

<sup>1</sup> Sexual selection, environmental variation, range size and speciation  
<sup>2</sup> in passerine birds

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<sup>4</sup> **Abstract**

<sup>5</sup> Sexual selection may influence patterns of diversification; yet controversy remains on whether sexual  
<sup>6</sup> selection leads to a net increase or decrease in speciation rate, or even elevates extinction. Sexual  
<sup>7</sup> selection is predicted to increase speciation rate as it can facilitate adaptation to new environments, and  
<sup>8</sup> work alongside divergent natural selection to swiftly promote reproductive isolation. However, sexual  
<sup>9</sup> selection frequently favours investment in costly or harmful traits that may reduce adaptation and affect  
<sup>10</sup> diversification. Here, we investigate the association of sexual selection with speciation and extinction in  
<sup>11</sup> passerine birds. We use two measures of sexual selection: sexual dichromatism ( $n = 5,812$  species) and a  
<sup>12</sup> multivariate measure of male-biased sexual selection (sexual dimorphism, polygyny and paternal care;  
<sup>13</sup>  $n = 2,465$ ), three distinct measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one measure of extinction  
<sup>14</sup> ( $\mu_{BAMM}$ ). Importantly, we test whether the effects of sexual selection on speciation are dependent upon  
<sup>15</sup> ecological pressures such as temperature variability across time and space, primary productivity and  
<sup>16</sup> range size. We find that male-biased sexual selection but not sexual dichromatism predicts speciation.  
<sup>17</sup> Additionally, we find that birds with smaller ranges have higher speciation rates; although the direction  
<sup>18</sup> of causality is unclear.

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## 19 Introduction

20 Selection pressures are the main engine of speciation. As populations diverge they accumulate genetic and  
21 phenotypic changes that ultimately erect barriers against gene flow (Presgraves 2010; *but see* Shaw and Mullen  
22 2011). In this view, populations will speciate and adapt more readily to new and different environments  
23 if selection is strong and/or persistent. Hence, the rate at which speciation occurs is likely dependent on  
24 both the populations response to selection (adaptation) and the potential for divergent phenotypic traits to  
25 evolve (*e.g.* morphology or colour Hugall and Stuart-Fox 2012; Rabosky et al. 2013). Sexual selection is an  
26 evolutionary force likely to affect fitness components of a population (Cally et al. 2018 *in review*), such as  
27 reproductive success or viability, as well as the evolution of ornaments involved in mating displays or weapons  
28 used in male-male competition (McCullough et al. 2016). Sexual selection is therefore hypothesised to be a  
29 key driver of diversification through shifting the rates of adaptation, speciation and extinction.

30 Sexual selection is applied by one sex on the other — more often by females on males (Kokko and Jennions  
31 2008; Fromhage and Jennions 2016; Janicke et al. 2016) and the strength of sexual selection can increase  
32 or decrease the average fitness of a population; often termed population fitness (*reviewed in* Kokko and  
33 Brooks 2003; Whitlock and Agrawal 2009; Holman and Kokko 2013). Specifically, in line with the ‘good  
34 genes’ perspective, sexual selection may purge deleterious mutations (Agrawal 2001; Siller 2001) and fix  
35 beneficial mutations in a population (Whitlock 2000). Thus, sexual selection is thought to be a key process  
36 in mitigating extinction risk and facilitating adaptation. Sexual selection can also increase the fitness of a  
37 population when the genotypes under sexual selection (*e.g.* those that increase male mating/fertilisation  
38 success) are genetically positively correlated with traits affecting fitness (*e.g.* female fecundity or survival).  
39 However, this positive correlation is not ubiquitous; indeed sexual selection frequently favours traits having  
40 negative pleiotropic effects on female fitness (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth  
41 2009; Pennell and Morrow 2013; Berger et al. 2014). For instance, in species with high levels of sexual  
42 selection, mating success becomes more variable and uncertain; thus individuals must invest heavily in costly  
43 weaponry and sexual signals to increase their chances of successfully reproducing. Such high investment,  
44 may trade off against strategies that would improve offspring fitness (*e.g.* parental care). This is a costly  
45 consequence of sexual selection that affects persistence, adaptation and extinction (Kokko and Brooks 2003).

46 Alongside changes to fitness, sexual selection has been proposed to facilitate speciation through the evolution  
47 of divergent signals/ornaments associated with improved mating success (Lande 1981, 1982). For instance,  
48 in antbirds (Thamnophilidae), genera with complex songs and striking dichromatism, are more species rich  
49 (Seddon et al. 2008). Under this model of speciation, divergent sexual signals in one sex (usually males)  
50 co-evolve with divergent preferences for those signals in the opposite sex, leading to behavioural reproductive  
51 isolation (Safran et al. 2013). Concurrently, sexual selection can increase the extent to which populations  
52 diverge by enlarging the phenotypic space diverging species can evolve into. These predictions emerge as  
53 sexual selection may increase genetic diversity as a result of trade-offs between naturally- and sexually-selected  
54 traits or trade-offs under intra-locus sexual conflict between male and female trait expressions (Lorch et  
55 al. 2003; Bonduriansky 2011; Radwan et al. 2016). However, the genetic architecture (*per se* heritability)  
56 of fitness and sexually selected traits may vary due to different sex determination systems across taxa. In  
57 male homogametic species (ZZ/ZW or ZZ/ZO) — such as birds — males are predicted to have increased  
58 heritability of male-specific genotypes on the Z chromosome associated with mating success: such as elaborate  
59 ornamentation or plumage colouration (Hastings 1994; Reeve and Pfennig 2003). If fitness and associated

60 mating traits are more heritable in birds we might expect bird populations experiencing stronger sexual  
61 selection to have increased adaptation and speciation rates compared to male heterogametic taxa.

62 Importantly, the effects of sexual selection on adaptation and speciation may depend on environmental  
63 conditions. Both theoretical and empirical studies suggest that under stressful/changing environments, sexual  
64 selection may have greater fitness benefits than under benign environments. Stressful environments strengthen  
65 the positive correlation between male mating success and female fitness, reducing the burden of negative  
66 pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016; Martinossi-Allibert et  
67 al. 2017). Conversely, benign or stable environments ensure consistent selection, preferentially eroding  
68 genetic variation at sexually concordant loci (*i.e.* loci where the optimum genotype is equivalent for both  
69 sexes). In this situation, genetic variation remains disproportionately at sexually antagonistic loci; causing  
70 displacement of male and female traits from their optimum. It follows from these predictions that populations  
71 with stronger sexual selection would have increased fitness and adaptive benefits, allowing them to adapt to  
72 novel environments (*reviewed in* Candolin and Heuschele 2008). In certain circumstances, sexual selection will  
73 reinforce locally adapted phenotypes through mate choice on phenotypes that effectively advertise quality  
74 in a specific ecological context (Boughman 2002; Maan and Seehausen 2011). Additionally, if mate choice  
75 operates on both sexes — or there is a correlation in trait values between a pair — assortative mating is likely  
76 to speed-up the evolution of divergent mating signals (Lande 1981). In several bird taxa, beak morphology is  
77 a trait that arose under natural selection and is now a trait under sexual selection (a.k.a. “magic traits”;  
78 Servedio et al. 2011). In Darwin’s finches (*Geospiza fortis*) divergent beak morphology is an adaptation to  
79 local food availability that has been maintained through assortative mating (Huber et al. 2007). Therefore,  
80 strong sexual selection and strong natural selection — such as environmental change over space and time —  
81 may work synergistically to increase speciation rates.

