

1 Male-biased sexual selection, but not sexual dichromatism, predicts
2 speciation in birds

3

4 **Abstract**

5 Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates.
6 However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many of
7 the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes. Here,
8 we test whether the strength of sexual selection predicts variation in speciation and extinction rates across
9 passerine birds (up to 5,812 species, covering most genera). We use two measures of sexual selection
10 (sexual dichromatism and a multivariate measure of male-biased sexual selection) and adjust for range
11 size and environmental variability. Male-biased sexual selection, but not sexual dichromatism, predicted
12 speciation rates (λ_{DR}) in passserines. This relationship was independent of range size or environmental
13 variability, though species with smaller ranges had higher speciation rates. There was no association
14 between sexual selection and extinction rate (μ_{BAMM}). Our findings suggest that sexual dichromatism is
15 a poor proxy for sexual selection at least a broad-scale and support the view that sexual selection has
16 shaped diversification in songbirds.

17 INTRODUCTION

18 Sexual selection is a ubiquitous evolutionary process whose effect on diversification is much debated (Lande
19 1981, 1982; West-Eberhard 1983; Seddon et al. 2008; Cooney et al. 2018). Sexual selection can promote
20 speciation because it operates on traits that can create reproductive isolation when they diverge between
21 lineages, such as signals and preferences involved in mate selection (Lande 1981, 1982; Safran et al. 2013),
22 sperm-egg interactions (Swanson and Vacquier 1998), or genital morphology (Sloan and Simmons 2019).
23 Sexual selection could also promote speciation or prevent extinction by purging deleterious mutations
24 (Whitlock and Agrawal 2009), fixing beneficial ones (Whitlock 2000), and accelerating adaptation in different
25 environments (Lorch et al. 2003; Candolin and Heuschele 2008; Cally et al. 2019). Conversely, sexual
26 selection might hinder speciation or make extinction more likely by favouring traits that improve mating
27 success but reduce population fitness (Kokko and Jennions 2008; Rankin et al. 2011; Holman and Kokko
28 2013; Fromhage and Jennions 2016). For example, species with costly sexual signals may be less resilient to
29 environmental change (Kokko and Brooks 2003). Extinction risk may also be exacerbated by sexual selection
30 causing maladaptation ('gender load') in female traits that are genetically correlated with sexually-selected
31 male traits (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009; Harano et al. 2010; Pennell
32 and Morrow 2013; Berger et al. 2014). Although numerous studies have examined the relationship between
33 sexual selection and speciation or extinction rates (Barraclough et al. 1995; Morrow et al. 2003; Seddon et al.
34 2008, 2013; Kraaijeveld et al. 2011; Huang and Rabosky 2014), the availability of more complete phenotypic,
35 ecological and phylogenetic data (Jetz et al. 2012), together with significant advances in phylogenetic methods
36 (Rabosky 2014; Harvey Michael et al. 2017), present new opportunities to test whether and how sexual
37 selection drives diversification.

38 The relationship between sexual selection and diversification may depend on the environment. Theoretical
39 work predicts that sexual selection should have a more positive effect on adaptation and population fitness
40 in variable environments relative to stable ones (Long et al. 2012; Connallon and Hall 2016). In stable
41 environments, consistent selection depletes genetic variation at sexually concordant loci (i.e. loci where the
42 same allele is fittest for both sexes). In these environments, genetic variation remains disproportionately
43 at sexually antagonistic loci, leading to stronger gender load and reduced net benefits of sexual selection
44 (Connallon and Hall 2016). By contrast, in spatially or temporally variable environments, sexual selection can
45 enhance local adaptation. For example, in Darwin's finches (*Geospiza fortis*) divergent beak morphology is an
46 adaptation to local food availability that has been maintained through assortative mating (Huber et al. 2007).
47 Despite the potential interaction between sexual selection and environmental variability in diversification,
48 phylogenetic tests are currently lacking.

49 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (Bar-
50 raclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014) because
51 their biology and phylogenetic relationships are comparatively well-known. A 2011 meta-analysis covering 20
52 primary studies of birds and other taxa found a small but significant positive association between sexual
53 selection and speciation, with the average effect size in birds stronger than in mammals but weaker than in
54 insects or fish (Kraaijeveld et al. 2011). However, there was large variation in effect size estimates across the
55 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and
56 sexual selection, in addition to true biological differences. More recently, Huang and Rabosky (2014) found no
57 association between sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric

58 measurements of museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only
59 phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on
60 diversification across 1,306 pairs of species, using dichromatism scores provided by human observers. More
61 recently, social polygyny (a proxy for sexual selection) was found to have a positive association with speciation
62 rate across 954 species of birds (Iglesias-Carrasco et al. 2019).

