1 **RECONCILING ECOGEOGRAPHICAL RULES: RAINFALL AND TEMPERATURE PREDICT GLOBAL**

2 **COLOUR VARIATION IN THE LARGEST BIRD RADIATION**

3 Kaspar Delhey[1], James Dale[2], Mihai Valcu[3] & Bart Kempenaers[3]

4 [1]School of Biological Sciences, Monash University, Clayton, Victoria, Australia. Corresponding author:

5 E-mail: kaspar.delhey@monash.edu

6 [2]Institute of Natural and Mathematical Science, Massey University, Auckland, New Zealand. E-mail:

7 J.Dale@massey.ac.nz

8 [3]Max Planck Institute for Ornithology, Seewiesen, Germany. E-mail: valcu@orn.mpg.de and

9 b.kempenaers@orn.mpg.de

10 **Running title:** Climatic effects on bird colour

11 **Authorship:** KD conceived the study. MV and KD analysed the data. JD, MV and BK contributed data.

12 KD wrote the manuscript with input from BK, JD and MV.

13 **Data availability:** upon acceptance of the manuscript data will be made available through online

14 repositories (eg Dryad) and the DOI of the data will be included in the article.

15 **Keywords:** climate, adaptation, thermoregulation, camouflage, birds, Passeriformes, biogeography,

16 plumage, Gloger's rule, Bogert's rule.

17 **Type of article:** Letter

18 **Number of words:** abstract = 151; main text = 5029;

19 **Number of References:** 90

20 **Number of Figures:** 5; **Number of Tables:** 0; **Number of textboxes:** 0.

21 **Corresponding author:** Kaspar Delhey, 25 Rainforest walk, School of Biological Sciences, Monash
22 University, 3800 Clayton, Victoria, Australia. Phone: +61-409 149 668/ +61-(0)3-9902 0377. E-mail:
23 kaspardelhey@gmail.com

Abstract

24

25   Ecogeographical rules that associate climate with organismal form and function can reveal patterns

26   of climatic adaptation. Two rules link animal coloration with climate: Gloger's rule (darker coloration

27   where wet and warm), and Bogert's rule (darker coloration where cold). Whereas Gloger's rule was

28   proposed for endotherms, and Bogert's rule for ectotherms, both rules may apply more broadly,

29   despite their seemingly opposing effects. Here we test this contradiction on a global scale across

30   passerine birds. Consistent with Gloger's rule, birds were darker in wetter areas and, following

31   Bogert's rule, lighter where warm, although birds became lighter again at very low temperatures.

32   Rainfall and temperature had antagonistic or additive effects depending on their pattern of

33   covariation, and this predicted whether birds followed the rules. We integrate both rules into a

34   general framework to explain heterogeneity in climatic effects on coloration, which has implications

35   to understand patterns of diversification, climatic adaptation and climate change impacts.

36

37

38   **INTRODUCTION**

39   Certain patterns of global spatial variation in organismal form and function are strong and general

40   enough to have been formalised as ecogeographical rules (Gaston *et al.* 2008). However, the

41   generality of these rules has been debated (Zink & Remsen 1986; Lomolino *et al.* 2006; Hagen 2017).

42   Currently, even some of the best-studied ecogeographical rules, such as Bergmann's rule (which

43   links body size with temperature variation), are sources of controversy (Olson *et al.* 2009; Salewski &

44   Watt 2017; Riemer *et al.* 2018). These debates are relevant today, because adaptive patterns of

45   phenotypic variation linked to climate may help us predict potential responses to human-induced

46   climate change (Millien *et al.* 2006; Roulin 2014; Teplitsky & Millien 2014). Hence, identifying the

47   reasons why ecogeographical rules apply in some cases but not in others, is essential to establish

48   their general validity and utility. However, our current knowledge is mainly restricted to body size

49   variation, and this limits our understanding of the broad palette of adaptations to climate variation

50   which include, among many others, appendage size, physiology, insulation, behaviour and

51   coloration.

52

53   One of the oldest ecogeographical rules that links variation in animal coloration with climatic

54   variation is Gloger's rule (Delhey 2017). This rule was inspired by the work of CWL Gloger who

55   recognised in 1833 that birds and mammals tend to be more intensively pigmented in tropical

56   regions (Gloger 1833). In its simple modern interpretation, Gloger's rule predicts that animals should

57   be darker in warm and humid areas, such as tropical rainforests (Rensch 1929; Delhey 2017).

58   Evidence supporting Gloger's rule has been found in different groups of animals (Miskimen 1972;

59   Zink & Remsen 1986; Lai *et al.* 2008, 2016; Roulin *et al.* 2009; Pannkuk *et al.* 2010; Friedman &

60   Remeš 2017; Delhey 2018). However, because the tropics are associated with a variety of climatic

61   factors, different patterns of variation have been considered consistent with Gloger's rule, including

62   correlations with rainfall, temperature, UV radiation, latitude, evapotranspiration or combinations

3

63   thereof (Gipson *et al.* 2002; Caro 2005; Kamilar & Bradley 2011; Singaravelan *et al.* 2013; Bastide *et*

64   *al.* 2014; Koski & Ashman 2015).

65

66   Indeed, recent comparative analyses on birds have revealed patterns that seemingly oppose some

67   aspects of Gloger's rule, namely that species with darker plumage are often found in colder rather

68   than warmer regions (Friedman & Remeš 2017; Delhey 2018; Galván *et al.* 2018; Medina *et al.*

69   2018). These conflicting results have also been found by some studies of intraspecific variation

70   (Aldrich & James 1991; Morales *et al.* 2017; Fargallo *et al.* 2018). However, darker animals occurring

71   in colder regions is consistent with another ecogeographical rule: Bogert's rule (Bogert 1949; Clusella

72   Trullas *et al.* 2007; Gaston *et al.* 2009). Also called the thermal melanism hypothesis, this rule was

73   originally proposed for ectothermic animals and argues that darker animals occur in colder regions

74   for thermoregulatory reasons because dark coloration absorbs more solar radiation (Clusella Trullas

75   *et al.* 2007).

76

77   Discrepancies between studies suggests that the correlation between climatic variables and animal

78   light-to-dark variation differs across the globe. For example, the relationship between lightness and

79   temperature could be positive in places such as Australia (Friedman & Remeš 2017; Delhey 2018) or

80   Spain (Galván *et al.* 2018), where the need for thermoregulation to avoid overheating may play an

81   important role, and negative at higher latitudes, driven by the need for camouflage against snowy

82   surfaces. Thus, heterogeneous patterns of correlations in different biogeographic regions are not

83   unexpected. An effective way to disentangle these possibilities is to assess the links between specific

84   climatic variables and animal coloration on a global scale.

85

4

86   Resolving the nature and generality of correlations between climate and coloration is a first

87   necessary step to identify the key drivers of ecogeographic rules. Positive correlations between

88   animal lightness and temperature as suggested by Bogert's rule are usually interpreted in terms of

89   thermoregulation (Clusella Trullas *et al.* 2007), while the mechanisms behind Gloger's rule are more

90   elusive. Camouflage is widely considered a valid explanation for the occurrence of darker animals in

91   more humid and vegetated environments, and of lighter animals in polar regions or deserts (Zink &

92   Remsen 1986; Caro 2005), but other explanations exist (Burtt & Ichida 2004; Ducrest *et al.* 2008;

93   Delhey 2017). If adaptive mechanisms underlie the patterns of geographic variation in coloration,

94   then climate change and human-driven habitat transformation may disrupt these with potential

95   negative consequences (Delhey & Peters 2017). For example, consistent with Bogert's rule, insect

96   assemblages have become lighter in regions experiencing increases in temperature, caused by shifts

97   in distribution and local extinctions (Zeuss *et al.* 2014; Bishop *et al.* 2016). Historical changes in

98   coloration across different species of birds and mammals have also been linked to climatic or

99   environmental change (Galeotti *et al.* 2009; Maloney *et al.* 2009; Sandoval-Castellanos *et al.* 2017)

100   and failure to adapt may result in local extinctions (Mills *et al.* 2013). Knowing the generality of

101   climatic effects on colour variability is thus essential to help us understand and predict the effects of

102   future changes.

103   Here we present a global test of both Gloger's and Bogert's rules by assessing the relationship

104   between climatic (temperature and rainfall) and environmental variables (tree cover), and plumage

105   lightness across nearly all species of passerine birds (Order Passeriformes).

106

107   **MATERIAL AND METHODS**

108   **Plumage lightness.** We quantified plumage lightness using Red-Green-Blue (RGB) values of plumage

109   colours obtained from the plates of the Handbook of the Birds of the World (del Hoyo, J., Elliott, A. &

110   Christie n.d.) as described in Dale et al. (Dale *et al.* 2015) for all species of the order Passeriformes (n

5

111   = 5831). Briefly, we obtained RGB values from scanned plates for nine different plumage patches

112   (nape, crown, forehead, throat, upper breast, lower breast, belly, vent and back). Each separate

113   channel (R, G, and B) can vary between 0 and 255, and we compute plumage lightness as (R+G+B)/3,

114   which therefore also varies between 0 (pure black) and 255 (pure white, see Supplementary

115   Information and Figs. S1-S2). For each species, we averaged these values across all patches, but

116   separately for each sex, to obtain sex-specific estimates of plumage lightness. Male and female

117   lightness scores were positively correlated (r = 0.8, 95%CI = 0.79 – 0.81, t = 102.3, df = 5807, p <

118   0.001). As shown in other studies using reflectance spectrometry (Delhey 2018) or book plates

119   (Negro *et al.* 2018), males are usually darker than females (mean differences within species [female

120   lightness – male lightness] = 8.3, 95%CI = 7.7 – 8.8, paired t=28.5, df=5808, p < 0.001).

