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Cooney, C.R. [orcid.org/0000-0002-4872-9146](https://orcid.org/0000-0002-4872-9146), MacGregor, H.E.A., Seddon, N. [orcid.org/0000-0002-1880-6104](https://orcid.org/0000-0002-1880-6104) et al. (1 more author) (2018) Multi-modal signal evolution in birds: re-examining a standard proxy for sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, 285 (1889). ISSN 0962-8452

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1 **Multi-modal signal evolution in birds: re-examining a standard**  
2 **proxy for sexual selection**

3

4 **Christopher R. Cooney<sup>1,2\*</sup>, Hannah E. A. MacGregor<sup>1,3</sup>, Nathalie Seddon<sup>1†</sup> & Joseph A.**  
5 **Tobias<sup>1,4†</sup>**

6

7 <sup>1</sup>*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.*

8 <sup>2</sup>*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield*  
9 *S10 2TN, UK.*

10 <sup>3</sup>*School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK.*

11 <sup>4</sup>*Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road,*  
12 *Ascot, Berkshire, SL5 7PY, UK.*

13 †Equal contribution

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15

16 **\*Author for correspondence:** [c.cooney@sheffield.ac.uk](mailto:c.cooney@sheffield.ac.uk)

17

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29 **Abstract**

30 Sexual selection is proposed to be an important driver of speciation and phenotypic diversification in  
31 animal systems. However, previous phylogenetic tests have produced conflicting results, perhaps  
32 because they have focused on a single signalling modality (visual ornaments), whereas sexual  
33 selection may act on alternative signalling modalities (e.g. acoustic ornaments). Here we compile  
34 phenotypic data from 259 avian sister species pairs to assess the relationship between visible  
35 plumage dichromatism—a standard index of sexual selection in birds—and macroevolutionary  
36 divergence in the other major avian signalling modality: song. We find evidence for a strong negative  
37 relationship between the degree of plumage dichromatism and divergence in song traits, which  
38 remains significant even when accounting for other key factors, including habitat type, ecological  
39 divergence and interspecific interactions. This negative relationship is opposite to the pattern  
40 expected by a straightforward interpretation of the sexual selection-diversification hypothesis,  
41 whereby higher levels of dichromatism indicating strong sexual selection should be related to greater  
42 levels of mating signal divergence regardless of signalling modality. Our findings imply a ‘trade-off’  
43 between the elaboration of visual ornaments and the diversification of acoustic mating signals, and  
44 suggest that the effects of sexual selection on diversification can only be determined by considering  
45 multiple alternative signalling modalities.

46

47 **Keywords:** birds, dichromatism, divergence, plumage, sexual selection, song, trade-off

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51

## 52 **Introduction**

53 Previous studies have provided theoretical and empirical evidence that sexual selection can stimulate  
54 the rapid divergence of traits involved in mate choice and species recognition [1, 2], supporting the  
55 longstanding view that sexual selection is an important driver of speciation and lineage diversification  
56 [3-6]. However, direct support for this hypothesis is relatively weak and inconsistent among taxa [7],  
57 with a series of studies finding no evidence of significant correlations between sexual selection and  
58 either species richness or speciation rate when studied across birds [8-11], mammals, butterflies and  
59 spiders [12], and certain fish taxa [13]. Although these observations suggest that sexual selection has  
60 limited effects on diversification at macroevolutionary scales, an alternative possibility is that standard  
61 comparative analyses are simply ineffective because they rely on crude phenotypic proxies to  
62 estimate variation in sexual selection across species.

63 To quantify the intensity of sexual selection, most existing large-scale studies in birds have  
64 used visible sex-differences in plumage colouration [e.g. 2, 8, 9, 10, 14, 15]. This metric—usually  
65 termed ‘plumage dichromatism’—has become a standard proxy for sexual selection because it is  
66 easily measured and positively correlated with other indices of sexual selection such as testes size,  
67 the degree of polygyny, and the frequency of extra-pair paternity [16-19]. Nonetheless, the extent to  
68 which plumage dichromatism provides an accurate and consistent estimate of the overall intensity of  
69 sexual selection across all lineages remains uncertain, not least because it focuses on a single sexual  
70 signalling modality, whereas many taxa engage in multimodal signalling [5]. Indeed, if the intensity of  
71 sexual selection targeted at one signalling modality (e.g. visual signals) trades off or is negatively  
72 correlated with the intensity of sexual selection targeted at another (e.g. acoustic signals) [3, 20], then  
73 such interactions could lead to a breakdown in the relationship between the underlying intensity of  
74 sexual selection across species and the visual traits used as proxies for sexual selection, therefore  
75 obscuring the true relationship between sexual selection and diversification [2, 8].

76 Progress in resolving this question has been slow because previous studies investigating the  
77 macroevolutionary consequences of sexual selection have generally focused exclusively on visual  
78 signalling traits [2, 21], leaving open the possibility that comparisons across different sexual signalling  
79 modalities may reveal contrasting patterns. Furthermore, most studies have failed to address the role  
80 of other important selection pressures potentially shaping the evolution of signal phenotypes, such as  
81 habitat differences, ecological divergence and interspecific interactions [22, 23], and have typically  
82 focused on geographically, taxonomically and/or ecologically restricted datasets, rather than sampling  
83 more broadly across major clades.

84 Here we address these issues by compiling data for a global sample of 259 avian species  
85 pairs from 33 passerine families to test the relationship between visible plumage dichromatism—used  
86 as a standard proxy for sexual selection in birds and other animals [7]—and macroevolutionary  
87 divergence in the other major avian signalling modality: song. We focus on birds because they offer

88 an unequivocal example of multimodal sexual signalling in which both traits—avian plumage  
89 colouration (a visual ornament) and song (an acoustic ornament)—are known to function in inter- and  
90 intra-sexual selection in many avian taxa [5, 24-27]. In addition, the availability of complementary  
91 species-level data on avian morphological traits, ecology, biogeography and phylogeny allows us to  
92 assess the importance of plumage dichromatism in relation to a suite of key variables known to  
93 influence patterns of signal evolution.

94 Our analyses can be divided into three stages. First, we use published song recordings to  
95 estimate the extent of song divergence within species pairs. Second, we assess the relationship  
96 between sexual dichromatism and degree of song divergence across pairs. Third, we use multiple  
97 regression combined with model averaging techniques to assess the relative association between  
98 dichromatism and song divergence in relation to other factors. If sexual selection has reinforcing or  
99 independent effects on traits from different signalling modalities [28], we expect the relationship  
100 between plumage dichromatism and song divergence to be positive, or non-significant, respectively.  
101 Conversely, if the effects of sexual selection on traits in different signalling modalities are negatively  
102 correlated, we expect a negative relationship between plumage dichromatism and song divergence  
103 across species pairs.

104

## 105 **Methods**

### 106 SPECIES SAMPLING AND PHYLOGENETIC FRAMEWORK

107 We used published molecular phylogenies to select a sample of passerine species pairs for which  
108 high quality song recordings were available [see 2, 8]. Each pair consisted of sister species, i.e. pairs  
109 of lineages that represent each other's closest relative. We note that a few of our study pairs contain  
110 species that are not true sisters, both because of incomplete sampling in published phylogenies, and  
111 because we included some near-sisters in which one member of the pair belonged to a sister clade  
112 (or both species from a polytomy). This approach is based on the assumption that comparisons  
113 between near-sisters are informative about phenotypic divergence during recent evolutionary history  
114 [2]. Overall, our sample contained 518 species from 259 species pairs (including 243 sister species  
115 and 13 near-sisters) widely distributed across the passerine radiation (Fig. S1). For full details, see  
116 the supplementary online material. To provide a phylogenetic framework for our analyses, we  
117 sampled 1000 molecular-only trees from [www.birdtree.org](http://www.birdtree.org) [29], which were pruned to include only  
118 the species included in our dataset. We then used TreeAnnotator [30] to generate a maximum clade  
119 credibility (MCC) tree, which was then pruned so that each pair was represented by a single tip.

120

### 121 SONG DIVERGENCE

122 To quantify the extent of song divergence within species pairs, we downloaded songs for all species  
123 from the Macaulay Library of Natural Sounds ([www.macaulaylibrary.org](http://www.macaulaylibrary.org)) and the online database

124 Xeno Canto ([www.xeno-canto.org](http://www.xeno-canto.org)). We digitized sound files in Raven Pro v1.4 using standard  
125 settings, then measured seven key temporal and spectral traits that together capture important  
126 interspecific differences in overall signal structure [for full details see 31, 32]: (i) maximum frequency  
127 (kHz), (ii) minimum frequency (kHz), (iii) peak frequency (kHz; frequency in the signal with the greatest  
128 amplitude), (iv) bandwidth (kHz; maximum frequency minus minimum frequency), (v) signal duration  
129 (s), (vi) number of notes and (vii) pace (number of notes s<sup>-1</sup>). For each species, at least three high-  
130 quality recordings were measured (mean 4.8 recordings per species), providing a total sample of  
131 2476 songs. To reduce the dimensionality of the dataset, we conducted a principal components (PC)  
132 analysis on the covariance matrix of individual (log-transformed) song measurements. The first three  
133 PCs from this analysis accounted for over 83% of the variance in the original acoustic dataset, with  
134 each PC capturing a distinct component of overall signal structure (Table S1). Specifically, PC1 (41%)  
135 loaded heavily with variables related to song pitch, PC2 (24%) loaded heavily with variables related  
136 to song length, and PC3 (18%) primarily loaded with song pace. We therefore interpreted these PCs  
137 as axes of variation in song pitch (PC1), length (PC2) and pace (PC3), respectively, with variation in  
138 overall song structure captured by position in this three-dimensional acoustic space (Fig. S2). Using  
139 these PCs, we estimated within-pair song disparity for all pairs as the Euclidean distance between  
140 species' mean PC scores in terms of overall song structure (PC1-3), and in terms of song pitch, length  
141 and pace separately (Fig. 1). To assess the sensitivity of our results, we also generated an alternative  
142 version of our dataset in which within-species song disparity estimates were corrected for observed  
143 levels of intraspecific variation (see Appendix S1 for full details).

144

#### 145 SEXUAL DICHROMATISM

146 To quantify the degree of sexual dichromatism within pairs, we used published [8] species-level  
147 scores of dichromatism estimated by eye from handbook illustrations (see Appendix S1 for  
148 justification). Briefly, we used standard methodology [17, 33] to score the difference in plumage  
149 colouration between the sexes over five body regions (head, nape-rump-back, throat-belly, tail, and  
150 wings) for each species in our sample. Each region was scored separately using three scores: 0, no  
151 difference between the sexes; 1, difference between the sexes only in shade or intensity of colour; 2,  
152 difference in colour or pattern between the sexes. The dichromatism scores for all five body regions  
153 were then summed to give species-specific scores of plumage dichromatism on a scale from 0  
154 (monochromatic) to 10 (maximum dichromatism).

155

#### 156 ADDITIONAL PREDICTORS OF SONG DIVERGENCE

157 To explore the role of other factors known to influence estimates of phenotypic (particularly song)  
158 divergence in birds, we collected data for a suite of additional explanatory variables including  
159 divergence time [34], life history and allometric effects [35], migration status [36], habitat [37, 38],  
160 breeding latitude and insularity [39, 40], interspecific interactions [41], niche divergence [42-44] and

161 song learning [45]. Because the key habitat attribute linked to song evolution in birds is vegetation  
162 density [32] we used a score of forest dependency (i.e. degree of association with densely forested  
163 habitat). See Appendix S1 for full details of methods, data and data sources.

164

## 165 STATISTICAL ANALYSES

### 166 *Estimating phylogenetic signal of song divergence*

167 We used a generalised least squares (GLS) approach to test the phylogenetic signal of song  
168 divergence in our dataset. This approach, implemented in the R package *caper* [46], estimates a  
169 maximum likelihood (ML) value for phylogenetic signal ( $\lambda$ ) [47], which typically varies between zero  
170 (trait variance is independent of phylogeny) and one (trait variance follows a Brownian motion model  
171 of evolution). In the context of analysing song divergence, a value of  $\lambda = 0$  indicates that extent of  
172 song divergence within pairs is random with respect to phylogeny, whereas a value of  $\lambda = 1$  implies  
173 that closely related pairs have more similar levels of song disparity than would be expected by chance.  
174 We found that ML values of  $\lambda$  were zero for all four measures of song divergence, with values of  $\lambda =$   
175 1 (i.e. a Brownian motion model of evolution) significantly rejected in all cases (Table S2). Results  
176 were qualitatively similar for an alternative dataset corrected for observed levels of intraspecific  
177 variation (Table S2), indicating that variation in the extent of within-pair song divergence in our dataset  
178 is unrelated to phylogeny. This allowed us to use non-phylogenetic regression techniques with more  
179 flexible error structures than currently possible in a statistical phylogenetic comparative framework,  
180 which was necessary for our dataset (see below).