82 Birds are notorious for the variety of ornaments that have evolved in response to sexual selection, such  
83 as plumage colour, size dimorphism, complex courtship rituals and male song (Gontard-Danek and Møller  
84 1999). The association between sexual selection and speciation has been investigated previously in birds  
85 using macroevolutionary approaches. A meta-analysis of 64 effect sizes from 20 studies found a small,  
86 but significant positive association between sexual selection and speciation across a wide range of taxa  
87 (Kraaijeveld et al. 2011). Within birds, they found a positive association but much lower than that for  
88 insects and fish. However, there was large variation in effect sizes due to variation in the measures of sexual  
89 selection used and diversification proxies (*e.g.* species/subspecies richness *vs* rate estimates). Contrary to  
90 this, Huang and Rabosky (2014) found no association between sexual dichromatism and speciation using  
91 tip-rate estimates from a genetic-only phylogeny (Jetz et al. 2012) and sexual dichromatism data from a  
92 limited spectrophotometry dataset ( $n = 918$ ; Armenta et al. 2008); similarly Cooney et al. (n.d.) found no  
93 effect of sexual dichromatism on diversification rates when using 1,306 pairs of species and human estimates  
94 of dichromatism. Given methodological advancements in tip-rate estimates (Rabosky and others 2018),  
95 the association between sexual selection and speciation is worth revisiting in order to overcome previous  
96 limitations. Firstly, the strength of sexual selection in macroevolutionary studies is often estimated using  
97 measures of sexual dimorphism or dichromatism; but these are often partial measures of sexual selection and  
98 may not account for the true variation in sexual selection across taxa. Secondly, until recently, studies on the  
99 association between sexual selection and speciation have largely ignored the contribution and interaction  
100 with environmental variables to explain variation in speciation rates. Thirdly, many studies use incomplete  
101 taxon sampling, with family-level analysis restricted to well sampled avian clades (Seddon et al. 2008; Huang

and Rabosky 2014). Fourthly, phylogenetic uncertainty in the avian tree (Jetz et al. 2012; *but see* Rubolini et al. 2015) and uncertainty in tip-rate measures of speciation such as the diversification rate statistic ( $\lambda_{DR}$ ) or node density ( $\lambda_{ND}$ ) (Rabosky and others 2018) as well as speciation and extinction tip-rates from models using BAMM (Bayesian Analysis of Macroevolutionary Mixtures) (*see*, Beaulieu and O'Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017) continue to plague efforts to identify drivers of speciation and extinction.

Here, we perform a macroevolutionary analysis of the relationship between sexual selection and speciation or extinction in passerine birds (Order: Passeriformes), arguably the largest group for which there exists comprehensive data. We build on these previous studies by using published datasets of sexual dichromatism measured from images ( $n = 5,812$ ; Dale et al. 2015) alongside smaller datasets of sexual dichromatism measured from spectrophotometry ( $n = 581$ ; Armenta et al. 2008) and a composite measure of male-biased sexual selection ( $n = 2,465$ ; Dale et al. 2015). We assess the relationship between sexual selection, environmental variability and their interaction with three tip-rate measures of speciation and one measure of extinction ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ). Using expert range maps and bioclimatic variables we are able to investigate whether the effect of sexual selection on speciation is dependent on range size, seasonal variation in temperature, spatial temperature variation (across a species' range), long-term variation in temperature between now and the last inter-glacial (LIG) as well net primary productivity (NPP).

## Materials and methods

We examined the effect of sexual selection on speciation and extinction rate in 97 % of passerines ( $n = 5,812$  species; 58 % of all birds). Specifically, we (*i*) compiled datasets for sexual dichromatism/selection strength and environmental variability, (*ii*) obtained estimates of speciation and extinction rates across passerines, and (*iii*) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented with reproducible code in the [electronic supplementary material \(ESM\)](#).

## Compiling data for sexual selection and environmental stress

### Sexual dichromatism

We used a previously published measure of sexual selection for 5,983 species of passerines (Dale et al. 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body patches (nape, crown, forehead, throat, upper breast and lower breast) from *Handbook of the Birds of the World* (volumes 8–16) (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values were averaged across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use the absolute difference between male and female plumage scores as an estimate of sexual dichromatism. Additionally, we used a measure of dichromatism from spectral data, used to estimate colour distance in avian colour space (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from taxonomic samples (as opposed to colour drawings). However, this spectrophotometry data is not as extensive as the RGB measures; with only 581 passerine species available for this analysis. While there is a correlation between these two measures, there is residual variation ( $r = 0.79$ ; [Figure S9](#)).

**139 Male-biased sexual selection**

140 Sexual dichromatism is a widely used indicator of sexual selection in birds (*e.g.*, Barraclough et al. 1995;  
141 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014), but only partially  
142 captures variation in the strength of sexual selection across taxa. Therefore, we also use an existing dataset  
143 (Dale et al. 2015) of male-biased sexual selection based on the first component of a phylogenetic principle  
144 component analysis (PPCA) of three characteristics associated with sexual selection (sexual size dimorphism,  
145 social polygyny and [lack of] paternal care). This measure of male-biased sexual selection is available for only  
146 2,465 species and is weakly correlated with the absolute values of sexual dichromatism using RGB measures  
147 ( $r = 0.34$ ; [Figure S11](#)).

**148 Environmental variables**

149 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook  
150 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database  
151 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism  
152 dataset (Dale et al. 2015). From these distributions we obtained estimates of climatic conditions that  
153 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19  
154 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature  
155 and precipitation) with 30 seconds ( $\sim 1 \text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017). From these values  
156 we obtained means and standard deviations for each species. Using the same spatial sampling we extracted  
157 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial  
158 (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the  
159 energy available to species we obtained the mean and standard deviation of net primary productivity (NPP)  
160 values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution  
161 and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production  
162 products stage 3 (MOD17A3) (Zhao et al. 2005). Using this data, which we provide as a potentially useful  
163 data resource (see ESM), we generated five predictors of speciation associated with different patterns in  
164 environmental variability (see below).

**165 Generating biologically relevant predictors for environmental variation**

166 Using the extracted environmental variables from each species range size we developed biologically meaningful  
167 predictors of environmental variation/stress relating to (*i*) seasonal climate variation, (*ii*) spatial climate  
168 variation and (*iii*) long-term climate variation. To obtain seasonal climate variation we used mean values  
169 of temperature seasonality (BIO4) for each range. To estimate levels of spatial environmental variation a  
170 species may endure we used the first principle component (PC1) from a PCA on standard deviations from all  
171 bioclimatic variables, excluding temperature (BIO4) and precipitation seasonality (BIO15). PC1 was heavily  
172 loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature  
173 across a species' range ([Table S1](#)). Given that species range is a potentially informative predictor of speciation  
174 and extinction we controlled for the correlation between spatial variation and range size — where larger  
175 ranges have larger variation in PC1 — by taking the residuals of a fitted general additive model (GAM; [Figure](#)  
176 [S1](#)). To obtain long-term variation in climates for each species range we take the first principal component of

177 the absolute difference in the bioclimatic variables between the LIG and current values. Similarly to spatial  
178 variation, the long-term climate variation is primarily loaded to temperature differences between the LIG  
179 and current climates ([Table S2](#), [Figure S2](#)). The five predictors of environmental variability are not strongly  
180 correlated ([Figure S3](#)). Details and code to generate these predictors can be found within the [ESM](#).

