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9 **Sympatry drives colour and song evolution in wood-warblers**10 **(Parulidae)**

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## 19 ABSTRACT

20 Closely related species often exhibit similarities in appearance and behaviour, yet when related  
21 species exist in sympatry, signals may diverge to enhance species recognition. Prior comparative  
22 studies provided mixed support for this hypothesis, but the relationship between sympatry and  
23 signal divergence is likely non-linear. Constraints on signal diversity may limit signal  
24 divergence, especially when large numbers of species are sympatric. We tested the effect of  
25 sympatric overlap on plumage colour and song divergence in wood-warblers (Parulidae), a  
26 speciose group with diverse visual and vocal signals. We also tested how number of sympatric  
27 species influences signal divergence. Allopatric species pairs had overall greater plumage and  
28 song divergence compared to sympatric species pairs. However, among sympatric species pairs,  
29 plumage divergence positively related to degree of sympatric overlap in males and females,  
30 while male song bandwidth and syllable rate divergence negatively related to sympatric overlap.  
31 In addition, as the number of species in sympatry increased, average signal divergence among  
32 sympatric species decreased, which likely due to constraints on warbler perceptual space and  
33 signal diversity. Our findings reveal that sympatry influences signal evolution in warblers,  
34 though not always as predicted, and that number of sympatric species can limit sympatry's  
35 influence on signal evolution.

36

37 **Key words:** birdsong, colour space, plumage, signal evolution, song space, visual models

## 38 INTRODUCTION

39           Animals exhibit an incredible diversity of communication signals. Many signals play a  
40 vital role in mate choice and intrasexual competition (hereafter: “sexual signals”), and divergent  
41 sexual signals among species often serve as important indicators of species identity [1].

42 Traditional speciation models assume that sexual signal divergence occurs as a by-product of  
43 ecological adaptation or genetic drift [2], however, sexual signals can diverge under the direct  
44 influence of sexual selection. For example, sexual selection can promote signal divergence due  
45 to receivers favouring individuals with signals that are more effective in different environments,  
46 leading to the evolution of divergent signals, even among closely related species [3,4].

47           Signals are expected to diverge between closely-related species with overlapping  
48 geographic ranges (e.g. Figure 1a) to maintain reproductive isolation and prevent hybridization  
49 [2,5]. Prior studies have revealed that signals used for mate choice, and the preference for those  
50 signals, are more divergent in areas where closely related species co-occur (i.e. sympatry) versus  
51 areas where each species occurs separately (i.e. allopatry) [6,7]. These studies provide evidence  
52 for sexual signals facilitating species identification of prospective mates, and thus maintaining  
53 reproductive isolation between sympatric species. Comparative studies offer limited additional  
54 evidence of sexual signal divergence for species recognition. For example, sympatric species  
55 exhibit greater divergence compared to allopatric species in song characteristics [8] and plumage  
56 colour [9] in birds. Similarly, the degree of sympatry between species pairs correlates with  
57 plumage colour divergence in temperate birds in North America [10].

58           The effect of sympatry on sexual signal divergence should not always be linear. As more  
59 species co-occur, the degree to which sexual signals can diverge will be limited by the perceptual  
60 space and signal production mechanisms of those species. For example, colour perceptual space

61 has a fixed size, based on the sensory capabilities of a given animal group (e.g. birds) [11]. As  
62 this colour space becomes increasingly crowded with more species, there should be a reduction  
63 in how much any particular species can simultaneously diverge in colour from multiple other  
64 species (Figure 1b). Many animals are even further constrained by their available colour  
65 production mechanisms [12], with certain colour production mechanisms producing only a  
66 specific set of colours [13]. For instance, due to colour production limitations, birds can only  
67 produce a subset (ca. 30%) of the colours they can perceive [12].

68         Other signals can also be limited by perceptual space or production mechanisms.  
69 Acoustic signals, for example, are also constrained by physiological and morphological  
70 limitations [14,15]. Body size constrains the frequencies produced by birds, especially at lower  
71 frequencies [15], and vocal tract morphology constrains vocal performance [14]. Outside of  
72 signal production constraints, other factors can restrict sexual signal diversity, such as predation  
73 pressures [16]. Given these constraints, when many species occur in sympatry it should be  
74 difficult for each species to exhibit high signal divergence from all other species (Figure 1b).  
75 Consequently, we predict that sympatry should favour signal divergence, but that the magnitude  
76 of signal divergence should decrease as the number of species in sympatry increases, due to  
77 bounded signal spaces becoming crowded.