181

### 182 *Testing the relationship between predictors and extent of song divergence*

183 To model the observed variation in estimates of within-pair song divergence, accounting for the right-  
184 skewed distribution of disparity estimates (Fig. S3), we used generalised linear models (GLMs) with  
185 a gamma error distribution and log link. Using this approach, we (i) examined the relationship between  
186 song disparity and degree of plumage dichromatism, (ii) tested for an interaction effect between  
187 dichromatism and habitat type (forest dependency) and (iii) assessed the combined influence of all  
188 predictor variables on the extent of song disparity using single and multi-predictor regression and  
189 Akaike information criterion-based model averaging [48] corrected for small sample sizes ( $AIC_c$ ).

190 To perform model averaging, following [49] and [50], we fitted models encompassing all  
191 possible additive combinations of our predictor variables (see above), including a null (intercept-only)  
192 model, calculating the  $AIC_c$  score of each model. We then calculated the relative importance (RI) for  
193 each predictor variable as the sum of relative Akaike weights for models in which they appear. RI  
194 values scale from 0 to 1, where a variable with a score of 0 is associated with very low Akaike weights  
195 (i.e. low importance) and 1 is consistently associated with high weights (i.e. high importance). We  
196 also calculated model-averaged estimates of regression parameters and standard error values,  
197 calculated as the sum of the parameter estimates for each model including that predictor, multiplied

198 by the relative Akaike weight of each of those models. To give further insight into the relative  
199 importance of predictor variables, we also identified the variables included in the top-ranked (i.e. best  
200 fitting) model in each case. We used this procedure to assess the effect of predictors on response  
201 variables, including overall song disparity (PC1-3), as well as separate estimates of disparity in pitch  
202 (PC1), length (PC2) and pace (PC3) separately. For multipredictor models, we restricted the dataset  
203 to include only those species pairs for which complete data for all predictors were available (246 of  
204 259 pairs) and pseudo- $R^2$  values for GLMs were estimated using the method of [51]. Pair age,  
205 generation length, body mass disparity and beak disparity were ln-transformed prior to analysis and  
206 models were inspected to ensure they complied with modelling assumptions (e.g. normality of  
207 residuals). We also checked for issues related to collinearity among predictors, which we found were  
208 unlikely to affect our results (see Appendix S1 for details). To improve the interpretability of regression  
209 coefficients, predictor variables were centered and standardised prior to model fitting [52]. All  
210 analyses were conducted in R version 3.3.1 and model averaging was performed using the R package  
211 *MuMIn* [53].

212

## 213 **Results**

### 214 RELATIONSHIP BETWEEN DICHROMATISM AND EXTENT OF SONG DIVERGENCE

215 Our models revealed that plumage dichromatism was significantly negatively correlated with overall  
216 song divergence between species (Table S3). Species pairs with a greater degree of plumage  
217 dichromatism tended to have less divergent songs than more monochromatic species pairs (Fig. 2).  
218 Analysing patterns of divergence in each song trait separately revealed that the overall effect of  
219 dichromatism was primarily driven by significant negative relationships with divergence in song pitch  
220 (PC1) and length (PC2), with more marginal effects on song pace (PC3) (Table S3). Furthermore,  
221 including an interaction effect with forest dependency in these models revealed no significant  
222 statistical support for the hypothesis that the relationship between dichromatism and song divergence  
223 is mediated by variation in habitat type across taxa (Table S3). Rerunning analyses correcting for  
224 observed levels of intraspecific variation produced highly similar results (Table S3).

225

### 226 ADDITIONAL PREDICTORS OF SONG DIVERGENCE

227 Single predictor regression models focused on our additional predictors of song divergence identified  
228 several variables that were individually correlated with variation in song disparity across pairs (Fig.  
229 S4-S7). In terms of total song disparity (PC1-3), the strongest individual predictor was pair age (Table  
230 S4). Furthermore, variation in overall song disparity was also significantly correlated with disparity in  
231 beak morphology, with more marginal effects detected for several other variables, including forest  
232 dependency and mass disparity (Table S4). We also detected additional significant correlations  
233 between individual predictors and estimates of disparity in specific components of song structure  
234 (Table S5).



235 We then assessed the relative importance of all predictors using AIC<sub>c</sub> model averaging  
236 techniques (Fig. 3). The best-supported predictor of total song disparity (PC1-3) was pair age (RI =  
237 0.99), which exhibited a strong and highly significantly positive relationship with disparity (Table S6).  
238 However, even after accounting for this relationship, the negative effect of dichromatism remained  
239 strong (RI = 0.98) (Fig. 3). The AIC<sub>c</sub> best model for total song disparity accounted for 17% of the total  
240 variation, and retained these two variables plus mean pair body mass, forest dependency and within-  
241 pair beak disparity mass as positive effects, and confamilial sympatry as a negative effect (Fig. 3;  
242 Table S6).

243 Analysing relationships in each component song trait separately revealed that predictor  
244 variables had contrasting effects depending on the axis considered (Fig. S8; Table S7). On the one  
245 hand, divergence in song pitch (PC1) was best predicted by significant effects of dichromatism (RI =  
246 0.97), pair age (RI = 0.96), body mass (RI = 0.93), confamilial sympatry (RI = 0.92) and forest  
247 dependency (RI = 0.89), whereas divergence in song length (PC2) was best explained by significant  
248 effects of only pair age (RI = 0.92) and dichromatism (RI = 0.91). In contrast, the only significant  
249 predictor of divergence in song pace (PC3) was a positive effect of within-pair beak disparity (RI =  
250 0.82). Overall, AIC<sub>c</sub> top models for these variables accounted for 22%, 12% and 6% of the total  
251 variation in disparity in song pitch, length and pace, respectively (Table S8). Rerunning models  
252 accounting for intraspecific variation produced qualitatively similar results (Table S9-S11).

253

## 254 **Discussion**

255 Our analyses reveal that the degree of sexual dichromatism is negatively related to the extent of  
256 divergence in song structure among closely related bird species, a pattern that remained strong after  
257 accounting for a suite of potentially correlated or confounding variables, as well as for intraspecific  
258 trait variation. This contrasts with the findings of previous studies reporting evidence for significant  
259 positive correlations between indicators of sexual selection and signal divergence in birds, supporting  
260 the view that sexual selection can drive parallel divergence across multiple signals [2, 21]. However,  
261 these studies assessed patterns of divergence in visual signalling traits (i.e. plumage colouration),  
262 using proxies for the intensity of sexual selection derived from the same signalling modality (e.g.  
263 dichromatism). In contrast, we have focused across major avian signalling modalities, finding the  
264 opposite relationship: that dichromatism (a visual signal) is negatively associated with divergence in  
265 song (an acoustic signal). Our results are therefore incompatible with a straightforward interpretation  
266 of the sexual selection-diversification hypothesis, whereby higher levels of dichromatism indicating  
267 strong sexual selection should be related to greater levels of mating signal divergence regardless of  
268 signalling modality. Instead, our findings are consistent with the alternative view that negative  
269 interactions between alternative signalling modalities play an important role in shaping  
270 macroevolutionary patterns of signal evolution in birds.

271 One intuitive explanation for the negative correlation between plumage dichromatism and  
272 song divergence is that it reflects an underlying link between sexual selection and acoustic signal  
273 divergence in species that do not rely on visual signals. This makes sense because single-species  
274 studies have demonstrated an important role for female choice and/or male-male competition in  
275 shaping many aspects of avian acoustic signal design [24], and many avian taxa with drab or  
276 monochromatic plumage are known to possess highly elaborate acoustic signals which often provide  
277 the best means of differentiating among lineages (e.g. Old World leaf warblers; Phylloscopidae) [54].  
278 Thus, increased sexual selection on acoustic traits relative to visual traits in monochromatic taxa  
279 provides a plausible explanation for a negative relationship between plumage dichromatism and song  
280 disparity at broad macroevolutionary scales.

281 A key challenge facing this interpretation is to explain why, within species, selection would  
282 favour signals from one rather than multiple signalling modalities, thus generating negative  
283 relationships across modalities at a macroevolutionary scale. It is possible that the relative costs and  
284 benefits of signalling via a given sensory modality are shaped by the prevailing environmental  
285 conditions [38], such that ecological differences among species should play a role in determining the  
286 relative prominence of one signal type over another [27]. In line with this idea, bird species inhabiting  
287 dense habitats such as reedbeds, thickets, and the understorey of forests often have more elaborate  
288 songs than visual signals. However, our models including forest dependency as an interaction term  
289 provided no support for the idea that the relationship between plumage dichromatism and song  
290 divergence is mediated by broad-scale habitat differences among taxa.

291 An alternative explanation is that our findings reflect the signature of evolutionary trade-offs  
292 between alternate signalling modalities. Under a resource- or cost-based trade-off scenario—such as  
293 that envisaged by Darwin [3] and later termed the ‘transfer hypothesis’ [20]—constraints on sexual  
294 selection within species make it costly for males to signal in (or females to choose between) multiple  
295 signalling modalities [55, 56], generating the potential for interspecific trade-offs in ornament  
296 elaboration (and diversification) between alternate signalling modalities [57]. This explanation relies  
297 on the assumption that investment in one signalling modality constrains investment in another, which  
298 is plausible given that avian plumage and song traits may both be costly to produce [58]. However,  
299 the energetic costs of signal production may be relatively low [59] and potentially offset by differences  
300 in how such signals are produced and displayed [27]. A different trade-off scenario is suggested by  
301 the concept of ‘redundancy’ among alternate signal types. Under a redundancy-based model, the  
302 spread of an attractive signal in one modality leads simultaneously to increased selection for detecting  
303 the novel signal and a weakening of selection for elaborate signals in alternate modalities, which  
304 occurs not because of costs associated with producing or maintaining multiple sexual signals, but  
305 because sexual selection on the latter trait is weak or non-existent, due to redundancy [60]. Such  
306 redundancy-based trade-offs can theoretically occur in the absence of any habitat differences among  
307 taxa, or resource limitation underlying the production of signalling traits. Thus, whether selection

308 favours one signal type (e.g. song) over another (e.g. plumage) largely depends on which signal type  
309 evolved first, which may largely be due to historical contingencies [61-63].

310

### 311 CONTRIBUTORY FACTORS

312 In addition to variation in the strength and targets of sexual selection, our results support a role for  
313 several other factors in shaping patterns of acoustic signal divergence in birds. We found strong  
314 evidence for a positive relationship between species pair age and degree of song disparity, in line  
315 with previous studies [e.g. 2, 39, 64, 65], as well as the general consensus that patterns of phenotypic  
316 divergence are primarily dictated by the time available for trait differences to evolve [34, 66]. Body  
317 mass also emerged as a significant predictor of song divergence, in line with previous studies  
318 indicating positive relationships between body mass and patterns of signal evolution in birds [2, 19].  
319 Furthermore, we found support for links between song divergence and both habitat and the degree  
320 of confamilial sympatry. First, we found evidence for increased pitch disparity in species pairs with  
321 higher levels of forest dependency, consistent with the idea of stronger (divergent) selection on  
322 acoustic traits in taxa signalling in densely vegetated habitats [37, 38]. Second, we found that pairs  
323 which co-occurred with a greater proportion of confamilial species had lower levels of song divergence  
324 than those with lower levels of overlap. This accords with the view that interactions among related  
325 species can constrain phenotypic divergence [67], in part because acoustic communities appear to  
326 'partition' finite aspects of acoustic signalling space [31, 68-70]. Finally, we found that divergence in  
327 song pace was significantly positively correlated with disparity in species' beak morphology. Previous  
328 studies have found evidence of correlated evolution of morphology and vocal signal structure in  
329 particular clades (e.g. Darwin's finches, Neotropical woodcreepers) [43, 71, 72], presumably because  
330 biophysical constraints on song production generate correlated evolution between songs and beaks.  
331 Our results in relation to beak morphology support this view, and imply that this effect holds across  
332 passerines more generally. Nonetheless, even when we accounted for these significant effects in  
333 statistical models, the strong negative association between song divergence and dichromatism was  
334 retained.

