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Widespread correlations between climatic niche evolution and species diversification in birds

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Summary

1. The adaptability of species' climatic niches can influence the dynamics of colonisation and gene flow across climatic gradients, potentially increasing the likelihood of speciation, or reducing extinction in the face of environmental change. However, previous comparative studies have tested these ideas using geographically, taxonomically and ecologically restricted samples, yielding mixed results, and thus the processes linking climatic niche evolution with diversification remain poorly understood.

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2. Focusing on birds, the largest and most widespread class of terrestrial vertebrates, we test whether variation in species diversification among clades is correlated with rates of climatic niche evolution, and the extent to which these patterns are modified by underlying gradients in biogeography and species' ecology.

3. We quantified climatic niches, latitudinal distribution and ecological traits for 7657 (~75%) bird species based on geographical range polygons, and then used Bayesian phylogenetic analyses to test whether niche evolution was related to species richness and rates of diversification across genus and family-level clades.

4. We found that the rate of climatic niche evolution has a positive linear relationship with both species richness and diversification rate at two different taxonomic levels (genus and family). Furthermore, this positive association between labile climatic niches and diversification was detected regardless of variation in clade latitude or key ecological traits.

5. Our findings suggest either that rapid adaptation to unoccupied areas of climatic niche space promotes avian diversification, or that diversification promotes adaptation. Either way, we propose that climatic niche evolution is a fundamental process regulating the link between climate and biodiversity at global scales, irrespective of the geographical and ecological context of speciation and extinction.

Key-words: Climate, diversification, ecological traits, latitudinal gradient, niche evolution, niche conservatism

Introduction

Environmental conditions (e.g. temperature and precipitation) have long been viewed as key predictors of species richness across spatial and temporal scales (Wallace 1876). These conditions are often considered to be extrinsic factors that primarily shape patterns of diversity indirectly, for instance through their effects on productivity and habitat complexity, both of which correlate with species richness (MacArthur 1964; Hawkins, Porter & Diniz-

Filho 2003). In recent years, however, the focus has shifted away from examining the importance of particular environmental conditions (e.g. temperature), and towards understanding the role of intrinsic processes linked to climate, including the relationship between climatic niche evolution and species diversification (e.g. Kozak & Wiens 2007; Kozak & Wiens 2010; Cadena *et al.* 2012; Gómez-Rodríguez, Baselga & Wiens 2014; Title & Burns 2015). This link is intuitively appealing because it suggests that abiotic environmental factors influence patterns of diversity directly via deterministic evolutionary processes, such as local adaptation and the breakdown of gene flow. However, the role of climatic niches in diversification remains unclear, not least because contrasting hypotheses linking niche evolution and diversification have been proposed.

One hypothesis, focusing on niche lability, predicts that species' diversification is greatest among lineages in which climatic niches evolve rapidly (Moritz *et al.* 2000; Kozak & Wiens 2007; 2010). These labile climatic niches could facilitate colonisation of novel environments, leading to local adaptation in ecological or sexual traits, thereby reducing gene flow between populations and promoting reproductive isolation (Sobel *et al.* 2010; Hua & Wiens 2013). Similarly, lineages with wide environmental tolerances may have large geographic ranges that are more susceptible to vicariance events leading to speciation (Rosenzweig 1995) or be better able to resist extinction in periods of environmental change (Holt 1990). In contrast, a second hypothesis predicts that diversification may be greatest when climatic niches evolve slowly. This may occur when conserved climatic niches promote allopatric speciation by limiting dispersal across unsuitable habitats or climatic gradients, for example in lineages specialised to a particular climatic regime (Janzen 1967; Wiens 2004; Kozak & Wiens 2006; Cadena *et al.* 2012). If gene flow is consequently interrupted between previously contiguous populations, then diversification may be greatest in groups where climatic niche evolution is most constrained (Hua & Wiens 2013). The central tenet of both these hypotheses is that the dynamics of climatic niche evolution within lineages directly

influences species diversification, but they make contrasting predictions as to the direction of the correlation between diversification and rates of climatic niche evolution.