78         In this study, we test the hypotheses that sympatry promotes sexual signal divergence,  
79 and that the number of species co-occurring in sympatry limits sexual signal divergence in wood-  
80 warblers (Family: Parulidae), a widespread and speciose group of birds (Figure 1). Wood-  
81 warblers exhibit tremendous variation in degree of sympatric overlap (i.e. 1 to 70 species in  
82 sympatry), even among species within the same genus (e.g. *Setophaga*). Nevertheless, wood-  
83 warblers effectively maintain species integrity [17]. Wood-warblers also show little divergence

84 in morphology (e.g. body size) [17], but exhibit remarkable diversification in sexual signals,  
85 including in plumage colour and song [18], which function in mate choice and intrasexual  
86 competition [19,20]. We predicted that plumage colour and song divergence would be greater in  
87 sympatric species and increase with degree of sympatric overlap. We also predicted that an  
88 increase in the number of sympatric species would decrease the average colour and song  
89 divergence among those sympatric species, due to wood-warbler signal space becoming too  
90 crowded. Sexual signals are also expected to diverge among species through a variety of other  
91 factors, such as genetic drift [19]. Therefore, we tested and controlled for the relationship  
92 between signal divergence and phylogenetic distance in our analyses. We also acknowledge the  
93 possibility that sexual signal divergence could facilitate sympatric overlap (i.e. the reverse of the  
94 above-described hypothesis), such that more-distinct species could remain reproductively  
95 isolated during secondary contact, while less-distinct species would have higher rates of  
96 hybridization due to lack of species recognition. While our analyses cannot completely  
97 distinguish between these alternatives, both hypotheses stem from the same underlying idea that  
98 signal divergence is important for species recognition to maintain reproductive isolation.

99

## 100 METHODS

### 101 *Plumage colour analysis*

102 We measured plumage reflectance from 818 museum specimens of 93 species (see  
103 Supplemental File S1 for specimen information), using established methods [20] (see Text S1 for  
104 details). Whenever possible, we measured five males and five females for each species. For each  
105 specimen, we measured the reflectance of 15 body regions: belly, breast, cheek (i.e. auricular),  
106 crown, eyebrow (i.e. supercilium), flank, mantle, nape, rump, inner tail (excluding outermost

107 feathers), outer tail (the two outermost tail feathers), throat, undertail coverts (hereafter under-  
108 coverts), lower wing (i.e. primaries and secondaries), and upper wing (i.e. wing coverts).

109 We processed reflectance spectra in R [21] using the package *pavo* [22]. We averaged  
110 spectra such that each species was represented by one average spectrum per body region per sex.  
111 We converted the spectra into avian tetrachromatic colourspace [11], using the average ultra-  
112 violet (UV) sensitive avian visual model [23] under an idealized light environment (i.e. we made  
113 no assumptions about each species' light environment), and calculated the absolute cone  
114 stimulation values for each avian photoreceptor [22]. We used the absolute cone stimulation  
115 values to calculate the just-noticeable differences (JNDs) [24] for each colour patch between all  
116 species, and used these JND values as our measures of pairwise species colour distances (i.e. a  
117 separate species pairwise distance matrix per body region). To reduce the overall number of  
118 matrices (15 per sex) and therefore reduce the number of statistical tests we ran, we averaged the  
119 individual body region matrices into biologically relevant body region groups as follows: (1)  
120 head: cheek, crown, eyebrow, throat; (2) upper-body: nape, mantle, rump; (3) under-body: belly,  
121 breast, flank, under-covert; (4) flight feathers: inner tail, outer tail, lower wing, upper wing. We  
122 also calculated an average JND colour distance matrix for all body regions together (“whole-  
123 body colour distance”). We conducted these analyses separately for males and females. Finally,  
124 for our analyses testing the effect of number of sympatric species on colour divergence, we used  
125 the JND data to create a JND-colourspace [25], where all distances within this space are in units  
126 of JND and are perceptually equivalent [25].

127

128 *Song analysis*

129           We obtained recordings of singing male warblers from public repositories and personal  
130 collections (see Supplemental File S2 for recording information). We only tested male song  
131 because female song occurs in only a small subset of species ( $n = 25$ ) [23]. For each species, we  
132 attempted to obtain five recordings that each contained one or more songs with high signal-to-  
133 noise ratio, no overlapping sounds, and no distortion, as determined aurally and by visual  
134 inspection of waveforms and spectrograms in Raven Pro software (v. 1.4; Cornell Lab of  
135 Ornithology, Ithaca, NY, USA). Multiple recordings of the same species were from different  
136 years or from locations at least 5 km apart to reduce the risk of including multiple recordings of  
137 the same individual, although these criteria were relaxed for rare and extinct species (e.g.  
138 *Vermivora bachmanii*). In total, we included 494 recordings from 102 species (only 10 species  
139 with fewer than 5 recordings). All recordings were converted to a standard format (WAVE  
140 format, 16-bit amplitude encoding, 44.1 kHz sampling rate) prior to analysis using Sample  
141 Manager software (version 3.1; Audiofile Engineering, St. Paul, MN, USA). Using Raven Pro,  
142 we measured duration, syllable rate, minimum frequency, maximum frequency, frequency range,  
143 and entropy (a measure of tone purity or disorder) for the highest quality song per recording after  
144 each song was filtered with a 1.1-kHz high-pass filter and normalized to a peak amplitude of -1  
145 dB (see Text S2 for full descriptions of each song variable). We then calculated the average of  
146 each song variable per species and calculated species pairwise differences for each song variable  
147 across species.