335

### 336 IMPLICATIONS FOR COMPARATIVE STUDIES

337 Our finding that dichromatism is negatively related to song divergence across a broad sample of avian  
338 species pairs has important implications for studies testing macroevolutionary hypotheses related to  
339 sexual selection. Most importantly, it implies that plumage dichromatism provides a relatively  
340 ineffective proxy for the intensity of sexual selection in taxa primarily using non-visual signals. This  
341 potential limitation of dichromatism has previously been proposed [2, 8] with reference to bird species  
342 such as the common nightingale (*Luscinia megarhynchos*), common whitethroat (*Sylvia communis*)  
343 and sedge warbler (*Acrocephalus schoenobaenus*), passerine species with largely monomorphic  
344 plumage colouration, elaborate song traits and strong sexual selection [73-75]. Our results provide

345 broad-scale empirical support for this view, and indicate that dichromatism will underestimate sexual  
346 selection in these taxa, potentially being negatively related to the intensity of sexual selection in  
347 samples dominated by non-visual signallers. Thus, the underlying effect of sexual selection may often  
348 be obscured in comparative studies based solely on dichromatism, perhaps helping to explain the  
349 weak or non-existent correlations between dichromatism and speciation rates in birds and other taxa  
350 with multimodal signalling [7-11].

351

## 352 CONCLUSIONS

353 Taken together, our findings are consistent with the view that sexual selection plays a major role in  
354 shaping sexual signal evolution, in conjunction with ecological factors [23, 76, 77]. However, whereas  
355 most previous studies have focused on a single signalling modality, we found evidence of a negative  
356 relationship between visual and acoustic signalling in birds, supporting the more general view that  
357 negative interactions between signalling modalities can explain general patterns of signal evolution  
358 [3, 20]. Not only do these results suggest that such 'trade-offs' are important in shaping phenotypic  
359 diversity, they also indicate that phylogenetic tests based on phenotypic metrics for the intensity of  
360 sexual selection will underestimate the association between sexual selection and diversification. We  
361 conclude that the rigour and accuracy of any comparative analysis testing the effects of sexual  
362 selection will be improved by considering phenotypic proxies for sexual selection that span all relevant  
363 signalling modalities, be they visual, acoustic, or olfactory.

364

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372

## 373 **Data accessibility**

374 The full dataset has been uploaded to Dryad Data Repository, and is available via the link:  
375 <https://datadryad.org/review?doi=doi:10.5061/dryad.b4p43t7>.

376

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378

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555  
556



557 **Figure and table captions**

558

559 **Figure 1.** A phylogenetic tree of passerine species pairs ( $n = 259$ ), showing within-pair disparity in  
560 overall song (PC1-3; innermost, black), pitch (PC2; red), length (PC3; blue) and pace (PC3;  
561 outermost, green). Size of points corresponds to relative within-pair song disparity. A version including  
562 species names is available in the supporting online material.

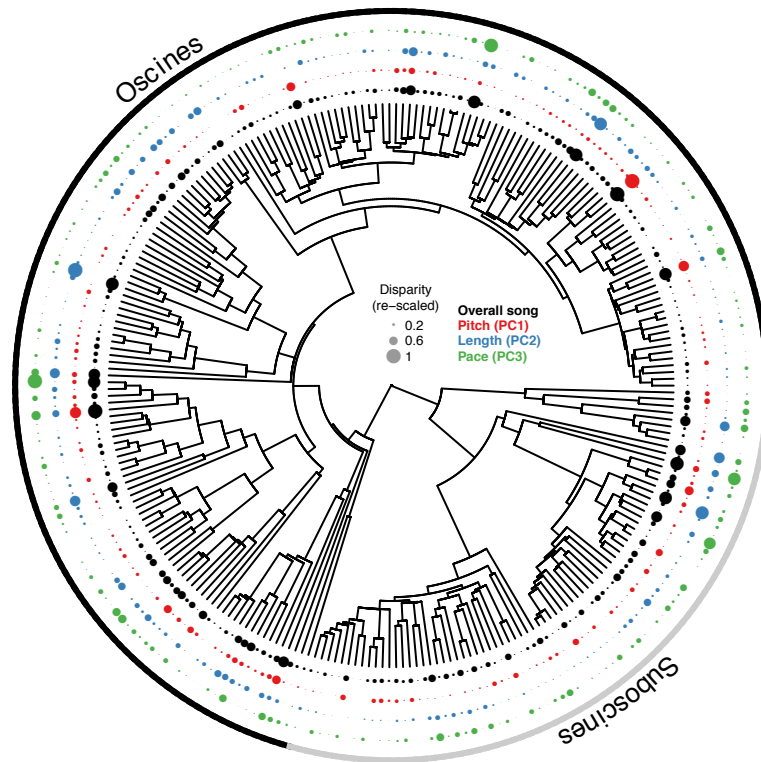
563

564 **Figure 2.** Scatterplot showing the relationship between total within-pair song disparity (PC1-3) and  
565 plumage dichromatism across 259 species pairs of passerine birds. Regression line (with prediction  
566 intervals, shaded) indicates the best-fitting relationship between the two variables.

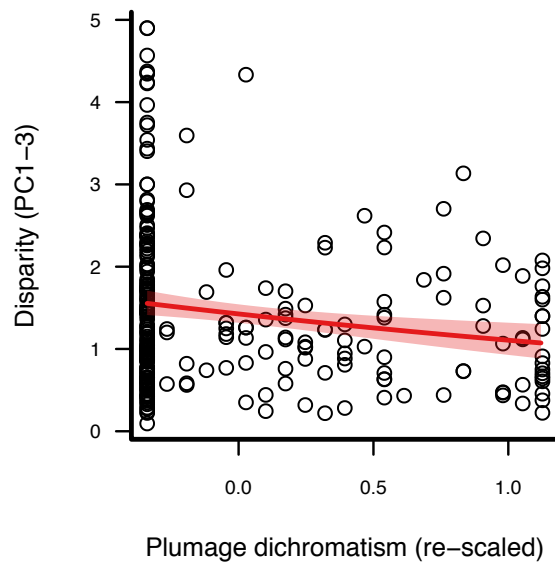
567

568 **Figure 3.** Model averaged coefficient estimates from multipredictor GLMs predicting variation in  
569 within-pair song disparity (PC1-3) among passerine species pairs ( $n = 259$ ). Points indicate the  
570 standardised effect sizes for each of the (scaled) predictor variables and lines indicate 95%  
571 confidence intervals (CI). Sizes of points represent the relative importance (RI) of each of the predictor  
572 variables, where a value of  $RI = 0$  indicates low importance and a value of  $RI = 1$  indicates high  
573 importance. Predictors included in the  $AIC_c$  top model are coloured (blue = negative effect; red =  
574 positive effect), with significant ( $P < 0.05$ ) model-averaged coefficients shown in darker colours.

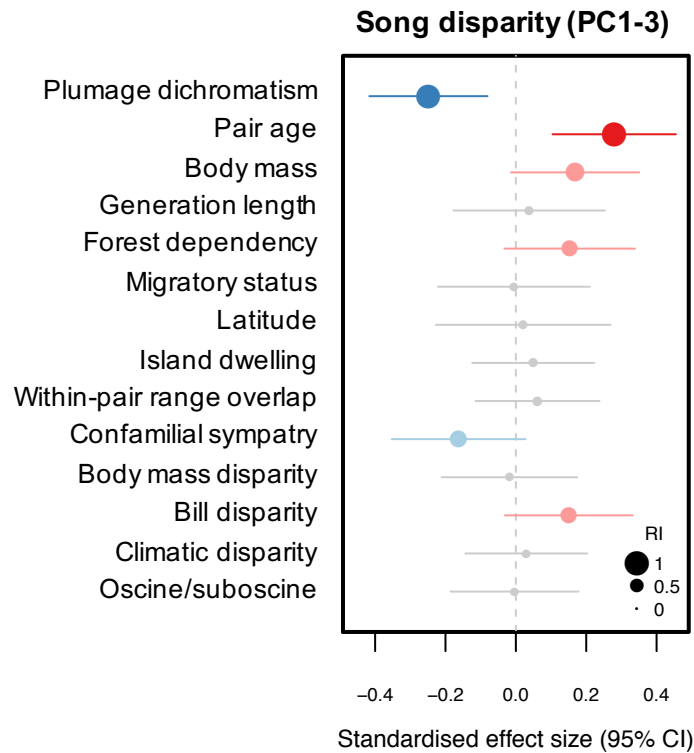
575



**Figure 1.** A phylogenetic tree of passerine species pairs (n = 259), showing within-pair disparity in overall song (PC1-3; innermost, black), pitch (PC2; red), length (PC3; blue) and pace (PC3; outermost, green). Size of points corresponds to relative within-pair song disparity. A version including species names is available in the supporting online material.



**Figure 2.** Scatterplot showing the relationship between total within-pair song disparity (PC1-3) and plumage dichromatism across 259 species pairs of passerine birds. Regression line (with prediction intervals, shaded) indicates the best-fitting relationship between the two variables.



**Figure 3.** Model averaged coefficient estimates from multipredictor GLMs predicting variation in within-pair song disparity (PC1-3) among passerine species pairs ( $n = 259$ ). Points indicate the standardised effect sizes for each of the (scaled) predictor variables and lines indicate 95% confidence intervals (CI). Sizes of points represent the relative importance (RI) of each of the predictor variables, where a value of  $RI = 0$  indicates low importance and a value of  $RI = 1$  indicates high importance. Predictors included in the  $AIC_c$  top model are coloured (blue = negative effect; red = positive effect), with significant ( $P < 0.05$ ) model-averaged coefficients shown in darker colours.

1 **SUPPLMENTARY MATERIAL FOR**

2  
3 **COONEY ET AL. – MULTI-MODAL SIGNAL EVOLUTION IN BIRDS: RE-EXAMINING A**  
4 **STANDARD PROXY FOR SEXUAL SELECTION**

5  
6 APPENDIX 1

7  
8 Supplementary methods

9  
10 Supplementary figures (S1-S10) and tables (S1-S12)

11

12 **APPENDIX 1**

13

14 **SUPPLEMENTARY METHODS**

15

16 **Compiling species pair datasets**

17 Following Seddon et al. (2013) and Cooney et al. (2017), we assembled a dataset of passerine  
18 species pairs for which we could collect detailed data on song traits. We compiled a list of species  
19 pairs from published phylogenetic trees of passerine families or genera generated using genetic  
20 data. We only included trees in which (i) > 70% of taxa had been sampled, and (ii) node support  
21 was high, with either posterior probability > 95% or ML bootstrap support > 70%. When several  
22 phylogenies were presented in a paper, we only selected species pairs resolved in all trees. When  
23 nodal support varied with the method of phylogenetic reconstruction, ML bootstrap values took  
24 precedence. We assumed that consensus trees and trees based on concatenated molecular  
25 datasets provided the most reliable source of phylogenetic information and thus, whenever possible,  
26 we assessed nodal support based on the values given in these trees.

27

28 **Principal component analysis of song measurements**

29 Raw song traits were correlated across species (Table S1). Such correlations can lead to  
30 overinflated divergence estimates if each trait axis is treated as independent. Therefore, to avoid  
31 this issue and to reduce the dimensionality of our dataset, following previous studies (Tobias et al.  
32 2014a; Tobias et al. 2014b) we conducted a principal components (PC) analysis on the covariance  
33 matrix of individual (log-transformed) song measurements. The first three PCs from this analysis  
34 accounted for over 83% of the variance in the original acoustic dataset, with each PC capturing a  
35 distinct component of overall signal structure (Table S1). Specifically, PC1 (41%) primarily loaded  
36 with variables related to song pitch, PC2 (24%) with variables related to song length, and PC3  
37 (18%) with song pace. We chose not to retain PC4 (14%) in our analysis because of its  
38 comparatively small eigenvalue (1.006) (Kaiser 1960) and because the loadings indicated that it  
39 was primarily related to variation in minimum song frequency (loading = 0.66), which is more difficult  
40 to quantify from song spectra and therefore potentially subject to greater levels of error. By focusing  
41 exclusively on variation in the first three PCs, which are interpretable in terms of song pitch (PC1),  
42 length (PC2) and pace (PC3), respectively, our analyses are directly comparable with previous  
43 studies (e.g. Tobias et al. 2014b) using the same combination of traits (PCs) to define a three-  
44 dimensional acoustic space (Fig. S2).

45

46 **Alternative dataset: accounting for intraspecific variation**

47 Intraspecific trait variation can generate overinflated estimates of interspecific disparity, especially  
48 when sample sizes are low relative to levels of intraspecific variation and/or measurement error

49 (Silvestro et al. 2015). To test whether our results were sensitive to these issues, we repeated our  
50 main analyses using an alternative version of our dataset in which within-species song disparity  
51 estimates were corrected for observed levels of intraspecific variation using an approach based on  
52 ANOVA (Weir and Wheatcroft 2011; Weir et al. 2012).