121   The lightness estimates used in this study did not cover the entire body, and were derived from book

122   plates rather than from plumage reflectance spectra. Hence, we assessed how well they correlated

123   with spectrometric measurements of plumage lightness derived from the entire plumage of museum

124   specimens (Delhey 2018) for the subsample of species for which we had both types of

125   measurements (n = 309). For both sexes, RGB values correlated with measurements of real plumage

126   lightness (males: r = 0.72, females: r = 0.70, both p < 0.001). To further determine whether

127   differences between methods could affect our conclusions, we tested whether climatic effects were

128   consistent between both methods (for the subsample of 309 species). This was the case; both

129   conclusions and effects are similar (Fig. S3). Hence, we consider the RGB values used here to

130   constitute an appropriate estimate of overall plumage lightness.

131   **Climatic variables and vegetation.** Based on the breeding range of each species from (Dale *et al.*

132   2015) we obtained species-specific average estimates of mean annual temperature (bio1, in °C) and

133   annual average precipitation (bio12, in mm, square-root transformed) from the database in (Karger

134   *et al.* 2017) and percent forest cover from (DeFries *et al.* 2000), sampled on a grid of 0.05° cell size

135   using the package 'RangeMapper' (Valcu *et al.* 2012). Similarly, for assemblage level analysis we

6

136   obtained average estimates for annual mean temperature, annual rainfall (square-root transformed)

137   and forest cover within each 1° cell (~100 x 100 km).

138   **Statistical Analyses**

139   **Analysis at species level.** We used the function phylolm from the R package 'phylolm' (Tung Ho &

140   Ané 2014) with plumage lightness as the dependent variable and temperature, rainfall and percent

141   tree cover as independent variables. We also included the quadratic effects for precipitation,

142   temperature and tree cover to assess for possible non-linear effects. All variables were centred and

143   scaled prior to analyses to facilitate the interpretation of linear and quadratic effects (Schielzeth

144   2010). We controlled for phylogenetic relatedness using Pagel's lambda model. A sample of 1000

145   phylogenetic trees for the species included was obtained from birdtree.org (Jetz *et al.* 2012). Models

146   were run on the 1000 phylogenies and we obtained average effect sizes and their SEs using model

147   averaging procedures (Symonds & Moussalli 2011) across all models. In addition, we also computed

148   median, minimum, and maximum p-values, as well as the proportion of phylogenies yielding a p-

149   value < 0.05 for each parameter. Analyses were carried out separately for male and female lightness.

150   Complete environmental and phylogenetic data were available for 5809 out of a total of 5831

151   species for which we had colour data (99.6%). Since the function phylolm does not include R^2-values

152   in its output, we assessed fit by correlating predicted and observed lightness values. To determine

153   the extent of taxonomic heterogeneity in the relationships between plumage lightness and rainfall,

154   temperature and tree cover, we ran the comparative analyses separately for each family comprising

155   10 or more species. However, in this case, we used only a sample of 100 phylogenies. Inspection of

156   model residuals did not reveal major departures from normality or heterogeneity of variance.

157   **Analysis at assemblage level.** For each 1° cell we computed a mean plumage lightness value for all

158   species in the assemblage, separately for males and females. Only cells with more than 5 species

159   were included, yielding a total of 9715 cells. Climatic variables and tree cover were also summarised

160   in the same manner. Mean assemblage lightness was the dependent variable, while precipitation,

161 temperature and percent tree cover were included as explanatory variables (as linear and quadratic

162 effects). All variables were centred and scaled prior to analyses (Schielzeth 2010). We also included

163 zoogeographical realm (11 levels, (Holt *et al.* 2013)) as a random intercept to account for differences

164 in lightness across the globe. These zoogeographic realms define terrestrial areas that harbour

165 subsets of species that are closely related, and which are often part of clades that have radiated in,

166 and are restricted to, specific regions of the globe. Terrestrial realms therefore constitute units

167 representing largely independent macro-ecological and -evolutionary patterns. We further included

168 random-slope effects for temperature, precipitation and percent tree cover (linear and quadratic

169 where relevant) in each realm to allow the possibility of different patterns in each realm. We

170 accounted for spatial autocorrelation of residuals based on the approach outlined by Crase et al.

171 (Crase *et al.* 2012) which involves fitting a residual autocorrelation covariate derived from a 5x5 cell

172 focal region around each cell. This procedure reduced spatial autocorrelation as revealed by visual

173 inspection of variograms. Model residuals did not show major departures from normality or

174 heterogeneity of variance. We computed marginal (fixed effects) and conditional (mixed+fixed

175 effects) R^2-values following (Nakagawa & Schielzeth 2013) using the package MUMin (Barton 2017).

176 Because the spatial autocorrelation covariate accounts for much of the unexplained variation (and

177 thus increases R^2-values beyond the contribution of the other fixed effects), R^2-values were

178 computed on the model without this variable. Assemblage-level analyses were carried out with the R

179 package lme4 (Bates *et al.* 2015).

180 **Simulations.** Assemblage level analyses that seek to link climatic variables with trait data and use

181 averages for each assemblage, suffer from a high probability of type I errors, even after accounting

182 for spatial autocorrelation (Friedman & Remeš 2017; Delhey 2018). To assess whether this affected

183 our conclusions we simulated the evolution of plumage lightness values for each species across the

184 phylogeny assuming Brownian motion for each of the 1000 phylogenies used in the species-level

185 analyses. Simulations were carried out using the function 'fastBM' from the package 'phytools' (0.6-

186 44) (Revell 2012), separately for female and male lightness. For each phylogeny we first quantified

8

187   the parameters λ and σ^2 based on the real lightness values, and we then used these parameters to

188   simulate lightness values. Given that these simulated values of species lightness should only be

189   influenced by phylogenetic relatedness, we would not expect any correlation with climatic variables

190   beyond those that are inherent when related species share climatic niches. Based on the simulated

191   data we re-ran the final best model for the assemblage-level analyses 1000 times to obtain a

192   distribution of simulated effects. We then compared the observed effects from the real data with

193   the simulated data, and computed the proportion of simulated effects that were larger than the

194   observed effect.

195

196   **Meta-regressions.** We used a meta-regression approach to determine whether variability in the

197   patterns of precipitation-temperature covariance could explain variability in climatic or tree cover

198   effects across bird families or zoogeographic realms. A meta-regression is a meta-analysis that

199   includes the effect of a continuous covariate (also called moderator (Nakagawa & Santos 2012)).

200   Meta-analyses combine statistical effects from different analyses, while accounting for their

201   measurement error, to obtain an average effect across analyses, and test for variables that explain

202   differences between analyses. We ran two groups of meta-regressions, one using each family-

203   specific effect of precipitation, temperature or tree cover on plumage lightness, as derived from

204   linear models accounting for phylogenetic relatedness (see species-level analyses above). We used

205   only families with at least 10 species but results are comparable if we only used families with at least

206   15 species (see Results). For the second group of meta-regressions we used each zoogeographic

207   realm specific effect, while controlling for spatial effects (see assemblage-level analyses above). In

208   both cases we used the function 'rma' (method='REML') in the package metafor (Viechtbauer 2010)

209   to run the meta-regressions, which weigh each effect by its variance.

210

211   **RESULTS**

9

212   Birds living closer to the equator have darker plumage (Figs. 1-2). This pattern was consistent at both

213   the species level (latitude effect: estimate females = 0.173, SE = 0.015, median p < 0.001; estimate

214   males = 0.128, SE = 0.015, median p < 0.001), and the assemblage level (latitude effect: female

215   estimate = 0.398, SE = 0.003, p < 0.001; male estimate = 0.573, SE = 0.003, p < 0.001). At the

216   assemblage level, plumage became darker at higher latitudes (Fig. 1, quadratic latitude effect:

217   female estimate = -0.414, SE = 0.003, p < 0.001, male estimate = -0.361, SE = 0.003, p < 0.001), but

218   this was not as evident at the species level (Fig. 1, quadratic latitude effect: female estimate = -

219   0.009, SE = 0.000, median p = 0.316, male estimate = -0.011, SE = 0.009, median p = 0.215).

220   At the species level, the main correlate of plumage lightness was annual precipitation (Figs. 1, 3).

221   Species living in areas with high levels of precipitation and tree cover were darker (Figs. 1, 3). The

222   quadratic precipitation and tree cover effects were never significant and excluded from the models

223   (Fig. 3). The quadratic temperature effect was positive and statistically significant indicating that

224   lightness was lowest at intermediate temperatures (~10 °C annual mean temperature, Fig. 1, 3). The

225   overall linear effect of temperature was positive (Fig. 3). In general, effects were stronger for female

226   plumage (model R^2 = 0.11) than for male plumage (model R^2 = 0.06), but patterns were similar (Fig.