148           We used a cross-correlation approach to measure the overall song similarity of species  
149 pairs [8]. Cross-correlation values range from 0 (dissimilar songs) to 1 (identical songs), and  
150 incorporate both frequency and temporal aspects of song co-variances [8] (see Text S2 for

151 details). We used Raven Pro to calculate the song cross-correlation matrix using all individual  
152 songs, and then calculated an average value for each species dyad.

153 For our analyses testing the effect of number of sympatric species on song divergence,  
154 we created a “song space” to calculate Euclidean distances between species for their songs. We  
155 used principal components analyses on our six song variables (see Table S1 for song variable  
156 correlations), resulting in three principal components (PCs) with eigenvalues above 1.0, which  
157 we used as x, y, z axes for this song space (Table S2). Song space x (PC1) had positive loadings  
158 with minimum frequency, maximum frequency, and song entropy; song space y (PC2) had  
159 positive loadings with song bandwidth and entropy and negative loadings with minimum  
160 frequency; and song space z (PC3) had positive loadings with duration and negative loadings  
161 with syllable rate (Table S2).

162

### 163 *Sympatry quantification*

164 To quantify degree of sympatric overlap within species dyads, we obtained digital  
165 polygons of warbler breeding ranges from BirdLife International and NatureServe [26] (datum:  
166 World Geodetic System 1984). Using the R package *rgdal* [27], we projected each breeding  
167 range using the Lambert Azimuthal Equal Area projection (latitude at projection centre = 45°;  
168 longitude at projection centre = -100°; false northing = 0 m; false easting = 0 m), which converts  
169 locations on the surface of an ellipsoid into locations on a plane, without distorting the areas  
170 contained in each range. We used the R package *rgeos* [28] to calculate the degree of sympatric  
171 overlap for every species pair (hereafter “degree of sympatric overlap”). We specifically  
172 calculated the proportion of species 1’s breeding range that was overlapped by species 2’s  
173 breeding range [29,30], and separately calculated the proportion of species 2’s breeding range



174 that was overlapped by species 1's breeding range, which allowed us to account for the  
175 asymmetry in degree of sympatric overlap within a species pair. For example, the Kirtland's  
176 warbler's (*Setophaga kirtlandii*) breeding range is completely overlapped by the American  
177 redstart's breeding range, whereas less than 1% of the American redstart's breeding range is  
178 overlapped by the Kirtland's warbler's range.

179

### 180 *Statistical analyses*

181 All statistical analyses were conducted in R [21], and we occasionally used natural log or  
182 square root transformations to meet statistical assumptions. We used a time-calibrated warbler  
183 phylogeny [31] and removed species with missing data using the R package *ape* [32]. To test for  
184 the effect of phylogenetic relatedness, we calculated patristic distances for each species pair (i.e.  
185 the sum of branch lengths between each pair of species in the trimmed phylogeny; hereafter  
186 "phylogenetic distance").

187 We first tested whether colour and song divergence were greater in sympatric or  
188 allopatric species pairs. We categorized all species pairs with no sympatric overlap as allopatric  
189 and all species pairs with sympatric overlap greater than zero as sympatric. We then created  
190 linear mixed models with both sympatric categorization and phylogenetic distance as fixed  
191 effects predicting pairwise species colour or song distances, with each species in a pair as a  
192 separate random effect, using the R package *lme4* [33]. We also tested whether sympatric species  
193 pairs exhibited higher phylogenetic relatedness, with each species in a pair as a separate random  
194 effect, and found that allopatric species pairs exhibited higher phylogenetic distances ( $t = -15.59$ ,  
195  $p < 0.001$ ). This result is not solely explained by deep phylogenetic relationships or  
196 biogeographical isolation, such as the allopatry between the North American *Oreothlypis* species

197 and the South American *Myioborus* species, because an average of 65% of species pairs within  
198 genera and an average of 78% of species pairs within breeding continent were allopatric (Table  
199 S3).

200 We then removed all allopatric species pairs from the dataset and tested whether degree  
201 of sympatric overlap predicted colour and song divergence in sympatric species pairs. Using only  
202 the sympatric species pairs, we created linear mixed models with degree of sympatric overlap  
203 and phylogenetic distance as fixed effects (these variables were not correlated in this dataset:  $t =$   
204  $0.17$ ,  $p = 0.87$ ) predicting pairwise species colour or song distances, with each species in a pair  
205 as separate random effects. We accounted for a false discovery rate of these multiple  
206 comparisons [34] following the recommendations of Nakagawa [35]. Our results were robust to  
207 this issue (Tables S4-9). We also tested whether sympatric overlap predicted colour and song  
208 divergence using all species pairs, however, due to the large number of allopatric species pairs  
209 (e.g. 3043 of 4095 species pairs were allopatric in our male colour dataset), these results roughly  
210 mirrored the sympatric categorization results above (Tables S8-9).