A number of previous studies have tested these predictions indirectly by assessing whether specific speciation events are associated with shifts in climatic niche. This approach has revealed that amphibian sister species inhabit both similar (e.g. Kozak & Wiens 2006) and dissimilar (Kozak & Wiens 2007) climatic conditions, while recent speciation events in other taxa, such as insects, birds and mammals, are also associated with (e.g. Rice, Martínez-Meyer & Peterson 2003; Eaton, Soberón & Peterson 2008) and without (e.g. Peterson, Soberón & Sánchez-Cordero 1999; Peterson & Nyári 2007) significant divergence in climatic niches. Similarly, more direct tests (i.e. those explicitly examining the relationship between rates of climatic niche evolution and species diversification) have also produced mixed results, finding either no association (Pyron & Wiens 2013) or positive associations (Kozak & Wiens 2010; Schnitzler *et al.* 2012; Title & Burns 2015) across taxa. However, such analyses have predominately focused on species diversification in the context of particular regions or clades, providing limited insight into the direction of relationships at larger spatial and temporal scales, and across groups with contrasting physiological traits. Moreover, comparative analyses have typically focused on linear relationships whereas species diversification may conceivably peak with intermediate levels of niche lability, producing non-linear associations.

Theoretically, the variation in previous results may also be partly explained by latitudinal and ecological variation among clades or species. Latitude, in particular, correlates strongly with many aspects of climatic variation. Increased thermal stability and zonation towards the equator potentially leads to narrower thermal tolerance, and hence reduced dispersal across climatic gradients, in tropical organisms (Janzen 1967). Thus, allopatric speciation among subdivided populations with conserved climatic niches may be more prevalent in tropical than temperate systems, modifying the relationship between

Accepted Article
climatic niche evolution and diversification (Kozak & Wiens 2007; Kozak & Wiens 2010; Cadena *et al.* 2012; Fisher-Reid, Kozak & Wiens 2012; Lawson & Weir 2014). Similarly, the association between niche evolution and diversification could be influenced by variation among species in ecological factors, such as habitat or dispersal ability (Gavrilets 2004; Cadena *et al.* 2012). The extent and direction of these associations is rarely considered because comprehensive data on phylogenetic history, climatic niche, latitudinal range and ecological traits have not been available for global samples of species.

To address this issue, we compiled distributional, environmental and ecological data to assess the relationship between climatic niche evolution and patterns of diversification across ~75% of extant bird species worldwide. We first quantified species' climatic niches using a suite of environmental variables extracted from mapped breeding range distributions. These geographical distributions do not provide direct insight into the environmental niche, yet their boundaries are predicted by climatic variables, even in migratory species (Pigot, Owens & Orme 2010). In line with many previous studies, we therefore assume that climatic variables extracted from breeding range distributions provide a valid estimation of the realised climatic niche of each species. We then used phylogenetic models to test for linear and non-linear associations between rates of niche evolution and lineage diversification. In addition, we investigated the mechanism driving rates of niche evolution by asking whether faster niche rates were positively or negatively associated with levels of climatic variance within species (estimated across the geographical range). Our assumptions were that intraspecific climatic variance will increase if diversification is predominantly driven by the colonisation of novel environments (niche expansion), but decrease if diversification reflects the splitting of wide-ranging parent lineages into daughter lineages with smaller ranges (niche subdivision). Finally, by incorporating latitudinal range and ecological traits into our models, we further considered whether the association between niche evolution and diversification was modified by major biogeographical or ecological factors, including habitat, behaviour, and migration.

Birds provide a useful system for these analyses for three main reasons. First, comprehensive and relatively accurate data are available on geographical ranges, habitat preferences and ecological traits for all avian species, most of which are included in comprehensive phylogenetic analyses (Jetz *et al.* 2012). Second, since birds occur across an almost full spectrum of climatic conditions, latitudes and habitats, we are able to explore the link between climatic niche evolution and diversification in unprecedented detail and with much improved sample size. Finally, the combination of datasets available for birds allows us to examine the association between climatic niche evolution and diversification at contrasting taxonomic scales. Specifically, we ran models across both genus- and family-level clades, which theoretically differ in their average age, offering two alternative perspectives on the role of climatic niche evolution over time.

Materials and methods

PHYLOGENETIC DATA AND CLADE SELECTION

As a phylogenetic framework, we used species-level molecular phylogenies compiled by Jetz *et al.* (2012). These trees were constructed in a Bayesian framework, combining multi-gene phylogenetic inference (6670 species) with a taxonomic placement approach (3323 species), overlaid on the Hackett *et al.* (2008) family-level backbone. To account for phylogenetic uncertainty, we sampled 500 trees from the posterior distribution of complete trees provided by Jetz *et al.* (2012). Each tree in this sample then formed the basis for an independent run of all subsequent analyses.

