

Climatic effects on niche evolution in a passerine bird clade depend on paleoclimate reconstruction method

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Climatic niches describe the climatic conditions in which species can persist. Shifts in climatic niches have been observed to coincide with major climatic change, suggesting that species adapt to new conditions. We test the relationship between rates of climatic niche evolution and paleoclimatic conditions through time for 65 Old-World flycatcher species (Aves: Muscicapidae). We combine niche quantification for all species with dated phylogenies to infer past changes in the rates of niche evolution for temperature and precipitation niches. Paleoclimatic conditions were inferred independently using two datasets: a paleoelevation reconstruction and the mammal fossil record. We find changes in climatic niches through time, but no or weak support for a relationship between niche evolution rates and rates of paleoclimatic change for both temperature and precipitation niche and for both reconstruction methods. In contrast, the inferred relationship between climatic conditions and niche evolution rates depends on paleoclimatic reconstruction method: rates of temperature niche evolution are significantly negatively related to absolute temperatures inferred using the paleoelevation model but not those reconstructed from the fossil record. We suggest that paleoclimatic change might be a weak driver of climatic niche evolution in birds and highlight the need for greater integration of different paleoclimate reconstructions.

KEY WORDS: Climate change, macroevolution, paleobiology, precipitation, temperature, trait evolution.

The climatic niche describes the climatic conditions in which a species can maintain a viable population in both space and time (Hutchinson 1957; Pearman et al. 2008). Examining how it changes over geological timescales is vital to our understanding of adaptation, speciation, and extinction and how climate shapes species diversity patterns (Hawkins et al. 2007; Moreno-Letelier

et al. 2014; Castro-Insua et al. 2018). Over the past millions of years, Earth has experienced strong climate variability (Zachos et al. 2001). Understanding the impact of these changes on organisms' climatic niches provides clues to their response to climate change and may help predict whether lineages are able to adapt their climatic niche to new conditions (Pearman et al. 2008;

Quintero and Wiens 2013a). However, this is not a simple task, requiring knowledge of the evolutionary history of taxa, as well as information on climatic change through time (Svenning et al. 2015).

There is a variety of indirect support for a relationship between climatic conditions and rates of niche evolution. For example, current macroecological patterns in climatic niches suggest a relationship with current climate and recent climate change; recent rates of climatic niche evolution are fastest at higher latitudes (Lawson and Weir 2014), where plio-pleistocene fluctuations were greatest (Janzen 1967; Quintero and Wiens 2013b; Liu et al. 2020). In addition, niche shifts in some lineages, as inferred using molecular phylogenies, have been found to coincide with periods of climatic change (Duran and Pie 2015; Nürk et al. 2015; Hua et al. 2019). However, in direct contrast, other studies have found no evidence for a relationship between climatic conditions and climatic niche changes (e.g., Schnitzler et al. 2012). It therefore remains unclear whether changes in climatic niches through time are driven by climate at deep time scales.

Many different aspects of climate may affect rates of climatic niche change (see Garcia et al. 2014 for a review). In particular, understanding the relationship between the potential speed of niche change (i.e., the rate) and the rate of climate change can help understand whether species are able to adapt their climatic niche to new conditions (Quintero and Wiens 2013a; Román-Palacios and Wiens 2020). Under changing climatic conditions, lineages that are able to tolerate novel conditions would be selected, resulting in climatic niche evolution following climatic conditions through adaptation within lineages, as well as through selective speciation and extinction of different lineages. A positive relationship between rates of climate change and rates of niche change would be expected as faster climatic changes should impose a stronger selection pressure on climatic niches, leading to higher apparent rates of niche change across surviving lineages (Benton 2009; Duran and Pie 2015). However, if climatic conditions change rapidly, species might not be able to adapt fast enough (Quintero and Wiens 2013a). Further, no relationship would be expected if organisms tolerate climatic changes through behavioral adaptations or range shifts, or if climatic niche changes are driven by other factors (e.g., avoiding competition; Pitteloud et al. 2017).

In addition, niche evolution rates might be influenced by absolute climatic conditions (i.e., the actual climate values at a particular point in time). If absolute climate conditions drive the evolution of the climatic niche, then we would expect to find a positive relationship between climate conditions and rates of niche evolution. Previous studies suggest different expectations for the direction of this relationship concerning absolute temperature. Temperature is known to influence biological processes at a variety of levels. For example, mutation rates increase with

temperature (Gillooly et al. 2005; Oppold et al. 2016; Foucault et al. 2018), whereas generation times decrease with temperature (Gillooly 2000), leading to faster rates of molecular evolution. These mechanisms may lead to increased rates of niche evolution under higher temperatures, assuming a positive relationship of molecular rates with rates of phenotypic evolution. However, empirical examination of the relationship between rates of genetic and phenotypic change has failed to confirm this assumption (Davies and Savolainen 2006).

Alternatively, if the rates of trait evolution that emerge at large phylogenetic scales are driven by underlying selection pressure rather than through direct effects of climate on mutation rates, a positive relationship between climate and rates of niche evolution might not be expected. For example, Clavel and Morlon (2017) found that body mass evolution of birds and mammals was faster during cold periods. A similar mechanism to this selection on body mass could directly apply to the physiological thermal limits of species, causing a negative relationship between absolute temperature and rates of climatic niche evolution through time.

Across extant species, the upper physiological limits of climatic niches are not correlated with ambient temperatures but the lower limits are, suggesting that lower temperatures exert a greater selective pressure across species and that rates of niche evolution may increase with cooling (Araújo et al. 2013; Khaliq et al. 2017). Further, physiological tolerances to heat apparently evolve more slowly than those to cold (Qu and Wiens 2020). Alternatively, as the variation in temperature globally is larger at the lower physiological limits of species' climatic niches, this may cause the negative relationship (Saupe et al. 2019). Temperate regions have experienced higher rates of climatic niche evolution and show much weaker phylogenetic conservatism in physiological limits of current species than the tropics over the past several million years (Lawson and Weir 2014; Khaliq et al. 2015), which could indicate that cold and dry conditions pose a stronger selection pressure than warm and moist conditions. Finally, no relationship between absolute climatic conditions and niche evolution rates would be expected if the climatic niche evolves by stochastic rather than adaptive processes. Such a lack of relationship has been suggested by modeling studies (Coelho et al. 2019), and by a lack of relationship between rates of niche evolution and climate in plants and terrestrial vertebrates (Liu et al. 2020).