211 We then tested whether the number of sympatric species predicts sympatric colour and  
212 song divergence through two sets of analyses. In our first analysis, we calculated the average  
213 colour or song difference between a given species and all its sympatric species; we refer to these  
214 values as “sympatric colour distance” (Figure S1a) or “sympatric song distance” (Figure S1b).  
215 For example, we identified every species that is sympatric with a particular warbler species  
216 (“species A”) and then calculated pairwise colour and song differences between “species A” and  
217 each sympatric species (body regions separately for colour; Figure S1a-b). For colour, we  
218 measured the Euclidean distances between two species in JND-colour space (Figure S1a), and  
219 for song we used the Euclidean distances between two species in the above described song space

220 (Figure S1b). However, when “species A” exhibits a 90% range overlap with “species B” and  
221 only a 10% range overlap with “species C”, we would expect “species B” to have a stronger  
222 influence on plumage divergence for “species A” compared to the influence of “species C”.  
223 Therefore, we weighted each pairwise colour or song distance by the degree of sympatric overlap  
224 between the focal species and that sympatric species (e.g. 0.9 for the “species A-B” pair and 0.1  
225 for the “species A-C” pair). We then averaged those weighted pairwise differences, such that  
226 there was a single, average sympatric colour and song distance (per body region and per sex for  
227 colour) between “species A” and all the species it is sympatric with (Figure S1a-b). We then  
228 averaged each body region such that we had one average sympatric colour distance, per sex  
229 (Figure S1a). We used phylogenetic generalized least squares (PGLS) analyses on log-  
230 transformed values to test whether the number of sympatric species predicts sympatric colour or  
231 song distance, using the R-package *caper* [36]. Finally, we re-ran these analyses without  
232 weighting each pairwise colour or song distance by the degree of sympatric overlap and obtained  
233 similar results (Table S10).

234 In our second analysis, we tested whether the number of sympatric species predicts  
235 sympatric colour and song diversity, which we measured as colour or song volume encompassed  
236 by sympatric species; we refer to these values as “sympatric colour volume” (Figure S1c) and  
237 “sympatric song volume” (Figure S1d). To calculate sympatric colour volume, we computed the  
238 smallest geometric shape (i.e. convex hull in 3 dimensions) that enclosed the colours across body  
239 regions for a particular species and its sympatric species in JND-colour space (Figure S1c), and  
240 we calculated the volume of that shape using the *convhulln* function in the R package *geometry*  
241 [37]. To calculate sympatric song volume, we computed the smallest geometric shape that  
242 enclosed the songs of a given species and its sympatric species in our song space (1 average song

243 per species), and calculated the shape's volume as we did for colour volume (Figure S1d). For  
244 song, when a given species occurred only with one or two other species in sympatry, we were  
245 unable to calculate a song volume ( $n = 5$  species), but this was not an issue for colour volume  
246 because we calculated the volume using each body region (i.e. 15 colours per species). We  
247 calculated sympatric colour and song volume for each species for which we had both song and  
248 colour data ( $n = 85$  species; sexes analyzed separately for colour). We then used PGLS analyses  
249 on log-transformed values to test how the number of species that occur in sympatry predicts  
250 sympatric colour and song volume.

251 Our results for both sympatric signal distance and sympatric signal volume were robust to  
252 pseudoreplication as shown by re-running the above analyses using a randomized resampling  
253 technique repeated 10,000 times (Text S3, Table S11). Finally, we calculated the total colour and  
254 song volume for all wood-warblers and compared those volumes to the sympatric species colour  
255 and song volumes.

256

## 257 RESULTS

### 258 *Colour and song divergence between allopatric and sympatric species pairs*

259 Contrary to our predictions, allopatric wood-warbler species pairs had higher male and  
260 female plumage colour divergence than sympatric species pairs. Allopatric species pairs  
261 exhibited more divergent male and female whole-body colouration, head colouration, and under-  
262 body colouration (Table S4). Conversely, sympatric species pairs exhibited more flight feather  
263 colouration in males only (Table S4). Male and female upper-body colour divergence and female  
264 flight feather colour divergence were not different between allopatric and sympatric species pairs  
265 (Table S4). All measures of male and female plumage colour divergence were positively related

266 to phylogenetic distance (Table S4), such that more distantly related species pairs had more  
267 divergent colouration.

268         Allopatric species also had higher male song divergence than sympatric species pairs.  
269 Specifically, allopatric species pairs had more divergent song duration and minimum song  
270 frequencies, and less correlated songs (Table S5). Sympatric species pairs had more divergent  
271 song syllable rates (Table S5). Other male song variables were not different between allopatric  
272 and sympatric species pairs (Table S5). Song duration, minimum frequency, maximum  
273 frequency, entropy, and syllable rate were positively related to phylogenetic distance (Table S5),  
274 such that more distantly related species pairs had more divergent songs. Male song bandwidth  
275 was not related to phylogenetic distance (Table S5). Finally, male song cross-correlation was  
276 negatively related to phylogenetic distance (Table S5), such that more distantly related species  
277 pairs had more different songs (i.e. less correlated songs).