63 Here, we investigate the association between sexual selection and diversification in birds while building upon
64 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual
65 dichromatism (Dale et al. 2015), as well as an index of male-biased sexual selection (Dale et al. 2015),
66 which captures (co)variation in sexual size dimorphism, social polygyny and paternal care. We use these two
67 measures because sexual dichromatism does not always signal the presence of strong sexual selection and *vice*
68 *versa* (Dale et al. 2015). For example, male and female dunnocks (*Prunella modularis*) are similarly coloured
69 yet sexual selection appears to be strong (Davies and Houston 1986). Furthermore, a recent comparative
70 study found a negative relationship between dichromatism and another sexually-selected trait (song) across
71 species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity (Cooney et
72 al. 2018). Additionally, our analysis includes multiple ecological and environmental variables, allowing us to
73 adjust for potential confounds, to identify environmental factors driving diversification, and to test whether
74 environmental factors interact with sexual selection as theory predicts (Connallon and Hall 2016). We use
75 multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including
76 BAMM (Bayesian Analysis of Macroevolutionary Mixtures) (Beaulieu and O'Meara 2015; Rabosky 2016;
77 Moore et al. 2016; Rabosky et al. 2017), as well as older but reliable tip-rate statistics, namely diversification
78 rate (λ_{DR}) and node density (λ_{ND}) (Jetz et al. 2012). Our results show that (i) a composite measure
79 of sexual selection, but not sexual dichromatism, significantly predicts speciation rates, (ii) species with
80 smaller ranges have higher speciation rates and (iii) there is no evidence that environmental variables or their
81 interaction with sexual selection have an impact on diversification rates. Therefore, we provide evidence at a
82 very large scale that sexual selection can have positive effects on diversification in the largest radiation of birds.
83 Furthermore, we suggest that the use of sexual dichromatism as the sole proxy for sexual selection should be
84 reconsidered, since it can misguide conclusions about the role of sexual selection in different scenarios.

85 MATERIALS AND METHODS

86 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$
87 species; 58% of all birds). Specifically, we (i) compiled datasets for sexual dichromatism/selection strength
88 and environmental variability, (ii) obtained estimates of speciation and extinction rates across passerines,
89 and (iii) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented
90 with reproducible code in the Electronic Supplementary Material (ESM).

91 Compiling data for sexual selection and environmental stress

92 Sexual dichromatism

93 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines (Dale et
94 al. 2015). Briefly, Dale et al. (Dale et al. 2015) obtained sex-specific RGB (red-green-blue) values across
95 six body patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the*
96 *Birds of the World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values
97 were averaged across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use
98 the absolute difference between male and female plumage scores as an estimate of sexual dichromatism.
99 Technically, this measures differences in the ‘degree of male-ness’ between males and females, rather than
100 sex differences in colour *per se* (i.e. dichromatism in the strict sense). For example, the metric would fail to
101 capture dichromatism when both the male and female possess a single, but differently coloured ‘male-like’
102 patch. However, the metric is highly correlated with dichromatism measured from spectral data (see below).
103 Additionally, we used another measure of dichromatism corresponding to colour distance in avian colour space
104 derived from spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet
105 and bird-visible range and — unlike the RGB measures — are sourced from museum specimens as opposed
106 to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB
107 data), although there was a substantial correlation between the two dichromatism measures ($r = 0.79$; Figure
108 S10).

109 Male-biased sexual selection

110 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual
111 selection across taxa, we sourced an additional measure of sexual selection (Dale et al. 2015), referred to here
112 as the ‘index of male-biased sexual selection’. This index is the first principal component from a phylogenetic
113 principal component analysis (PPCA) of three characteristics positively associated with sexual selection
114 (sexual size dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual
115 selection is available for only 2,465 species, and shows a moderate correlation with the RGB measure of
116 sexual dichromatism ($r = 0.34$; Figure S12).

117 Environmental variables

118 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
119 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the Birdlife database
120 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism
121 dataset (Dale et al. 2015). From these distributions, we obtained estimates of climatic conditions that
122 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
123 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
124 and precipitation) with 30-second ($\sim 1 \text{ km}^2$) spatial resolution (Fick and Hijmans 2017). From these values,
125 we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted
126 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial

(LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). To estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3 (MOD17A3) (Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource (see ESM), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

Generating biologically relevant predictors for environmental stress

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. Firstly we used (*i*) the average NPP in each species' range and (*v*) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (*iii*) mean values of temperature seasonality (BIO4) for each range. (*iv*) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species' range (Table S1). Species range is a potentially informative predictor of speciation and extinction, so we controlled for the correlation between environmental spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model (GAM; Figure S1) as a predictor. To obtain long-term variation in climates for each species range we take (*v*) the first principal component of the absolute difference in the bioclimatic variables between the LIG and current values. Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences between the LIG and current climates (Table S2, Figure S2). The five predictors of environmental variability are not strongly correlated (Figure S3). Details and R code to generate these predictors can be found within the ESM.