Although many studies have hypothesized that rates of climatic niche change are driven by variations in temperature and precipitation (Evans et al. 2009, Duran and Pie 2015), a lack of temporally resolved information on terrestrial environmental conditions from the deep past has largely precluded explicitly testing for a temporal relationship (e.g., Duran and Pie 2015; Nürk et al. 2015, but see Stigall 2012; Saupe et al. 2014). Previous studies have explored the evolution of climatic niches

across deep time in relation to distribution, diversification, and traits (Meseguer et al. 2015, 2018; Rolland et al. 2018), but to our best knowledge, no previous study has explicitly tested for a temporal relationship between paleoclimatic conditions and rates of change in climatic niches inferred across multiple lineages. Further, many studies that have related trait evolution to climatic conditions in the past have relied on global temperature curves derived from marine proxies (Zachos et al. 2008; Nürk et al. 2015; Clavel and Morlon 2017), which are unlikely to adequately represent regional terrestrial climatic conditions. Additionally, studies have been limited to examining temperature despite precipitation being an important aspect of species' climatic niche (IPCC 2014; La Sorte et al. 2019; Boyle et al. 2020).

Paleoclimate simulations of atmospheric circulation models with temporally explicit temperature and precipitation estimates across the globe exist, but are only available for a limited set of time intervals (Brown et al. 2018) and come with uncertainty, for example, results are highly sensitive to model settings such as atmospheric CO₂ content (Forrest et al. 2015; Varela et al. 2015). In particular, very few models are available for the Miocene and Pliocene; Paleoclim, a database of paleoclimate simulations using the HadCM3L model, currently comprises just two climatic layers older than the Pleistocene (for 3.205 and 3.3 million years ago). Finally, terrestrial paleoclimate proxies from fossil records, for example, plant assemblages or paleosols, have mostly been investigated in local archives and have not been compiled for entire continents or over long geological periods (e.g., Hamer et al. 2007; Royer 2012).

In this study, we test for a relationship between climatic conditions and phylogenetically reconstructed rates of niche change using terrestrial paleoclimate estimates inferred independently from two sources: (i) a paleoelevation model (Hagen et al. 2019) and (ii) from the mammal fossil record (Liu et al. 2012). The paleoelevation model reconstructs air surface temperatures at a 1-million-year temporal resolution and a 1° spatial resolution, which were estimated by Hagen et al. (2019) using lithological indicators of past climatic conditions, and present-day temperature lapse rates with elevation. We additionally inferred regional mean annual temperature (MAT) and precipitation (MAP) through time from fossil occurrences of large mammalian herbivores based on a functional relationship between tooth structure and environment (Liu et al. 2012). The distribution of dental functional traits in ungulates that occur in a location reflects the type of resources available, and in turn ambient climatic conditions (Liu et al. 2012, see also Fortelius et al. 2014). Although the paleoclimate record reconstructed with the paleoelevation model has a much higher temporal and spatial resolution, it is only indirectly based on geological evidence, whereas paleoclimate reconstructions based on the mammal fossil record constitute a widely accepted proxy for both temperature and precipitation from in situ evidence, albeit patchy in time and space.

We predicted and tested for relationships between estimated rates of climatic niche change and (i) rates of paleoclimatic change and (ii) absolute climatic conditions, by comparing changes in both temperature and precipitation niches in an extant passerine bird clade with corresponding climatic conditions estimated by each paleoclimate dataset. Our first hypothesis was that rates of niche change are positively associated with the rate of climate change for both temperature and precipitation. Second, we hypothesized that estimated rates of niche change are negatively related to absolute temperature and precipitation, that is, we expected to find faster rates of niche change occurring in cold dry conditions. We tested these hypotheses using the monophyletic, broadly distributed wheatear-chat clade (Aves: Passeriformes: Muscicapidae, genera *Oenanthe*, *Monticola*, *Saxicola*, *Myrmecocichla*, *Emarginata*, *Campicoloides*, *Pinarochroa*, and *Thamnolaea*). This is a suitable clade to test these hypotheses for ecological and practical reasons. Species are widely distributed and occupy a variety of climatic conditions and habitats. In addition, the clade's geographic and temporal distribution matches the areas and time period for which paleoclimatic data from the mammalian fossil record were available.

Methods

SPECIES SAMPLING AND PHYLOGENETIC INFERENCE

We investigated climatic niche evolution in a monophyletic clade comprising 71 species (following IOC taxonomy version 3.01; Gill and Donsker 2012, see Table S1) of Old-World flycatchers (the wheatear-chat clade). Phylogenetic relationships within the group were obtained from Phillips et al. (2018, 2020) who obtained and vetted sequence data for three genes (one nuclear and two mitochondrial) from GenBank (www.ncbi.nlm.nih.gov/genbank) for 65 species. These genes were selected as having the greatest coverage across the group and evolving at differing rates. Sequence data were missing for six species. The phylogeny was estimated using Beast version 2.4.4 (Bayesian Evolutionary Analysis Sampling Trees; Bouckaert et al. 2014). Four independent runs, each for 50 million generations, were combined after removing the burn-in. A maximum clade credibility (MCC) tree was calculated using Tree Annotator (also in Beast version 2). Finally, Phillips et al. (2018, 2020) derived absolute dates based on a *Luscinia* fossil (Jenő and János 2012), a closely related outgroup to our clade of interest. Although it is possible that this tree is not the true representation of all relationships within the group, the majority of branches were strongly supported with only seven nodes with posterior support below 0.9. Further, relationships and dates were mostly consistent with previous phylogenetic studies (Fig. S1; Phillips et al. 2018). In addition to the MCC tree, we used 100 trees sampled randomly from the posterior distribution to account for phylogenetic uncertainty.

For an overview of the methods, see Figure S2. All following analyses were performed in R (version 3.6.1) unless stated otherwise.

CLIMATIC NICHE QUANTIFICATION

The fundamental climatic niche is often assumed to be best represented by physiological tolerance data (Pearman et al. 2008). Despite birds being well-studied, necessary physiological data are not available for the vast majority of species (Khaliq et al. 2014). Therefore, climatic niches were quantified using climatic conditions within the species distribution. Geographic distributions may be shaped by other factors such as competition (Yackulic 2017), meaning that they most likely provide an imperfect estimation of a species fundamental climatic niche and instead represent the realized niche (Soberón 2007). However, despite this, it is usually assumed that carefully vetted broad-scale geographic distributions provide a reasonable approximation of climatic niches (Pigot et al. 2010; Khaliq et al. 2017). Here, we make use of a newly compiled dataset of extent-of-occurrence range maps that comprised both the breeding and nonbreeding ranges of bird species (Eyres et al. 2020). Despite limitations for climatic niche quantification (Graham and Hijmans 2006), such maps represent the most consistent coverage of a species range that are currently available at a global scale across large numbers of species (Kearney et al. 2010; Wisz et al. 2013; Meyer et al. 2015).

As 22 out of the 65 species included in our analyses are classified as migratory (Eyres et al. 2017), we made use of a new database of nonbreeding ranges of migratory bird species (GeoMiB; see Eyres et al. 2020 and Supporting Information for details) to ensure that our niche quantifications take into account the climatic conditions experienced by species in their breeding and nonbreeding range (Eyres et al. 2017). The final species occurrences used in the analyses were seasonal presences in 1° latitude-longitude grid squares. For a complete description of datasets, see methods in the Supporting Information.