181 **Estimating extinction and speciation.**

182 Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade  
183 credibility (MCC) tree from 2,500 samples of the posterior distribution that were subset to the passerine bird  
184 order ( $n = 5,965$ ) as the main phylogenetic tree in our comparative analysis. Additionally, a random draw of  
185 100 full trees (including species without genetic data) from the posterior distribution of phylogenetic trees  
186 was used for diversification analyses using tip-rate measures and BAMM (Rabosky 2014). These trees used  
187 a ‘Hackett backbone’ (Hackett et al. 2008) and were constructed using the a pure birth (Yule) model. We  
188 calculated three different tip-rate metrics of speciation and one of extinction across all trees.

189 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes  
190 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating  
191 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),  
192 also known as diversification rate (DR) (e.g., Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),  
193 is derived from the sum of edge lengths branching from a node, with each more basal node having the sum of  
194 lengths down-weighted. Studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  $\lambda_{ND}$ )  
195 are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Rabosky and others  
196 2018). Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events  
197 and  $\lambda_{ND}$  is a measure of speciation across the root-to-tip path. These tip-rate measures are alternatives  
198 to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE). But,  
199 based on previous simulation studies  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high  
200 power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized  
201 Least Squares (PGLS) models (Harvey Michael et al. 2017).

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

217 2017). All analyses were conducted on log-rates.

## 218 Statistical analysis

### 219 Phylogenetic comparative analysis

220 To test the association between speciation/extinction and sexual selection, environmental variability and  
221 their interaction, we used phylogenetic least squares (PGLS) models in the `n1me` package (Pinheiro et al.  
222 2018). We began by estimating the phylogenetic signal — Pagel's  $\lambda$  (Pagel 1999) — using the `corPagel`  
223 function in the `ape` package (Paradis et al. 2004) on the MCC tree. The estimate of  $\lambda$  was then fixed for  
224 model selection, which was conducted on the same MCC tree derived from 2,500 draws of the posterior  
225 distribution (Jetz et al. 2012). Model selection used either  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  tip-rate estimates  
226 from the MCC tree as the response variable. For  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  we were also able to use model weights  
227 sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution ( $n$   
228 = 1,000). Model weights thus reflect the degree of precision to which each species tip-rate is measured in  
229 BAMM. Using model selection we only compared interaction terms between a measure of sexual selection  
230 (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the  
231 individual predictors of: dichromatism/male-biased sexual selection measures, log-transformed range size,  
232 seasonal temperature variation, spatial temperature variation, long-term temperature variation and NPP  
233 while comparing 32 models with different combinations of interactions (including none). Model selection was  
234 done in `MuMIN` using the `dredge` function (Bartoń 2017). Using the terms from the top-ranking model (lowest  
235 AICc), we ran the equivalent model for each of the 100 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$   
236 and  $\mu_{BAMM}$ , using the unique response variables and phylogenetic tree correlation structure in each model.  
237 This method enabled us to present model estimates for an MCC tree alongside 100 trees from the posterior  
238 distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets  
239 corresponding to each measure of sexual selection: dichromatism derived from RGB values of images ( $n$  =  
240 5,812); dichromatism from spectrophotometry ( $n$  = 581) and the multivariate measure of male-biased sexual  
241 selection ( $n$  = 2,465).

242 Finally, using data subsetted for species with measurements of male-biased sexual selection, we conducted  
243 a phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis  
244 was used to assess causal paths between variables not able to be modelled within the univariate response of  
245 PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables  
246 used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection and  
247 range size to have effects on each other and not just on speciation rate. To minimise path complexity we use  
248 temperature seasonality (BIO4) as the single measure for environmental variability and use  $\lambda_{DR}$  as the single  
249 measure of speciation. The phylogenetic path analysis used tip-rates and correlation structure from the MCC  
250 tree. Further details of the path analysis including reasons for path directions can be found within the [ESM](#)  
251 along with all other analyses and the relevant R code to reproduce results.

## 252 Results

### 253 Effects of sexual dichromatism/selection on speciation are not dependent on 254 environmental variability

255 PGLS models with interaction terms between each measure of sexual dichromatism/selection and the five  
256 measures of environmental variability (seasonal temperature variation, log-range size, long-term temperature  
257 variation, spatial temperature variation and NPP) were included in model selection. However, no interaction  
258 terms were significant or present in the top models ( $\delta \text{ AICc} > 4$ ) for any measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  
259  $\lambda_{BAMM}$ ) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection;  $\delta \text{ AICc}$   
260  $> 4$ ; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual  
261 selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no  
262 evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,  
263 spatial temperature variation and NPP) predict speciation independently from sexual dichromatism/selection  
264 ([Figure 1](#), [Figure S10](#)).

### 265 No evidence that sexual dichromatism affects speciation

266 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.  
267 Using three response measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ), the effect of sexual dichromatism was not  
268 significant in any PGLS model based on tip-rate estimates and correlation structures from the MCC tree.  
269 Specifically, sexual dichromatism showed no association with  $\lambda_{DR}$  ( $\beta = -1.279e-03$ ,  $p = 0.147$ ; [Figure 1a](#),  
270 [Figure 2a](#)) or  $\lambda_{ND}$  ( $\beta = -5.745e-05$ ,  $p = 0.078$ ; [Figure 1a](#)). Furthermore, speciation rates from BAMM  
271 ( $\lambda_{BAMM}$ ) were also unaffected by sexual dichromatism ( $\beta = -1.430e-05$ ,  $p = 0.872$ ; [Figure 1a](#)). PGLS analyses  
272 using subsetted data ( $n = 581$ ), where sexual dichromatism was measured using spectrophotometry (Armenta  
273 et al. 2008) yielded results concordant to the full data set; that is, no association between sexual dichromatism  
274 and speciation or extinction ([Figure S10](#)). Our results from MCC models are largely corroborated by model  
275 estimates from PGLS analyses of the rates and correlation structures from 100 random trees. Model estimates  
276 are normally distributed around zero when using complete taxon sampling models and RGB measures of  
277 sexual dichromatism ([Figure 1a](#), see HPD (highest posterior density) intervals in [Table S8](#)). For PGLS models  
278 using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the  
279  $\lambda_{DR}$  models are positively skewed (-1.781e-02, 3.488e-02) but normally distributed around zero for  $\lambda_{ND}$  and  
280  $\lambda_{BAMM}$  ([Table S12](#)).

### 281 Male-biased sexual selection increases speciation

282 We found a significant positive association between male-biased sexual selection ( $n = 2,465$ ) and  $\lambda_{DR}$  ( $\beta$   
283 = 3.887e-02,  $p = 0.012$ ; [Figure 1b](#)). However, this associate was not significant for the other two measures  
284 of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.381e-04$ ,  $p = 0.351$ ;  $\lambda_{BAMM}$ :  $\beta = 9.422e-04$ ,  $p = 0.764$ ; [Figure 1b](#)). The  
285 distribution of estimates from PGLS models on 100 random trees was similar to the estimate from an MCC  
286 tree: among the 100 trees there was a positive association between sexual selection and  $\lambda_{DR}$  (HPD Interval =  
287 9.115e-03, 6.085e-02), and a smaller positive association between sexual selection and  $\lambda_{ND}$  (HPD Interval =

<sup>288</sup> -3.104e-04, 1.536e-03; ) as well as  $\lambda_{BAMM}$  (HPD Interval = -1.297e-02, 3.089e-02). Complete HPD intervals  
<sup>289</sup> for models using male-bias sexual selection PPCA as a predictor can be found within [Table S15](#).