Estimating extinction and speciation

Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution ($n = 5,965$) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1,000 trees) and BAMM (100 trees) (Rabosky 2014). These trees used a 'Hackett backbone' (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),

also known as diversification rate (DR) (Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018), is derived from the sum of edge lengths branching from a node, with each edge towards the root having the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and λ_{ND}) are more reflective estimates of speciation than diversification; this is because λ_{DR} and λ_{ND} cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and Rabosky 2018). Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events while λ_{ND} measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous simulation studies, λ_{DR} and λ_{ND} are robust and intuitive measures that provide high power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models (Harvey Michael et al. 2017).

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo) to generate probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the 100 BAMM runs are detailed in full in the ESM; briefly, we used a time-variable model with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the BAMMtools R package (Rabosky et al. 2014). Each BAMM model (one MCC tree and 100 random draws of the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and number of rate shifts (Table S3, Table S4). Further details of BAMM parameters and output are available in the ESM, with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al. 2017). All analyses were conducted on log-rates.

Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the `n1me` package (Pinheiro et al. 2018). Firstly, we conducted model selection to compare models in which λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior distribution (Jetz et al. 2012)). For models of λ_{BAMM} and μ_{BAMM} we used the inverse of the variance associated with each tip rate estimate as weights, to account for the variable precision of the estimates provided by BAMM. The most complicated model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main

205 effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in MuMIn using
206 the `dredge` function (Bartoń 2017). Using the terms from the top-ranked model (ranked by AICc), we ran the
207 equivalent model for each of the 1,000 phylogenetic trees used to derive λ_{DR} , λ_{ND} and each of the 100 trees
208 used to derive λ_{BAMM} and μ_{BAMM} . In each model we used the unique response variables and phylogenetic
209 tree correlation structure. Specifically, for models using tip-rate metrics (λ_{DR} , λ_{ND}) we estimated the
210 phylogenetic signal — Pagel's λ (Pagel 1999) — using the `corPagel` function in the `ape` package (Paradis et
211 al. 2004) independently for each of the 1,000 trees/models. Alternatively, for models using speciation and
212 extinction estimates derived using BAMM (λ_{BAMM} and μ_{BAMM}) we found λ was consistently estimated at 1
213 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure.
214 This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the
215 posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three
216 datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images
217 ($n = 5,812$); dichromatism from spectrophotometry ($n = 581$) and the index of male-biased sexual selection
218 ($n = 2,465$).

219 Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic
220 path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was used to assess
221 causal paths between variables not able to be modelled within the univariate response of PGLS. That is,
222 a phylogenetic path analysis allowed us to model relationships between the predictor variables used in our
223 PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to
224 have effects on each other and not just on speciation rate. To minimise path complexity we used temperature
225 seasonality (BIO4) as the single measure for environmental variability, λ_{DR} as the single measure of speciation
226 and the tip-rates from the MCC tree. Further details of the path analysis, including our rationale for each
227 path's directions, can be found within the ESM along with all other analyses and the relevant R code to
228 reproduce results.

229 RESULTS

230 Male-biased sexual selection, but not sexual dichromatism, affects speciation

231 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$
232 species; 58% of all birds). To do this, we tested the association between speciation/extinction and sexual
233 selection, environmental variability and their interaction using phylogenetic least squares (PGLS) models
234 with λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} as the response variable. These are three different tip-rate metrics of
235 speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one of extinction (μ_{BAMM} , see Methods for details). Predictors included
236 one measure of sexual selection (one of two measures of sexual dichromatism or the index of male-biased
237 sexual selection), four measures of environmental variation, range size and 2-way interactions between the
238 measure of sexual selection and each of the environmental measures including range size, with subsequent
239 model simplification using AIC model selection.

240 We found a significant positive association between the index of male-biased sexual selection ($n = 2,465$) and
241 λ_{DR} maximum credibility (MCC) tree ($\beta = 3.89 \times 10^{-2}$, $p = 0.01$; Figure 1b). However, this association
242 was not significant for the other two measures of speciation rate (λ_{ND} : $\beta = 4.38 \times 10^{-4}$, $p = 0.35$; λ_{BAMM} :

$\beta = 9.42 \times 10^{-4}$, $p = 0.76$; Figure 1b). When we took into account phylogenetic uncertainty by running the models using 1,000 trees, the distribution of estimates from PGLS models was similar to the estimate from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR} (highest posterior density (HPD) Interval = 4.51×10^{-3} , 5.72×10^{-2}), and the distribution skewed towards a positive association between sexual selection and λ_{ND} (HPD Interval = -5.04×10^{-4} , 1.58×10^{-3} ;) as well as the 100 models using λ_{BAMM} (HPD Interval = -1.30×10^{-2} , 3.09×10^{-2} ; Table S15).