53

#### 54 **Sexual dichromatism**

55 Although it would be preferable to estimate dichromatism using more objective measurements of  
56 bird plumage colouration, such as those generated by a spectrophotometer, these types of  
57 measurements are currently unavailable for most species. However, the high correlation between  
58 spectrophotometric and human estimates of dichromatism indicate that human vision can provide a  
59 reliable estimate of avian colouration in general (Bergeron and Fuller 2018) and sexual  
60 dichromatism in particular (Armenta et al. 2008; Seddon et al. 2010). To test this assumption in our  
61 dataset, we used spectrophotometric measurements of plumage colouration from museum  
62 specimens described in (Cooney et al. 2017) to calculate objective estimates of dichromatism for  
63 species and pairs common to both datasets, following methods outlined previously (Seddon et al.  
64 2013; Cooney et al. 2017). This resulted in dichromatism estimates for 264 species (132 pairs),  
65 which we compared to our scores based on handbook illustrations using Spearman's rank  
66 correlation. We found that estimates of dichromatism based on spec measurements and human  
67 vision were highly positively correlated (Fig. S9) across both species (Spearman's  $r = 0.76$ ,  $P <$   
68  $0.001$ ) and species pairs (Spearman's  $r = 0.79$ ,  $P < 0.001$ ). Thus, we conclude that scores of  
69 dichromatism based on published illustrations are valid for our dataset, in line with previous studies  
70 (e.g. Dale et al. 2015).

71

#### 72 **Additional predictors of song divergence**

73 To explore the role of other factors known to influence song divergence in birds, we collected data  
74 for a suite of additional explanatory variables. Details are given below.

75 *Pair age.* We generated estimates of pair age (i.e. time from the present to the most recent  
76 common ancestor) by calculating the mean height of the node connecting the pair in the (pruned)  
77 Jetz et al. (2012) phylogenies (see above).

78 *Body mass.* Estimates of body mass were extracted from Wilman et al. (2014) and we used  
79 the mean of species (ln-transformed) values to generate pair-level averages.

80 *Generation length.* Data on species' generation length, forest dependency and migratory  
81 status were compiled from BirdLife International (<http://www.datazone.birdlife.org>; accessed 18-10-  
82 2017), and we used the mean of species' generation length values to provide pair-level averages.

83 *Forest dependency.* In the BirdLife dataset species are assigned to one of four categories,  
84 depending on whether they "do not normally occur in forests", or exhibit "low", "medium" or "high"  
85 levels of forest dependency. To convert this into a quantitative variable capturing broad differences

86 in habitat usage, we converted this classification system into a 4-point scoring scheme, giving each  
87 species a score of 0, 1, 2 or 3 based on whether they were recorded as having no, low, medium or  
88 high forest dependency, respectively. To capture the average level of forest dependency within a  
89 pair, we took the mean score for each pair.

90 *Migratory status.* Similarly, in the BirdLife dataset species are categorised as “not a migrant”,  
91 “nomadic”, “altitudinal migrant” or “full migrant”, so again we converted this classification system into  
92 a 2-point scoring scheme, giving each species a score of 0 (not a migrant) or 1 (nomadic, altitudinal  
93 migrant or full migrant) and then took the mean score for each pair.

94 *Latitude.* All variables relating to species’ geographical distributions are based on (breeding)  
95 range maps provided by BirdLife International and NatureServe (2016, version 9;  
96 <http://www.datazone.birdlife.org>). To estimate the latitudinal midpoint of each pair, we first  
97 calculated each species’ range centroids using the R package *PBSmapping* (Schnute 2015) and  
98 then took the mean of species (absolute) latitudinal values (Weir and Schluter 2007; Weir and  
99 Wheatcroft 2011; Weir et al. 2012).

100 *Island-dwelling.* To characterise species as island-dwelling, we used a high-resolution  
101 database of global geography (GSHHG version 2.3.6; <http://www.soest.hawaii.edu/pwessel/gshhg/>)  
102 to identify all landmasses >1 km<sup>2</sup> in size surrounded by ocean and smaller than Greenland  
103 (following Weigelt et al. 2013). We then overlaid species range maps on top of this dataset and  
104 calculated the proportion of species’ ranges occurring on islands. We consider species with >80%  
105 of their range occurring on islands to be primarily island dwelling and turned this into a pair-level  
106 variable by counting whether neither (0), one (1) or both (2) of the species in a pair were  
107 characterised as island dwelling.

108 *Within-pair range overlap.* To calculate range overlap between species within a pair, we took  
109 the standard approach of calculating the area of overlap between species, divided by the area of the  
110 smaller species’ range (Pigot and Tobias 2013; Tobias et al. 2014a; Cooney et al. 2017).

111 *Confamilial sympatry.* To quantify the extent of interactions with related species, we used the  
112 taxonomy of Jetz et al. (2012) and the range maps to tally up the number of same-family  
113 (confamilial) species that are sympatric with the focal species (Morinay et al. 2013), where sympatry  
114 is defined as >20% range overlap between species—a threshold commonly used to define  
115 ‘substantial’ sympatry (Tobias et al. 2014a). We then divided this number by the total number of  
116 species in the family and took the mean of these values to generate a pair-level average.

117 *Climatic disparity.* To quantify divergence in species’ climatic niches, we extracted range-  
118 wide climatic information for each species from WorldClim (<http://www.worldclim.org/>) using a global  
119 resolution of 10 arc minutes (~100 km<sup>2</sup>). Following Lawson and Weir (2014), we focused on 48  
120 climatic variables, 36 related to temperature (maximum, minimum and mean for each month of the  
121 year) and 12 to precipitation (mean for each month of the year). We then conducted a PC analysis  
122 on these (sorted) values across all species (Lawson and Weir 2014), retaining the first four PC axes



123 that together accounted for 96% of the variation. Euclidean distances between the species' midpoint  
124 (median) values in each of the four axes were used as an overall measure of climatic divergence  
125 within a pair.

126 *Body mass disparity.* To calculate within-pair disparity in body mass, we took the absolute  
127 difference between (ln-transformed) body mass values for species within a pair.

128 *Beak disparity.* Variables relating to species' beak traits are based on a dataset of biometric  
129 measurements collected from museum specimens. For each species, we measured linear  
130 measurements of beak morphology (length, width and depth, measures at the nares) for multiple  
131 individuals per species (mean = 6.5) per sex. To quantify divergence in beak morphology, we  
132 followed the methods outlined in Pigot and Tobias (2013) and calculated beak divergence as the  
133 Euclidean distance between species mean (ln-transformed) values for all three axes.

134 *Song learning.* Finally, we identified whether species pairs belonged to the oscine (Passeri)  
135 or suboscine (Tyranni) passerine suborders, which do and do not exhibit song learning,  
136 respectively.

137

### 138 **Collinearity among predictor variables**

139 Collinearity among predictor variables is a potential problem in multiple regression modelling  
140 (Graham 2003). However, methods based on the type of information theoretic-based model  
141 averaging approach we employ here are generally robust to collinearity (Graham 2003; Freckleton  
142 2011). Nonetheless, we checked for collinearity among predictors by calculating pairwise Pearson  
143 correlation coefficients ( $r^2$ ) and variance inflation factors (VIF) for all variables. Only one pair of  
144 predictors (latitude and migration) showed evidence of (strong) collinearity ( $r^2 = 0.75$ ; Table S12),  
145 and calculating VIFs for our full dataset revealed no evidence of severe ( $VIF > 10$ ) or even  
146 moderate ( $VIF > 4$ ) multicollinearity (range = 1.16 – 3.14; mean = 1.61), indicating that  
147 multicollinearity is unlikely to affect our results.