So that niche quantification represented the climatic conditions of migratory species, we used the climate data for the season when each species is present in a particular part of their range (i.e., when a species is in its breeding range and when it is in the nonbreeding range). The three peak breeding months for each species were determined from the literature (Handbook of the Birds of the World; del Hoyo et al., 2019, see Eyres et al. 2020 and Table S1). The three nonbreeding months for each species were defined as starting six months later than the breeding season (Laube et al. 2015). To ensure comparability across species, climatic niches were calculated in the same way for residents and migrants.

Monthly climatic data were obtained from the WorldClim *raw climate data* dataset (averages from 1970 to 2000, resolution 10 arc minutes; Fick and Hijmans 2017). The following four cli-

matic variables were obtained: minimum, maximum, and average daily temperatures within each month and total monthly precipitation, hereafter referred to as T_{\min} , T_{\max} , T_{mean} , and Precipitation, respectively. We chose to investigate the rates of change of these three aspects of temperature niche (T_{\min} , T_{\max} , and T_{mean}) as well as precipitation as they are most likely to be related to the climatic variables that we were able to infer from the paleoelevation model (temperature) and from the fossil record (temperature and precipitation). All climate data were resampled into the same grid cells as the occurrence data, so that a given species occurring in a given grid cell had either three monthly values for each climatic variable (breeding or nonbreeding occurrence) or six-monthly values (year-round occurrence). As a measure of average climatic conditions that species are exposed to, highest-density values from this entire distribution of grid square values across the entire species range throughout the six months (breeding and nonbreeding) were determined from density plots using the *hdr* function from the R package *hdr* (Hyndman et al. 2013) for each of the four climatic variables (T_{\min} , T_{\max} , T_{mean} , and Precipitation). These highest-density values for each climatic variable were used rather than the mean because climatic conditions tolerated by species are often not normally distributed (Evans et al. 2009). These values represent the most common conditions each species is exposed to across its range, and were assumed to be representative of the central niche position for each species.

RATES OF NICHE EVOLUTION

Rates of climatic niche change were reconstructed from the inferred climatic niches of extant species combined with their phylogeny. We calculated rates of climatic niche change for each of the four climatic variables for four different time bin schemes to match the time bins of the paleoclimate data (for more details see below and Supporting Information). We assumed that the fundamental climatic niche is captured by our niche position quantification from geographic range maps, and therefore follow previous studies in considering the evolutionary rates of change in these inferred climatic niches as a meaningful approximation of climatic niche evolution (Schnitzler et al. 2012; Title and Burns 2015; Cooney et al. 2016). We recognize that the observed climatic niche is not necessarily an evolving species trait (Dormann et al. 2010; Soberón and Peterson 2011). Rates of realized niche change were estimated using the variable rates model in BayesTraits, version 2 (Venditti et al. 2011). This model assumes trait evolution by Brownian motion (BM) but allows variable rates between branches, permitting us to explore how the rate of evolution varies across the tree. This analysis was carried out on the MCC tree of Phillips et al. (2020). The model was run using default priors and two independent MCMC chains for 1 billion iterations each. For each climatic variable, we carried out two independent runs and removed the first 10,000 samples as

burn-in. From each chain, we retained every 100,000th tree post burn-in yielding 10,000 samples. The branches in each posterior tree had been scaled proportionally to the rate of evolution. All subsequent analyses were carried out on the pooled 20,000 posterior trees from both chains to account for uncertainty in the inferences of rates of climatic niche change across the phylogeny.

We calculated temporal variation in rates of niche change following Cooney et al. (2016). For each time bin, we calculated the weighted mean rate of evolution across all branches present in that time bin. Branches were weighted by the proportion of the time bin they covered (so that a branch that is present for the whole time bin has more weight than one that is only present for part of the time bin). This was carried out for each posterior tree and then averaged across trees. In addition, to test for significant shifts on particular branches or clades, we calculated the probability of a rate shift across all posterior trees for each node in the tree.

MODEL FITTING AND ADEQUACY

The variable rates model in BayesTraits is a modification of the BM model that allows variable rates of niche evolution across the tree, and allows the identification of branches and clades where the rate of niche evolution varies significantly. To determine whether this model was better supported by the data than the simpler constant-rate BM model, we ran two nested models: one allowing the rates of evolution to vary across the phylogeny (as above), and one where the rates were held constant. We then calculated the log Bayes factors from the log marginal likelihoods of the two models.

To ensure BM was an appropriate underlying model of niche evolution for our data, we additionally fit three single process models (BM, early burst [EB], and Ornstein-Uhlenbeck [OU]; see Harmon et al. 2010) using the *fitContinuous* function in the R package Geiger version 2.0.6.4 and included the standard error of each climatic niche estimate to incorporate uncertainty. Models were run across the MCC tree and 100 posterior phylogenies to assess the influence of phylogenetic uncertainty. The adequacy of these models, that is, potential violations of the assumptions underlying each model, was also assessed using the *arbutus* function in the R package *arbutus* version 0.1 (Pennell et al. 2015) for the MCC tree.

PALEOCLIMATIC CONDITIONS: PALEOELEVATIONAL MODELING

Reconstructions of paleoclimatic conditions for the Neogene (~23–3 million years ago) were obtained from Hagen et al. (2019). These reflect air surface temperature at a 1-million-year temporal resolution and 1° spatial resolution for the study region (Africa and Eurasia). They combine reconstructions of broad climatic zones (Köppen zones) based on the geographic

distributions of lithological climate indicators with paleotopographic reconstructions. The resulting reconstructions provide an estimate of average surface temperature that accounts for the decrease of temperature with elevation (Fig. S3). For details, see Hagen et al. (2019).

Average temperature was calculated as the mean across the study region for each time point (every million year). Rate of climate change was calculated as mean of the differences in climatic conditions between successive time points for each grid square. To ascertain whether differences in temperature inferred from the mammal fossil record were sensitive to spatially non-random sampling in the fossil record, we additionally calculated mean temperature values for each time point only using those grid cells that had fossil occurrences.

PALEOCLIMATIC CONDITIONS: MAMMAL FOSSIL DATA

Temperature and precipitation were estimated from the mammal fossil record for the Neogene, ~23–2 million years ago following Liu et al. (2012), using a linear regression method that estimates MAT and MAP based on the dental traits of herbivore assemblages. In total, MAT and MAP were estimated for 1735 unique fossil localities (Fig. S4). To incorporate a measure of uncertainty in each of these point estimates, we calculated the minimum and maximum possible value with the error term in the regression analyses used to derive climatic estimates (Liu et al. 2012).

Geo-referenced and dated fossil records for large mammals (Orders: Artiodactyla, Perissodactyla, Primates, Proboscidea) were obtained from the NOW database (New and Old Worlds Database of Fossil Mammals, www.helsinki.fi/science/nov/) for continents occupied by the study clade (Europe, Asia, and Africa). To examine climatic trends through time, we used MN (Mammal Neogene) temporal units. MN zonation is a stratigraphic timescale of 16 consecutive zones used to date European mammal fossil localities in the Miocene and Pliocene (Table S2). Mammal fossil assemblages were assigned to each of these biozones based on their age estimates using two assignment methods that we refer to here as “strict” and “mid-point” assignment (full description in Supporting Information). MAT and MAP were estimated for 1735 unique fossil localities (fossil assemblages with a unique combination of location and age-estimate; see Table S2 for final numbers of fossils in each time bin).