In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation. Sexual dichromatism showed no association with λ_{DR} ($\beta = -1.28 \times 10^{-3}$, $p = 0.15$; Figure 1a, Figure 2), λ_{ND} ($\beta = -5.75 \times 10^{-5}$, $p = 0.08$; Figure 1a) or λ_{BAMM} ($\beta = -1.43 \times 10^{-5}$, $p = 0.87$; Figure 1a). PGLS analyses using sexual dichromatism ($n = 581$) measured by spectrophotometry (Armenta et al. 2008) yielded results concordant with the full dataset; i.e. no association between sexual dichromatism and speciation (Figure S11). Our results from models based on the MCC tree are largely corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} . The HPD intervals show model estimates are distributed around zero when using complete taxon sampling models and RGB measures of sexual dichromatism (λ_{DR} : HPD Interval = -1.63×10^{-3} , 1.66×10^{-3} , λ_{ND} : HPD Interval = -4.26×10^{-5} , 5.50×10^{-5} , Figure 1a, Table S8). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the λ_{DR} models are positively skewed (HPD Interval = -1.78×10^{-2} , 3.49×10^{-2}) but normally distributed around zero for λ_{ND} and λ_{BAMM} (Table S12).

No interaction terms were present in the top models ($\Delta \text{AICc} > 4$) for any measure of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and the index of male-biased sexual selection; $\Delta \text{AICc} > 4$; Table S5, Table S6, Table S10, Table S13). Thus we found no evidence that the effect of sexual selection on speciation is dependent on our measures of environmental variation or range size. Furthermore, we found no evidence that these environmental factors — seasonal temperature variation, long-term temperature variation, spatial temperature variation, and Net Primary Productivity (NPP) — predict speciation independently from sexual dichromatism/selection (Figure 1, Figure S11).

Species with smaller ranges have increased rates of speciation

Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size and speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.58 \times 10^{-3}$, $p = 0$; λ_{ND} : $\beta = -1.46 \times 10^{-4}$, $p = 0.03$; Figure 1a, Figure 2). This association was also evident across the estimates from models using the 1,000 trees (λ_{DR} : HPD Interval = -8.87×10^{-3} , -6.61×10^{-4} ; λ_{ND} : HPD Interval = -1.51×10^{-4} , 1.72×10^{-5} ; Figure 1a). Subset models with reduced sample size and different measures of sexual selection — but the same measure of range size — showed equivocal evidence that range size is negatively associated with speciation. Range size significantly predicted λ_{DR} (Figure 1b) using data subset for species with an index of male-biased sexual selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subset for spectrophotometry-based dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets we draw our conclusions from the models with the highest power using near-complete taxon sampling ($n = 5,812$).

283 Phylogenetic path analysis

284 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
285 (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
286 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism (β = 0.07) and strongly
287 affected range size (β = 0.52). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect}$ =
288 -0.02; Figure 3), given the negative association we identified between λ_{DR} and range size in PGLS models.

289 Extinction rate

290 We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
291 full-taxon sampling ($\beta = 2.38 \times 10^{-5}$, $p = 0.93$; Figure 1a), nor spectrophotometry-based measures of sexual
292 dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table
293 S15).

294 Variability across phylogenetic trees and speciation rate measures

295 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in
296 the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % HPD interval across PGLS model estimates from
297 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single PGLS
298 model using the MCC tree. This contrasts with variation across trees for the other rate estimates (λ_{DR} and
299 λ_{ND}), where the 95 % HPD interval of model estimates for pglss models using 1,000 trees was near-equivalent
300 to the 95 % confidence interval calculated for PGLS model estimates of the MCC tree (Table S9). Given
301 the computational requirements of BAMM, the great majority of earlier studies have based their estimates
302 on a single consensus tree, and so the inconsistency of the BAMM estimates between different phylogenies
303 with similar statistical support is notable. Mean measures of speciation rate across 100 trees were positively
304 correlated between measures ($\lambda_{DR} - \lambda_{BAMM}$: $r=0.75$, $\lambda_{DR} - \lambda_{ND}$: $r=0.65$, $\lambda_{ND} - \lambda_{BAMM}$: $r=0.51$; Figure
305 S15). Given that the calculation of BAMM rates can be affected by the settings of the run and the use of
306 different priors, we compared the estimate of our MCC tree with that of previous published analyses on
307 birds, and found a high correlation ($r=0.81$, Figure S8). Full details of the BAMM results are presented as
308 supplementary materials.