148

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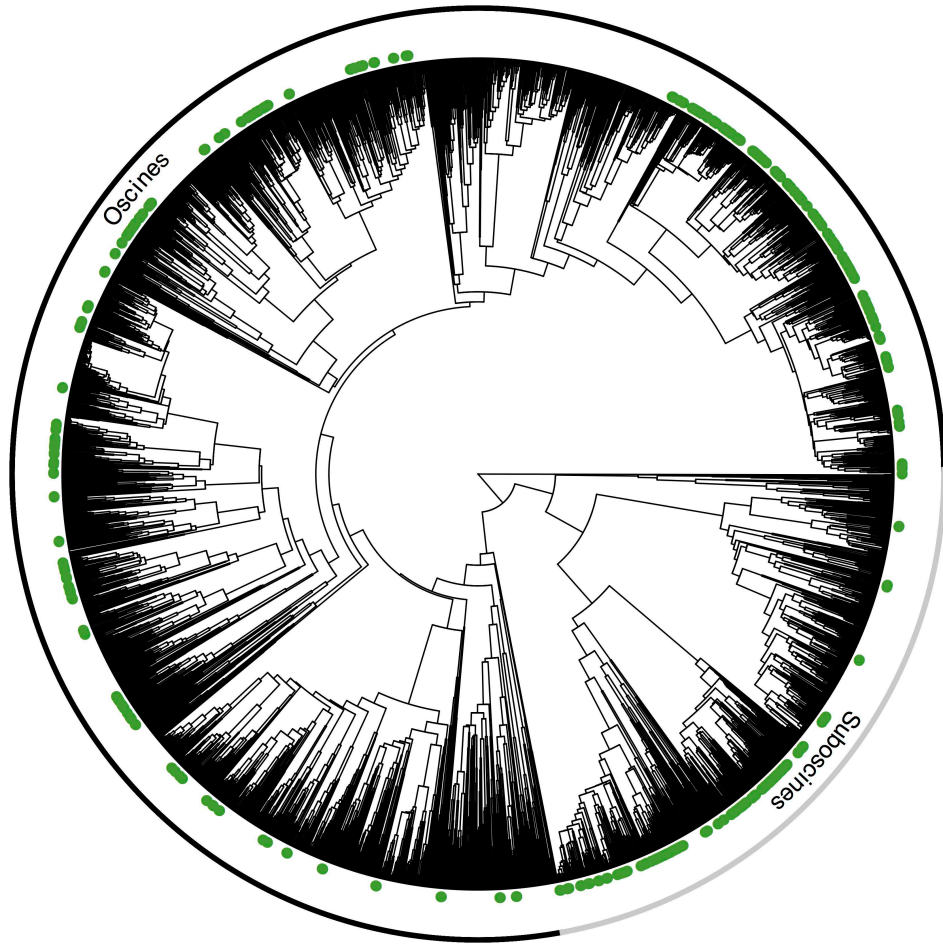
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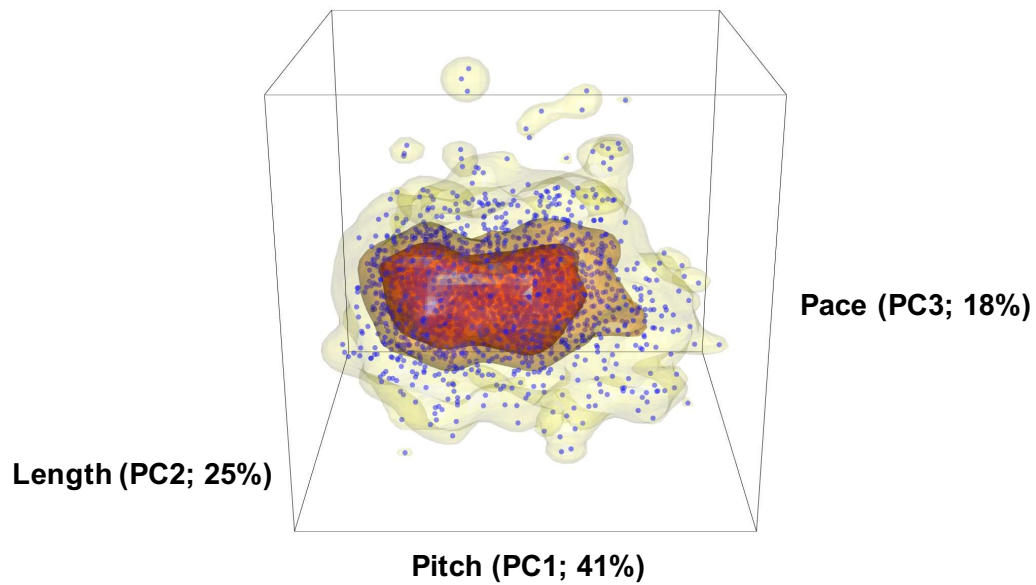
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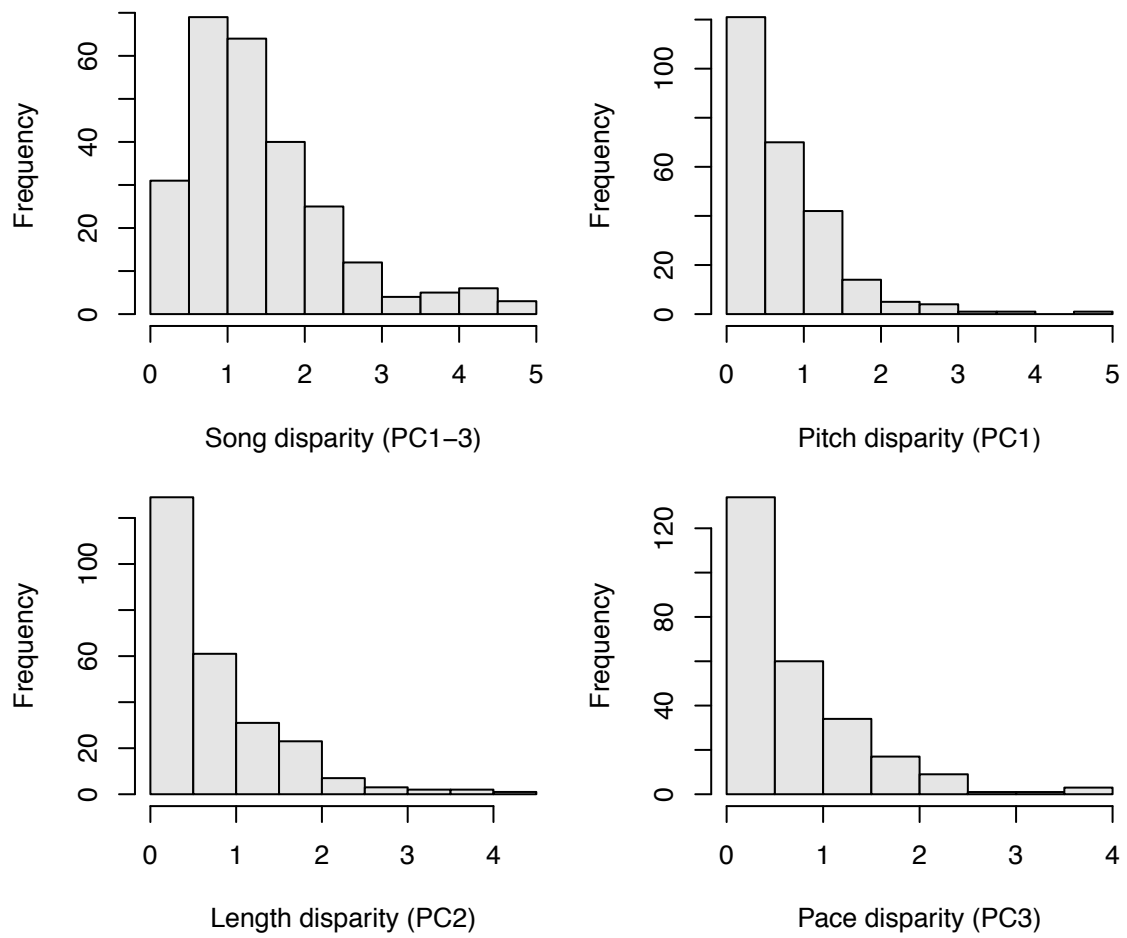
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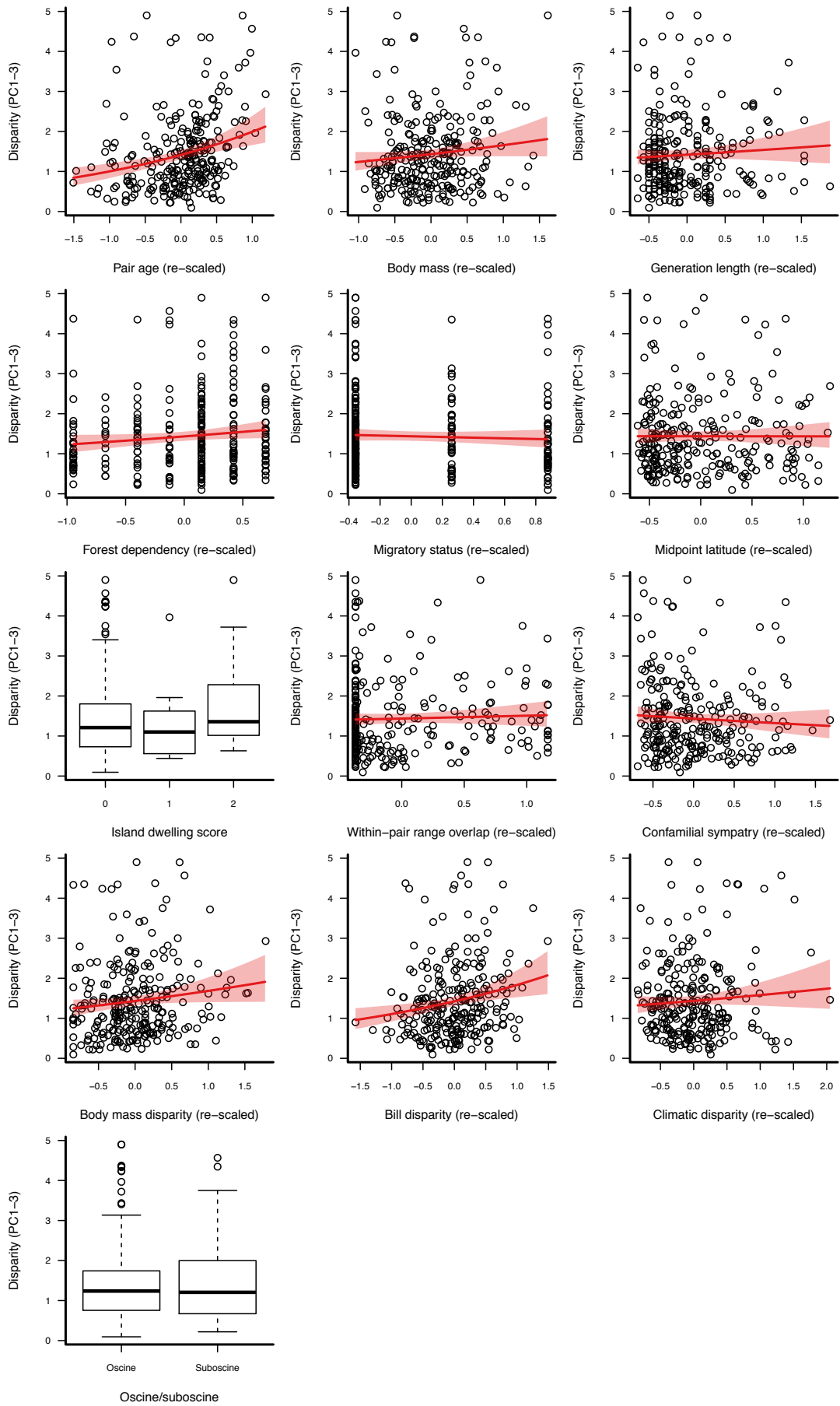
**Figure S1.** A representative phylogeny of passerines from Jetz et al. (2012) showing the location of species sampled in this study (green points).



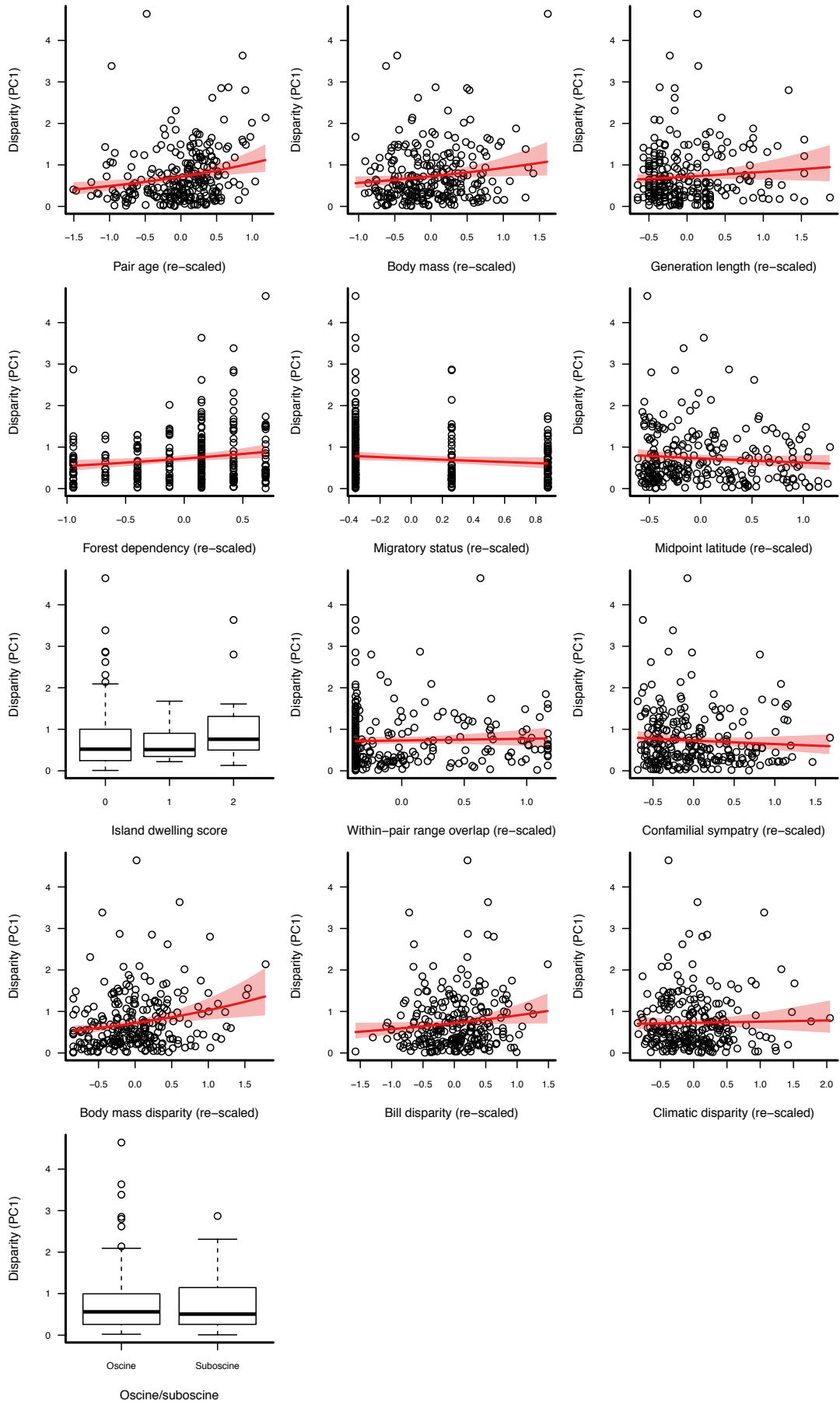
**Figure S2.** Plot showing the distribution of individual song recordings ( $n = 2476$ ) in acoustic 'trait space', a defined by the first three principal component (PC) axes of variation, corresponding to variation among song in pitch (PC1), length (PC2) and pace (PC3). Coloured areas represent kernel density estimates of 50% (red), 75% (orange) and 100% (yellow) of the data (for illustrative purposes only).