278

279 *Degree of sympatry and phylogenetic distance versus colour and song divergence in sympatric*  
280 *species*

281         Across sympatric wood-warblers, both degree of sympatry and phylogenetic distance  
282 predicted male and female plumage colour divergence. Species pairs with greater sympatric  
283 overlap exhibited more divergent male and female whole-body colouration (Figure 2a,b), male  
284 head colouration, and female under-body colouration (Table S6). Colour divergence in other  
285 body regions were not related to degree of sympatry (Table S6). Additionally, all measures of  
286 male and female colour divergence, except for female head colour were positively related to  
287 phylogenetic distance (Table S6).

288         Across sympatric wood-warblers, song divergence was negatively related to degree of

289 sympatry and positively related to phylogenetic distance. Species pairs with greater sympatric  
290 overlap had males with less divergent song bandwidth and syllable rate (Table S7; Figure 2c,d).  
291 Other male song variables were not related to degree of sympatry (Table S7). Male song  
292 minimum frequency, maximum frequency, bandwidth, entropy, and syllable rate divergence  
293 were positively related to phylogenetic distance (Table S7). Male song duration was not related  
294 to phylogenetic distance (Table S7). Finally, male song cross-correlation was negatively related  
295 to phylogenetic distance (Table S7), such that more distantly related species pairs had more  
296 different songs.

297

298 *The influence of the number of sympatric species on sexual signal divergence and diversity*

299         The number of sympatric species negatively predicted sexual signal divergence in wood-  
300 warblers. Specifically, male warbler sympatric colour distance was negatively related to the  
301 number of sympatric species (PGLS:  $F_{1,83} = 31.76$ ,  $p < 0.001$ ,  $\lambda = 0.59$ ), such that as the number  
302 of sympatric species increased, the average colour divergence between those species decreased  
303 (Figure 3a). Similarly, female sympatric colour distance was negatively related to the number of  
304 sympatric species ( $F_{1,83} = 29.99$ ,  $p < 0.001$ ,  $\lambda = 0.00$ ; Figure 3b). Male sympatric song distance  
305 was negatively related to the number of sympatric species ( $F_{1,83} = 5.37$ ,  $p = 0.02$ ,  $\lambda = 0.46$ ), such  
306 that as the number of sympatric species increased, the average song divergence between those  
307 species decreased (Figure 4a), although this relationship was weaker than the plumage colour  
308 relationships.

309         Across wood-warblers, the number of sympatric species positively predicted sympatric  
310 colour volumes and song volumes. Male warbler sympatric colour volume was positively related  
311 to the number of sympatric species ( $F_{1,83} = 268.6$ ,  $p < 0.001$ ,  $\lambda = 0.38$ ); that is, as the number of

312 sympatric species increased, male colour volume of sympatric species also increased (Figure 3c).  
313 Similarly, female warbler sympatric colour volume was positively related to the number of  
314 sympatric species ( $F_{1,83} = 155.7$ ,  $p < 0.001$ ,  $\lambda = 0.69$ ). For both sexes, as sympatric colour volume  
315 approached the total wood-warbler colour volume, the relationships between the number of  
316 sympatric species and sympatric colour volume plateaued (Figure 3c,d). Male warbler sympatric  
317 song volume also had a positive relationship to the number of sympatric species ( $F_{1,78} = 226.10$ ,  
318  $p < 0.001$ ,  $\lambda = 0.56$ ); as the number of sympatric species increased, the male song volume of  
319 sympatric species increased. However, male warbler sympatric song volume did not exhibit the  
320 same logarithmic relationship as sympatric colour volume (Figure 4b).

321

## 322 DISCUSSION

323 Our findings suggest that sympatry influences signal evolution in wood-warblers. We  
324 found allopatric species have more divergent sexual signals than sympatric species. Among  
325 sympatric species, however, increased sympatric overlap predicted increased divergence in male  
326 and female plumage colouration, but decreased divergence in male song. Additionally, our data  
327 demonstrate that the number of sympatric species constrains sexual signal divergence: higher  
328 numbers of sympatric species result in reduced average signal divergence. Overall, our results  
329 provide insight into the complex relationship between sympatry and signal evolution, and  
330 uniquely demonstrate that the number of species in sympatry impacts sexual signal evolution.

331 To our knowledge, we provide the first evidence for sexual signal evolution in multiple  
332 signal modalities related to sympatry, though not always in the predicted direction nor by the  
333 predicted evolutionary mechanisms. Our finding that degree of sympatric overlap is positively  
334 related to plumage colour divergence among sympatric species expands upon the small number

335 of comparative studies supporting the hypothesis that sympatry drives increases in sexual signal  
336 divergence [8–10]. While our analyses demonstrated that other factors, such as genetic drift, may  
337 contribute to colour divergence, it is not surprising that signal evolution should be driven by  
338 multiple selection pressures [19,20]. Therefore, the reported relationships between signal  
339 divergence and sympatric overlap demonstrate how sympatry, above and beyond other selection  
340 pressures, influences signal evolution, especially since sympatric overlap and phylogenetic  
341 distance were not related among sympatric species.