227   3, for full statistical results see Table S1). Separate analyses for each bird family showed that the

228   effects of precipitation, tree cover and temperature can vary substantially among families (Fig. 1).

229   At the assemblage level, bird communities in areas with higher levels of precipitation and tree cover

230   contained, on average, species with darker plumage (Figs. 1-3). While the quadratic tree cover effect

231   was not significant (and therefore excluded), the model revealed a significant quadratic precipitation

232   effect in males and the same trend in females (Fig. 1), indicating that the precipitation effect

233   weakens at very high levels of precipitation (Fig. 1). Linear temperature effects were largely positive

234   (but not statistically significant in males), with lighter assemblages occurring in warmer areas (Figs.

235   1-2); no significant quadratic temperature effects were detected (Fig. 3). Fixed effects alone

236   explained a substantial amount of variation in assemblage lightness (marginal $R^2_{females}$ = 0.32;

237   marginal R^2_{males} = 0.25); when random effects were taken into account the amount of variation

238   explained was even higher (conditional $R^2_{females}$ = 0.78, conditional R^2_{males} = 0.75). For full statistical

239   results see Table S2.

240   Since assemblage-level analyses can be prone to inflated type I error rates (Friedman & Remeš 2017;

241   Hawkins *et al.* 2017; Delhey 2018), we compared the observed results with those obtained from a

242   sample of 1000 phylogenetic simulations (see methods). This approach indicated that our

243   conclusions are robust: observed effects in the final assemblage model (Fig. 3) were always larger

244   than the most extreme simulated effects.

245   Across zoogeographic realms (Holt *et al.* 2013), there was substantial variation in average plumage

246   lightness and the magnitude and direction of the temperature effect (Fig. 1, and as indicated by

247   random intercept and slope variances, Table S2). Separate plots for each realm confirmed this,

248   showing in particular negative effects of temperature for the Neotropical and Sino-Japanese realms

249   (Fig. S4). Further exploratory plotting (Fig. S5) revealed that these realms showed some of the

250   strongest positive correlations between annual precipitation and average temperature.

251   To evaluate this further, we tested whether variation in the correlation between temperature and

252   precipitation could explain heterogeneity in climatic effects detected at the family and realm levels.

253   If both climatic variables correlate in a strong positive manner, temperature and rainfall effects may

254   oppose each other, weakening their correlation with plumage lightness. We used a meta-regression

255   approach to test whether the effects of temperature, precipitation and tree cover – estimated

256   separately for each family or realm and weighted by their uncertainty – co-varied with the strength

257   of the temperature-rainfall correlation. For these analyses we only considered models with linear

258   effects, rather than also including the quadratic effects. The main aim of these tests was to

259   determine whether the overall positive or negative effects of temperature, precipitation and tree

260   cover can be affected by antagonistic or additive effects of temperature and precipitation. Including

11

261   quadratic effects makes interpreting these linear effects more difficult. Moreover, quadratic effects

262   were statistically significant in only 5 families of birds.

263   At the species level, across passerine families, the positive effect of temperature on plumage

264   lightness became significantly weaker as the correlations between precipitation and temperature

265   became more positive (Table S3, Fig. 4a). Similarly, the negative effect of tree cover on plumage

266   lightness became less marked with stronger positive temperature-precipitation correlation values

267   (Table S3, Fig. 4c). The precipitation effect was not as affected by this correlation (Table S3, Fig. 4b).

268   Results for males followed similar patterns, but effects were weaker (Table S3). It could be argued

269   that the reason why effects become weaker when precipitation and temperature are highly

270   correlated is simply due to the statistical effect of collinearity (F. Dormann *et al.* 2007). However, the

271   fact that patterns are similar and in some cases became stronger if we tested for effects of each

272   variable separately (thereby avoiding collinearity issues) (Table S3) argues against this.

273   At the assemblage level, the effect of temperature on plumage lightness decreased with strong and

274   positive temperature-precipitation correlations across the 11 zoogeographic realms (Table S4, Fig.

275   4d), while the effect of precipitation and tree cover became less marked (Table S4, Fig. 4ef). As

276   above, results are qualitatively similar but weaker for males (Fig. 4d-f, Table S4), but again become

277   more marked when we run models for each predictor separately (Table S4).

278

279   **DISCUSSION**

280   Our global analysis is broadly supportive of the observations made by Gloger nearly 200 years ago:

281   birds tend to be darker towards the equator (Gloger 1833). Assessing the effect of three possible

282   environmental drivers behind this correlation reveals that annual precipitation is the most consistent

283   correlate of plumage lightness: both at the species and assemblage levels, passerine birds are darker

284   in areas with higher rainfall. Tree cover had a similar but weaker effect with darker birds inhabiting

12

285   areas with higher tree cover. The effect of temperature was less strong, but in general birds tended

286   to be lighter, not darker in warmer areas. Note, however, that at the species (but not assemblage)

287   level, lightness increased again at very low temperatures. In sum, precipitation effects followed

288   predictions by Gloger's rule while temperature effects largely contradicted it, and were more

289   consistent with Bogert's rule.

290   These global patterns are in general agreement with recent work on Australian birds both at the

291   species and assemblage levels, which showed similar negative precipitation effects and positive

292   temperature effects (Friedman & Remeš 2017; Dalrymple *et al.* 2018; Delhey 2018). However, some

293   of these effects vary in strength depending on the specific region (Dalrymple *et al.* 2018; Delhey

294   2018) or taxonomic group assessed (Friedman & Remeš 2017). Similarly, work on Spanish birds also

295   reported a positive correlation between plumage lightness and temperature, but not with rainfall

296   (Galván *et al.* 2018). This variability in climatic effects is reflected by our own analysis because the

297   strength and direction of climatic effects varied across bird families and zoogeographic realms (Figs.

298   1, 4).

299   Our observations suggest that spatial and taxonomic heterogeneity of climatic effects can be partly

300   explained by patterns of covariation between rainfall and temperature. When the correlation is

301   strong and positive, the effects of rainfall and temperature on plumage lightness weaken (Fig. 4),

302   because both gradients oppose each other (lightness correlates mostly positively with temperature

303   and negatively with precipitation). This effect is more evident on temperature effects, which are

304   generally much weaker than precipitation effects. Antagonistic climatic effects could provide a

305   general explanation for a lack of agreement between studies. Trade-offs between different selective

306   forces (which may or may not be summarised as ecogeographical rules) are not un-common, and

307   have been used to explain, for example, departures from Bergmann's rule (Medina *et al.* 2007;

308   Gutiérrez-Pinto *et al.* 2014; De Keyser *et al.* 2015; Busso & Blanckenhorn 2018). However, previous

309   studies have not explicitly identified the antagonistic or reinforcing effects of different climatic

13

310 variables. We note that because we generated this explanation based on the data, proper

311 confirmation will require further tests in different taxonomic groups and/or at a different level of

312 variation (e.g. intraspecific variation).

313 The effects of temperature and precipitation are also constrained by the shape of the climatic space.

314 This space, as defined by precipitation and temperature, is triangular in shape (Fig. 5), because very

315 high levels of precipitation are always found in warm areas, while very cold regions always have low

316 levels of precipitation. Very high levels of precipitation never coincide with very low temperatures.

317 The consequence of this is that patterns of colour variation seem to follow the predictions of

318 Gloger's rule: birds are darker where it is warm and wet (and to some extent lighter where very

319 cold). Yet, when assessing the underlying effects of the climatic variables, it becomes evident that

320 this is only because at high temperatures the precipitation effects overwhelm temperature effects.

321 Birds are dark despite high temperatures, not because of them. On the other hand, the lightening of

322 plumage at cold temperatures (<10°C) does match the prediction of Gloger's rule of lighter 'polar

323 coloration' (Rensch 1929). We note, however, that this effect was only detected at the species-level

324 analysis and that it applies to comparatively few species (~10%); most passerines inhabit warmer

325 areas, where temperature effects lead to lighter plumage (Fig. 5).

326 Because Gloger's rule generally predicts darker animals in warmer areas, and our temperature

327 effects do not seem to follow this expectation in general, it is tempting to reformulate the rule in

328 terms of precipitation alone rather than precipitation and temperature together. We therefore

329 propose a general framework to explain climatic effects on plumage coloration that integrates and

330 reconciles Gloger's and Bogert's rules, by taking into account their reinforcing or antagonistic effects

331 (Fig. 5). Within this framework, for most species of passerines (and at the assemblage level)

332 temperature effects on coloration seem to fall in the realm of Bogert's rule. Gloger's rule on the

333 other hand, could be re-defined in terms of precipitation effects alone.

14

334 Traditionally, Bogert's rule has been applied mainly to ectotherms (Clusella Trullas *et al.* 2007) and

335 Gloger's rule was formulated for endotherms, although the possibility that it also applies to

336 ectotherms was left open (Rensch 1929). Past and recent work indicates that these rules could apply

337 more broadly across animals (Amtmann 1965; Xing *et al.* 2016; Friedman & Remeš 2017; Cheng *et al.*

338 2018; Delhey 2018; Galván *et al.* 2018), fungi (Cordero *et al.* 2018) and perhaps even in plants

339 (Watson & Hanham 1977; Burns 2015; Cuthill 2015). Whether patterns follow more strongly Gloger's

340 or Bogert's rule could depend on the selective pressures behind the mechanisms in each rule. For

341 example, for ectotherms thermoregulation may be more important such that correlations between

342 lightness and temperature would be more prevalent. In contrast, for endotherms camouflage or

343 parasite resistance (two popular adaptive explanations for Gloger's rule (Delhey 2017)) could exert

344 stronger selection, such that correlations with rainfall become more marked (as seems the case in

345 birds).