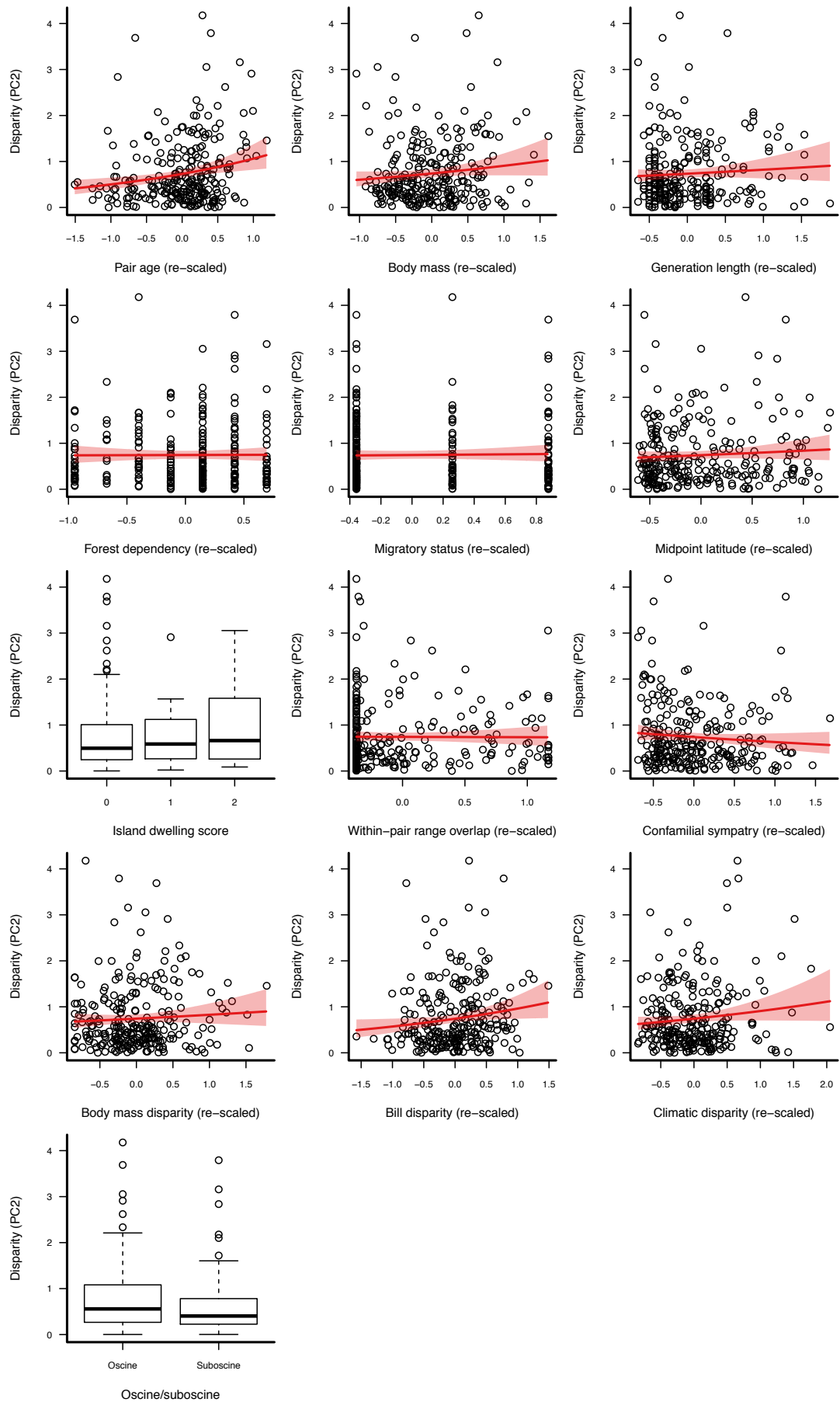
**Figure S3.** Histograms showing the distribution of within-pair song disparity estimates for species pairs ( $n = 259$ ).



**Figure S4.** Plots showing the relationship between overall within-pair song disparity (PC1-3) and each of the additional predictors included in our analysis. For all continuous predictors, regressions lines (with prediction intervals, shaded) indicate the best-fitting relationship between the two variables.

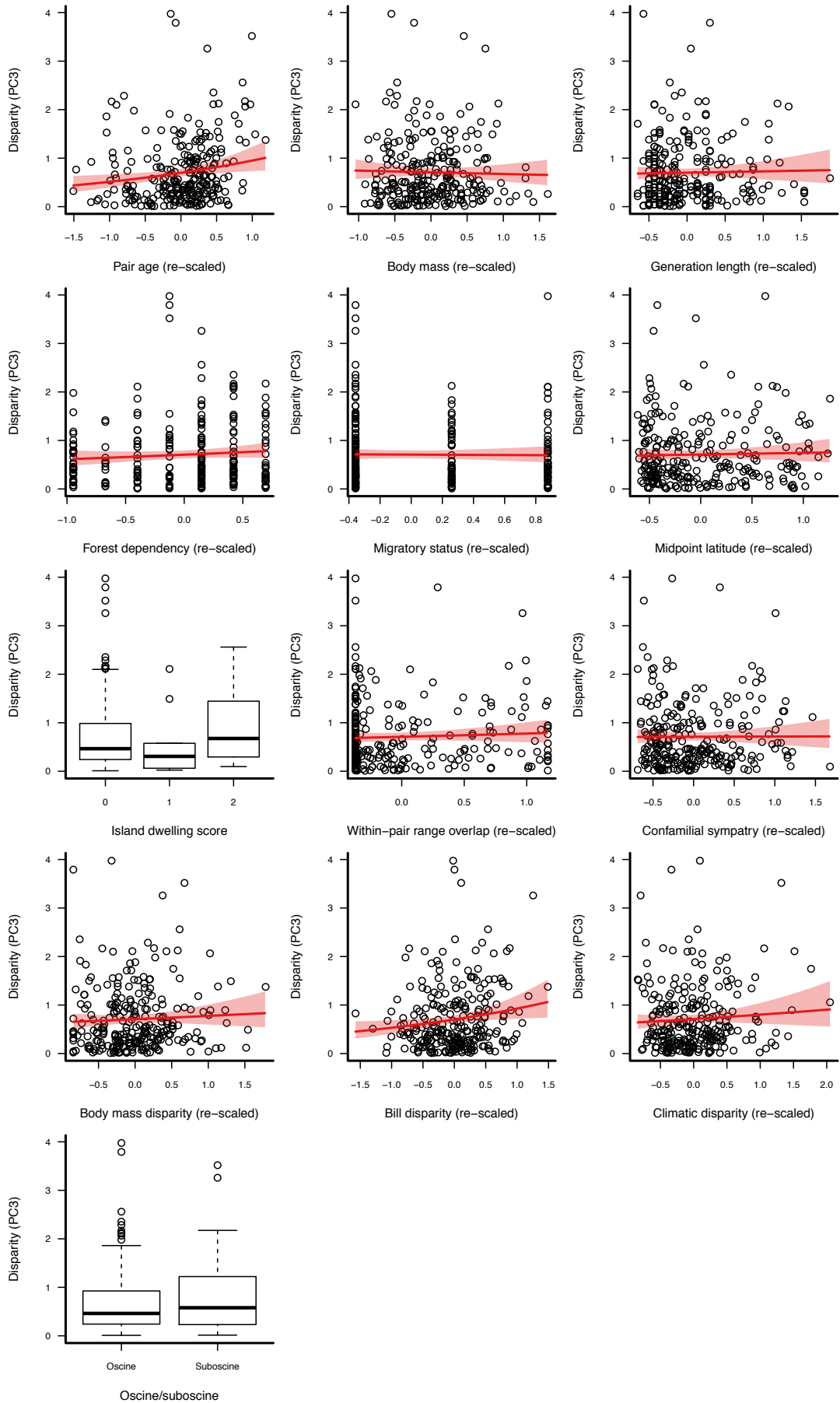


**Figure S5.** Plots showing the relationship between within-pair disparity in pitch (PC1) and each of the additional predictors included in our analysis. For all continuous predictors, regressions lines (with prediction intervals, shaded) indicate the best-fitting relationship between the two variables.

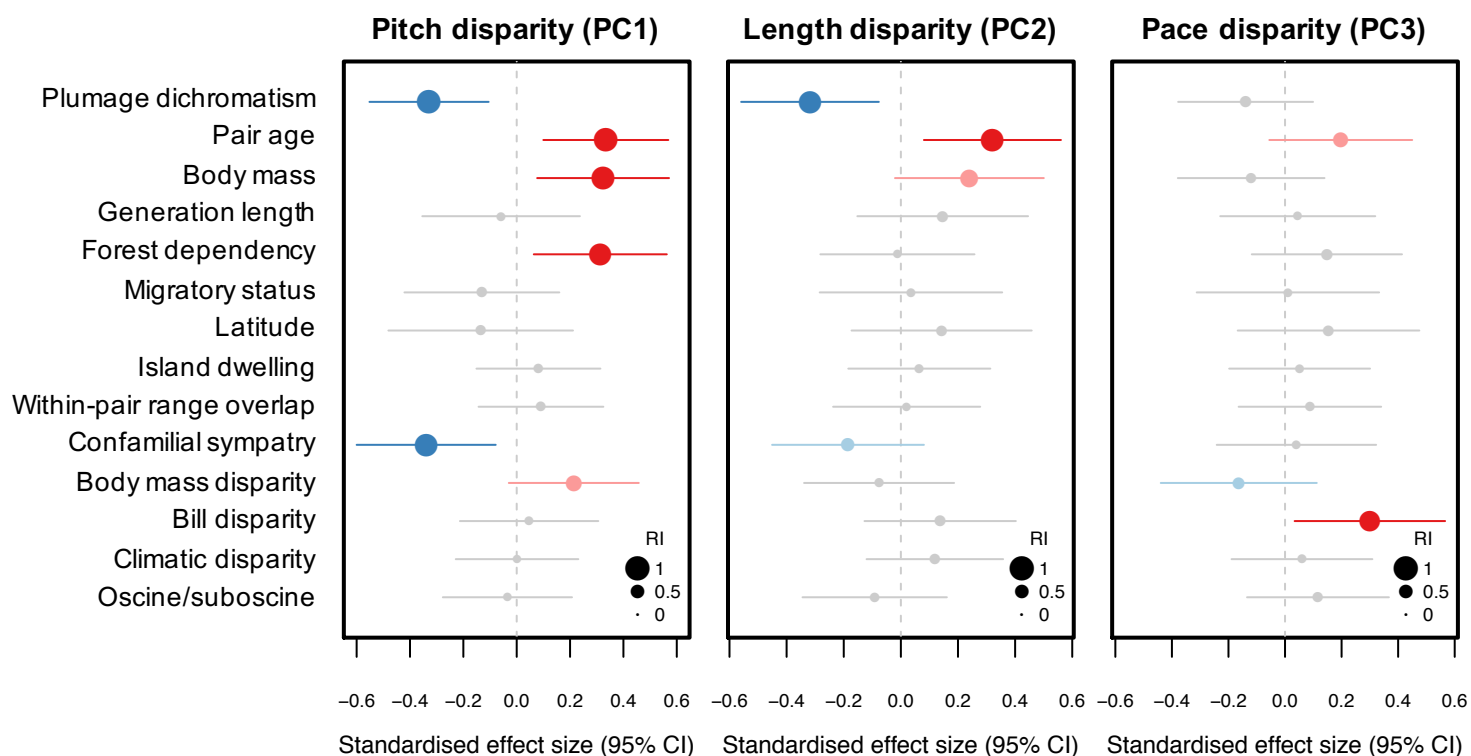


**Figure S6.** Plots showing the relationship between within-pair disparity in length (PC2) and each of the additional predictors included in our analysis. For all continuous predictors, regressions lines (with prediction intervals, shaded) indicate the best-fitting relationship between the two variables.