342         Interestingly, our comparison of plumage divergence between sympatric and allopatric  
343 species ran contrary to our predictions and other prior work within a species and across bird  
344 families [6,9]. Across all warblers, we found that allopatric species exhibited greater plumage  
345 divergence than sympatric species in both sexes. We speculate that these results demonstrate the  
346 effect of habitat divergence on plumage colour evolution. Species that occur in allopatry likely  
347 do not share similar habitats, while those within sympatry likely do (i.e. light environment, visual  
348 background, predatory species), though future work is needed to confirm this hypothesis.  
349 Therefore, species within a similar habitat should be selected to optimize colour signal  
350 conspicuousness, colour crypsis, or both in similar ways [3].

351         Our study also presents novel evidence that the number of sympatric species constrains  
352 the extent sexual selection can drive signal divergence. In wood-warblers, as the number of  
353 sympatric species increased, sexual signal divergence between sympatric species decreased, and  
354 for plumage colouration, we found this negative relationship to be explained by constraints on  
355 avian perceptual space and wood-warbler colour diversity. The types of colour production  
356 mechanisms found in wood-warblers typically produce a specific set of colours, such as the red  
357 to yellow continuum found in carotenoid pigments [13], which is likely a primary driver of



358 limitations in wood-warbler colour diversity. However, even when considering all possible  
359 colour production types in birds, avian colour diversity only occupies a small fraction of avian  
360 colour space (i.e. 30% of the colours birds can see) [12]. Wood-warbler plumage colouration  
361 occupies only 3.7% of avian perceptual colour space, and therefore represents only 12.6% of  
362 total avian colour diversity (calculated from [12]). Thus, while degree of sympatric overlap does  
363 drive increased male sexual signal divergence in wood-warblers, the number of sympatric  
364 species dampens the effect of sympatry on colour divergence such that the effect plateaus at high  
365 numbers of sympatric species. This damping effect suggests that the influence of sympatry on  
366 sexual signal divergence estimated in our study is likely conservative. Further, variation in the  
367 number of sympatric species could mask the influence of sympatry on sexual signal divergence  
368 in other studies (e.g. [38]). Therefore, we strongly recommend that future studies account for the  
369 number of species in sympatry when testing the effect of sympatry on signal divergence.

370 Our results for male song divergence were opposite to our predictions: among sympatric  
371 species pairs, those with greater sympatric overlap had less divergent song syllable rates and  
372 bandwidth. As with plumage divergence, however, song divergence was greater in allopatric  
373 species compared to sympatric species across all warbler species pairs. While song divergence,  
374 like colour, was also influenced by other factors like genetic drift, we posit that the negative  
375 relationship between sympatry and song divergence is a consequence of the acoustic adaptation  
376 hypothesis [39]. In other words, species that exhibit higher degrees of sympatric overlap likely  
377 occur in more similar habitats, and these habitats are driving song evolution so that songs are  
378 optimally transmitted within the local environment [39], though again, future work in wood-  
379 warblers is needed to confirm this idea. While we used a similar explanation to explain our  
380 colour divergence results between allopatric and sympatric species pairs, unlike colour, song

381 divergence still exhibited a negative relationship with sympatric overlap, even among sympatric  
382 species pairs only. Therefore, we suspect that sympatry is not directly driving song evolution in  
383 wood-warblers but is indirectly related to song evolution due to shared habitats among sympatric  
384 species.

385 Further, as with our colour results, we found that the number of sympatric species is  
386 negatively related to song divergence, though the relationship was not as strong. Contrary to our  
387 colour results, however, we found no evidence that sympatric song volume approached the total  
388 song volume of wood-warblers. While some aspects of song are constrained by physiology or  
389 morphology [14,15], the temporal properties of songs add a dimension for song diversity not  
390 present in wood-warbler colour signals. Additionally, temporal song features might be less  
391 constrained than frequency characteristics, since some birds are known to take mini-breaths  
392 between syllables within a song, thereby allowing them to sing very long songs [40]. Therefore,  
393 further work is needed to understand why the number of sympatric species does still seem to  
394 limit song divergence.

395 Sexual signal diversity has long interested biologists, and speciation has often been  
396 implied as an important mechanism in this process [5]. Our results demonstrate a two-layered  
397 explanation for plumage colour evolution in wood-warblers: first, allopatric species are more  
398 divergent than sympatric species, likely due to habitat differences, and second, among sympatric  
399 species, sympatric overlap predicts plumage colour divergence. We also offer evidence that song  
400 evolution is likely driven by shared habitat occurring via sympatry. Our results also demonstrate  
401 that testing for a relationship between degree of sympatric overlap and sexual signal divergence  
402 alone does not capture the entire picture, because the number of sympatric species can  
403 significantly limit sexual signal divergence. Therefore, we strongly encourage future work

404 investigating the relationship between sympatry and signal divergence to also test the influence  
405 of the number of sympatric species, so that we can better understand how sympatry drives  
406 diversity in sexual signals.