## <sup>290</sup> Species with smaller ranges have increased rates of speciation

<sup>291</sup> Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation we found a negative association between range size and  
<sup>292</sup> speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This negative  
<sup>293</sup> association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.578e-03$ ,  $p = 0.001$ ;  $\lambda_{ND}$ :  
<sup>294</sup>  $\beta = -1.462e-04$ ,  $p = 0.034$ ; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from  
<sup>295</sup> models using the 100 trees ( $\lambda_{DR}$ : HPD Interval = -8.438e-03, -1.823e-03;  $\lambda_{ND}$ : HPD Interval = -1.899e-04,  
<sup>296</sup> 9.112e-06; [Figure 1a](#)). Subsetted models with reduced sample size and different measures of sexual selection —  
<sup>297</sup> but the same measure of range size — showed variable evidence that range size is negatively associated with  
<sup>298</sup> speciation. Range size significantly predicted  $\lambda_{DR}$  ([Figure 1b](#)) using data subsetted for male-biased sexual  
<sup>299</sup> selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ . Model using data subsetted for spectrophotometry-based  
<sup>300</sup> dichromatism ( $n = 581$ ) gave non-significant estimates for the effect of range size on all measures of speciation  
<sup>301</sup> ([Figure S10](#), [Table S11](#), [Table S12](#)). Because the range size dataset is the same across the three data subsets  
<sup>302</sup> we draw our conclusions from the models with highest power using near-complete taxon sampling ( $n = 5,812$ ).

## <sup>303</sup> Phylogenetic path analysis

<sup>304</sup> Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS  
<sup>305</sup> ([Figure 3](#); [Figure S13](#)). Notably, environmental variability (temperature seasonality) directly affected sexual  
<sup>306</sup> dichromatism ( $\beta = 0.07$ ) and the path from male-biased sexual selection to sexual dichromatism was relatively  
<sup>307</sup> weak, ( $\beta = 0.22$ ), despite dichromatism being widely used as an indicator of the strength of sexual selection.  
<sup>308</sup> Additionally, the large direct effect of temperature seasonality on range size ( $\beta = 0.52$ ) suggests an indirect  
<sup>309</sup> effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta = -0.02$ ; [Figure 3](#)), given the negative we identified between  $\lambda_{DR}$   
<sup>310</sup> and range size in PGLS models.

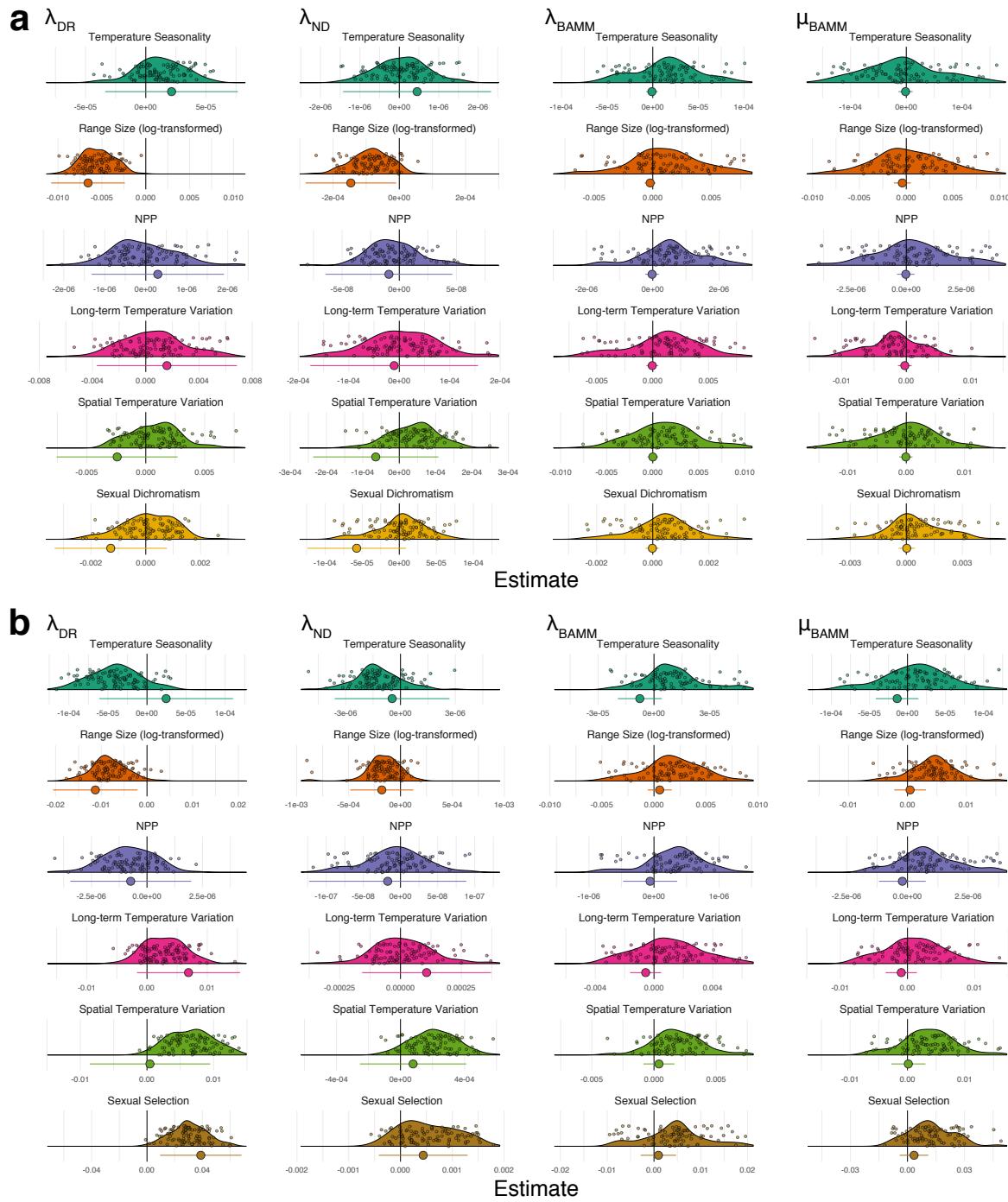
## <sup>311</sup> Extinction rate

<sup>312</sup> We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
<sup>313</sup> full-taxon sampling ( $\beta = 2.390e-05$ ,  $p = 0.93$ ; [Figure 1a](#)), nor spectrophotometry-based measures of sexual  
<sup>314</sup> dichromatism ([Figure S10](#), [Table S11](#), [Table S12](#)) or male-biased sexual selection ([Figure 1b](#), [Table S14](#), [Table  
<sup>315</sup> S15](#)).

