climatic divergence were not significantly correlated in our data, and geographical distance separating sisters was not significantly greater at high latitudes. Even without a latitudinal increase in geographical distance between sisters, a latitudinal increase in geographical heterogeneity in climate (see Fig. 1a–c) could promote increased opportunities for climatic-niche divergence towards the poles (Vázquez & Stevens 2004). While our data set does support increased geographical variance in seasonality at high latitudes (Fig. 1c), the same is not generally true for temperature (Fig. 1a), suggesting that other factors may also play a role.

Alternatively, increased intensity of Plio–Pleistocene climatic fluctuations towards the poles may have likewise increased opportunities for climatic-niche divergence in high latitude species (Colinvaux *et al.* 1996; Bush & De Oliveira 2006; Sandel *et al.* 2011). In contrast, the tropics experienced less severe climatic fluctuations over the past several million years (especially at low altitudes), and this relatively more stable climate may have promoted increased climatic specialisation of



**Figure 3** The relationship between standardised climatic divergence and evolutionary rates ( $\beta$ ) of body mass and song while correcting for latitude. The darkness of lines increases with increasing latitude. Lines are plotted every  $10^\circ$  between  $0^\circ$  and  $60^\circ$  degrees latitude. The best fit models in a, c, d and e include an interaction term between climatic divergence and latitude, in (f) includes only the effect of seasonality and not latitude, and in (b) shows only a minor effect of latitude.

tropical species, as supported by the reduced climatic ranges for tropical species in our data set (Fig. 3d–f) and reported elsewhere (e.g. Hua & Wiens 2010; Cadena *et al.* 2012). While climatic specialisation could potentially allow species to overlap less in climatic-niche than generalists, our data do not exhibit strong latitudinal trends in climatic overlap, with slightly greater overlap in the tropics for temperature and seasonality (as also supported by Cadena *et al.* 2012 for temperature across a variety of high elevation vertebrate groups, including birds), and the opposite for precipitation (Fig. 1 e–g). Instead, we argue that tropical specialisation is likely to retard divergence in mean values of the climatic-niche for two reasons. First, ecological specialisation may narrow a species physiological tolerances to climate, and thereby reduce

its ability to readily adapt to novel conditions (Futuyma & Moreno 1988), whereas generalists may more easily respond to changes in climate. Second, competitive exclusion may prevent specialised species from expanding into novel climatic regimes already occupied by other specialist species, especially in species packed tropical environments. Thus the high species richness of the tropics can act as a constraint towards climatic-niche divergence, whereas low species richness, high levels of extinction (which opens up niche space), and reduced specialisation of higher latitude species may facilitate divergence in climatic-niche.

Faster divergence in climate away from the equator suggests that species at higher latitudes are experiencing stronger climate-induced divergent selection pressures. If climate is a

key driver of evolution, the stronger selection pressures mediated by climate should lead to faster evolutionary divergence in traits relevant to the climatic-niche. We tested whether strong climatic-niche divergence is associated with faster evolutionary rates in traits important to ecological differentiation (body mass) and reproductive isolation (song).

We find that stronger climatic divergence in temperature is associated with faster divergence in body mass, with the strongest effect at high latitudes (Fig. 3) as indicated by the interaction term between latitude and temperature divergence in the best fit model. Bergman's Rule describes the biogeographical pattern in which body mass increases with latitude, presumably to aid in heat conservation at high latitudes (though this explanation is not universally accepted; Anderson 1973; Katti & Price 2003; Millien *et al.* 2006), with larger-bodied species possessing a lower surface area to volume ratio, and thus better able to conserve heat in cold conditions (Riesenfeld 1981; Rodríguez *et al.* 2008). Many sister pairs in our data set vary geographically along a north–south axis and their mass differences could be heavily influenced by thermoregulatory factors. Recent meta-analyses of birds indicates that Bergman's rule often holds true – both at the intra- and interspecific levels – across northern temperate latitudes, but the signal is non-existent or weaker in the tropics (Meiri & Dayan 2003; Rodríguez *et al.* 2008). The association of evolutionary rates in body mass with temperature divergence is strong at high latitudes in our data set, but not in the tropics (Fig. 3a), consistent with the pattern of Bergman's rule operating primarily in extra-tropical regions.