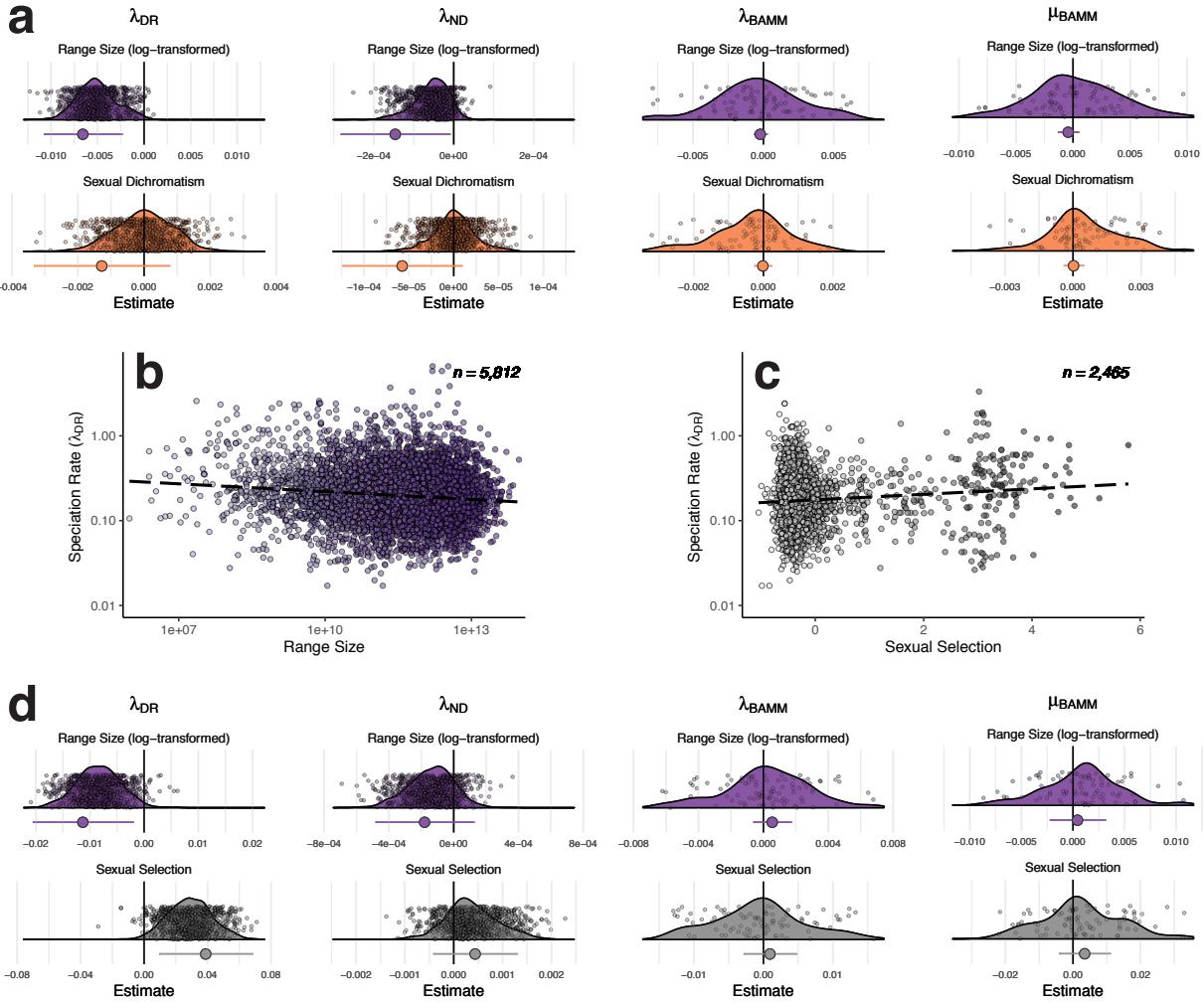


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate (λ_{DR}) and male-biased sexual selection ($n = 2,465$). Similar to (a), (d) presents model estimates for PGLS analyses using a restricted dataset with measures of an index of male-biased sexual selection ($n = 2,465$) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 1,000 randomly sampled trees (for λ_{DR} and λ_{ND}) or 100 randomly sampled trees for λ_{BAMM} and μ_{BAMM} can be found in the ESM. Density curves are based on model estimates from 1,000/100 trees and the circle below with error bars is the estimate and 95% CIs from the MCC tree. For this figure we removed outliers from estimates coming from the 100 randomly sampled trees for BAMM models in order to be able to visualise the MCC 95% CIs.