In the Jetz *et al.* (2012) phylogenies, both genus and family-level clades are frequently reconstructed as para- or polyphyletic, so we used a standardised procedure to test for monophyly, and restricted our sample to monophyletic clades (see online supplementary material). We also excluded clades containing fewer than four species with climatic data. The removal of small or data-poor clades can potentially bias analyses (e.g. Ricklefs & Jönsson 2014), but some thinning of the dataset is necessary to avoid the

problems associated with calculating rates of evolution in very small clades (Kozak & Wiens 2010; Rabosky *et al.* 2013). We therefore attempt to strike a balance by including all but the very smallest clades (1–3 species). Applying this clade selection procedure across the distribution of trees provided 500 ‘pseudoreplicate’ samples of clades (Appendix; fig. S1) containing a median of 96 (range: 93–100) family-level clades and 507 (503–511) genus-level clades (total $n = 7657$ species). On average across all datasets, family-level clades were substantially older (mean = 31.5 Myr) than genus-level clades (11.9 Myr; fig. S2; t-test, $t_{601} = 17.83$, $P < 0.001$) across all pseudoreplicate datasets, and thus differ markedly in the temporal scale of evolutionary history that they represent. For further details of phylogenetic methods and clade selection see electronic supplementary material.

METRICS OF CLADE DIVERSIFICATION

We opted not to use the most sophisticated methods available for exploring lineage diversification (e.g. Etienne & Haegeman 2012) because fitting such models to large datasets is challenging. Furthermore, parameter estimates derived from these models can be strongly interrelated and subject to bias according to clade age and relative extinction intensity (see Etienne *et al.* 2012), potentially making them difficult to interpret when applied to a wide sample of clades. Instead, we focused on two relatively simple and transparent methods for estimating clade diversification, following a number of recent studies (e.g. Rabosky & Matute 2013; Title & Burns 2015; Wiens 2015). One approach involved calculating net diversification rates, which in its simplest form can be estimated by dividing ln-transformed (extant) species richness by clade age. Another focused on variation in (ln-transformed) clade richness, which captures the total time-integrated diversification experienced by a clade.

The validity of both these approaches depends on the relationships between species richness, diversification rate and clade age (Rabosky 2010). To explore this issue, we used Bayesian phylogenetic mixed models (BPMs; Hadfield 2010) to test the relationship

between both metrics of diversification and crown group age in our dataset. Although older clades were characterised by lower estimated diversification rates—indicative of non-constant rates of species accumulation over time—we also found weakly positive relationships between clade age and species richness in both families and genera (fig. S3), suggesting that each approach provides some useful information about diversification (see online supplementary material). As there was no conclusive evidence favouring the use of one diversification metric over another, we ran our final analyses using both metrics.

RATES OF CLIMATIC NICHE EVOLUTION

Although birds are arguably the best-known class of organisms, detailed data on physiological tolerance and fine-scale occurrence records are not available for most species. Thus, to characterise species' climatic niches, we used geographic range maps of species' breeding distributions from BirdLife International and NatureServe (available from www.birdlife.org) linked to global climate layers (Hijmans *et al.* 2005). We overlaid range maps with a ~10 x 10 km equal area grid in Behrman projection and then used grid cell occurrence to extract environmental conditions at the same resolution. For each grid cell occupied by one or more species, we extracted values for 19 bioclimatic variables plus elevation from the WorldClim dataset, which together provide a comprehensive set of environmental variables frequently used to characterise species' broad-scale climatic niches (e.g. Kozak & Wiens 2010; Pigot, Owens & Orme 2010; Cooper, Freckleton & Jetz 2011; Botero *et al.* 2014; Gómez-Rodríguez, Baselga & Wiens 2014).

It is worth noting that our niche estimates may not accurately capture the full range of climatic conditions experienced by migratory species because environmental data are only extracted from breeding ranges. While incorporating additional information from non-breeding ranges would be preferable in these cases, it is difficult to quantify the environmental conditions experienced by migratory birds over the course of a year because the timing of migrations and migratory stopovers are complex and often poorly documented,

Accepted Article

as are the true extent of non-breeding distributions. For these reasons, we follow other global studies of avian climatic niches (e.g. Pigot, Owens & Orme 2010; Botero *et al.* 2014) by focusing on breeding ranges, which are generally more accurately documented and likely to play a more crucial role than wintering ranges in the context of gene flow, speciation and diversification. See online supplementary material for further explanation and justification of our approach.