407

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413

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418

## 419 DATA ACCESSIBILITY

420 The data used in this study is available through Dryad: Simpson, Richard et al. (2020), Sympatry  
421 drives colour and song divergence in wood-warblers (Parulidae), Dryad,  
422 Dataset, <https://doi.org/10.5061/dryad.m63xsj410>

423

## 424 AUTHOR CONTRIBUTIONS

425 Conceptualization, RKS, DRW, AFM, DJM, SMD; Methodology, RKS, DRW, AFM, DJM,  
426 SMD; Investigation, RKS, DRW, AFM; Writing – Original Draft, RKS, DRW, AFM; Writing –  
427 Review & Editing, RKS, DRW, AFM, DJM, SMD; Funding Acquisition, DJM, SMD.

428

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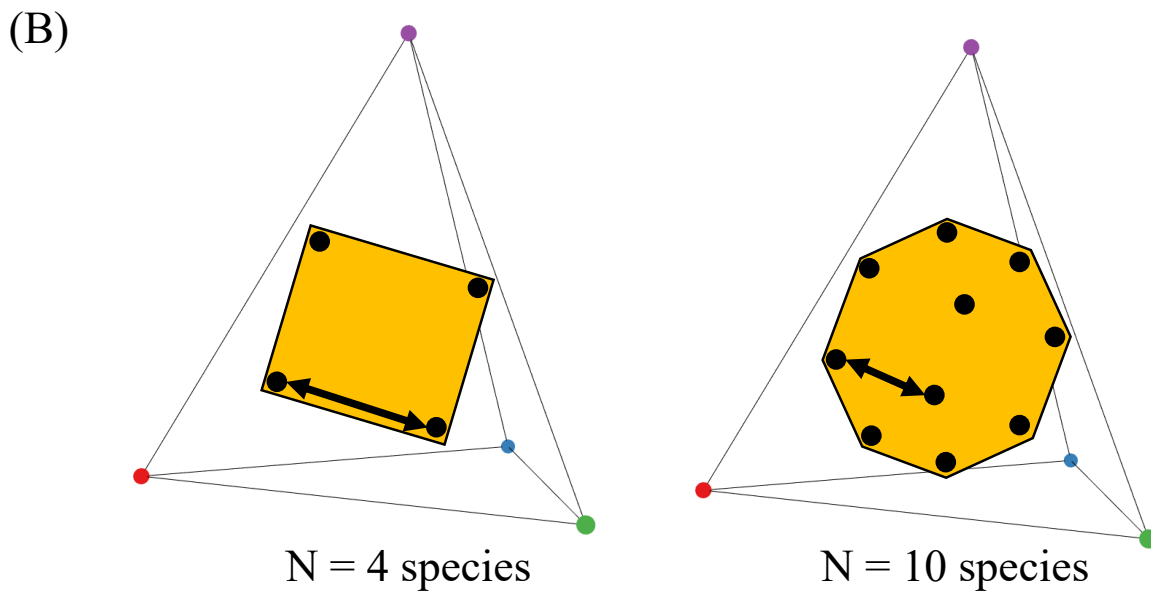
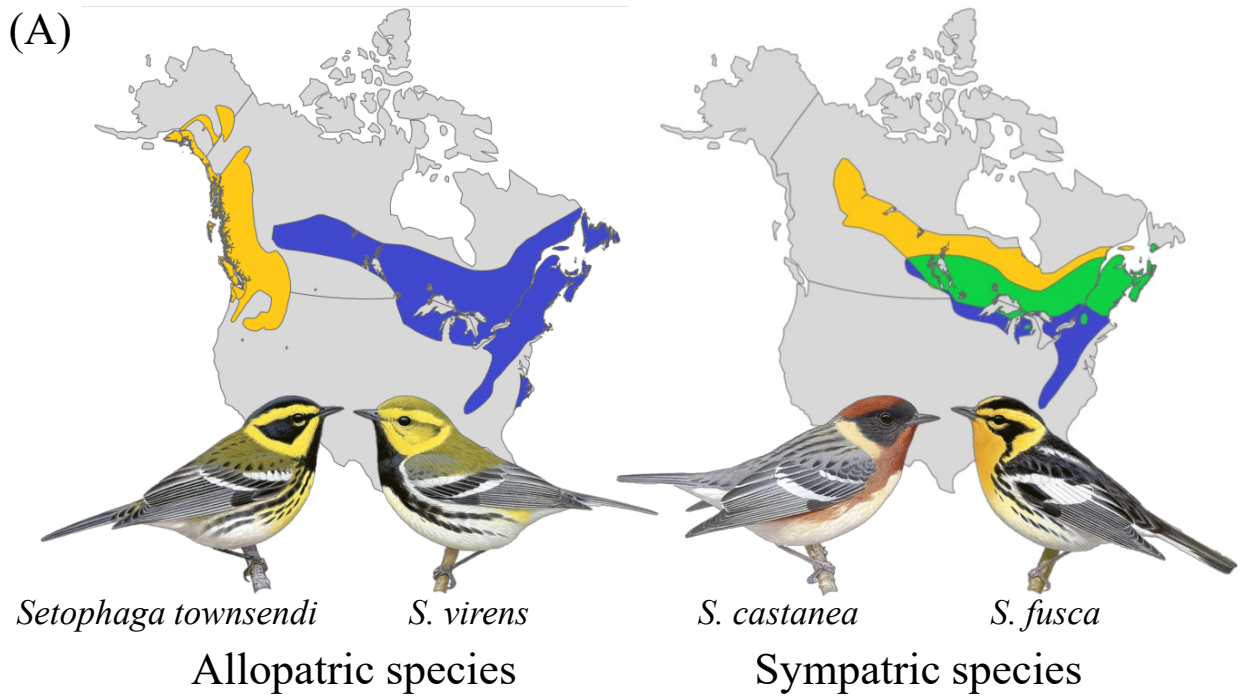
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525