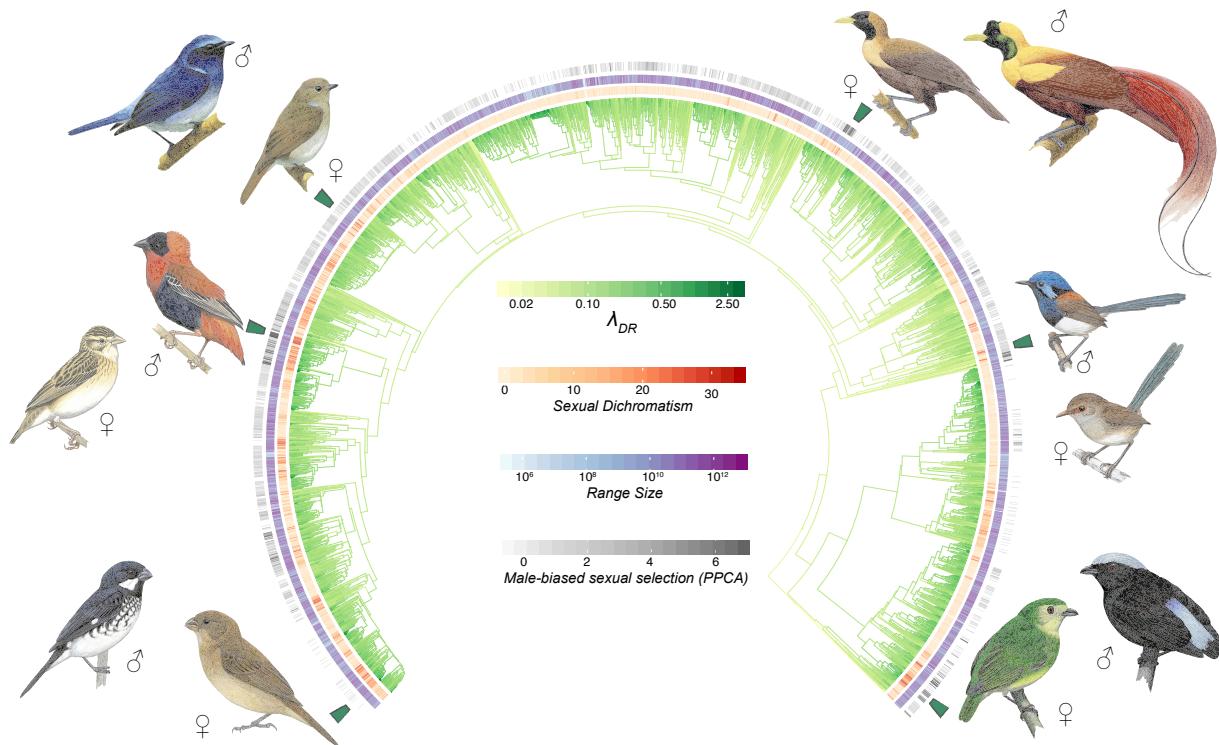


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} and log-range size as well as a significant positive association between λ_{DR} and male-biased sexual selection but no significant association between λ_{DR} and sexual dichromatism based on RGB measures. λ_{DR} are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the six species are: *Sporophila bouvronides*, *Euplectes franciscanus*, *Phainopepla nitens*, *Paradisaea rubra*, *Malurus pulcherrimus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to λ_{DR} but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted. Illustrations reproduced by permission of Lynx Editions.