346 This integrated framework has implications for further research. If climatic gradients where

347 precipitation and temperature effects oppose each other lead to reduced colour divergence, pre-

348 mating hybridization barriers may be reduced (Martin *et al.* 2010), and this could affect the

349 maintenance of incipient species in cases of secondary sympatry. Hence, not only the magnitude

350 (Jezkova & Wiens 2018) but also the nature of the climatic gradient may influence speciation in

351 organisms where visual signals are important pre-mating barriers between species (e.g. birds). For

352 example, together with song, differences in plumage coloration between subspecies of Song

353 Sparrow (*Melospiza melodia*) across a rainfall gradient contribute to the prevention of hybrid mating

354 (Patten *et al.* 2004). Hence, coloration could be considered as a "magic trait" (traits under divergent

355 selection that also result in non-random mating (Servedio *et al.* 2011)), being affected by climatic

356 conditions and playing a role in mate choice (Keller & Seehausen 2012). To our knowledge, no

357 studies have linked lineage diversification patterns with the nature of climatic gradients. We predict

358 that climatic gradients where rainfall and temperature effects reinforce each other (that is, negative

359   correlation between rainfall and temperature) should be associated with higher rates of lineage

360   diversification in animals that strongly rely on visual cues.

361   Furthermore, if patterns of covariation between climatic variables constrain the evolution of

362   coloration that is optimally suited for the prevailing temperature or rainfall levels, alternative

363   adaptations may evolve in compensation. These could include adaptations for thermoregulation

364   such as insulation properties of fur or plumage (Briscoe *et al.* 2015), physiology (Tattersall *et al.*

365   2012), body and appendage size (Symonds & Tattersall 2010), or anti-predator behaviour to

366   compensate for imperfect camouflage (Mcqueen *et al.* 2017). It could be argued that some of these

367   compensatory responses should be evident in males (e.g. (Briscoe *et al.* 2015)), because male

368   plumage lightness is less closely linked to climatic variation than female lightness. Males are under

369   stronger sexual selection than females (Dale *et al.* 2015) and this often selects for conspicuous

370   colours that function best when they stand out rather than blend in with the background. For

371   example, plumage signals are selected to be lighter in environments with dense vegetation

372   (Marchetti 1993), opposing the effects of Gloger's rule described here. The fact that plumage

373   coloration is a complex trait – the compromise of a variety of selection forces and evolutionary

374   constraints – probably accounts for the generally modest explanatory power of climatic effects (Fig.

375   1).

376   In general, compensatory mechanisms that mediate evolutionary compromises may provide clues

377   about possible alternative adaptive responses if future climate change disrupts current patterns of

378   climatic covariation (Wu *et al.* 2011). More broadly, assessing the simultaneous effects of climate on

379   a suite of adaptations can –not only help to establish why ecogeographical rules are not always

380   followed– but also provide a more complete understanding on the diversity of phenotypic responses

381   to climatic variation across taxa. To this end we need to expand the type of integrative framework

382   used here to encompass multiple ecogeographic rules.

383   In conclusion, we propose a general framework to understand the effects of temperature and

384   precipitation on the evolution of animal colours. Our data suggest that climatic effects on plumage

385   coloration are affected by the type of climatic gradient, and that the strength and direction of

386   climatic effects on plumage lightness can also vary across climatic space, while being constrained by

387   the specific shape of the climatic space (Fig. 5). Given that the patterns uncovered at the species and

388   assemblage levels should reflect selection at the individual level, studies on intraspecific variation in

389   coloration are needed to put these predictions to test. Here we have deliberately focused on the

390   two climatic variables that are most closely linked to the original ecogeographical rules. However,

391   other climatic (and non-climatic) variables may be playing additional roles (Dalrymple *et al.* 2018)

392   and correlations with temperature and precipitation may be driven by other causes. For example, it

393   has been suggested that Gloger's rule should be reformulated in terms of vegetation rather than

394   precipitation because the former is presumably more closely linked to the putative mechanism

395   (darker animals more camouflaged in darker environments)(Zink & Remsen 1986). This assumes that

396   the mechanism behind Gloger's rule is clear – an assumption that remains disputed (Burtt & Ichida

397   2004; Ducrest *et al.* 2008; Delhey 2017). More recently, research on the genetic basics melanin

398   pigmentation –the main pigment involved in Gloger's (Delhey 2017) and Bogert's rules (Clusella

399   Trullas *et al.* 2007), and the most common pigment in birds (Delhey 2015; Galván & Solano 2016)–

400   has revealed pleiotropic links between genes that underlie pigmentation and multiple adaptive

401   processes such as dispersal, aggressiveness, immune-responsiveness, stress-physiology, (Ducrest *et*

402   *al.* 2008; San-jose & Roulin 2018) and even thermoregulation behaviours (Dreiss *et al.* 2016). Such

403   links suggest that correlations between coloration and climate could be the consequence of

404   selection that is not acting directly on colour per se. Hence, determining the mechanism(s)

405   responsible for the correlations between climate and coloration may lead to further refinement and

406   reformulation of the rule(s). In the meantime, our results provide an integrated framework to assess

407   the generality of climatic effects on animal coloration, a necessary first step to determine their

408   status as biological rules.

409 **ACKNOWLEDGMENTS**

413 **REFERENCES**

414 Aldrich, J.W.. & James, F.C.. (1991). Ecogeographic Variation in the American Robin (Turdus

415   migratorius). *Auk*, 108, 230–249.

416 Amtmann, E. (1965). Zur geographischen Farbvariation des Afrikanischen Riesenhoernchens

417   Protoxerus stangeri (Waterhouse 1842). Eine quantitative Untersuchung zur Glogerschen

418   Regel. *Z. Morph. Oekol. Tiere*, 529, 515–529.

419 Barton, K. (2017). MuMIn: Multi-Model Inference. R package version 1.40.0.

420 Bastide, H., Yassin, A., Johanning, E.J. & Pool, J.E. (2014). Pigmentation in Drosophila melanogaster

421   reaches its maximum in Ethiopia and correlates most strongly with ultra-violet radiation in sub-

422   Saharan Africa. *BMC Evol. Biol.*, 14, 179.

423 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using

424   lme4. *J. Stat. Softw.*, 67, 1–48.

425 Bishop, T.R., Robertson, M.P., Gibb, H., van Rensburg, B.J., Braschler, B., Chown, S.L., *et al.* (2016).

426   Ant assemblages have darker and larger members in cold environments. *Glob. Ecol. Biogeogr.*,

427   25, 1489–1499.

428 Bogert, C.M. (1949). Thermoregulation in Reptiles, A Factor in Evolution. *Evolution (N. Y).*, 3, 195–

429   211.

430 Briscoe, N.J., Krockenberger, A., Handasyde, K.A. & Kearney, M.R. (2015). Bergmann meets

431   Scholander: Geographical variation in body size and insulation in the koala is related to climate.

18

432   *J. Biogeogr.*, 42, 791–802.

433   Burns, K.C. (2015). The color of plant reproduction: macroecological trade-offs between biotic

434   signaling and abiotic tolerance. *Front. Ecol. Evol.*, 3, 1–4.

435   Burtt, E.H. & Ichida, J.M. (2004). Gloger's Rule, Feather-Degrading Bacteria, and Color Variation

436   Among Song Sparrows. *Condor*, 106, 681–686.

437   Busso, J.P. & Blanckenhorn, W.U. (2018). Climatic factors shape plastic trade-offs in the polyphenic

438   black scavenger fly Sepsis thoracica (Diptera: Sepsidae). *J. Biogeogr.*, 45, 593–603.

439   Caro, T. (2005). The Adaptive Significance of Coloration in Mammals. *Bioscience*, 55, 125.

440   Cheng, W., Xing, S., Chen, Y., Lin, R., Bonebrake, T.C. & Nakamura, A. (2018). Dark butterflies

441   camouflaged from predation in dark tropical forest understories. *Ecol. Entomol.*, 304–309.

442   Clusella Trullas, S., van Wyk, J.H. & Spotila, J.R. (2007). Thermal melanism in ectotherms. *J. Therm.*

443   *Biol.*, 32, 235–245.

444   Cordero, R.J.B., Robert, V., Cardinali, G., Arinze, E.S., Thon, S.M. & Casadevall, A. (2018). Impact of

445   Yeast Pigmentation on Heat Capture and Latitudinal Distribution. *Curr. Biol.*, 28, 2657–2664.e3.

446   Crase, B., Liedloff, A.C. & Wintle, B.A. (2012). A new method for dealing with residual spatial

447   autocorrelation in species distribution models. *Ecography (Cop.).*, 35, 879–888.

448   Cuthill, I.C. (2015). Flower colour: Gloger's rule isn't just for the birds. *Nat. Plants*, 1, 14013.

449   Dale, J., Dey, C., Delhey, K., Kempenaers, B. & Valcu, M. (2015). The effects of life-history and social

450   selection on male and female plumage coloration. *Nature*, 527, 367–370.