In addition to body mass evolution, we tested the association of climatic divergence with accelerated rates of song evolution, a trait important for pre-mating reproductive isolation (Slabbekoorn & Smith 2002; Price 2008). We find that increased climatic divergence is associated with increased rates of divergence in song length (temperature, precipitation and seasonality) and song pitch (seasonality) even while correcting for latitude (Fig. 3). Climate influences vegetation density, which is known to have an influence on a variety of song features (e.g. simpler songs with less modulation in pitch in dense vegetation; Morton 1975; Padgham 2004; Tobias *et al.* 2010), thus divergence in climate could drive divergence in song in response to vegetation change. In contrast, climatic divergence was not associated with increased rates of syllable diversity evolution in our data set, suggesting that other factors, such as sexual selection, may drive faster evolutionary rates in this character at high latitudes (Weir & Wheatcroft 2011).

Climate has previously been proposed to accelerate either the initiation or the completion of the speciation process (Hua & Wiens 2010). Slow climatic-niche divergence (i.e. niche conservatism) could promote increased opportunities for the initiation of allopatric speciation (e.g. range fragmentation; Wiens 2004; Kozak & Wiens 2006), whereas ecological niche divergence could drive faster evolution of characters important to reproductive isolation (Wiens 2004), thus completing the speciation process (e.g. ecological speciation). Slower rates of climatic-niche evolution at tropical latitudes suggest that allopatric speciation may be commonly initiated there, but that reproductive isolation may take a longer time to develop (as further evidenced by slower divergence of song and plum-

age colouration in tropical birds, both of which are important to reproductive isolation; Martin *et al.* 2010; Weir & Wheatcroft 2011; Weir *et al.* 2012). In contrast, rapid climatic-niche divergence at high latitudes should accelerate the development of reproductive isolation towards the poles, as our data for song generally suggests. Likewise, species in more extreme climates at high latitudes have greater number of subspecies than those in benign tropical climates (Botero *et al.* 2014) suggesting that climate may be linked to rapid plumage differentiation between populations within species. Whether rapid niche divergence or niche conservatism ultimately drives faster rates of speciation is difficult to predict. Phylogenetic estimates in birds over the past several million years support recent higher speciation rates at high latitudes (Weir & Schluter 2007), suggesting the possibility that rates of climatic-niche divergence may be an important factor in driving latitudinal differences in rates of speciation in birds.

Climatic-niche divergence may drive trait evolution directly through adaptation to climatic differences (e.g. mass following Bergman's rule; song driven by vegetation density), but may also indirectly influence trait divergence. For example, divergence in body mass between sisters could occur if prey size varies between ecological communities in different thermal regimes, because body mass generally increases with prey size in animals (Brose *et al.* 2005). Likewise, different vocal competitors encountered in climatically dissimilar regions may result in signal interference (Gröning & Hochkirch 2008), leading to song differentiation. Further analyses are needed to determine whether direct or indirect effects of climatic divergence are driving trait evolution at high latitudes, or whether other factors are driving both climatic and trait divergence in a correlated fashion.

We find that rates of climatic-niche evolution increase with increasing latitude, and that climatic differentiation is often associated with divergence in traits indicative of ecological differentiation (body mass) and reproductive isolation (song). Our study also suggests a link between fast climatic divergence and rapid completion of the speciation process at high latitudes, suggesting a potential explanation for faster poleward speciation rates over the past several million years (Weir & Schluter 2007; Botero *et al.* 2014). Although the results of this study identify the importance of climate in accelerating evolution at high latitudes, it is unknown whether divergent selection driven by factors other than climate will follow a similar latitudinal trend.

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#### AUTHORSHIP

AL and JW designed the study; AL collected data; AL and JW carried out analyses; AL and JW wrote the manuscript.

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