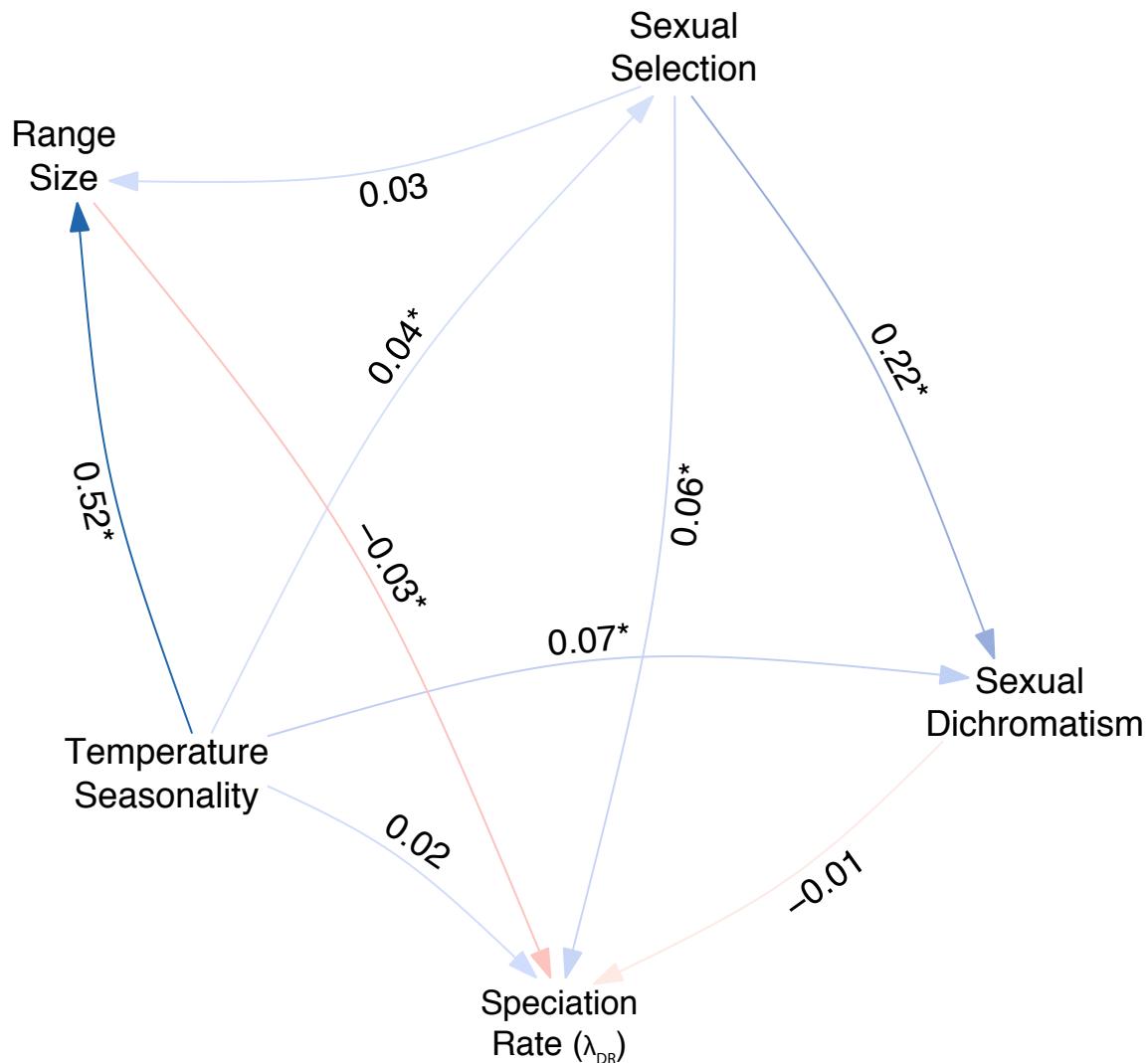


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals of this estimate do not overlap with zero. The confidence intervals were obtained from 500 bootstrapped iterations and the data used in this analysis was subset to species with both sexual dichromatism and an index of male-biased sexual selection measures ($n = 2,465$).

309 DISCUSSION

310 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual
311 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable
312 correlation between sexual dichromatism and speciation rate was consistent across different measures of
313 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB), and it cannot
314 be explained by a difference in statistical power since the sample size for the dichromatism analyses was
315 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was
316 measured using spectrophotometry (Huang and Rabosky 2014) or human observers (Cooney et al. 2017).
317 The correlation between speciation rate and the index of male-biased sexual selection (which encapsulates
318 variation in sexual size dimorphism, social polygyny, and paternal care) was statistically significant for
319 λ_{DR} , but not for λ_{ND} and λ_{BAMM} . Interestingly, we also found a consistent negative relationship between
320 range size and speciation rate, at least when this rate was quantified using λ_{DR} and λ_{ND} . None of the
321 bioclimatic measures of environmental variability that we investigated (i.e., temperature seasonality, long-term
322 temperature variation, and spatial temperature variation) significantly predicted speciation rate.
323 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection
324 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual
325 selection (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang
326 and Rabosky 2014). Given our findings, and the modest correlation between dichromatism and the sexual
327 selection index ($r = 0.34$; Dale et al. 2015), we suggest that sexual dichromatism may not be a robust
328 proxy for sexual selection. Although dichromatism almost certainly provides some insight into the operation
329 of sexual selection, it may be too indirect a measure to detect any association with speciation rate, even
330 with large sample size. There are several reasons why the use of sexual dichromatism as a proxy for sexual
331 selection is problematic. Firstly, sexual dichromatism can evolve for reasons other than sexual selection,
332 such as when males and females occupy different ecological niches (Wallace 1889; Kottler 1980; Slatkin 1984;
333 Shine 1989) or experience different selective pressures in contexts other than competition for mates (Price
334 and Eaton 2014). For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably
335 evolved in response to spatial variation in predation pressure, increasing dichromatism (Medina et al. 2017).
336 Ecological selection on sexual dichromatism was implicated by our path analysis, which found that sexual
337 dichromatism is positively affected by temperature seasonality (a measure of environmental variation), albeit
338 weakly. Secondly, colour is only one of the traits subject to sexual selection (Miles and Fuxjager 2018; Cally
339 et al. 2019). For instance, sexual selection may promote investments in other mating signals (e.g. song) that
340 trade-off against plumage colour, leading to variable investment in different sexually selected signals across
341 species (Cooney et al. 2018). Lastly, not all plumage colouration honestly reflects mate quality. A recent
342 meta-analysis found that converted carotenoids (but not carotenoids sourced from the diet) predict mate
343 quality through improvements in parasite resistance and reproductive success (Weaver et al. 2018). Given
344 the importance of honest signalling in sexual selection and the variability in colour production mechanisms
345 across birds, sexual dichromatism in many species may be an unreliable measure of mate quality for female
346 birds and sexual selection for researchers.
347 In line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that male-
348 biased sexual selection increases speciation rate, at least when speciation is measured by λ_{DR} . Additionally,
349 we found that this association appears to be independent of net primary productivity and spatiotemporal