451   Dalrymple, R.L., Flores-Moreno, H., Kemp, D.J., White, T.E., Laffan, S.W., Hemmings, F.A., *et al.*

452   (2018). Abiotic and biotic predictors of macroecological patterns in bird and butterfly

453   coloration. *Ecol. Monogr.*, 88, 204–224.

454   DeFries, R.S., Hansen, M.C., Townshend, J.R.G., Janetos, a C. & Loveland, T.R. (2000). A new global 1

455   km dataset of percentage tree cover derived from remote sensing. *Glob. Chang. Biol.*, 6, 247–

456   254\r.

457   Delhey, K. (2015). The colour of an avifauna: A quantitative analysis of the colour of Australian birds.

458   *Sci. Rep.*, 5.

459   Delhey, K. (2017). Gloger's rule. *Curr. Biol.*, 27, R689–R691.

460   Delhey, K. (2018). Darker where cold and wet: Australian birds follow their own version of Gloger's

461   rule. *Ecography (Cop.).*, 41, 673–683.

462   Delhey, K. & Peters, A. (2017). Conservation implications of anthropogenic impacts on visual

463   communication and camouflage. *Conserv. Biol.*, 31.

464   Dreiss, A.N., Séchaud, R., Béziers, P., Villain, N., Genoud, M., Almasi, B., *et al.* (2016). Social huddling

465   and physiological thermoregulation are related to melanism in the nocturnal barn owl.

466   *Oecologia*, 180, 371–381.

467   Ducrest, A.L., Keller, L. & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and

468   behavioural syndromes. *Trends Ecol. Evol.*, 23, 502–510.

469   F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., *et al.* (2007).

470   Methods to account for spatial autocorrelation in the analysis of species distributional data: A

471   review. *Ecography (Cop.).*, 30, 609–628.

472   Fargallo, J.A., Martínez, F., Wakamatsu, K., Serrano, D. & Blanco, G. (2018). Sex-Dependent

473   Expression and Fitness Consequences of Sunlight-Derived Color Phenotypes. *Am. Nat.*, 191,

474   000–000.

475   Friedman, N.R. & Remeš, V. (2017). Ecogeographical gradients in plumage coloration among

476   Australasian songbird clades. *Glob. Ecol. Biogeogr.*, 26, 261–274.

477   Galeotti, P., Rubolini, D., Sacchi, R. & Fasola, M. (2009). Global changes and animal phenotypic

478   responses: melanin-based plumage redness of scops owls increased with temperature and

479   rainfall during the last century. *Biol. Lett.*, 5, 532–534.

480   Galván, I., Rodríguez-Martínez, S. & Carrascal, L.M. (2018). Dark pigmentation limits thermal niche

481   position in birds. *Funct. Ecol.*, 32, 1531–1540.

482   Galván, I. & Solano, F. (2016). Bird integumentary melanins: Biosynthesis, forms, function and

483   evolution. *Int. J. Mol. Sci.*, 17.

484   Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., *et al.* (2009).

485   Macrophysiology: A Conceptual Reunification. *Am. Nat.*, 174, 595–612.

486   Gaston, K.J., Chown, S.L. & Evans, K.L. (2008). Ecogeographical rules: Elements of a synthesis. *J.*

487   *Biogeogr.*, 35, 483–500.

488   Gipson, P.S., Bangs, E.E., Bailey, T.N., Boyd, D.K., Dean Cluff, H., Smith, D.W., *et al.* (2002). Color

489   patterns among wolves in western North America. *Wildl. Soc. Bull.*, 30, 821–830.

490   Gloger, C.W.L. (1833). *Das Abändern der Vögel durch Einfluss des Klimas*. August Schulz., Breslau.

491   Gutiérrez-Pinto, N., McCracken, K.G., Alza, L., Tubaro, P., Kopuchian, C., Astie, A., *et al.* (2014). The

492   validity of ecogeographical rules is context-dependent: Testing for Bergmann's and Allen's rules

493   by latitude and elevation in a widespread Andean duck. *Biol. J. Linn. Soc.*, 111, 850–862.

494   Hagen, J.B. (2017). Bergmann's Rule, Adaptation, and Thermoregulation in Arctic Animals:

495   Conflicting Perspectives from Physiology, Evolutionary Biology, and Physical Anthropology After

496   World War II. *J. Hist. Biol.*, 50, 235–265.

497   Hawkins, B.A., Leroy, B., Rodríguez, M., Singer, A., Vilela, B., Villalobos, F., *et al.* (2017). Structural

498   bias in aggregated species-level variables driven by repeated species co-occurrences: a

499   pervasive problem in community and assemblage data. *J. Biogeogr.*, 44, 1199–1211.

500   Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S. a, Araújo, M.B., Dimitrov, D., *et al.* (2013). An

501   Update of Wallace's Zoogeographic Regions of the World. *Science (80-.).*, 339, 74–78.

502   del Hoyo, J., Elliott, A. & Christie, D.A. (n.d.). *Handbook of the Birds of the World Vols 8–16*. Lynx

503   Edicions, Barcelona.

504   Jetz, W., Thomas, G.H.H., Joy, J.B.B., Hartmann, K. & Mooers, a. O.O. (2012). The global diversity of

505   birds in space and tim. *Nature*, 491, 1–5.

506   Jezkova, T. & Wiens, J.J. (2018). Testing the role of climate in speciation: new methods and

507   applications to squamate reptiles (lizards and snakes). *Mol. Ecol.*, in press.

508   Kamilar, J.M. & Bradley, B.J. (2011). Interspecific variation in primate coat colour supports Gloger's

509   rule. *J. Biogeogr.*, 38, 2270–2277.

510   Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2017).

511   Climatologies at high resolution for the earth's land surface areas. *Sci. Data*, 4, 1–20.

512   Keller, I. & Seehausen, O. (2012). Thermal adaptation and ecological speciation. *Mol. Ecol.*, 21, 782–

513   799.

514   De Keyser, R., Breuker, C.J., Hails, R.S., Dennis, R.L.H. & Shreeve, T.G. (2015). Why Small Is Beautiful:

515   Wing Colour Is Free from Thermoregulatory Constraint in the Small Lycaenid Butterfly,

516   Polyommatus icarus. *PLoS One*, 10, e0122623.

517   Koski, M.H. & Ashman, T.-L. (2015). Floral pigmentation patterns provide an example of Gloger's rule

518   in plants. *Nat. Plants*, 1, 14007.

519   Lai, Y.C., Huang, S.W. & Yu, H.T. (2016). Gene structure and sequence polymorphism of the coat

520   color gene, Mc1r, in the black-bellied vole (Eothenomys melanogaster). *Zool. Stud.*, 55, 1–9.

521   Lai, Y.C., Shiroishi, T., Moriwaki, K., Motokawa, M. & Yu, H.T. (2008). Variation of coat color in house

522   mice throughout Asia. *J. Zool.*, 274, 270–276.

523   Lomolino, M. V., Riddle, B.R. & Brown, J.H. (2006). *Biogeography*. 3d edn. Sinauer Associates Inc.,

524   Sunderland, Massachusetts.

525   Maloney, S.K., Fuller, A. & Mitchell, D. (2009). Climate change: is the dark Soay sheep endangered?

526   *Biol. Lett.*, 5, 826–829.

527   Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species

528   divergence. *Nature*, 362, 149–152.

529   Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2010). Rapid sympatry explains greater color

530   pattern divergence in high latitude birds. *Evolution (N. Y).*, 64, 336–347.

531   Mcqueen, A., Naimo, A.C., Teunissen, N., Magrath, R.D., Delhey, K., Peters, A., *et al.* (2017). Bright

532   birds are cautious : seasonally conspicuous plumage prompts risk avoidance by male superb

533   fairy-wrens. *Proc. R. Soc. B*, 284, 20170446.

534   Medina, A.I., Martí, D.A. & Bidau, C.J. (2007). Subterranean rodents of the genus Ctenomys

535   (Caviomorpha, Ctenomyidae) follow the converse to Bergmann's rule. *J. Biogeogr.*, 34, 1439–

536   1454.

537   Medina, I., Newton, E., Kearney, M.R., Mulder, R.A., Porter, W.P. & Stuart-Fox, D. (2018). Reflection

538   of near-infrared light confers thermal protection in birds. *Nat. Commun.*, 9, 3610.

539   Millien, V., Kathleen Lyons, S., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006). Ecotypic

540   variation in the context of global climate change: Revisiting the rules. *Ecol. Lett.*, 9, 853–869.

541   Mills, L.S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T. & Lukacs, P.M. (2013). Camouflage

542   mismatch in seasonal coat color due to decreased snow duration. *Proc. Natl. Acad. Sci. U. S. A.*,

543   110, 7360–5.

544   Miskimen, G.W. (1972). Environmental Factors Affecting Soldier Beetle Distribution and Coloration in

545   Columbia. *Biotropica*, 4, 85–92.

546   Morales, H.E., Pavlova, A., Sunnucks, P., Major, R., Amos, N., Joseph, L., *et al.* (2017). Neutral and

547   selective drivers of colour evolution in a widespread Australian passerine. *J. Biogeogr.*, 44, 522–

548   536.