All climatic variables were log-transformed and standardised (Cooper, Freckleton & Jetz 2011) before being subjected to a principal components analysis (PCA). This procedure identified two dominant PCs (fig. S4; table S1) explaining more variation in climatic variables than expected under a neutral broken stick model (Kozak & Wiens 2010). These two PCs were used in all subsequent analyses. To characterise climatic variation between species, we calculated species' mean PC scores in each climatic axis, and then used these values to infer clade-level rates of niche evolution (see below). For each species, we estimated levels of within-species (intraspecific) variation in species' climatic niche traits by calculating the range-wide variance in climatic PC scores (both axes) generated for all grid cells overlapping the geographical distribution. In total, we estimated climatic niche parameters for 7499 (98%) species in our dataset.

To infer rates of climatic niche evolution, we followed established methodological approaches (e.g. Cooper, Jetz & Freckleton 2010; Cooper, Freckleton & Jetz 2011; Machac, Storch & Wiens 2013; Quintero & Wiens 2013; Title & Burns 2015) by using phylogenetic models of trait evolution in the R package *geiger* (Pennell *et al.* 2014) to estimate the Brownian rate parameter (σ^2) under Brownian motion (BM) and Ornstein-Uhlenbeck (OU) models of evolution. We estimated rates of niche evolution for all clades in our dataset under each model, and then assessed relative model fit by calculating Akaike weights based on AIC scores. Using these scores, we then calculated a model-averaged estimate of σ^2 for each PC within each clade using the weighted sum of σ^2 estimates derived from each

model. However, we also studied the effects of (i) using rates derived from a single model only (BM or OU) and (ii) using rates estimated from clade trees pruned to include only those species represented in the Jetz *et al.* (2012) phylogenies by genetic data. It is worth noting that by estimating σ^2 using phylogenetic methods, we assume that climatic variance within clades represents evolved differences among species rather than plasticity alone. Given that plasticity almost certainly contributes to climatic niche differences across our sample, the rates we calculate might best be viewed as climatic niche divergence. However, we refer to them as rates of climatic niche evolution, both for the sake of consistency with previous studies, and because evolutionary adaptation often plays a major role in setting bioclimatic limits at large spatial scales (e.g. transitions between biomes with contrasting vegetation). For further details and justification of our approach, see online supplementary material.

LATITUDE AND ECOLOGICAL TRAITS

To investigate the influence of geographical distribution and ecological traits on the relationship between climatic niche evolution and diversification, we quantified clade latitude and ecological traits for all species in our analysis. For clade latitude, we used range maps to calculate latitudinal centroid values for each species, and then generated mean (absolute) values as an estimate of the dominant latitudinal position of each clade. To capture ecological variation among clades, we quantified three key ecological attributes—habitat, territorial system, and migratory behaviour—all of which are related to dispersal ability, with important implications for gene flow (Salisbury *et al.* 2012). For each ecological axis, species were assigned to one of three categories based primarily on information provided in *The Handbook of the Birds of the World* series (del Hoyo *et al.* 1992–2011; see supplementary online material). In total, we collated data on latitude and ecological traits for 7648 (99%) species in our dataset. To convert species-level data to clade-level indices, we averaged the species means for each ecological trait across all species within a clade. Further details,

including an expanded justification for the use and classification of ecological variables, are presented in the electronic supplementary material.

PHYLOGENETIC COMPARATIVE ANALYSES

We used BPMMs (Hadfield & Nakagawa 2010) to assess the correlation between climatic niche evolution and diversification. As in phylogenetic generalised least-squares (PGLS) regression models, the BPMM approach is capable of estimating both phylogenetic and non-phylogenetic (i.e. residual) sources of variation, with the added benefit that it is possible to model data with alternative (i.e. non-Gaussian) error structures (see below). In the first set of analyses, we tested whether clade diversification was predicted by linear or non-linear (quadratic) relationships with model-averaged rates of climatic niche evolution. These analyses were performed across both family- and genus-level clades. To test the consistency of these relationships, we re-ran models using: (i) non-model-averaged niche rates estimated from single models (BM or OU), (ii) niche rates derived from clade trees pruned to contain only species placed by genetic data, and (iii) data restricted to clades containing 10 or more species. We also assessed whether rates of interspecific climatic niche evolution were positively or negatively correlated with levels of clade-averaged intraspecific variance in climatic conditions.