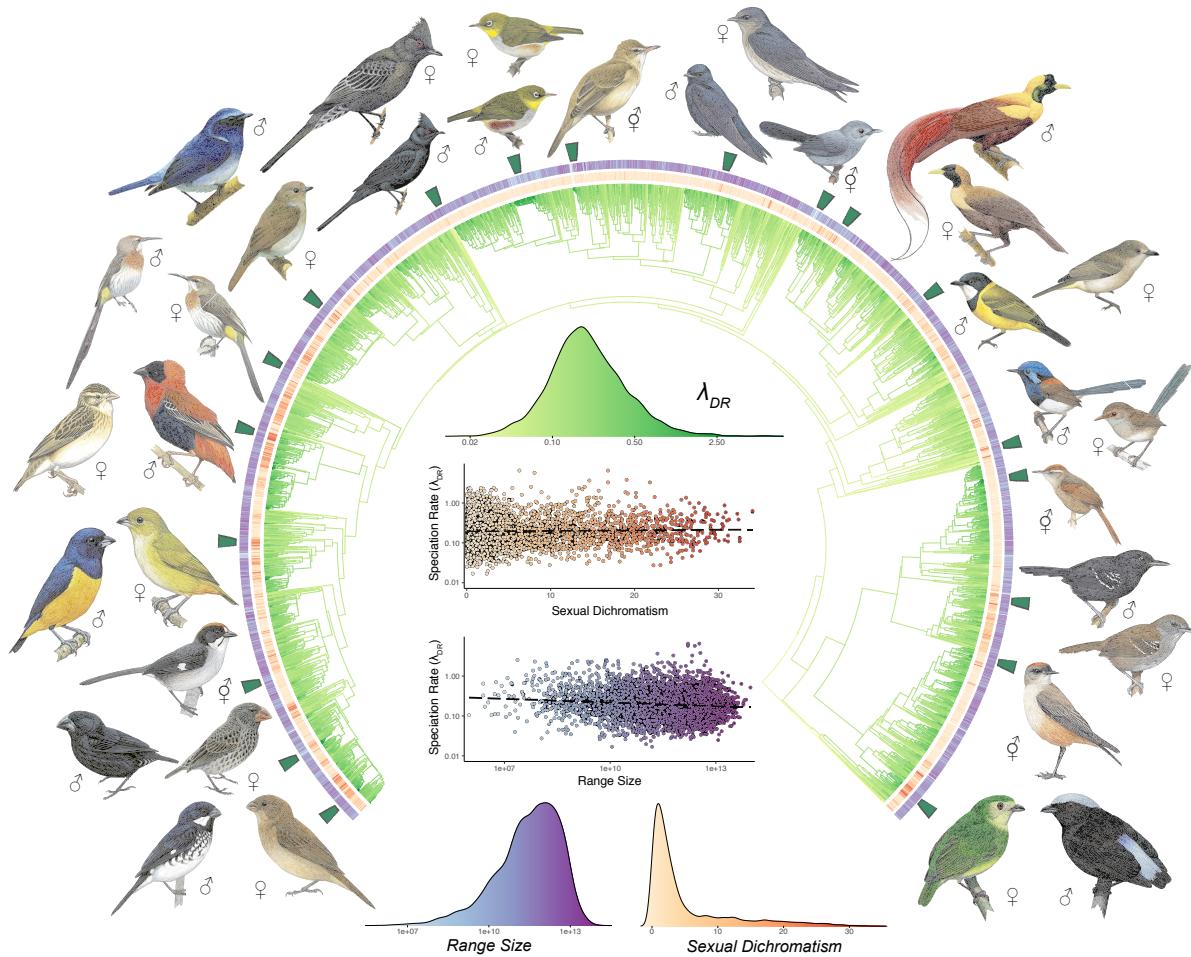
## <sup>316</sup> Variability across trees and methods

<sup>317</sup> We tested our hypothesis that sexual selection is associated with speciation using several methods and across  
<sup>318</sup> 100 trees drawn from the post burn-in posterior (Jetz et al. 2012). We used a range of methods to overcome  
<sup>319</sup> uncertainty in the power and precision of various tip-rate estimates as well as the variation between trees.  
<sup>320</sup> We found that that the tip-rate estimates across the 100 trees were quite variable for both  $\lambda_{DR}$  and  $\lambda_{BAMM}$   
<sup>321</sup> ([Figure S14](#)). Despite this, tip-rate estimates of speciation from the two methods were moderately correlated

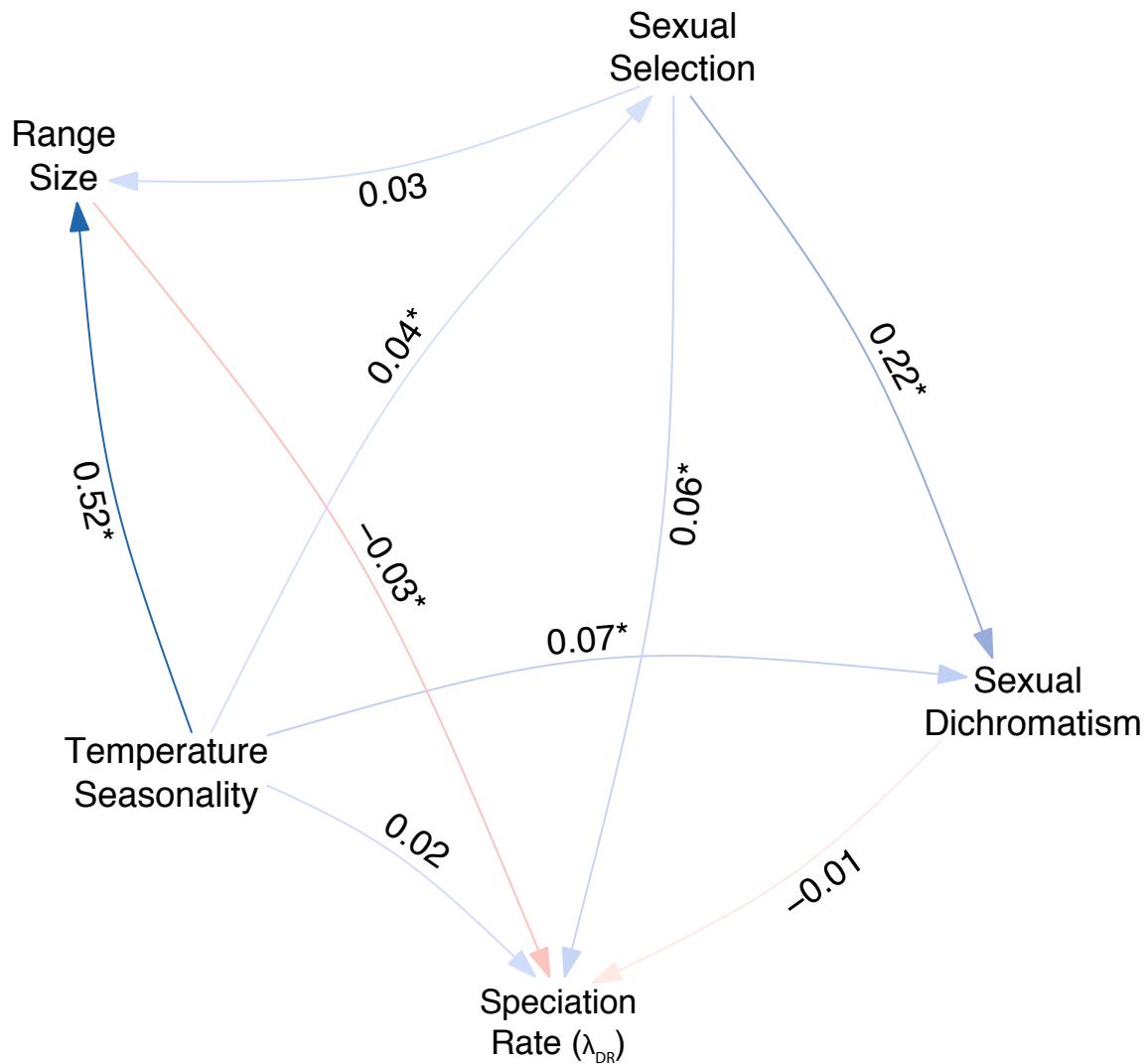
322 across the 100 trees ( $r = 0.75$ ) and for the MCC tree ( $r = 0.68$ ; [Figure S15](#)). However, in comparison to  $\lambda_{DR}$ ,  
323 the value of  $\lambda_{BAMM}$  was the *mean* drawn from a posterior distribution ( $n = 1,000$ ) of BAMM generations,  
324 thus estimates of  $\lambda_{BAMM}$  (and  $\mu_{BAMM}$ ) have an added level of variation. To account for this variation,  
325 weights (using the inverse of the variance) were used for the PGLS models. From 1000 posterior samples  
326 of the MCC BAMM run the coefficient of variation ( $CV$ ) for all log-rates of  $\lambda_{BAMM}$  was relatively low  
327 (*mean CV* = 21.49, *median CV* = 15.76 ; see [Figures S5](#) and [Figure S7](#)). Despite the convergence of the  
328 BAMM model in all runs — where effective sample sizes of the number of shifts and log-likelihood were all  
329 greater than 200 ([Table S3](#), [Table S4](#)) — we found that the unique combinations of rate shifts across the  
330 large phylogenetic tree ( $n = 5,966$  species) was high. This means that although the number of rate shifts  
331 reached convergence (*median* = 59; [Figure S6](#)), the locations of the rate shifts (*i.e.* the credible shift set)  
332 across the tree are highly heterogeneous. The variability in the locations for the shift configurations is a  
333 likely source of uncertainty in downstream tip-rates used as the response variable in PGLS models. Notably,  
334 the 95 % HPD interval for model estimates using BAMM rates from 100 trees was about 20-fold the 95 %  
335 confidence intervals of the estimate from the MCC tree; whereas for  $\lambda_{DR}$  and  $\lambda_{ND}$  the HPD 95 % interval  
336 width was equal to or less than the MCC 95 % CI ([Figure 1](#), [Table S9](#)).