Directly averaging paleoclimate records across the entire geographic region for each time bin would not take into account the spatial variation in sampling or the uncertainty in climate inferences. Therefore, we gridded the entire region using a 1° grid and summarized the records that fell into each grid square. For each grid square, we calculated an average value of temperature and precipitation and an uncertainty estimate (for details, see Supporting Information). The number of grid squares containing

fossil localities varied within each continent, that is, Africa, Europe, and Asia (Fig. S4). To ensure the estimated climatic conditions through time were not unduly influenced by the variation in spatial distribution of fossil localities, we first calculated climatic averages for each continent, and then averaged these to get an estimate for the entire study region. The average climate value for each continent in each time bin was calculated as the weighted mean of all the grid squares in a continent. The value from each grid square was inversely weighted by its uncertainty estimate to account for spatial heterogeneity in the uncertainty of climatic estimates.

Rates of paleoclimatic change were calculated as absolute differences in climatic conditions between successive time bins, divided by the time difference between the mid points of successive time bins. Rates were calculated for each continent separately and rates for the entire study region were subsequently calculated as the average of those values.

STATISTICAL ANALYSES

We tested for (i) a temporal relationship between paleoclimate averages and mean rates of change in climatic niches in each time bin, and for (ii) a relationship between rates of paleoclimatic change and mean rates of change in climatic niches among subsequent time bins. For each relationship, we tested two aspects of climate (MAT and MAP) for the mammal fossil data, and one aspect (MAT) for the paleoelevation model, as well as four aspects of climatic niches (precipitation niche and the three temperature variables). Because glacial-interglacial oscillations in the Pleistocene were not well resolved at the temporal resolution of either of our reconstructions (1 million years up to several millions of years), we did not include the last ~2 million years (i.e., Pleistocene and Holocene) in our analyses.

We first tested for temporal autocorrelation using the *acf* function in R and found a significant correlation between climate at time t and climate at time $t + 1$ for all analyses. As some relationships were nonlinear, we used generalized additive models (GAMs) that accounted for the temporal structure through first order autoregressive models, taking the correlation among subsequent time bins into account (Crawley 2007). Additionally, results of linear generalized least squares (GLS) models are reported in the supplement.

Results

RATES OF NICHE EVOLUTION

Using the molecular phylogeny, we inferred changes in temperature and precipitation niches across the tree (Figs. 1A, 1B, and S4) using the best-fitting variable rates model (see below for comparison to other models). There was little difference between

the results for the three aspects of temperature niche (T_{\min} , T_{mean} , and T_{\max}). We present the results from T_{\min} in the main text and the others in the Supporting Information. No significant branch or clade shifts in inferred rates of climatic niche change were detected for the temperature niche using any of the three temperature variables (Fig. 1A for T_{\min} ; Figs. S3A and S3B for T_{\max} and T_{mean}). The average rate of temperature niche change across the tree showed an overall positive trend through time (Figs. 1C, S4C, and S4D) indicating that temperature niche evolution accelerated toward the present.

In contrast to temperature, we identified four significant shifts in inferred rates of change in the precipitation niche within the phylogeny (Fig. 1B). Significant shifts were found in the branch leading to the *Oenanthe-Myrmecocichla* split, within *Oenanthe*, within *Myrmecocichla*, and finally within the branch leading to *Saxicola*. All four of these shifts were to faster rates of niche evolution (Fig. 1B). Average rates of precipitation niche change across the tree through time showed an overall positive trend with rates increasing through time (Fig. 1D). There were slight peaks in the rate of change for precipitation niche around 12 and 6 million years ago (Fig. 1D). Estimated rates of change in the precipitation niche were more variable through time than those of the temperature niche.

MODEL FITTING AND ADEQUACY

Model fitting and adequacy tests all supported the variable-rates model as the most appropriate to describe climatic niche evolution within the study group (a monophyletic clade within the Muscicapidae). Comparison of mean AIC_C and likelihood values for univariate models of BM, OU, and EB fitted across 100 posterior trees for the wheat-ear chat phylogeny showed strong support for BM as an adequate fit for the data for all niche metrics (Table S3). For all metrics of the temperature niche, AIC_C was lowest for the BM model. For the precipitation niche, mean AIC_C was lowest for models fitting an OU model of trait evolution. However, the difference in AIC_C values between models fitting OU and those fitting BM was less than 4 (2.673) indicating only slightly lower support for the BM model than the OU model. Likelihood values for all metrics of the climatic niche were highest for OU models, but never significantly different to those from the BM models. Therefore, there was no substantial evidence that OU is a better fit to the data than the simpler BM model, and the latter was therefore a reasonable model for this application.

For all six metrics of model adequacy in *arbutus*, all models (BM, OU, and EB) were confirmed as adequate for the three temperature niche traits (Table S4). For precipitation niche, three of the metrics suggested that none of the models were adequate. These metrics test for accurate estimation of rate heterogeneity (C_{var}), for accurate modeling of variation in ancestral state (S_{ASR}), and for deviations from the expected normal distributions