In a second set of analyses, we focused on the effect of latitude and ecology on the relationship between climatic niche evolution and diversification. We began by fitting models containing our niche rate variable plus latitude and all four ecological variables. We then examined whether the relationship between niche rate and diversification varied with latitude or ecology by fitting models in which diversification was predicted by the interaction between climatic niche rate and each latitudinal/ecological variable. We chose not to run models containing all variables and their interactions with climatic niche evolution to avoid problems associated with over-parameterisation and interpretation of highly complex models including multiple interactions. For clarity, therefore, we tested the interaction between niche rate and

each ecological variable separately. This second set of analyses focused specifically on genera because geographic and ecological variables are likely to provide a more accurate index of species' traits within genera than families because data are averaged across fewer species.

In all cases, we incorporated phylogenetic uncertainty in our parameter estimates by running each model set over the entire range of pseudoreplicate datasets. We inferred the overall significance of predictors using the median P_{MCMC} value across these datasets, and also by counting the frequency of models (f) in which the predictor was statistically significant ($P_{MCMC} < 0.05$), following Botero *et al.* (2014). Diversification rate models and models of (ln-transformed) family-level species richness were run using a Gaussian error structure, whereas for genus-level species richness we assumed a quasi-Poisson error with a ln-link because richness values were highly right-skewed (Botero *et al.* 2014). Rate variables were ln-transformed and all predictor variables were centered and standardised prior to analysis to aid interpretation of relative effect sizes (Schiegg 2010). To account for any region-specific effects, we also included 'Continent' as a random effect in all our models, with each clade being unambiguously assigned to a particular continent based on the position of the majority of occupied grid cells. BPMMs were run using the R package *MCMCglmm* and each model was run for 110000 iterations with a burn-in of 10000 iterations and thinning interval of 25 iterations, using flat uninformative priors and uniformly low levels of belief (Hadfield 2010).

Results

RATES OF CLIMATIC NICHE EVOLUTION

Using PCs describing two major axes of variation in avian climatic niches (Fig. 1, table S1), we estimated model-averaged rates of climate niche evolution for each clade in our analysis (>300000 clades tested across 500 pseudoreplicate trees). In general, across both families and genera, climatic niche evolution in both PC axes was best characterised by an OU

model of trait evolution (fig. S5), in which climatic niches evolve randomly within bounds. However, an unbounded BM model received slightly higher levels of support among genera than family-level clades (fig. S5), possibly because climatic niche evolution is less constrained in genus-level clades. We note however that this pattern could also reflect reduced statistical power to reject BM models among genera simply because they typically contain a smaller sample of species.

CLIMATIC NICHE EVOLUTION AND DIVERSIFICATION

We found strong evidence of a positive linear relationship between diversification and rates of climatic niche evolution across both families (Fig. 2A,C) and genera (Fig. 2B,D), regardless of whether we used (ln-transformed) species richness values (i.e. total diversification) or net diversification rates as our metric of clade diversification (table S2). However, we detected no significant non-linear (quadratic) relationships between either family- or genus-level diversification (table S2). In general, these findings were highly consistent across pseudoreplicate datasets (table S2) and alternative analytical approaches, including those based on (i) niche rates derived from either BM or OU models separately (tables S3 and S4), (ii) niche rates estimated using only those species in clades represented by genetic data (table S5), and (iii) only clades containing 10 or more species (tables S6).

When we assessed whether intraspecific variance in climatic conditions was correlated with rates of climatic niche evolution, we found that these two variables were significantly albeit weakly positively correlated across both family- and genus-level clades, irrespective of the dataset used (Table S7). In other words, across both families and genera, clades exhibiting the fastest rates of climatic niche evolution also had, on average, higher levels of within-species climatic variance (Fig. 3).

THE ROLE OF LATITUDE AND ECOLOGY

Habitat, territoriality and migration were uncorrelated with genus species richness, and thus do not explain the link between rates of climatic niche evolution and total diversification (table S8). Latitude was correlated with genus species richness, which increased moderately towards the tropics, but again this had little effect on the strong positive relationship between rates of niche evolution and total diversification (table S8). Similarly, we found that the association detected between climatic niche evolution and diversification rates across genera was not explained by the same set of biogeographic and ecological variables (table S8).

When we fitted separate models with interaction terms to explore these associations in more detail, we found no evidence that the slope of the relationship between climatic niche evolution and genus diversification varied deterministically with variation in either latitude or ecology (Table 1). In all cases, models containing an interaction term between niche rate variables and clade latitude or ecology provided no significant increase in explanatory power (interaction terms $P_{MCMC} \gg 0.05$; Table 1), a pattern found irrespective of the metric used (table S9). Taken together, these results imply that the linear association between rapid rates of niche evolution and genus-level diversification is largely consistent across both major clades of the avian tree (passerines and non-passerines), and regardless of differences in geography and ecology.