**Figure 1:** Model estimates for (a) PGLS analyses using sexual dichromatism ( $n = 5,812$ ) and (b) PGLS analyses using measures of male-biased sexual selection ( $n = 2,465$ ). Both datasets were used for analyses with three measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one measure of extinction ( $\mu_{BAMM}$ ) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 100 random trees can be found within the ESM. Density curves are based on estimates from 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 random trees for BAMM models in order to interpret the MCC 95 % CIs.



**Figure 2:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between  $\lambda_{DR}$  and log-range size but no significant association between  $\lambda_{DR}$  and sexual dichromatism based on RGB.  $\lambda_{DR}$  are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the species are: *Sporophila bouvronides*, *Geospiza magnirostris*, *Atlapetes leucopterus*, *Euphonia rufiventris*, *Euplectes franciscanus*, *Promerops gurneyi*, *Phainopepla nitens*, *Zosterops erythropleurus*, *Acrocephalus australis*, *Progne cryptoleuca*, *Mayrornis schistaceus*, *Paradisaea rubra*, *Pachycephala pectoralis*, *Malurus pulcherrimus*, *Cranioleuca curtata*, *Cercomacra manu*, *Muscisaxicola capistratus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to  $\lambda_{DR}$  but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.



**Figure 3:** Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values 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 male-biased sexual selection measures ( $n = 2,465$ ).

## 337 Discussion

338 We found no evidence that sexual dichromatism alters the rate of speciation in passerine birds independently  
339 or via interactions with environmental variability. This result is consistent across different measures of  
340 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and two measures of dichromatism (spectral and RGB). The results are  
341 also consistent with previous studies performed at a smaller scale (Huang and Rabosky 2014; Cooney et al.  
342 n.d.). However, we found that when using a measure of male-biased sexual selection — instead of sexual  
343 dichromatism — there was a positive association with speciation, though the strength of this relationship  
344 varied across different rate estimates. Our findings suggest that the components of the composite measure of  
345 male-biased sexual selection (sexual size dimorphism, social polygyny and [lack of] paternal care) are better  
346 predictors of speciation than sexual dichromatism. No bioclimatic measures of environmental variability  
347 (temperature seasonality, long-term temperature variation and spatial temperature variation) predicted  
348 speciation, but range size was negatively associated with two measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ). This  
349 suggests that species with smaller range sizes have increased speciation rate, however, small range size may  
350 be a cause or effect of elevated speciation rate and potentially even an artifact of taxonomic classification.  
351 Interestingly we found a discrepancy in the model results obtained from tip-rate statistics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and  
352 those using tip-rate estimates from a model-based approach ( $\lambda_{BAMM}$ ); whereby BAMM produced precisely  
353 null results for most associations between predictors and speciation as well as extinction.

354 The association between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin  
355 1871) that allows it to be commonly used as a proxy for the strength of sexual selection in comparative  
356 studies (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and  
357 Rabosky 2014). Despite the association between sexual selection and sexual dichromatism in passerine birds  
358 (Dale et al. 2015) we find that sexual dichromatism does not predict speciation rate, whereas male-biased  
359 sexual selection does. Given our results, we suggest that sexual dichromatism may not be a robust proxy  
360 for sexual selection, and that variance in the association between dichromatism and the strength of sexual  
361 selection may obscure any relationship with speciation rate, despite the high power of our comparative study.  
362 There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is problematic.  
363 Firstly, ecological pressures could drive sexual dichromatism in the absence of mate choice if sex-specific  
364 niches provide opportunity for the evolution of sex-limited traits (Wallace 1889; Kottler 1980; Slatkin 1984;  
365 Shine 1989). Specifically, natural selection on females may be important in explaining patterns of sexual  
366 dichromatism in birds (Price and Eaton 2014). In fairy-wrens (*Malurus cyaneus*), female colouration has  
367 evolved in response to environmental pressures, leading to increased sexual dichromatism in regions where  
368 females are under stronger selection from predation (Medina et al. 2017). Ecological impacts on sexual  
369 dichromatism are supported by our path analysis, which reveals that sexual dichromatism is positively affected  
370 by temperature seasonality (a measure of environmental variation) albeit relatively weakly. Secondly, colour  
371 is but one trait and sexual selection may drive the evolution of sex differences in a wide variety of traits  
372 used in mate choice or intrasexual competition (Miles and Fuxjager 2018). And thirdly, not all plumage  
373 colouration honestly reflects mate quality. A recent meta-analysis found that converted carotenoids (but not  
374 those sourced from diet) predict mate quality through improvements in parasite resistance and reproductive  
375 success (Weaver et al. 2018). Given the importance of honest signaling in sexual selection and the variability  
376 in colour production across birds, sexual dichromatism in many species may be an unreliable measure of  
377 mate quality for female birds and sexual selection for researchers.