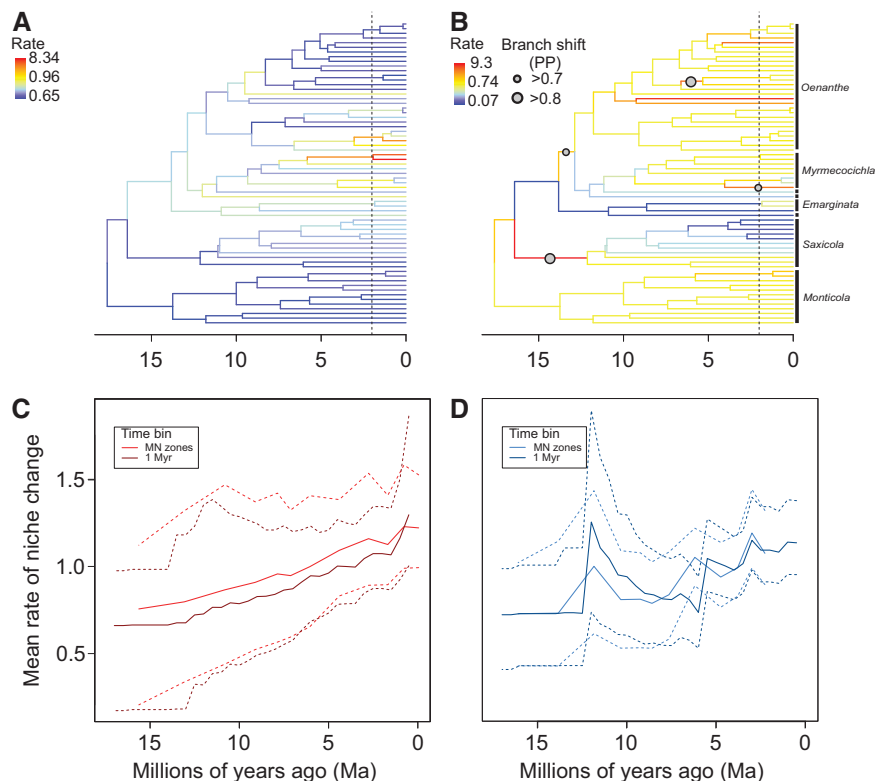


Figure 1. The maximum clade credibility (MCC) phylogeny for Wheatears and Chats ($n = 65$ species) colored by estimates of the mean rates of trait evolution for climatic niche aspects (A and B) and the mean rate of evolution through time estimated from 20,000 samples with a BayesTraits analysis (C and D), for minimum temperature (A and C) and precipitation (B and D). Rate values were log-transformed for visualization. Gray circles show rate shifts inferred on individual internal branches, with the relative size of each circle indicating the posterior probability (PP) of a rate shift. Mean rate of climatic niche evolution (C and D) with 95% confidence intervals (dashed lines) was calculated for each time period using the two time bin schemes (MN zones and every million years) as the weighted average of all branches that were present in a time period.

of contrasts (D_{cdf}). Therefore, these results suggest that all three univariate models underestimated the overall rate heterogeneity, providing further evidence in support of fitting a variable rates model.

Finally, there was strong support for fitting the more complex variable rates model over a univariate Brownian model of trait evolution from the log Bayes factors calculated between the variable rates model and fixed rate Brownian model in BayesTraits. These were greater than five for all niche metrics (Table S5).

PALEOCLIMATIC CONDITIONS

Paleoclimatic reconstructions of temperature for our study region (Africa and Eurasia) differed between the two methods (Fig. 2). Overall reconstructed temperature values from the mammal fossil record were much higher and slightly more variable than those reconstructed using a paleoelevation modeling approach (Fig. 2A). Mean air surface temperature values inferred using the paleoelevation reconstruction varied from 8.6 to 13.8°C (difference $\sim 6^\circ\text{C}$), with an overall decrease over the last 24

million years. In contrast, temperature reconstructed from the mammal fossil record was more variable, ranging from 14.0 to 21.9°C (difference $\sim 8^\circ\text{C}$), with a clear overall decrease over the last 24 million years.

Rates of reconstructed temperature change inferred from the mammal fossil record were also greater than those inferred from paleoelevation models (Fig. 2C). Temperature reconstructions (absolute values and rates) from the paleoelevation model were more similar to temperature inferred from the mammal record, when sampled at the same locations in time and space (Figs. 2A and 2C). However, even then, they still depict quite different temperature trajectories, indicating that the difference between the two methods is not only due to different spatiotemporal coverage and deserves further investigation.

For precipitation, only one source of paleoclimatic data was available, that is, the mammal fossil record. We observed stronger temporal patterns in this record than for temperature, with precipitation values varying more than twofold between ~ 700 and ~ 1700 mm (Fig. 2B). Rates of paleoclimatic change for precipitation were very variable through time, with a clear

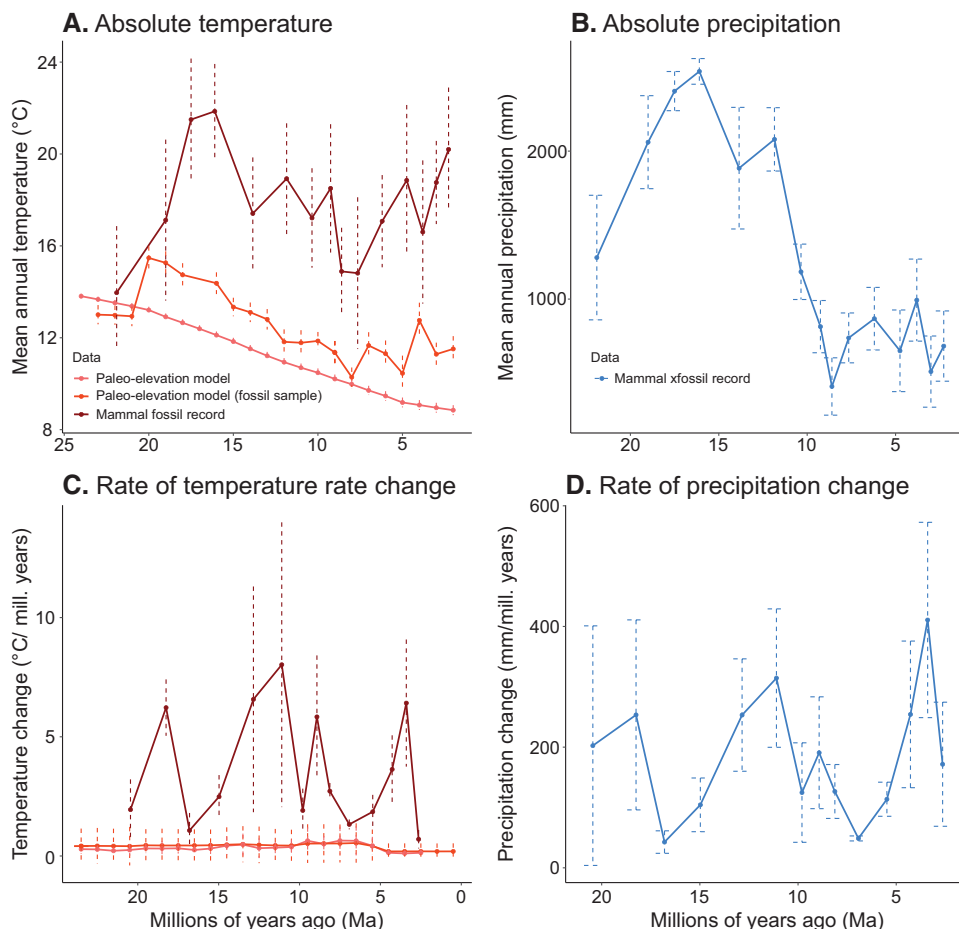


Figure 2. Absolute paleoclimatic values (A and B) and inferred rates of paleoclimatic change through time (C and D) for mean annual temperature (red) and precipitation (blue). Temperature values were inferred from the full mammal fossil record (dark red) and from reconstructions from Hagen et al. (2019) who used a paleoelevation modeling approach (red). In addition, we calculated temperature values from paleoelevation reconstructions only using localities for which we have fossil data (light pink). Rates of climatic change were calculated between successive time bins. Absolute precipitation (B) and rates of precipitation change (D) were only inferred from the mammal fossil record. Error bars for absolute climate variables inferred from the mammal fossil record were calculated as the mean of the standard errors for each region. Error bars show the standard error at each time point for each data source.

peak between MN5 and MN6 (roughly 12 million years ago; Fig. 2D).