549   Nakagawa, S. & Santos, E.S. a. (2012). Methodological issues and advances in biological meta-

550   analysis. *Evol. Ecol.*, 26, 1253–1274.

551   Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from

552   generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

553   Negro, J.J., Figueroa-Luque, E. & Galván, I. (2018). Melanin-based sexual dichromatism in the

554   Western Palearctic avifauna implies darker males and lighter females. *J. Avian Biol.*, 49, 1–8.

555   Olson, V.A., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., *et al.* (2009). Global

556   biogeography and ecology of body size in birds. *Ecol. Lett.*, 12, 249–259.

557   Pannkuk, E.L., Siefferman, L.M. & Butts, J.A. (2010). Colour phases of the eastern screech owl: A

558   comparison of biomechanical variables of body contour feathers. *Funct. Ecol.*, 24, 347–353.

559   Patten, M.A., Rotenberry, J.T. & Zuk, M. (2004). Habitat Selection, Acoustic Adaptation, and the

560   Evolution of Reproductive Isolation. *Evolution (N. Y).*, 58, 2144–2155.

561   Rensch, B. (1929). *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung*.

562   Gebrueder Borntraeger, Berlin.

563   Revell, L.J. (2012). phytools: An R package for phylogenetic comparative biology (and other things).

564   *Methods Ecol. Evol.*, 3, 217–223.

565   Riemer, K., Guralnick, R.P. & White, E.P. (2018). No general relationship between mass and

566   temperature in endothermic species. *Elife*, 7, 1–16.

567   Roulin, a., Wink, M. & Salamin, N. (2009). Selection on a eumelanic ornament is stronger in the

568   tropics than in temperate zones in the worldwide-distributed barn owl. *J. Evol. Biol.*, 22, 345–

569   354.

570   Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change. *Glob. Chang.*

571   *Biol.*, 1–7.

572   Salewski, V. & Watt, C. (2017). Bergmann's rule: a biophysiological rule examined in birds. *Oikos*,

573   126, 161–172.

574   San-jose, L.M. & Roulin, A. (2018). Toward Understanding the Repeated Occurrence of Associations

575   between Melanin-Based Coloration and Multiple Phenotypes. *Am. Nat.*, 192.

576   Sandoval-Castellanos, E., Wutke, S., Gonzalez-Salazar, C. & Ludwig, A. (2017). Coat colour adaptation

577   of post-glacial horses to increasing forest vegetation. *Nat. Ecol. Evol.*, 1–4.

578   Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.

579   *Methods Ecol. Evol.*, 1, 103–113.

580   Servedio, M.R., Doorn, G.S. Van, Kopp, M., Frame, A.M. & Nosil, P. (2011). Magic traits in speciation:

581   "magic" but not rare? *Trends Ecol. Evol.*, 26, 389–397.

582   Singaravelan, N., Raz, S., Tzur, S., Belifante, S., Pavlicek, T., Beiles, A., *et al.* (2013). Adaptation of

583   Pelage Color and Pigment Variations in Israeli Subterranean Blind Mole Rats, Spalax Ehrenbergi.

584   *PLoS One*, 8.

585   Symonds, M.R.E. & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and

586   model averaging in behavioural ecology using Akaike information criterion. *Behav Ecol*

587   *Sociobiol*, 65, 13–21.

588   Symonds, M.R.E. & Tattersall, G.J. (2010). Geographical Variation in Bill Size across Bird Species

589   Provides Evidence for Allen's Rule. *Am. Nat.*, 176, 188–197.

590   Tattersall, G.J., Sinclair, B.J., Withers, P.C., Fields, P.A., Seebacher, F., Cooper, C.E., *et al.* (2012).

591   Coping with thermal challenges: Physiological adaptations to environmental temperatures.

592   *Compr. Physiol.*, 2, 2151–2202.

593   Teplitsky, C. & Millien, V. (2014). Climate warming and Bergmann's rule through time: Is there any

594   evidence? *Evol. Appl.*, 7, 156–168.

595   Tung Ho, L.S. & Ané, C. (2014). A linear-time algorithm for gaussian and non-gaussian trait evolution

596   models. *Syst. Biol.*, 63, 397–408.

597   Valcu, M., Dale, J. & Kempenaers, B. (2012). RangeMapper: A platform for the study of macroecology

598   of life-history traits. *Glob. Ecol. Biogeogr.*, 21, 945–951.

599   Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.*, 36,

600   1–48.

601   Watson, L.J. & Hanham, R.Q. (1977). Flower Color and Environment: the Case of Butterfly Weed in

602   Oklahoma. *Prof. Geogr.*, 29, 374–377.

603   Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J. & Hungate, B.A. (2011). Responses of terrestrial

604   ecosystems to temperature and precipitation change: A meta-analysis of experimental

605   manipulation. *Glob. Chang. Biol.*, 17, 927–942.

606   Xing, S., Bonebrake, T.C., Tang, C.C., Pickett, E.J., Cheng, W., Greenspan, S.E., *et al.* (2016). Cool

607   habitats support darker and bigger butterflies in Australian tropical forests. *Ecol. Evol.*, 6, 8062–

608   8074.

609   Zeuss, D., Brandl, R., Brändle, M., Rahbek, C. & Brunzel, S. (2014). Global warming favours light-

610   coloured insects in Europe. *Nat. Commun.*, 5.

611   Zink, R.M. & Remsen, J. V. (1986). Evolutionary processes and patterns of geographic variation in

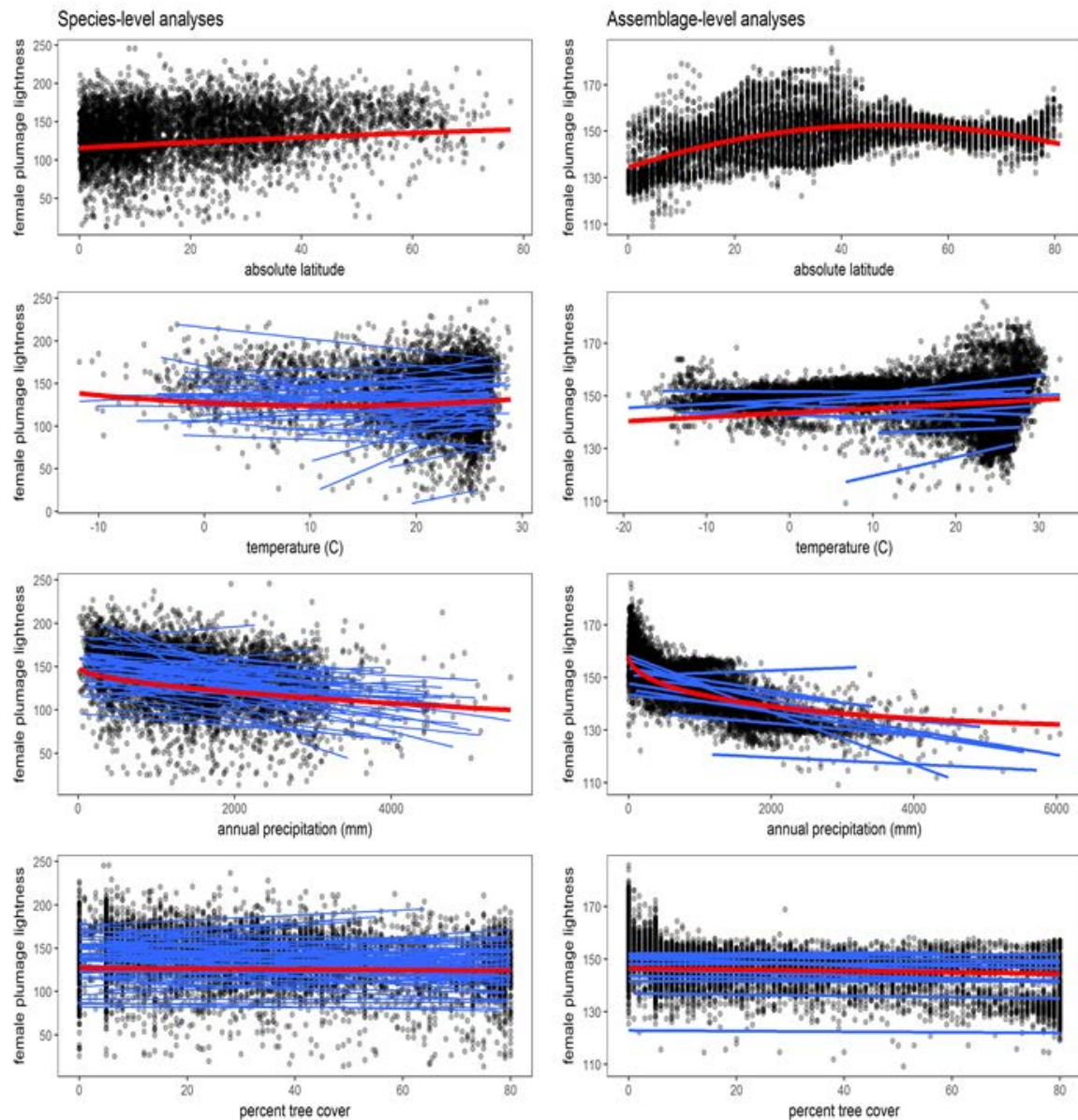612   birds. *Curr. Ornithol.*, 4, 1–69.