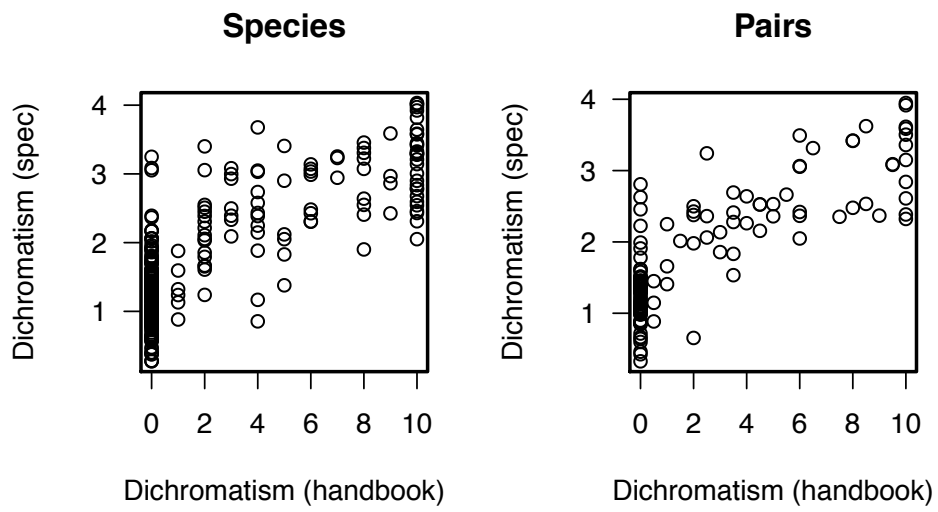




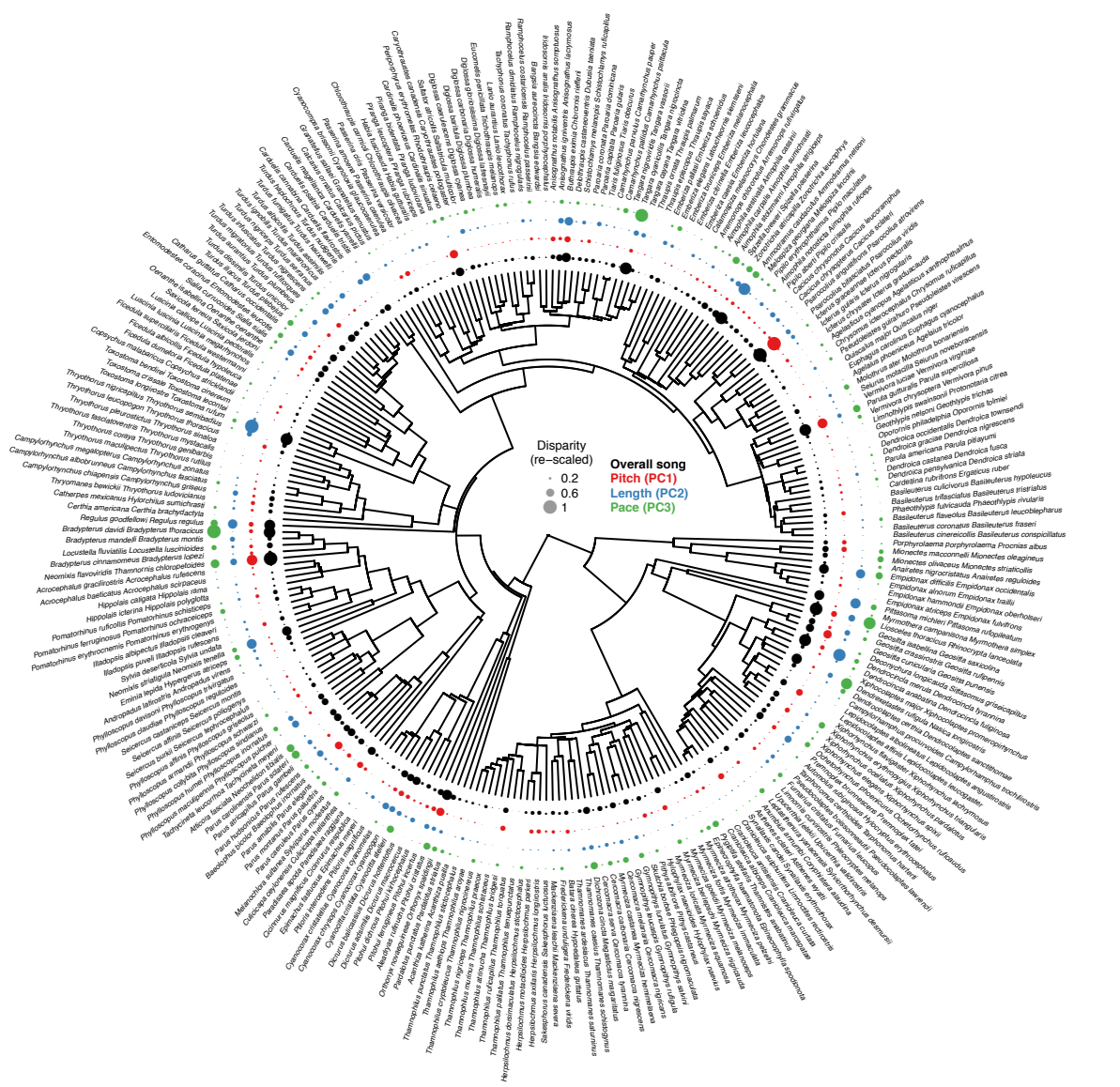
**Figure S7.** Plots showing the relationship between within-pair disparity in pace (PC3) and each of the additional predictors included in our analysis. For all continuous predictors, regressions lines (with prediction intervals, shaded) indicate the best-fitting relationship between the two variables.



**Figure S8.** Model averaged coefficient estimates from multipredictor GLMs predicting variation in within-pair disparity in song pitch (PC1), length (PC2) and pace (PC3) among passerine species pairs ( $n = 246$ ). Within each dataset, points indicate the standardised effect sizes for each of the (scaled) predictor variables and lines indicate 95% confidence intervals (CI). Sizes of points represent the relative importance (RI) of each of the predictor variables, where a value of  $RI = 0$  indicates low importance and a value of  $RI = 1$  indicates high importance. Predictors included in the  $AIC_c$  top model for each dataset are coloured (blue = negative effect; red = positive effect), with significant ( $P < 0.05$ ) model-averaged coefficients shown in darker colours.



**Figure S9.** Scatterplots showing the relationship between dichromatism estimates based on spectrophotometric measurements of colouration from museum specimens and handbook illustrations for species ( $n = 264$ ) and species pairs ( $n = 132$ ) of birds.



**Figure S10.** A phylogenetic tree of passerine species pairs ( $n = 259$ ), showing within-pair disparity in overall song (PC1-3; black), pitch (PC2; red), length (PC3; blue) and pace (PC3; green).

	Pitch (PC1)	Length (PC2)	Pace (PC3)
Maximum frequency	<b>-0.57</b>	0.06	0.11
Minimum frequency	-0.27	-0.26	0.41
Peak	<b>-0.54</b>	-0.08	0.22
Bandwidth	<b>-0.48</b>	0.16	-0.07
Duration	0.12	<b>0.64</b>	0.45
Note number	-0.09	<b>0.70</b>	-0.16
Pace	-0.25	0.07	<b>-0.73</b>
Eigenvalue	2.85	1.72	1.25
Cumulative variance explained (%)	41	65	83

**Table S1.** Variable loadings and variance explained by the first three principal components (PCs) of an analysis of measurements of individual song recordings ( $n = 2476$ ) for the species included in our analyses ( $n = 518$ ). Standardised loadings of the main contributors to each component are highlighted in bold.

Variable	Full dataset			Alternative dataset		
	$\lambda$ (95% CI)	$P$ ( $\lambda = 0$ )	$P$ ( $\lambda = 1$ )	$\lambda$ (95% CI)	$P$ ( $\lambda = 0$ )	$P$ ( $\lambda = 1$ )
Total disparity (PC1-3)	0.00 (NA, 0.39)	1.000	<0.001	0.00 (NA, 0.29)	1.000	<0.001
Pitch disparity (PC1)	0.00 (NA, 0.09)	1.000	<0.001	0.00 (NA, 0.08)	1.000	<0.001
Length disparity (PC2)	0.00 (NA, 0.50)	1.000	<0.001	0.00 (NA, 0.14)	1.000	<0.001
Pace disparity (PC3)	0.00 (NA, 0.18)	1.000	<0.001	0.01 (NA, 0.30)	0.719	<0.001

**Table S2.** Maximum likelihood estimates (and 95% confidence intervals; CI) of phylogenetic signal (Pagel's lambda;  $\lambda$ ) for each measure of within-pair song disparity across passerine species pairs ( $n = 259$ ).

Response variable	Term	Full dataset			Alternative dataset		
		Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>	Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>
Total disparity (PC1-3)	Dichromatism	-0.25 (0.08)	0.002	0.04	-0.16 (0.06)	0.001	0.03
Pitch disparity (PC1)	Dichromatism	-0.27 (0.11)	0.015	0.03	-0.13 (0.05)	0.015	0.04
Length disparity (PC2)	Dichromatism	-0.33 (0.12)	0.005	0.04	-0.14 (0.06)	0.019	0.03
Pace disparity (PC3)	Dichromatism	-0.21 (0.12)	0.074	0.02	-0.08 (0.05)	0.137	0.01
Total disparity (PC1-3)	Dichromatism	-0.26 (0.08)	0.001	0.06	-0.17 (0.06)	0.005	0.06
	Forest dependency	0.17 (0.08)	0.039		0.15 (0.06)	0.013	
	Interaction	-0.08 (0.15)	0.585		-0.05 (0.11)	0.627	
Pitch disparity (PC1)	Dichromatism	-0.25 (0.10)	0.009	0.07	-0.14 (0.05)	0.009	0.07
	Forest dependency	0.30 (0.10)	0.006		0.13 (0.05)	0.011	
	Interaction	-0.10 (0.21)	0.633		-0.02 (0.10)	0.803	
Length disparity (PC2)	Dichromatism	-0.33 (0.12)	0.005	0.04	-0.14 (0.06)	0.019	0.04
	Forest dependency	0.02 (0.12)	0.875		0.06 (0.06)	0.311	
	Interaction	-0.10 (0.22)	0.641		-0.06 (0.11)	0.623	
Pace disparity (PC3)	Dichromatism	-0.22 (0.12)	0.065	0.02	-0.09 (0.05)	0.116	0.02
	Forest dependency	0.16 (0.12)	0.181		0.06 (0.05)	0.261	
	Interaction	-0.06 (0.22)	0.796		0.02 (0.10)	0.820	

**Table S3.** Standardised coefficient estimates from GLMs predicting variation in within-pair disparity in song traits among passerine species pairs (*n* = 259). SE, standard error. *R*<sup>2</sup>, pseudo-*R*<sup>2</sup>.

	Full dataset			
	N pairs	Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>
Plumage dichromatism	259	-0.25 (0.08)	0.002	0.04
Pair age	259	0.34 (0.08)	<0.001	0.09
Body mass	259	0.15 (0.08)	0.081	0.02
Generation length	251	0.08 (0.08)	0.334	<0.01
Forest dependency	259	0.15 (0.08)	0.063	0.02
Migratory status	259	-0.06 (0.08)	0.467	<0.01
Latitude	257	0.00 (0.08)	0.987	<0.01
Island dwelling	259	0.12 (0.08)	0.150	0.01
Within-pair range overlap	257	0.05 (0.08)	0.565	<0.01
Confamilial sympatry	257	-0.08 (0.08)	0.330	0.01
Body mass disparity	259	0.16 (0.08)	0.053	0.02
Bill disparity	257	0.25 (0.08)	0.003	0.04
Climatic disparity	254	0.10 (0.08)	0.252	0.01
Oscine/suboscine	259	0.01 (0.08)	0.919	<0.01

**Table S4.** Standardised coefficient estimates from single predictor GLMs predicting variation in within-pair song disparity (PC1-3) among passerine species pairs (*n* = 259). SE, standard error. *R*<sup>2</sup>, pseudo-*R*<sup>2</sup>.

	N pairs	Full dataset								
		Pitch disparity (PC1)			Length disparity (PC2)			Pace disparity (PC3)		
		Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>	Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>	Estimate (SE)	<i>P</i>	<i>R</i> <sup>2</sup>
Plumage dichromatism	259	-0.27 (0.11)	0.015	0.03	-0.33 (0.12)	0.001	0.04	-0.21 (0.12)	0.074	0.02
Pair age	259	0.38 (0.12)	0.001	0.07	0.37 (0.12)	0.002	0.06	0.31 (0.12)	0.010	0.04
Body mass	259	0.25 (0.11)	0.028	0.03	0.20 (0.12)	0.088	0.02	-0.05 (0.12)	0.677	<0.01
Generation length	251	0.15 (0.12)	0.203	0.01	0.11 (0.12)	0.353	0.01	0.04 (0.12)	0.741	<0.01
Forest dependency	259	0.29 (0.11)	0.008	0.04	0.01 (0.12)	0.941	<0.01	0.14 (0.12)	0.229	0.01
Migratory status	259	-0.21 (0.11)	0.060	0.02	0.03 (0.12)	0.783	<0.01	-0.02 (0.12)	0.868	<0.01
Latitude	257	-0.15 (0.11)	0.180	0.01	0.12 (0.12)	0.299	0.01	0.05 (0.12)	0.701	<0.01
Island dwelling	259	0.19 (0.11)	0.096	0.02	0.14 (0.12)	0.234	0.01	0.08 (0.12)	0.518	<0.01
Within-pair range overlap	257	0.06 (0.11)	0.621	<0.01	-0.01 (0.12)	0.937	<0.01	0.09 (0.12)	0.448	<0.01
Confamilial sympatry	257	-0.12 (0.11)	0.281	0.01	-0.16 (0.12)	0.182	0.01	0.01 (0.12)	0.954	<0.01
Body mass disparity	259	0.36 (0.11)	0.002	0.06	0.11 (0.12)	0.371	<0.01	0.09 (0.12)	0.441	<0.01
Bill disparity	257	0.23 (0.11)	0.047	0.02	0.26 (0.12)	0.030	0.03	0.28 (0.12)	0.018	0.03
Climatic disparity	254	0.04 (0.12)	0.738	<0.01	0.20 (0.12)	0.086	0.02	0.12 (0.12)	0.315	0.01
Oscine/suboscine	259	-0.01 (0.11)	0.919	<0.01	-0.14 (0.12)	0.234	0.01	0.15 (0.12)	0.215	0.01

**Table S5.** Standardised coefficient estimates from single predictor GLMs predicting variation in within-pair disparity in three independent axes of song variation among passerine species pairs (*n* = 259). SE, standard error. *R*<sup>2</sup>, pseudo-*R*<sup>2</sup>.