Discussion

We have shown that positive relationships between rates of climatic niche evolution and diversification are pervasive at global scales in birds: labile climatic niches are associated with greater species richness and faster rates of diversification across both avian genera and families. Moreover, the same linear relationships were also detected regardless of the methods used to quantify niche evolution and diversification. These findings are consistent with the view that rapid adaptation to novel climatic regimes drives diversification, and that

this coupling between fast rates of niche evolution and diversification is maintained over a range of evolutionary timescales.

The link we identify between rapid shifts in climatic regimes and the build up of clade diversity is opposite to the pattern predicted by the niche conservatism hypothesis, and instead supports a positive association between niche lability and diversification. Similar relationships have now been reported in plants (Schnitzler *et al.* 2012), ectothermic vertebrates (Kozak & Wiens 2010), and endothermic vertebrates (Title & Burns 2015). However, while each of these previous studies was focused on restricted geographic or taxonomic sampling (the Cape Flora of South Africa, the plethodontid salamanders of the New World, and the thraupid tanagers of the Neotropics, respectively), our results confirm that the relationship holds for an entire globally distributed class of organisms, implying a much more general link between niche lability and diversification.

One possible explanation for this association is that climatic niche evolution has a direct effect on the likelihood of speciation and extinction, for example when populations inhabiting contrasting environments speciate as a result of reduced gene flow (Kozak & Wiens 2007; Sobel *et al.* 2010). In the most commonly postulated form of this scenario, niche evolution facilitates range expansion and larger ranges are then more likely to be subject to vicariance events than smaller ranges (Pigot *et al.* 2010). When populations colonise new environments they may be subjected to different environmental conditions, which in turn drive divergence in ecological traits and mating signals (Schluter 2001; Hua & Wiens 2013). This may apply either to geographically isolated populations, or to contiguous populations under the gradient model of speciation (Moritz *et al.* 2000), in which reproductive isolation evolves as a result of local adaptation across steep environmental gradients (Rice, Martínez-Meyer & Peterson 2003; Eaton, Soberón & Peterson 2008). Regardless of spatial context, the adaptability of individual lineages to divergent climatic conditions may directly promote speciation, potentially driving the positive relationship between rates of climatic niche evolution and diversification.

An alternative explanation is that the relationship is a by-product of indirect processes. For instance, when diversification occurs through vicariance events, a link between diversification and fast rates of climatic niche evolution could emerge if descendent species are forced to diverge rapidly into novel environments due to range expansion, or through competition among daughter species (Weir & Price 2011). Under this scenario, fast rates of climatic niche evolution are a consequence, rather than a cause, of species diversification. Nonetheless, range expansion is necessary for repeated rounds of speciation in birds (Rosenzweig 1995; Weir & Price 2011), and thus the ability to adapt rapidly to divergent climatic conditions may promote diversification, either because it permits range expansion directly through colonisation of novel environments, or indirectly through the displacement of competing species to unoccupied areas of climatic niche space. For similar reasons, climatic niche lability theoretically reduces the risk of extinction (Title & Burns 2015). Thus, although it is not possible to determine the direction of causality underlying the correlations we detect, the most likely interpretation is that climatic niche lability promotes species diversification through direct and indirect effects on speciation and extinction.

Because of the global scale of our sampling, we are able to test whether the positive associations identified between climatic niche evolution and diversification are mediated by underlying correlations with latitude and ecology. When we tested for these effects across genera, we found no evidence that the relationship is altered towards the equator. This is contrary to the prediction that increased climatic zonation in the tropics will facilitate greater specialisation to climatic conditions, thereby reducing gene flow and increasing speciation when populations with conserved climatic niches are separated by regions of unsuitable climate (Janzen 1967; Cadena *et al.* 2012). We also find no evidence that climatic niche lability and species diversification are more strongly coupled among high latitude genera, despite greater opportunities for climate-mediated divergent selection in the temperate zone and the observation that rates of climatic niche evolution among recently diverged species peaks at high latitudes (Lawson & Weir 2014). Furthermore, the niche evolution–

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diversification relationship does not appear to be regulated by key ecological traits (habitat, territorial system, migration), despite their association with species' differences in dispersal ability (Moore *et al.* 2008; Salisbury *et al.* 2012). This is perhaps unexpected given that speciation occurs over a smaller geographic scale in non-dispersive organisms (Kisel & Barraclough 2010), frequently involving narrow geographic barriers that separate populations in essentially uniform climatic environments, particularly in the tropics (Kozak & Wiens 2006; Peterson & Nyári 2007; Cadena *et al.* 2012). The message of our analyses is that, while niche conservatism may drive speciation in some clades, it does not explain overall patterns of diversification.