613

614

Figure 1. Correlates of plumage lightness in female passerines. Scatterplots depict female plumage lightness for all species of passerine birds in relation to different geographic (latitude), climatic (annual mean temperature, annual precipitation) and environmental (percent forest cover) predictors at the species level (A) – D), n = 5809) and assemblage level (E) – H), n = 9715). Red lines depict the global line of best fit derived from the best models (except for latitude, which was fitted only to show broad patterns of variation); blue lines depict lines of best fit (linear effects only) derived separately for each family (species level analyses, n = 65 families with 10 or more species each) or zoogeographic realms (assemblage level analyses, 11 realms). Note that while scatterplots

624   of temperature effects suggest heterogeneity of variance, this was not evident in the model
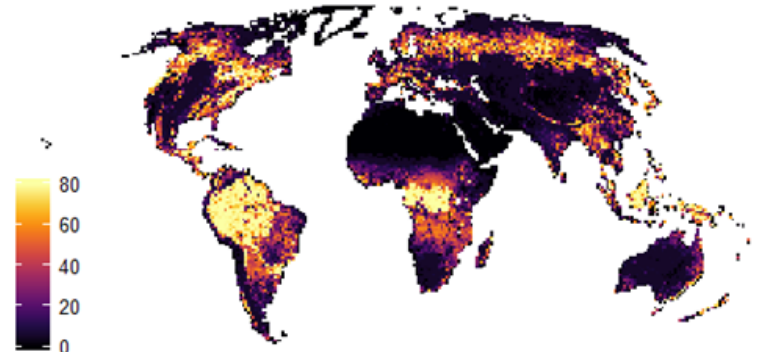
625   residuals.

626

(A) Female lightness
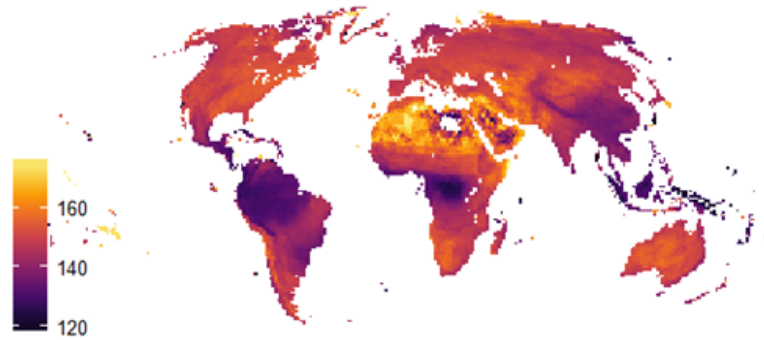
(B) Annual mean temperature
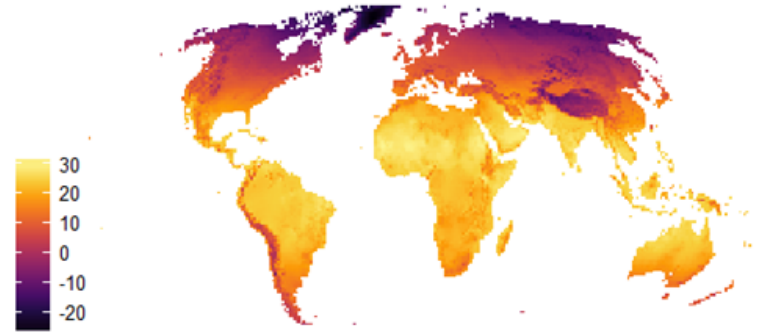
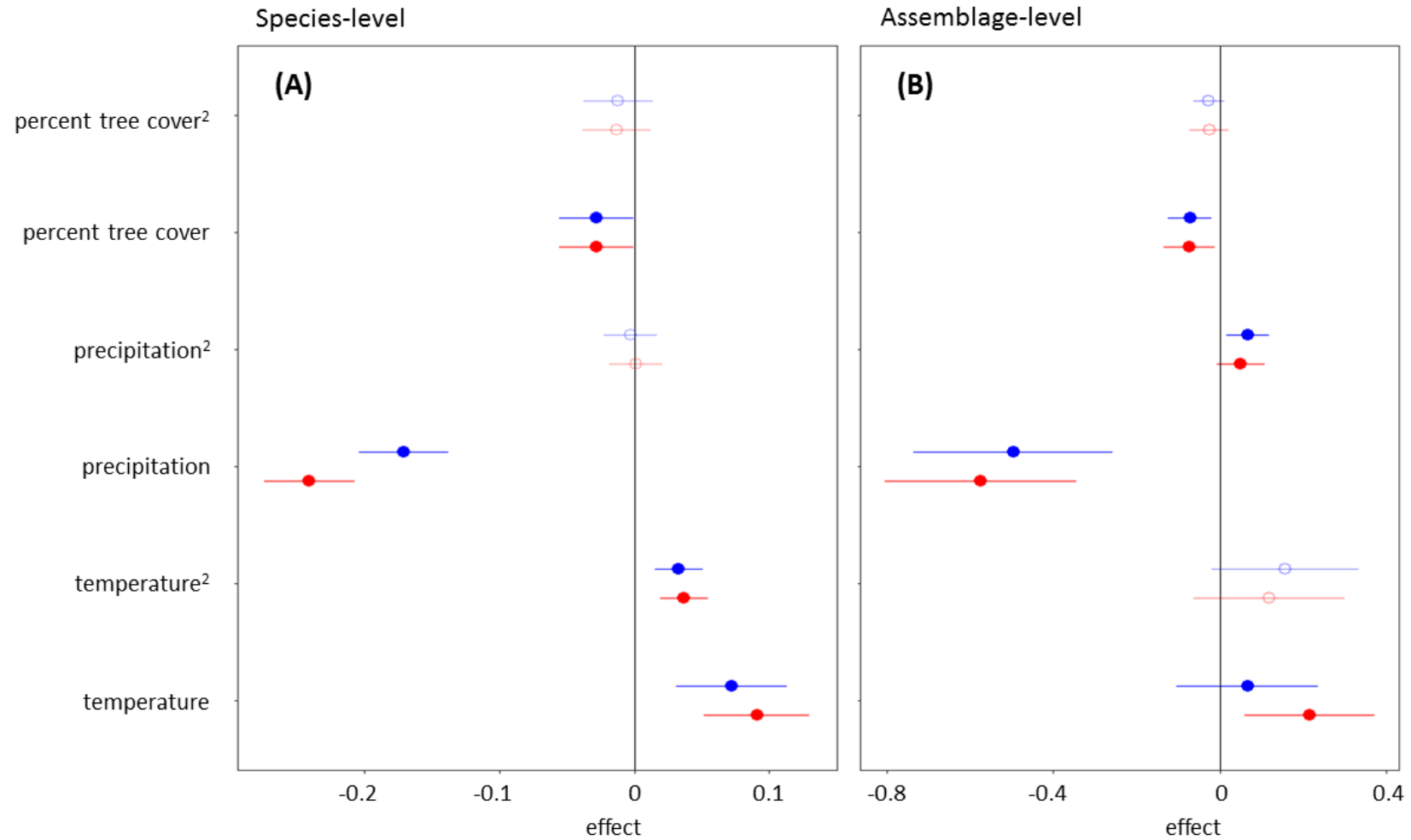## (C) Annual precipitation
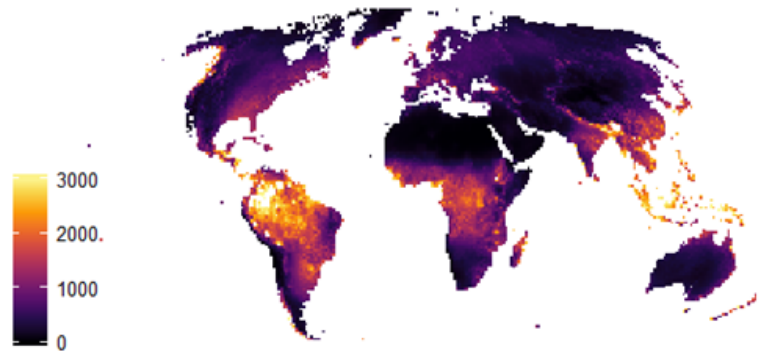
(D) Percent tree cover

627

628   Figure 2. Maps illustrating the geographic distribution of (A) mean female plumage lightness, (B) annual mean temperature, (C) annual precipitation and (D)

629   percent tree cover.