RELATIONSHIP BETWEEN PALEOCLIMATE AND RATES OF NICHE EVOLUTION

We found no or weak evidence for a relationship between rates of paleoclimatic change and rates of climatic niche evolution in the wheatear-chat clade. First, we found a weak but significant negative relationship between rates of temperature change inferred from the paleoelevation model and rates of evolution for the three measures of the temperature niche (T_{\min} , T_{mean} , and T_{\max} , P -values < 0.04 , $R^2 < 0.3$; Fig. 3A and Table 1 for GAM results; see Table S6 for consistent GLS results). However, these significant negative relationships were driven by two time points, the two most recent time intervals (Fig. 3C); when these

are removed, the relationship is no longer significant for any of the three measures of temperature niche (P -values > 0.2). Second, we found no significant relationship between rates of paleoclimatic change inferred from the mammal fossil record and rates of evolution of the climatic niche for both temperature (Fig. 3D) and precipitation (Fig. S5 and Table S1).

We found mixed support for relationships between absolute paleoclimate and rates of climatic niche evolution. Specifically, we found a significant nonlinear relationship between absolute temperature conditions reconstructed using paleoelevation modeling and rates of evolution of the temperature niche (Fig. 3A and Table 1). With increasing temperature (between 9 and 11°C), estimated rates of niche evolution decreased almost linearly. Beyond 11°C, estimated rates of niche evolution did not change with temperature. Absolute temperature consistently explained

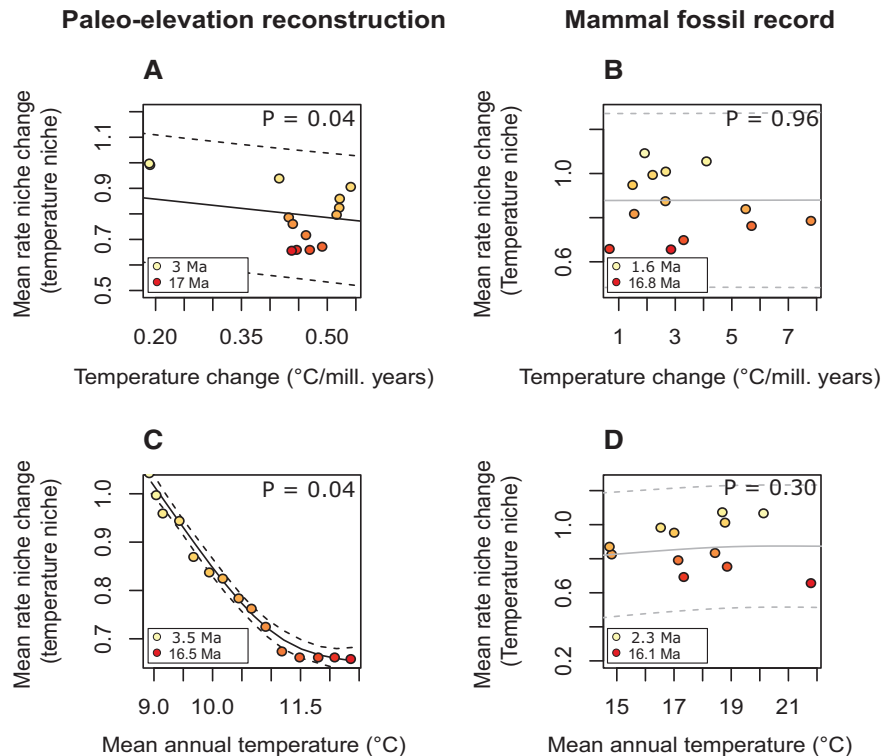


Figure 3. Relationship between temperature and rates of temperature niche evolution (T_{\min}) for rates of paleoclimate change (A and B) and absolute paleoclimate values (C and D). Results were consistent for the other two values of temperature niche (T_{mean} and T_{max}). Figure shows results using the two methods of paleoclimate reconstruction: Paleoclimate was inferred using a paleoelevation approach (A and C) and from the mammal fossil record (B and D). Prediction lines are shown in black for statistically significant relationships with confidence intervals. To highlight the temporal structure of the data, points are colored by the midpoint age of the time zones. Paleoclimatic conditions reconstructed from the mammal fossil record were calculated using the full fossil data set (mid-point assignment method).

a large amount of the variation across all metrics of temperature niche (all R^2 values > 0.9).

In direct contrast to this, we did not find a significant relationship between absolute temperature inferred from the mammal record and rates of evolution of any of the temperature niche values (Fig. 3D and Table 1). We also found no significant relationship between absolute precipitation inferred from the mammal fossil record and rates of evolution of precipitation niche (Table 1 and Fig. S4).

Discussion

For the study clade, estimated mean rates of niche change for both precipitation and temperature niche increased over time, indicating that niches changed faster closer to the present. In addition, we found four significant shifts in the precipitation niche across the wheatear-chat phylogeny. These changes were generally toward niches characterized as tolerating warmer and drier conditions. Despite these changes in the climatic niche, we found relatively little overall support for a relationship between

climatic conditions and rates of niche evolution through time. We inferred very different paleoclimatic temperature conditions depending on the method of reconstruction used. However, our inferences from both methods broadly match well-known trends that characterize the late Neogene with both methods showing an overall decline in temperature over the last 20 million years (e.g., see Fortelius et al. 2014).

We set out to test two hypotheses: (1) that there would be a positive relationship between rates of climate change and rates of niche evolution and (2) that there would be a (negative) relationship between absolute climatic conditions and rates of niche evolution. Support for the two hypotheses was found to vary depending on the aspect of the climatic niche studied (i.e., temperature vs. precipitation) and for temperature depending on the source of paleoclimatic reconstruction. Contrary to our first hypothesis, and expectations from the literature, we did not find a significant positive relationship between rates of climate change and rates of niche evolution for the period of interest for either temperature or precipitation, regardless of the method of paleoclimatic reconstruction. Although we did find a

Table 1. Results from the final GAMs testing for a relationship between rates of climatic niche evolution with (1) rates of change in paleoclimatic conditions and (2) absolute paleoclimatic conditions. Response variables were rates of climatic niche evolution (either temperature variables or precipitation) inferred based on phylogeny for the wheatear-chat clade. In the first set of models (1), the rates of paleoclimatic change in MAT and MAP were used as respective fixed effects. (2) Absolute paleoclimatic values for mean annual temperature and precipitation (MAT and MAP, respectively) were included as the fixed effects. In the second set of models, paleoclimate data were inferred using two different methods: (a) reconstructions of temperature using a paleoelevation model were used and (b) temperature and precipitation were inferred using the mammal fossil record. Temporal autocorrelation in the data structure was accounted for in the model.