Theoretically, the link between climatic niche lability and species diversification should weaken if clades reach the limits of accessible climatic niche space (e.g. those set by impermeable biogeographic barriers, such as oceans), as new species must then originate within areas of niche space already occupied by existing members of the clade. After this stage is reached, continued lineage diversification may become more strongly regulated by mechanisms facilitating species coexistence through ecological (e.g. MacArthur 1972) or reproductive (e.g. Gröning & Hochkirch 2008) isolation, rather than bioclimatic limits. However, our findings are consistent with the idea that many avian families have not yet reached limits of accessible niche space, supporting the notion that niche lability influences patterns of species richness and diversification rates in older clades (Title & Burns 2015), presumably because they continue to accumulate new species by expanding their 'adaptive zone' and thus by filling unoccupied areas of climatic niche space (Vermeij 1973; Rabosky & Adams 2012; Rabosky *et al.* 2013).

A major caveat in large-scale comparative studies of climatic niche evolution is that results are partly contingent on the method used to characterise species' climatic tolerances. Given the lack of unbiased fine-scale distributional data for most species at global scales, we used standard methods based on geographical range polygons (e.g. Pigot, Owens &

Orme 2010; Cooper, Freckleton & Jetz 2011; Botero *et al.* 2014). This approach is based on the assumption that the spatial range of each species reflects their fundamental climatic niche—that is, the full combination of climatic variables in which that species could exist (Soberón 2007). However, the coarse grain sizes of such analyses, combined with the fact that geographical distributions may be shaped by other factors including competitive exclusion (Pigot & Tobias 2013) and dispersal limitation (Pigot & Tobias 2015), mean that they realistically provide only an imperfect approximation of species' realised climatic niches (Wisz *et al.* 2013). Nonetheless, broad-scale geographical distributions can provide a reasonable estimate of physiological tolerances or the maximum extent of the environmental niche, even in endothermic organisms like birds (Tingley *et al.* 2009; Pigot, Owens & Orme 2010; Khaliq *et al.* 2014; Khaliq *et al.* 2015). Moreover, although it can be argued that the approach increases error, there is no reason to suspect that this issue should consistently bias our results towards detecting a positive effect, and thus if anything it merely weakens the relationship between climatic niche evolution and diversification. Our results therefore represent a conservative test of climatic niche–diversification relationships.

The error introduced in climatic niche estimation provides one explanation for the relatively low explanatory power of our analyses, but there are at least two other possible interpretations. First, the relationship between climatic niche evolution and diversification may be relatively weak in birds because they are endotherms, and thus geographical ranges are less tightly constrained by climatic tolerances (Buckley & Jetz 2008; Araújo *et al.* 2013). Second, the relationship may be strong but offset by an opposing effect. For example, niche lability and niche conservatism may both be driving speciation in different contexts, thereby weakening the inferred relationship between these variables at broad scales. However, given that our analyses revealed only positive associations between rates of niche evolution and diversification, we suggest that any such positive effect of niche conservatism on speciation is outweighed to a large extent by the strong diversifying effect of niche lability. Further support for this conclusion is provided by our finding that clades characterised by

faster rates of climatic niche evolution between species also exhibited greater average levels of climatic variance within species.

Although our results do not identify the extent or direction of causality, they indicate that climatic niche lability is an important correlate of avian diversification across a comprehensive span of latitudes and contrasting ecological settings. These findings are consistent with the hypothesis that rapid adaptation to novel climatic niches promotes speciation and/or impedes extinction. The generality of this pattern across both avian genera and families highlights the importance of evolutionary processes in regulating the link between climate and biodiversity across broad temporal and spatial scales.

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Data accessibility

Data is available from Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4mp30> (Cooney, Seddon & Tobias 2016).

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Detailed methods for phylogenetic analyses and compilation of ecological trait data. Includes Tables S1–S9, and Figs S1–S5.