630

Fig. 3. Predictors of plumage lightness in passerine birds. Forest plots depict effects (±95% CI) of each predictor on plumage lightness of females (red symbols) and males (blue symbols) for analyses at the species (A) and assemblage (B) levels. Non-significant quadratic effects excluded from the final model

633   are depicted by open symbols, with the exception of the quadratic precipitation effect at the assemblage level which was not significant in females but

634   significant in males. Positive effects represent increases in plumage lightness with increases of the explanatory variable. All variables are scaled, hence each

635   effect represents the change in the response variable (in standard deviations) associated with a change in one standard deviation of the explanatory

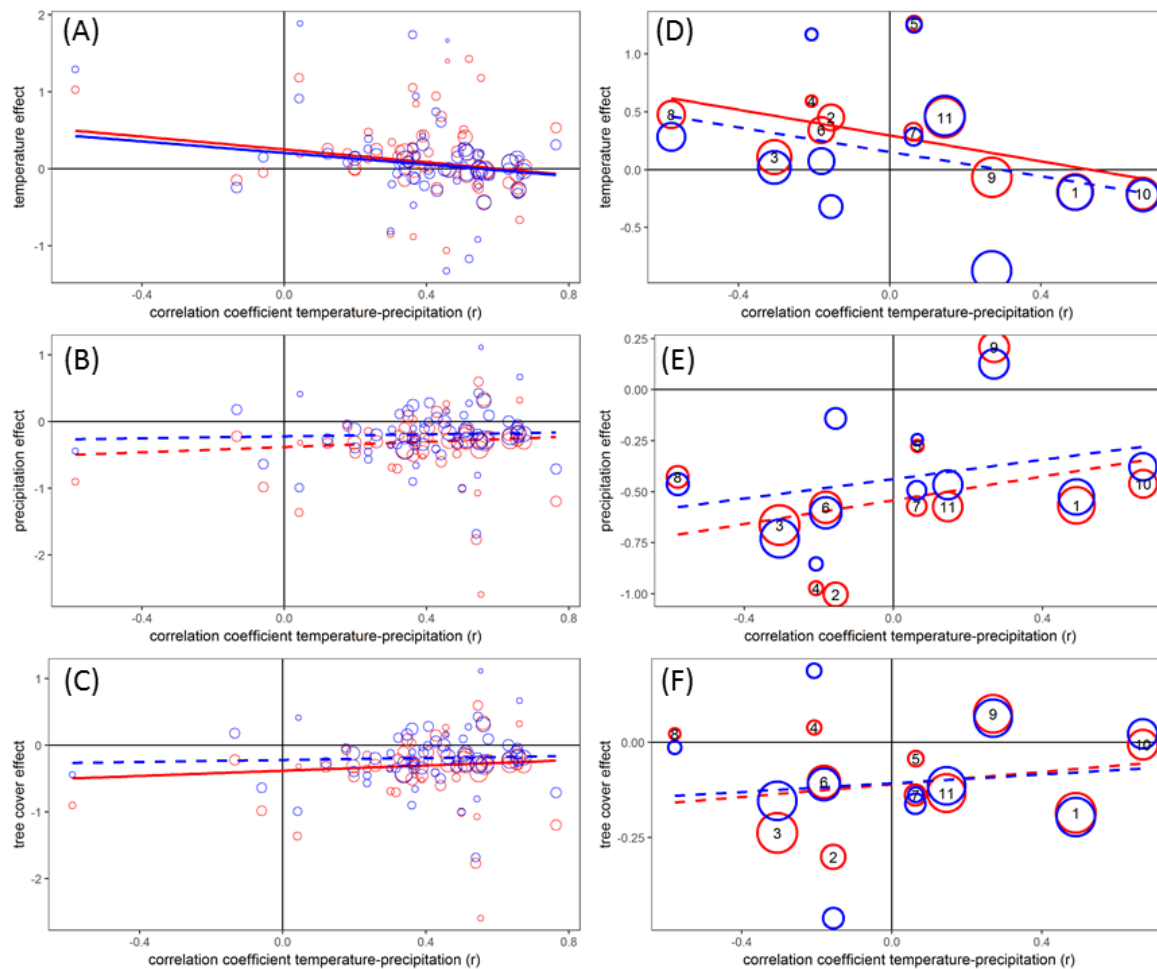636   variable. For full statistical results see Tables S1-S2.

Figure 4. The association between the strength of the climatic (temperature [A, D], annual precipitation [B, E]) and environmental (tree cover [C, F]) effects on female (red) and male (blue) plumage lightness and the correlation between temperature and rainfall for different bird families (A) - C), 65 families with 10 or more species, but results are similar using only families with 15 or more species, Table S3) or zoogeographic realm (D – F), 11 realms). Each dot depicts a family- or realm-specific effect. Dot size is proportional to 1/SE of the effect (but on a different scale in A-C versus D-F). The lines show the best fit derived from meta-regression analyses weighing each effect by its uncertainty, continuous lines represent statistically significant effects (p < 0.05, for full results see Tables S3-S4). Numbers in D-F correspond to zoogeographic realms: 1: Neotropical, 2: Australian, 3: Aftrotropical, 4: Madagascan, 5: Oceania, 6: Oriental, 7: Panamanian, 8: Saharo-Arabian, 9: Nearctic, 10: Sino-Japanese, 11: Palearctic.
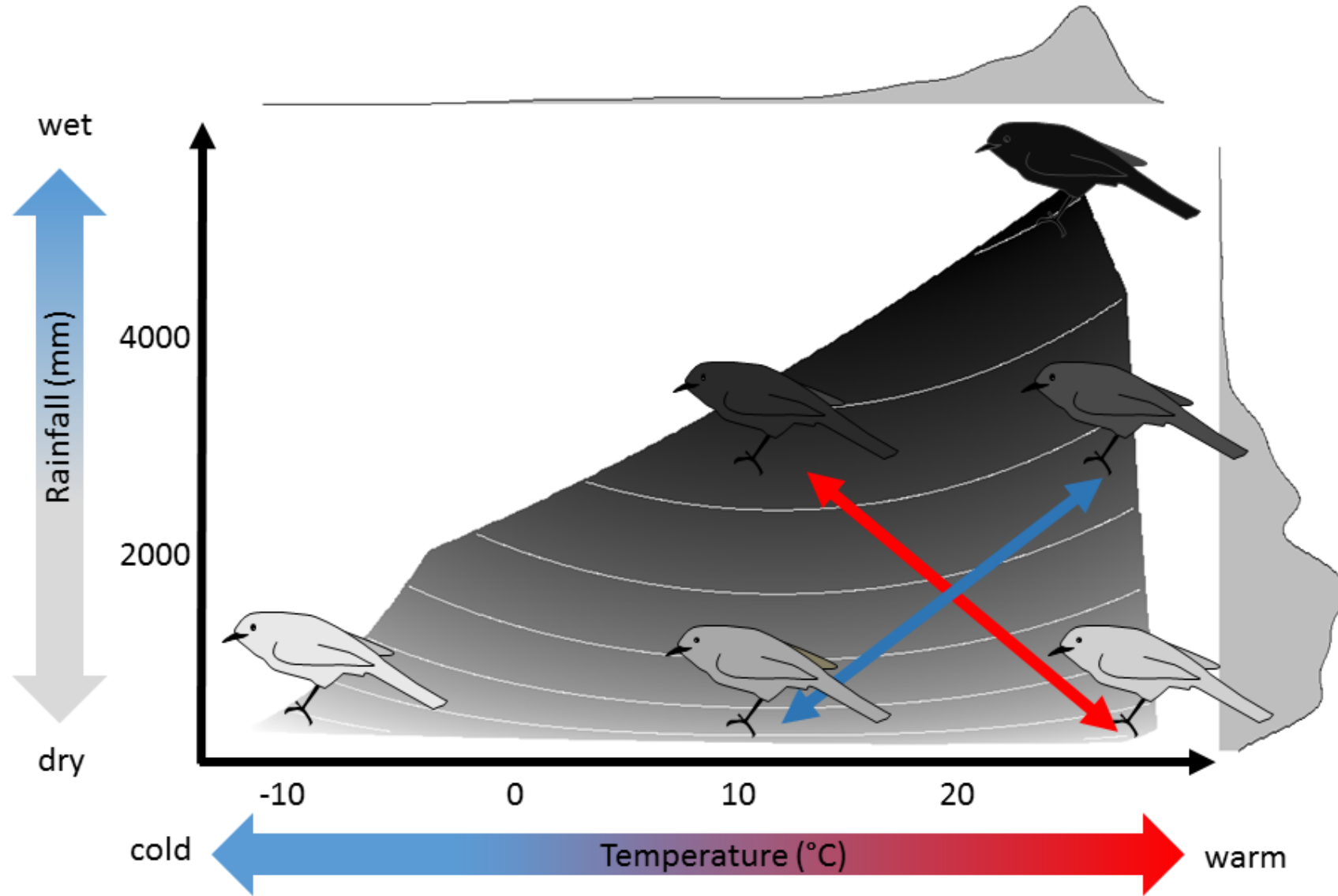
650   Figure 5. Proposed framework integrating the effects of precipitation (Gloger's rule) and temperature (Bogert's rule) on animal light-to-dark variation. The

651   shades of the background and bird icons are based on predictions from the species-level model (Fig. 3A), which are restricted to the range of temperatures

652   and precipitations present in the sample. The temperature effect shows a quadratic relationship: at high and low temperatures, plumage is lighter, at

653   intermediate levels plumage is darker. Marginal density plots depict where in climatic space most species are found. Note that the lightening of plumage at

654   low temperatures applies to comparatively few species because most passerines are found at higher temperatures where lightness increases with

655   temperature. The precipitation effect (darker plumage at higher precipitation) is much stronger than any temperature effects in birds and this is why in

656   warm and humid places birds are expected to have darker plumage. The two arrows depict two hypothetical climatic gradients. The red one is a gradient

657   that should lead to high levels of colour divergence because temperature and precipitation effects work together (note how the arrow crosses 5 contour

658   lines). The blue gradient leads to low levels of colour divergence because both gradients are working against each other (the arrow crosses only 3 contour

659   lines).

660