	R^2 adjusted	F	P -value
(1) Rates of paleoclimatic change			
(a) Paleoelevation reconstruction			
T_{\min}	0.122	5.567	0.036
T_{mean}	0.259	12.668	0.004
T_{\max}	0.237	8.995	0.012
(b) Mammal fossil record			
T_{\min}	-0.0919	0.003	0.957
T_{mean}	-0.0919	0.002	0.970
T_{\max}	-0.0781	0.255	0.624
Precipitation	-0.0122	0.342	0.570
(2) Absolute climate values			
(a) Paleoelevation reconstruction			
T_{\min}	0.985	226.042	<0.001
T_{mean}	0.988	195.490	<0.001
T_{\max}	0.960	51.882	<0.001
(b) Mammal fossil record			
T_{\min}	-0.138	0.818	0.296
T_{mean}	-0.105	1.008	0.339
T_{\max}	-0.097	0.836	0.382
Precipitation	0.076	0.855	0.377

slight negative relationship between rates of temperature niche evolution and rates of temperature change through time inferred from the paleoelevation model, the statistical significance of this relationship was entirely driven by the two most recent time intervals and their drastically warmer temperature and slightly higher rate of climatic niche evolution. We found no evidence of a relationship between rates of temperature niche evolution and rates of temperature change inferred from the mammal fossil record. Regarding the second hypothesis, we found evidence that partly rejected a relationship between absolute conditions and rates of niche evolution through time, with the two methods of temperature reconstruction providing different results. There was a strong and significant negative relationship with temperature as reconstructed from paleoelevation modeling, but there were no

significant relationships with either temperature or precipitation as reconstructed from the mammal fossil record.

MIXED RESULTS FOR ABSOLUTE TEMPERATURE

Consistent with expectations that surviving species would have adapted to changing climatic conditions through time, we find a significant relationship between temperature as inferred from the paleoelevation reconstruction and the inferred rates of temperature niche change through time. Rates of niche evolution were found to decrease with increasing temperature, seemingly challenging the hypothesis that evolution is faster under warm climates, as expected if high mutation rates occur at high temperatures and drive fast rates of thermal niche evolution (Gillooly et al. 2005). However, our results are consistent with the observation that faster rates of evolution occur at high latitudes (where conditions are cooler), and that phylogenetic niche conservatism of thermal limits is higher in the tropics (Lawson and Weir 2014; Khaliq et al. 2015). The results are also consistent with previous studies showing that traits can evolve faster under cool conditions (Clavel and Morlon 2017). However, it is possible that high rates of niche evolution are not driven by cold temperatures as such, but instead climatic heterogeneity. The latitudinal gradient in rates of evolution is largely attributed to greater spatial heterogeneity in climate (i.e., a greater diversity of climatic conditions in a given area) in temperate regions than in tropical regions. It may be that across long timescales, periods of cold temperature correspond to periods of temperate biomes and consequently greater heterogeneity of climate in space (Clavel and Morlon 2017).

In contrast, we found no relationship between the inferred rates of climatic niche change and major regional trends in either absolute climate values or rates of climate change when using climatic values reconstructed using the mammal fossil record. This was the case for temperature, but also for precipitation (for which we have no comparison due to lack of other large-scale paleoclimate datasets). If the relationship between temperature and rates of thermal niche evolution exists, as indicated by temperature from the paleoelevation model, the lack of relationship using temperature from the mammal fossil record may partly be explained by its spatial bias. Although we worked to correct this bias, the geographic distribution of fossils is heterogeneous through time and thus estimates of climate may not be representative of the average conditions species were experiencing through time (Fig. S4). This notion is strengthened somewhat by our finding that recalculating the temperature from paleoelevation modeling for the locations and time intervals with data in the mammal fossil record leads to a temperature trajectory through time that appears more similar to the one for temperature reconstructed from the mammal fossils (Fig. S4).

Nevertheless, temporal dynamics of paleotemperature and consequently results for a relationship with rates of niche evolution were very different depending on the method of reconstruction used. It is unclear which reconstruction provides a more accurate representation of the true paleoclimatic conditions that taxa were exposed to: although the paleoelevation model offers a nominally higher spatiotemporal resolution, it is only indirectly based on proxy data, and apparently recovers long-term trends better than local and short-term heterogeneity. In contrast, the mammal fossil record is subject to spatial and temporal sampling bias, so the reconstructed paleoclimate appears much noisier, but may provide better direct evidence for local climatic conditions. It is therefore very difficult to conclusively determine from our study whether there is a general relationship between absolute temperature and rates of temperature niche evolution through time.

DOES CLIMATE MATTER FOR CLIMATIC NICHE EVOLUTION IN BIRDS?

Our results indicate support for only some of the postulated relationships. In particular, we find little support for a relationship between rates of paleoclimate change and rates of niche evolution. Our results suggest that instead of changing their climatic niches through adaptation, the wheatear-chat lineages exposed to paleoclimate change may have altered their geographic distributions or behavior to cope with environmental conditions (Virkkala and Lehikoinen 2017; Nogués-Bravo et al. 2018). Considering the high mobility of birds, it is likely that instead of adapting their niches they buffer climatic change through adaptive behavior such as large-scale movements or small-scale habitat and microhabitat choices (Keppel et al. 2017). This is particularly relevant to this study clade, as a disproportionate number of species (>30%) are migratory, and therefore have the potential to be highly mobile.

Indeed, relatively fast range shifts and expansions have already been observed in birds in response to current and ongoing climate change (Gillings et al. 2015; Massimino et al. 2015) and in mammals in response to past changes (Eronen and Rook 2004). For mobile organisms, such as birds, other factors such as habitat, resources, and competition may be more important for niche dynamics than climate (Jønsson et al. 2012; Pitteloud et al. 2017). This idea is supported by Khaliq et al. (2014) who showed that thermal tolerance limits of many bird species do not match ambient climatic conditions, indicating that, although undeniably important, environmental climatic conditions do not strictly limit species' distributions. Our results are also consistent with previous studies that show that at narrow phylogenetic extents (such as ours) biotic interactions such as competition are more important than climatic factors for determining bird occurrences (Barraclough and Vogler 2000; Graham et al. 2018).

Our rather mixed results appear in contrast with those of other studies pointing toward consistent associations between climate change and rate of climate niche changes. This might reflect a taxonomic bias in the literature. Many previous studies examining niche dynamics have focused on terrestrial nonvolant organisms, for example, 38 out of the nearly 40 empirical studies reviewed by Pearman et al. (2008) or studies on plant biogeographical history (Meseguer et al. 2018). However, birds' responses to changing climatic conditions may systematically differ due to their high mobility, and could be expected to be more similar to marine organisms because movement in the marine realm is also much less restricted (Webb 2012). Consistent with our results for birds, studies that have examined niche dynamics in marine taxa found that niches are relatively stable even when faced with significant environmental change (e.g., Stigall 2012; Saupe et al. 2014). However, it is worth noting that Liu et al. (2020) found that overall rates of niche evolution are similar for mobile terrestrial vertebrates and immobile plants.