378 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we found that male-biased  
379 sexual selection increases speciation rate — at least for  $\lambda_{DR}$  and  $\lambda_{ND}$  estimates — but this association was  
380 not dependent on variable or stressful environments. When evolving under stressful conditions, sexually  
381 antagonistic selection is hypothesised to be weakened relative to selection that is concordant between the  
382 sexes (Connallon 2015; Connallon and Hall 2016). While these predictions are supported in several lab  
383 (experimental evolution) studies (Long et al. 2012; Punzalan et al. 2013; Berger et al. 2014), other studies  
384 have not found the association (Delcourt et al. 2009; Holman and Jacomb 2017; Martinossi-Allibert et al.  
385 2017). The environmental variability predictors used here often reflected changes in climate across space and  
386 time, whereby high environmental variation would likely increase the strength of natural selection on a given  
387 species. Given that we did not detect an effect of environmental variability (by itself or as an interaction  
388 with sexual selection) we are left with several possible explanations. Firstly, the effects of sexual selection on  
389 adaptation and thus speciation may depend on the type of environmental variability the species is evolving  
390 under. Specifically, sexual antagonism may be more easily purged in environments where cyclic pressures  
391 (*e.g.* seasonality) are perpetuated; whereas when environmental variability is directional (*e.g.* long-term  
392 climatic change) sexual antagonism can remain indefinitely as a fitness burden (Connallon and Hall 2016).  
393 Secondly, the environmental predictors used here may not account for the key ecological forces/natural  
394 selection pressures that interact with sexual selection to drive speciation. Specifically, access to dietary  
395 resources, and the impacts of predation or parasitism are unaccounted for here: arguably these are key  
396 processes affecting sexual selection and speciation (*reviewed in* Maan and Seehausen 2011). Thirdly, it is also  
397 possible that there is no effect of environmental variability on speciation rates; at least not in the species  
398 investigated here.

399 The most consistent finding uncovered in this comparative analysis is that smaller range sizes are associated  
400 with increased speciation rates; however reduced range size can be a cause or consequence of speciation.  
401 Intuitively, large range size should promote speciation by creating greater opportunities for geographic barriers  
402 to form (Rosenzweig 1995). However, birds with smaller range sizes are predicted to have lower dispersal  
403 ability. This ensues that individuals might not be able to overcome geographical barriers and maintain gene  
404 flow; which would promote reproductive isolation and speciation (Birand et al. 2012; Claramunt et al. 2012).  
405 Several studies have used morphological measures of wing shape (Hand-wing index/ Kipp's distance) — a  
406 proxy for dispersal ability — as predictors of speciation and coexistence (*e.g.*, Kennedy et al. 2016; Pigot et  
407 al. 2016). But currently, published datasets of these measurements are not available for many passerines.  
408 Alternatively, reduced range size may be a consequence of speciation. Under this view, high speciation rate  
409 may lead to smaller range sizes as niche filling by recently diverged species will suppress the expansion of  
410 newly speciated relatives. Within Himalayan songbirds, range expansions are prevented by the competition  
411 for resources by related species (Price and Eaton 2014); this suppression on range expansion is then expected  
412 to prevent future speciation events (Rosenzweig 1995; Weir and Price 2011). Unlike Himalayan songbirds,  
413 species undergoing adaptive radiation in new niches are unlikely to be limited by competition for resources  
414 from existing taxa. Across islands we expect to see a correlation between speciation and small range size  
415 because they reflect newly formed environments with empty niches. Thus, our findings may be heavily  
416 dependent on species whose range size is restricted to a single island within an archipelago (*e.g.* *Geospiza*  
417 sp.; a.k.a. Darwin's finches). One further explanation for the negative association between range size and  
418 sexual dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting  
419 of species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller  
420 ranges. Given the problems of determining causality and mode of speciation the reason for the negative

421 association found here remains obscured.

422 In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual  
423 selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated  
424 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in* Kokko  
425 and Brooks 2003). Using BAMM, we found no association between extinction rate and sexual dichromatism,  
426 male-biased sexual selection or measures of environmental variability. Extinction is notoriously hard to  
427 estimate accurately (*see* Rabosky 2016). It can be estimated from phylogenetic inference, fossil record, records  
428 of recent extinctions and IUCN extinction threat status. Phylogenetic methods — like BAMM — allow for  
429 speciation and extinction rates to be measured using moderately sized phylogenies. However, BAMM has  
430 been subject to controversy in its ability to model rate shifts and extinction rates (*see*, Beaulieu and O'Meara  
431 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017), and while several tip-rate estimates exist for  
432 speciation (*e.g.*,  $\lambda_{DR}$  and  $\lambda_{ND}$ ) extinction estimates are not as easily obtained. Here, we found that BAMM  
433 often produced homogeneous speciation and extinction rates for clades with few rate shifts; arguably this  
434 could reduce our power to detect small differences in extinction rates among closely related taxa (Rabosky  
435 et al. 2017; Rabosky and others 2018). The ability to detect extinction rates rarely improves when fossil  
436 records are used, as many clades (*e.g.* birds) lack the stratigraphic sampling across time to statistically  
437 calculate extinction rates. But, there are exceptions: ostracods — a group of marine invertebrates — have  
438 extensive fossil records and show identifiable sexual dimorphism. Across 93 species of ostracods, Martins et  
439 al. (2018) found that ostracod taxa with larger sexual dimorphism (representing exaggerated investment by  
440 males in reproductive organs) had higher extinction rates; implying that sexual selection increases extinction  
441 risk. Alternatively, when comparative studies have assessed the relationship between sexual selection and  
442 extinction in extant birds (Mitra et al. 1996; Doherty et al. 2003; Morrow and Pitcher 2003) and mammals  
443 (Morrow and Fricke 2004; Bro-Jorgensen 2014) there has been no consensus. Unfortunately, these methods  
444 often rely on extinction threat status from the International Union for Conservation of Nature (IUCN) Red  
445 List (*e.g.*, Morrow and Pitcher 2003; Morrow and Fricke 2004; Bro-Jorgensen 2014) and may be biased to  
446 species under greater anthropogenic threat, culturally valued or well researched.

447 Improvements in estimating tip-rates of speciation has allowed us to revisit the association between sexual  
448 selection and speciation. With high power and alongside extensive ecological predictors we find support that  
449 male-biased sexual selection predicts speciation. If sexual selection promotes speciation through improvements  
450 in fitness and adaptation the implications are manifold with sexual selection a potentially valuable utility in  
451 conservation (*reviewed in*, Holman and Kokko 2013) and captive breeding programs for threatened species  
452 (*reviewed in*, Charge et al. 2014). Furthermore, our finding that high speciation rate is associated with  
453 smaller range size has pronounced significance to the future survival of these rapidly speciating species in a  
454 world with increased habitat loss and anthropogenic stress. Range size is the best predictor of extinction risk  
455 (Harris and Pimm 2008) and the association found here ensues that many newly speciated clades may be at  
456 greater risk of extinction due to their reduced range being impacted by anthropogenic effects.

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## Critical analysis

*[On Darwinism]... But it by no means follows that slight differences in the shape, pattern, or colours of the ornamental plumes are what lead a female to give the preference to one male over another; still less that all the females of a species, or the great majority of them, over a wide area of country, and for many successive generations, prefer exactly the same modification of the colour or ornament.*

— ALFRED RUSSEL WALLACE

### Strengths and limitations

Perhaps one of the biggest unravelings of this project was the decoupling of male-biased sexual selection from sexual dichromatism, remarkably this same controversy engrossed Wallace and Darwin 130 years ago (Kottler 1980). The widespread use of sexual dichromatism largely goes unchallenged as our instinctive Darwinian mind reminisces of peacocks and birds of paradise; my thoughts were such when I began this scientific inquiry. Of course, I was expecting sexual dichromatism from RGB measures to be a noisy measure of sexual selection, but across 5,831 species I anticipated a signal would permeate through the noise. And despite the correlation between sexual dichromatism and male-biased sexual selection is present, the relationship is surprisingly weak (see [Figure 3](#) in main text). With this in mind, the practical use of sexual dichromatism in macroevolutionary research is severely weakened. This finding is particularly pertinent as efficient proxy measurements are incredibly valuable in comparative analyses: that's because they increase the accessibility, available sample size and transferability of a study, making it more conducive to research synthesis. But, as Wallace remarks, the matter is inevitably more complex despite the irresistibility of the Darwinian argument<sup>1</sup> (Kottler 1980; Caro 2017). On the bright side, the multivariate measure of male-biased sexual selection that is: sexual dimorphism, social polygyny and [lack of] paternal care is a dataset that better predicts speciation and would benefit from being expanded across birds.