	Full dataset				
	Model averaged			AIC <sub>c</sub> top model	
	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>
Plumage dichromatism	-0.25 (0.09)	0.004	0.98*	-0.25 (0.08)	0.003
Pair age	0.28 (0.09)	0.002	0.99*	0.26 (0.09)	0.002
Body mass	0.17 (0.09)	0.070	0.74*	0.16 (0.09)	0.057
Generation length	0.04 (0.11)	0.731	0.29	-	-
Forest dependency	0.15 (0.09)	0.106	0.61*	0.17 (0.09)	0.064
Migratory status	-0.01 (0.11)	0.959	0.26	-	-
Latitude	0.02 (0.13)	0.868	0.28	-	-
Island dwelling	0.05 (0.09)	0.576	0.29	-	-
Within-pair range overlap	0.06 (0.09)	0.492	0.31	-	-
Confamilial sympatry	-0.16 (0.10)	0.093	0.65*	-0.18 (0.09)	0.045
Body mass disparity	-0.02 (0.10)	0.854	0.27	-	-
Bill disparity	0.15 (0.09)	0.104	0.62*	0.14 (0.09)	0.098
Climatic disparity	0.03 (0.09)	0.737	0.27	-	-
Oscine/suboscine	0.00 (0.09)	0.968	0.26	-	-

**Table S6.** Standardised coefficient estimates from model averaged and AIC<sub>c</sub> top model multipredictor GLMs predicting variation in within-pair song disparity (PC1-3) among passerine species pairs (n = 246). SE, standard error; RI, relative importance. Pseudo-*R*<sup>2</sup> for AIC<sub>c</sub> top model = 0.17.



	Full dataset								
	Pitch disparity (PC1)			Length disparity (PC2)			Pace disparity (PC3)		
	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>	RI
Plumage dichromatism	-0.33 (0.11)	0.004	0.97*	-0.32 (0.12)	0.010	0.91*	-0.14 (0.12)	0.252	0.39
Pair age	0.33 (0.12)	0.005	0.96*	0.32 (0.12)	0.009	0.92*	0.20 (0.13)	0.126	0.56*
Body mass	0.32 (0.13)	0.010	0.93*	0.24 (0.13)	0.071	0.69*	-0.12 (0.13)	0.366	0.34
Generation length	-0.06 (0.15)	0.698	0.28	0.15 (0.15)	0.337	0.38	0.04 (0.14)	0.748	0.27
Forest dependency	0.31 (0.13)	0.014	0.89*	-0.01 (0.14)	0.930	0.27	0.15 (0.13)	0.275	0.39
Migratory status	-0.13 (0.15)	0.378	0.35	0.04 (0.16)	0.829	0.28	0.01 (0.16)	0.951	0.28
Latitude	-0.13 (0.18)	0.444	0.34	0.14 (0.16)	0.375	0.36	0.15 (0.16)	0.348	0.37
Island dwelling	0.08 (0.12)	0.492	0.31	0.06 (0.13)	0.611	0.29	0.05 (0.13)	0.685	0.28
Within-pair range overlap	0.09 (0.12)	0.446	0.32	0.02 (0.13)	0.877	0.26	0.09 (0.13)	0.494	0.31
Confamilial sympatry	-0.34 (0.13)	0.011	0.92*	-0.19 (0.13)	0.172	0.49*	0.04 (0.14)	0.779	0.27
Body mass disparity	0.21 (0.12)	0.085	0.61*	-0.08 (0.13)	0.569	0.29	-0.16 (0.14)	0.245	0.42*
Bill disparity	0.05 (0.13)	0.725	0.28	0.14 (0.13)	0.309	0.38	0.30 (0.14)	0.027	0.82*
Climatic disparity	0.00 (0.12)	0.992	0.26	0.12 (0.12)	0.329	0.35	0.06 (0.13)	0.638	0.28
Oscine/suboscine	-0.03 (0.12)	0.778	0.26	-0.09 (0.13)	0.477	0.31	0.12 (0.13)	0.363	0.34

**Table S7.** Standardised coefficient estimates from model averaged multipredictor GLMs predicting variation in within-pair disparity in three independent axes of song variation among passerine species pairs ( $n = 246$ ). SE, standard error; RI, relative importance. \* Denotes predictor variables included in the  $AIC_c$  top model.

	Full dataset					
	Pitch disparity (PC1)		Length disparity (PC2)		Pace disparity (PC3)	
	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>
Plumage dichromatism	-0.34 (0.11)	0.002	-0.30 (0.12)	0.010	-	-
Pair age	0.31 (0.12)	0.007	0.34 (0.12)	0.004	0.21 (0.12)	0.095
Body mass	0.33 (0.11)	0.002	0.27 (0.12)	0.027	-	-
Generation length	-	-	-	-	-	-
Forest dependency	0.34 (0.12)	0.005	-	-	-	-
Migratory status	-	-	-	-	-	-
Latitude	-	-	-	-	-	-
Island dwelling	-	-	-	-	-	-
Within-pair range overlap	-	-	-	-	-	-
Confamilial sympatry	-0.31 (0.12)	0.010	-0.21 (0.12)	0.075	-	-
Body mass disparity	0.21 (0.12)	0.070	-	-	-0.20 (0.13)	0.131
Bill disparity	-	-	-	-	0.30 (0.13)	0.024
Climatic disparity	-	-	-	-	-	-
Oscine/suboscine	-	-	-	-	-	-

**Table S8.** Standardised coefficient estimates from  $AIC_c$  top models predicting variation in within-pair disparity in song traits among passerine species pairs ( $n = 246$ ). SE, standard error. Pseudo- $R^2$  for each model: PC1 = 0.22; PC2 = 0.12; PC3 = 0.06.

Alternative dataset					
	Model averaged			AIC <sub>c</sub> top model	
	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>
Plumage dichromatism	-0.16 (0.06)	0.010	0.94	-0.16 (0.06)	0.001
Pair age	0.21 (0.06)	0.001	0.99	0.20 (0.06)	0.001
Body mass	0.10 (0.07)	0.137	0.58	0.09 (0.06)	0.158
Generation length	0.03 (0.08)	0.722	0.29	-	-
Forest dependency	0.17 (0.07)	0.017	0.91	0.17 (0.06)	0.009
Migratory status	0.04 (0.08)	0.611	0.30	-	-
Latitude	0.06 (0.09)	0.497	0.34	-	-
Island dwelling	0.01 (0.07)	0.849	0.26	-	-
Within-pair range overlap	0.06 (0.07)	0.388	0.35	-	-
Confamilial sympatry	-0.15 (0.07)	0.040	0.80	-0.16 (0.07)	0.017
Body mass disparity	0.01 (0.07)	0.872	0.27	-	-
Bill disparity	0.10 (0.07)	0.124	0.58	0.09 (0.06)	0.134
Climatic disparity	0.03 (0.07)	0.647	0.28	-	-
Oscine/suboscine	0.07 (0.07)	0.298	0.40	-	-

**Table S9.** Standardised coefficient estimates from model averaged and AIC<sub>c</sub> top model multipredictor GLMs predicting variation in within-pair song disparity (PC1-3) using an alternative dataset of passerine species pairs (*n* = 246). SE, standard error; RI, relative importance. Pseudo-*R*<sup>2</sup> for AIC<sub>c</sub> top model = 0.16.

	Alternative dataset								
	Pitch disparity (PC1)			Length disparity (PC2)			Pace disparity (PC3)		
	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>	RI	Estimate (SE)	<i>P</i>	RI
Plumage dichromatism	-0.15 (0.05)	0.004	0.99*	-0.14 (0.06)	0.022	0.92*	-0.06 (0.06)	0.288	0.41
Pair age	0.16 (0.05)	0.004	0.99*	0.14 (0.06)	0.018	0.93*	0.10 (0.06)	0.085	0.71*
Body mass	0.15 (0.06)	0.009	0.97*	0.13 (0.07)	0.056	0.82*	-0.06 (0.06)	0.309	0.40
Generation length	-0.01 (0.07)	0.889	0.26	0.05 (0.08)	0.497	0.34	0.01 (0.07)	0.888	0.27
Forest dependency	0.16 (0.06)	0.005	0.98*	0.08 (0.07)	0.237	0.47*	0.07 (0.06)	0.264	0.44
Migratory status	0.00 (0.07)	0.970	0.26	0.04 (0.08)	0.599	0.32	0.01 (0.08)	0.928	0.29
Latitude	-0.01 (0.07)	0.885	0.26	0.09 (0.08)	0.262	0.47*	0.09 (0.07)	0.210	0.51*
Island dwelling	0.04 (0.05)	0.502	0.31	-0.01 (0.06)	0.819	0.26	0.03 (0.06)	0.579	0.30
Within-pair range overlap	0.02 (0.05)	0.702	0.27	0.03 (0.07)	0.615	0.30	0.03 (0.06)	0.597	0.29
Confamilial sympatry	-0.17 (0.06)	0.003	0.99*	-0.08 (0.07)	0.227	0.49	-0.01 (0.07)	0.911	0.27
Body mass disparity	0.10 (0.06)	0.078	0.69*	-0.04 (0.07)	0.595	0.30	-0.06 (0.06)	0.311	0.41
Bill disparity	0.01 (0.06)	0.810	0.27	0.07 (0.07)	0.319	0.41	0.14 (0.06)	0.026	0.90*
Climatic disparity	0.00 (0.05)	0.981	0.25	0.07 (0.06)	0.291	0.42	0.02 (0.06)	0.756	0.27
Oscine/suboscine	0.02 (0.06)	0.763	0.26	0.01 (0.06)	0.869	0.26	0.09 (0.06)	0.124	0.61*

**Table S10.** Standardised coefficient estimates from model averaged multipredictor GLMs predicting variation in within-pair disparity in song traits using an alternative dataset of passerine species pairs ( $n = 246$ ). SE, standard error; RI, relative importance. \* Denotes predictor variables included in the  $AIC_c$  top model.

	Alternative dataset					
	Pitch disparity (PC1)		Length disparity (PC2)		Pace disparity (PC3)	
	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>
Plumage dichromatism	-0.15 (0.05)	0.003	-0.14 (0.06)	0.018	-	-
Pair age	0.15 (0.05)	0.004	0.14 (0.06)	0.018	0.09 (0.06)	0.116
Body mass	0.14 (0.05)	0.007	0.14 (0.06)	0.021	-	-
Generation length	-	-	-	-	-	-
Forest dependency	0.16 (0.05)	0.003	0.09 (0.07)	0.175	-	-
Migratory status	-	-	-	-	-	-
Latitude	-	-	-0.13 (0.07)	0.055	0.08 (0.06)	0.145
Island dwelling	-	-	-	-	-	-
Within-pair range overlap	-	-	-	-	-	-
Confamilial sympatry	-0.17 (0.05)	0.002	-	-	-	-
Body mass disparity	0.10 (0.05)	0.066	-	-	-	-
Bill disparity	-	-	-	-	0.12 (0.06)	0.036
Climatic disparity	-	-	-	-	-	-
Oscine/suboscine	-	-	-	-	0.09 (0.06)	0.098

**Table S11.** Standardised coefficient estimates from  $AIC_c$  top models predicting variation in within-pair disparity in song traits using an alternative dataset of passerine species pairs ( $n = 246$ ). SE, standard error. Pseudo- $R^2$  for each model: PC1 = 0.23; PC2 = 0.12; PC3 = 0.08.

	Pair age	Body mass	Generation length	Forest dependency	Migratory status	Latitude	Island dwelling	Plumage dichromatism	Within-pair range overlap	Confamilial sympatry	Body mass disparity	Bill disparity	Climate disparity
<b>Body mass</b>	0.03												
<b>Generation length</b>	0.06	0.52											
<b>Forest dependency</b>	0.13	0.07	0.27										
<b>Migratory status</b>	-0.02	-0.34	-0.31	-0.31									
<b>Latitude</b>	0.01	-0.29	-0.27	-0.46	0.75								
<b>Island dwelling</b>	0.07	0.18	0.36	0.14	-0.16	-0.18							
<b>Plumage dichromatism</b>	0.02	0.15	0.30	0.08	0.03	-0.05	0.06						
<b>Within-pair range overlap</b>	0.14	-0.01	-0.05	-0.06	0.11	0.13	0.12	-0.02					
<b>Confamilial sympatry</b>	0.07	0.22	0.26	0.37	-0.40	-0.55	0.11	0.09	0.10				
<b>Body mass disparity</b>	0.25	0.18	0.09	-0.10	-0.10	-0.05	0.13	0.02	0.04	-0.01			
<b>Bill disparity</b>	0.26	0.18	0.10	-0.07	-0.03	-0.02	0.13	-0.05	0.13	0.04	0.47		
<b>Climate disparity</b>	0.00	0.02	0.02	-0.05	0.08	0.02	-0.07	0.02	-0.41	-0.10	0.06	0.06	
<b>Oscine/suboscine</b>	0.03	0.04	0.10	0.25	-0.29	-0.31	-0.18	0.11	-0.04	0.33	0.01	-0.03	-0.07

**Table S12.** Pearson correlation coefficients ( $r^2$ ) for all pairwise combinations of (standardised) predictor variables considered in our analysis