SCOPE AND CAVEATS OF THE ANALYSES

Based on our results, we cannot dismiss the role of aspects of climate other than those investigated here, such as changes in seasonality or the emergence of novel climates, as being important to birds. Instead of average conditions, rates of niche change might rather be affected by extreme events (Greenville et al. 2012; Grant et al. 2017). For example, although we do not find a relationship between precipitation conditions and rates of inferred niche change through time, we do observe a sudden drop in precipitation around 12 million years ago (which is also seen as a spike in the rate of precipitation change), which appears to coincide with a peak in the estimated rates of precipitation niche change in the wheatear-chat clade. Hence, some niche changes may be driven by exceptional periods of strong climate change, but our results imply that this is not consistent over time. Further, we examined whether there is a relationship between rates of niche change and average climatic conditions across a very broad geographic range. If highly heterogeneous local climatic conditions are driving rates of niche change, we might fail to find a relationship between macroevolutionary trends and broad scale macroclimatic trends, at the scale we investigated. Moreover, it is important to consider that uncertainty of paleoenvironmental reconstructions drastically increases deeper in time (Dolman et al. 2020). Similarly, we tested for a relationship between climate and mean clade-wide rates of niche change. If some lineages respond to climate and others do not, or if lineages respond in opposing ways, we would not detect this from average rates.

As well as mechanistic explanations, there are methodological reasons why we might not find a relationship between climate and niche evolution. Although we have two very reasonable sets of paleoclimatic data, the mammal fossil dataset is still

comparably small (in terms of number of climatic estimates for each time bin and continent). Therefore, we could only infer climatic conditions at a coarse temporal resolution, severely limiting the statistical power for analyses from the fossil record, including the only analysis that was possible for precipitation. This may explain why we found a significant relationship with temperature, when inferred using the paleoelevational model but not when using the mammal fossil record.

Our study further highlights the difficulties surrounding paleoclimatic reconstructions. We recovered very nonoverlapping estimates of paleotemperature and consequently results depending on reconstruction method. It is unclear which reconstruction provides a more accurate representation of the climatic conditions that our taxa were exposed to and it is difficult to obtain robust uncertainty measures for either reconstruction. The mammal fossil record provides good local estimates of climatic conditions (Eronen et al. 2012); however, our analyses show that although we use an extensive dataset (compared to other paleodata), impacts of geographic biases and temporal resolution remain. To guide future studies, we emphasize a need for more integrated records from multiple proxies to increase spatial and temporal resolution and extent of reconstructions (Forrest et al. 2015; Hollis et al. 2019). Comparisons among different proxies and reconstruction methods could provide valuable quantifications of uncertainty (Axford et al. 2011; Evans et al. 2018). Moreover, improving paleo reconstructions and applying mechanistic models could be a path toward disentangling rates of niche evolution and environmental dynamics. Specifically, eco-evolutionary mechanistic models accounting for trait evolution and fossilization observer functions could reveal insights on niche evolution dynamics when validated by empirical data such as fossils.

Finally, a major caveat of studies reconstructing rates of climatic niche evolution is that the results are highly dependent on niche characterization methods (Evans et al. 2009; Dormann et al. 2010). Here, we assumed that the spatial distribution of species is representative of the full range of climatic conditions that a species is able to survive under (i.e., its fundamental niche). However, other factors such as competition also shape species' distributions (Soberón 2007), further confounding inferences about climate-niche evolution relationships.

Conclusions

We found no or weak evidence of a relationship between rates of paleoclimatic change and rates of niche evolution. In contrast, we found mixed evidence of a negative relationship between temperature and rates of niche evolution depending on the method used for paleotemperature conditions. We suggest that climatic niches in birds are only weakly linked to paleoclimatic change, presum-

ably because they can more easily respond to climate change by redistributing in space rather than by adapting their climatic niches. We highlight the need for more integrated records from paleoclimatic proxies or improved paleoclimatic models to provide better spatiotemporal coverage of terrestrial paleoclimate.

AUTHOR CONTRIBUTIONS

AE, SAF, and JTE designed the study. AE, OH, and JTE carried out the analyses. AE wrote this article with help from OH, SAF, JTE, and KBG.

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DATA ARCHIVING

Mammal fossil data used for paleoclimatic inferences are freely available online (NOW: New and Old Worlds database of fossil mammals: <http://www.helsinki.fi/science/now/>). Climate inferred using this mammal fossil dataset is available on Dryad <https://doi.org/10.5061/dryad.zgmsbcc9r> (link for review: https://datadryad.org/stash/share/JImhpsmWWBApVL7xoXDz-PBEGdcccxBi1zBV_kgH858) as are climatic niche quantifications based on range map data. Phylogenetic data are available from the Treebase Digital Repository: <http://purl.org/phylo/treebase/phylo/study/TB2:S23275>.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

- Figure S1.** Maximum clade credibility tree for the wheatear-clade as obtained in a BEAST analyses (figure from Phillips et al. 2020).
- Figure S2.** Overview of the methods used. Rates of niche evolution (1) were inferred from current climatic niches and a dated phylogeny using a variable rates model in BayesTraits.
- Figure S3.** Air surface temperature inferred using a paleoelevation reconstruction at 1-million-year temporal resolution and a 1° spatial resolution for our study region (Africa, Asia and Europe).
- Figure S4.** Distribution of mammal fossil localities used to infer paleoclimatic conditions through time.
- Figure S4.** The maximum clade credibility (MCC) phylogeny for Wheatears and Chats ($n = 65$ species) colored by estimates of the mean rates of trait evolution for climatic niche traits and mean rate of evolution through time calculated from 20,000 samples from a BayesTraits analysis for mean temperature (A and C) and maximum temperature (B and D).
- Figure S5.** Relationship between climate and rates of niche evolution for rates of paleoclimatic change (A: D) and absolute paleoclimatic conditions (E:J).
- Table S1.** List of study species and peak breeding months determined from descriptions in the Handbook of birds of the world (del Hoyo et al. 2019).
- Table S2.** Start and end dates of the Mammal Neogene (MN) zonation system. Numbers show the number of unique fossil localities in each MN zone using the two methods of assignment (strict and mid-point, respectively).
- Table S3.** Comparison of three univariate evolutionary models; Brownian motion (BM), Ornstein-Uhlenbeck (OU) and Early Burst (EB) for four niche metrics.
- Table S4.** Comparison of model adequacy for three univariate evolutionary models; Brownian motion (BM), Ornstein-Uhlenbeck (OU) and Early Burst (EB) for four trait values using the six metrics in ABUTUS: M_{SIG} , C_{VAR} , S_{ASR} , S_{HGT} , and D_{CDF} .
- Table S5.** Values of log marginal likelihood as estimated using a stepping stone sampler for variable rates model and a univariate rates model fitted using BayesTraits to each climatic niche variable.
- Table S6.** Results from the final GLS models testing for a relationship between rates of climatic niche evolution with (1) rates of change in paleoclimatic conditions and (2) absolute paleoclimatic conditions.
- Table S7.** The list of sources used for each region in the GeoMiB database, the source type, and the priority ranking for combining different sources for each species range map.