Not only are the measurements of sexual selection under a cloud of uncertainty, the estimates of speciation and extinction are another point of controversy. Macroevolutionary research is a field plagued by methodological uncertainty and conflicts. Originally, I had planned to continue my meta-analysis by investigating extinction rate across a large taxonomic group. There were signs that extinction rate could be measured from phylogenetic methods with relative confidence (Pyron and Burbrink 2016). However, these hopes soon dissipated, and with them the seeming *raison d'être* of the project. Extinction rate is arguably the best measure of population fitness. And while a high profile study has measured extinction rate in experimental evolution (Lumley et al. 2015), it has been rarely measured accurately over long, evolutionarily meaningful timescales (*but see* Martins et al. 2018). We included measurements of extinction rate within the paper, however these findings were played down. The reason for this movement away from extinction and towards speciation is the controversy surrounding extinction rate measures as well as phylogenetic uncertainty. Measuring extinction rates within the bird phylogeny is problematic because of the nature of phylogenetic construction; for passerine birds a birth-only model of tree construction and incomplete genetic taxon sampling are large barriers that limit the

<sup>1</sup>Wallace was initially supportive of the evolution of sexual dichromatism as a result of mate choice but later took more interest in a view where natural selection on predator-prone nesting females generated dullness in females but not males.

ability to use model-based methods to detect extinction rate (Beaulieu and O'Meara 2015). Furthermore, the very detection of an absence of data — which is what such methods attempt to do — is a hard sell both conceptually and methodically come peer review: see Rabosky (2016) for a cautionary tale on measuring extinction rate with BAMM. The mechanisms and rates at which speciation and extinction occur are an active area of research. In a recent pre-print Henao Diaz et al. (2018) used BAMM across 104 time-calibrated molecular phylogenies and found that despite variation in ecology, biogeography and taxonomy, younger clades consistently had higher rates of speciation and extinction. This finding of time-dependency in rates of diversification makes comparative analyses between clades challenging and calls into question countless studies (Henao Diaz et al. 2018). Similar to Wallace's view of sexual dichromatism we are left with a view of diversification rate measures where we cannot yet account for the underlying true variation; which is vastly more complex than we can currently measure.

As with sexual dichromatism and macroevolutionary rates, the most severe limitation for environmental variation was the coarseness of the measures. In total, for 5,831 species we extracted 338,203,831 point measures<sup>2</sup> of environmental variability, but our measures may not account for variation in biotic components such as nutritional resources or predation. However, the methods employed here are arguably much better than those traditionally implemented; where the range mid-point is used to obtain a single measure of temperature, precipitation or seasonality or where only one bioclimatic variable is used. I would argue that reducing the multivariate data into several biologically meaningful predictors is a conceptually challenging exercise, but researchers should not feel limited by the amount of raw data that they can access<sup>3</sup>. In fact, previous to our study on birds the same methodology was applied to ~ 100 species of bovids with speciation, extinction and environmental variability obtained. This study was prematurely halted as there was homogeneity in the response variable (speciation and extinction rates) across the smaller bovid phylogeny. However, this workflow was easily transferred over to passerine birds with similar methods used for extracting environmental predictors. The use of extensive bioclimatic predictors and spatial data in macroevolutionary research is imperative as we scale up studies. At very least, if bioclimatic variables do not encapsulate key ecological parameters (e.g., resources, predation, habitat structure) these predictors may account for some of the noise in the dataset and may help isolate the effect of the key moderator variables of interest.

## Future Directions

I had initially envisaged that this comparative study would allow for the reliable measure of extinction rate, utilise multiple taxonomic groups and use more robust measures of sexual selection (see Anthes et al. 2016). As such, many questions regarding this topic remain unanswered. Here I discuss the broader directions that we may follow in order to consolidate our understanding of sexual selection and its effects on fitness and diversification. I will draw heavily on the discussions from a Royal Society meeting on '*Sexual selection: patterns in the history of life*'<sup>4</sup> in the UK this year. This meeting spurred further inquiry into the subject and how interdisciplinary approaches can be harnessed to liberate ourselves from conventional comparative methodologies.

<sup>2</sup>5,831 species x 1000 samples per range x 59 environmental variability measures including bioclimatic predictors now, in the last inter-glacial and the last glacial maximum as well as NPP.

<sup>3</sup>This statement applies to species with documented range sizes, which varies across taxa but is comprehensive for birds, mammals, amphibians and many marine groups. The [IUCN](#) has a large and accessible database for research use. Details of how we extracted data from these ranges is provided as a potentially useful resource in the [ESM](#).

<sup>4</sup>Specifically, the following two sections are spurred from dialogue with [Dr Gene Hunt](#) and [Associate Professor Erin E. Saupe](#)

The study by Martins et al. (2018) has already been referred to several times in the main text of both papers and for good reason. This elegant study was able to do what no one else has; reliably measure extinction rate over meaningful time scales. Using fossil ostracods with various levels of sexual dimorphism, Martins et al. (2018) found that species with high levels of sexual dimorphism were quickly swept to extinction. From stratigraphic occurrence data a capture–mark–recapture model was used to determine the rate of extinction for 93 species. Their finding challenges the results from experimental evolution studies (Jarzebowska and Radwan 2010; Plesnar-Bielak et al. 2012; Lumley et al. 2015) and our meta-analysis that find sexual selection in mitigates extinction. Moving forward, it would be incredibly valuable to see whether other groups of marine invertebrates have the fossil data and recognisable sexual dimorphism to conduct such a study. In the interim I would be eager to see how BAMM would perform on an ostracod phylogeny and whether the same positive association between extinction rate and sexual dimorphism could be detected among extant taxa. For me, this will be a true test of the applicability of BAMM and a key step in the effort to reliably measure extinction from phylogenetic inference.

One aspect and only foreseeable shortcoming of the ostracod study is that it did not account for environmental variability; a challenging proposal for extinct species nevertheless. However the use of paleoclimate models in evolution is now a reality; with recent studies incorporating averaged values across multiple paleoclimate models as predictors of speciation (*see* Quintero and Jetz 2018). While the uncertainty surrounding paleoclimates was beyond the scope of the study, future studies should remain vigilant of the everlasting need to incorporate key ecological processes in macroevolutionary research (*reviewed in* Weber et al. 2017). In our study on passerine birds we found that range size is negatively associated with speciation. The role of range size in speciation may be further investigated through ancestral geographic range reconstruction (Quintero et al. 2015), as ancestral ranges may be beneficial in understanding modes of speciation and the causality of range size expansions and contractions (Losos and Glor 2003). Within Palaeobiology the role of range size and niche breadth on diversification patterns has been the subject of recent interest (*e.g.* Saupe et al. 2015; Qiao et al. 2016). Across 92 bivalve species that lived during a mid-Pliocene warming period, Saupe et al. (2015) used environmental niche modelling to assess the impact of ecological processes on extinction. Harnessing ecological niche modelling in macroevolutionary studies across extant taxa such as passerine birds is a daunting challenge but offers an Eco-evo synthesis that may be particularly pertinent in questions relating to extinction; especially if the taxonomic group under inquiry is of high conservation value, for which the songbirds certainly are.