350 variation in the environment. The lack of an effect of these environmental variables on speciation rate
351 has several possible interpretations. Firstly, the effects of sexual selection on adaptation and speciation
352 may depend on the type of environmental variability under which the species is evolving. Specifically,
353 speciation rates might be impacted by genetic constraints on adaptation, that vary across environments.
354 Theory suggests that sexual antagonism (which is often exacerbated in species with strong sexual selection)
355 may be lower in habitats experiencing cyclical environmental variation (e.g. seasonality), relative to those
356 experiencing directional change in the environment (Connallon and Hall 2016). Another possibility is that the
357 environmental predictors we chose may not account for the key ecological sources of selection that interact
358 with sexual selection to drive speciation. For example, our study does not include direct measure of food
359 availability or the severity of predation and parasitism, which are both hypothesised to affect sexual selection
360 and speciation (reviewed in Maan and Seehausen 2011). Finally, it is possible that environmental variability
361 genuinely has little effect on speciation rates, at least in the taxa investigated here.

362 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation
363 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates
364 in taxa with smaller range size (Greenberg and Mooers 2017). Intuitively, large range size should promote
365 speciation by creating more opportunities for geographic barriers to form (Rosenzweig 1995; Castiglione
366 et al. 2017). However, the opposite pattern is also plausible because birds with limited dispersal or more
367 specialised niches can have more fragmented populations, which would promote vicariant divergence and
368 higher speciation rates (Jablonski and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). It is also
369 possible that high speciation rates cause smaller range sizes, rather than the other way around, for example
370 because repeatedly-speciating lineages tend to fill niches in ways that hinder the geographical expansion of
371 new species (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014). However, species undergoing
372 adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing taxa.
373 One further explanation for the negative association between range size and sexual dichromatism/sexual
374 selection is the potential bias of taxonomic classification, whereby over-splitting of species in clades with
375 large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

376 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based
377 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,
378 male-biased sexual selection, or our measures of environmental variability. However, these extinction results
379 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from
380 phylogenies, principally because different combinations of speciation and extinction rates can give rise to
381 similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation
382 and extinction rates to be estimated using moderately-sized phylogenies, although the ability of BAMM to
383 model evolutionary rate shifts and extinction rates is debated (see, Beaulieu and O'Meara 2015; Rabosky
384 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for
385 speciation rate (e.g., λ_{DR} and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without
386 complex Bayesian models which are sensitive to sampling bias (Davis et al. 2013). Although extinction rates
387 can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation
388 extinction, or IUCN red list status (Greenberg and Mooers 2017), each approach has its limitations. Across
389 the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction
390 rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences
391 in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this

392 methodological constraint likely decreases our ability to accurately measure the correlation between metrics
393 of sexual selection and the probability of extinction.

394 One outcome of our analyses was that different measures of speciation rates presented different results. This
395 is not completely surprising, because each of the rates is calculated differently (Title and Rabosky 2018). For
396 instance, λ_{DR} is weighted more towards speciation events close to the tips and allows more rate heterogeneity
397 compared to BAMM estimates. This leads to greater variation in λ_{DR} relative to the BAMM estimates,
398 potentially explaining the difference in results. The BAMM estimates were also more sensitive to phylogenetic
399 uncertainty.

400 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts
401 speciation in passerines, that the magnitude of this effect is modest, and that this relationship is not markedly
402 affected by environmental variability. These findings imply that sexual dichromatism is not a reliable proxy for
403 sexual selection, and that alternative measures of sexual selection are more directly related to diversification.
404 Our results also add indirect support to the hypothesis that sexual selection promotes adaptation, which
405 has implications for conservation (Holman and Kokko 2013) and captive breeding programs for threatened
406 species (Charge et al. 2014). Furthermore, our finding that high speciation rate is associated with smaller
407 range size highlights the threat to the persistence of rapidly-speciating lineages in a world with increased
408 habitat loss and anthropogenic stress. This concern arises as the best predictor of extinction risk is range size
409 (Harris and Pimm 2008) and the association found here implies that many newly-specified clades have small
410 range sizes and could thus be at greater risk of extinction.

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