Author contributions

C.R.C., N.S. and J.A.T. developed the conceptual framework and collected data. C.R.C. conducted the analyses. C.R.C. and J.A.T. wrote the manuscript.

Figure captions

Figure 1. Climatic niche variation across 7499 bird species plotted in relation to the global extent of available environmental conditions, depicted in grey. Coloured points show the position of each occupied $\sim 10 \times 10$ km grid cell in bivariate climatic niche space, as quantified by the first two principal components (PCs) derived from 19 climatic variables, plus elevation (see table S1); colours indicate variation in species richness. Grey points show unoccupied grid cells and thus unexploited regions of climatic niche space, occurring primarily at the coldest and wettest extremes (e.g. polar regions).

Figure 2. The relationship of total diversification (i.e. ln-transformed species richness; A, B) and diversification rate ($\epsilon = 0.45$; C, D) with model-averaged climatic niche rates derived from BM and OU models across avian family- and genus-level clades. For clarity, plotted points are from one pseudoreplicate dataset whereas regression lines indicate significant relationships between variables based on median parameter values (solid black line) from BPMM models fitted to 500 pseudoreplicate datasets (grey lines). Median sample size of clades: 96 at family level and 507 at genus level.

Figure 3. The relationship of between-species (i.e. interspecific) climatic niche rate with levels of within-species climatic variance for family (A) and genus-level (B) clades. Shown are clade-averaged intraspecific variance estimates and model-averaged climatic niche rates derived from BM and OU models fit to both climate PC axes. For clarity, plotted points are from one pseudoreplicate dataset whereas regression lines indicate significant relationships between variables based on median parameter values (solid black line) from BPMM models fitted to 500 pseudoreplicate datasets (grey lines). Median sample size of clades: 96 at family level and 507 at genus level.

Table 1. Summary of results of BPMM models of genus diversification including interactions with latitudinal and ecological variables, using model-averaged climatic niche rates derived from BM and OU models. Results shown are median values for models fitted to 500 pseudoreplicate datasets, and the frequency of models (f) in which the predictor was statistically significant ($P_{MCMC} < 0.05$). Total diversification, diversification rate and niche rate were ln-transformed and predictor variables were standardised prior to analysis.

Parameter	Total diversification			Diversification rate ($\epsilon = 0.45$)		
	β (95% CI)	P_{MCMC}	f	β (95% CI)	P_{MCMC}	f
Niche rate	1.44 (1.19, 1.70)	<0.001	1.00	0.39 (0.29, 0.49)	<0.001	1.00
Latitude	-0.67 (-0.95, -0.40)	<0.001	1.00	-0.11 (-0.24, 0.02)	0.112	0.27
Niche rate * latitude	-0.05 (-0.54, 0.44)	0.680	0.00	0.12 (-0.07, 0.31)	0.228	0.12
Niche rate	1.40 (1.14, 1.67)	<0.001	1.00	0.38 (0.28, 0.48)	<0.001	1.00
Habitat	-0.35 (-0.62, -0.09)	0.010	0.93	0.01 (-0.12, 0.15)	0.694	0.00
Niche rate * habitat	0.17 (-0.33, 0.66)	0.490	0.01	0.09 (-0.11, 0.30)	0.364	0.03
Niche rate	1.32 (1.06, 1.57)	<0.001	1.00	0.37 (0.27, 0.47)	<0.001	1.00
Territoriality	-0.05 (-0.31, 0.20)	0.684	0.00	0.15 (0.01, 0.30)	0.037	0.60
Niche rate * territoriality	0.17 (-0.31, 0.65)	0.479	0.03	0.08 (-0.11, 0.28)	0.392	0.05
Niche rate	1.36 (1.12, 1.62)	<0.001	1.00	0.38 (0.28, 0.48)	<0.001	1.00
Migration	-0.41 (-0.69, -0.14)	0.004	1.00	-0.01 (-0.14, 0.12)	0.706	0.00
Niche rate * migration	0.06 (-0.44, 0.56)	0.679	0.00	0.12 (-0.07, 0.30)	0.224	0.11
Niche rate	1.32 (1.07, 1.57)	<0.001	1.00	0.38 (0.28, 0.49)	<0.001	1.00
Passnonpass:pass	0.13 (-0.19, 0.45)	0.399	0.00	0.36 (-0.29, 1.01)	0.284	0.00
Niche rate * passnonpass	0.29 (-0.19, 0.77)	0.246	0.12	-0.09 (-0.29, 0.11)	0.380	0.04