## 526 FIGURE LEGENDS



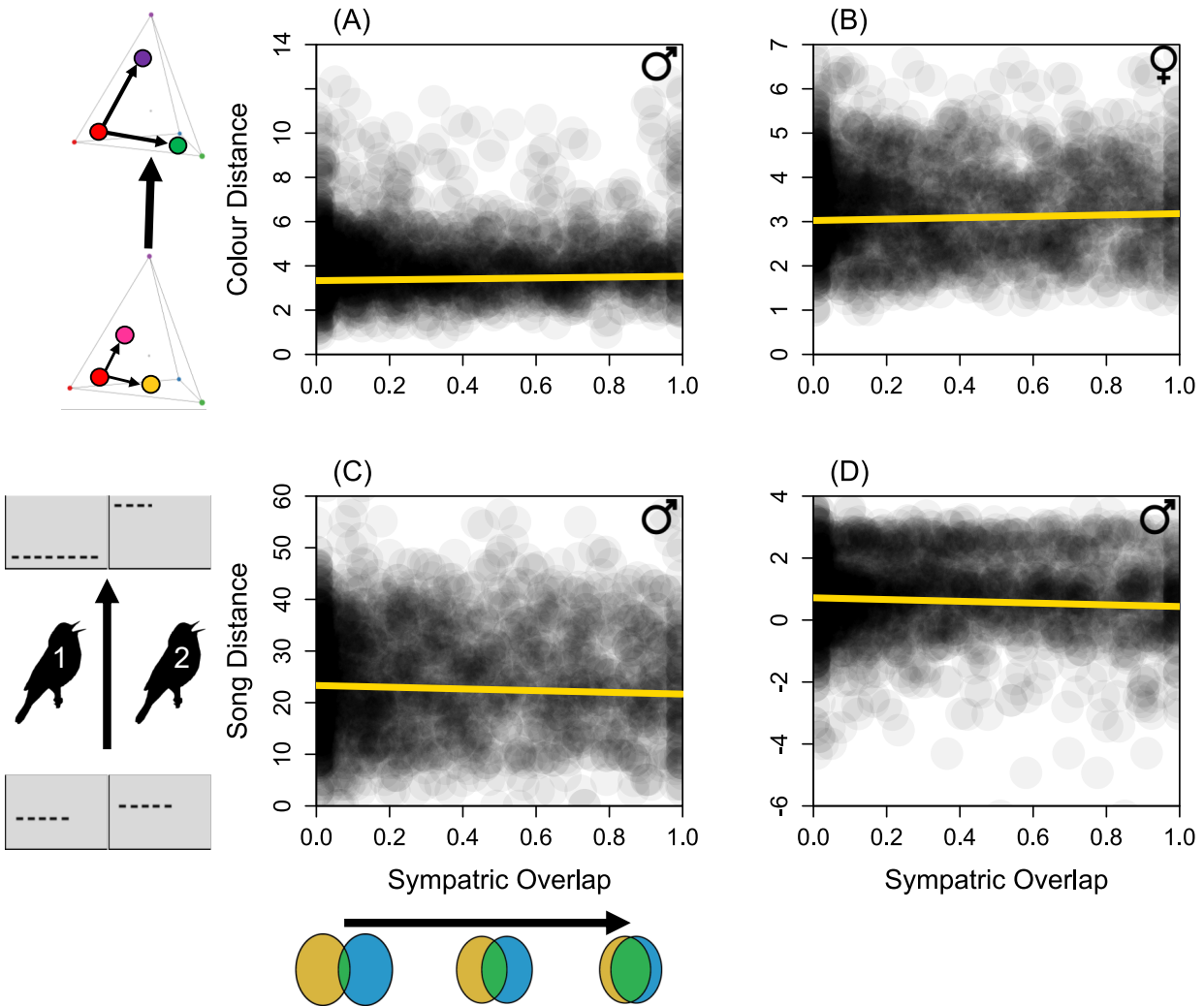
527

528 **Figure 1.** (A) Two example pairs of wood-warbler species, illustrating the effect of sympatry on529 sexual signal divergence. Male plumage colour divergence between the sympatric species (*S.*530 *castanea* in gold; *S. fusca* in blue, range overlap in green) is much greater than between the

531 allopatric species (*Setophaga townsendi* in gold; *S. virens* in blue) in this example. (B) An  
532 illustration of how we predict the number of sympatric species to influence sexual signal  
533 divergence and sexual signal diversity. The tetrahedrons represent avian tetrachromatic  
534 perceptual space. The golden polygons represent the colour volume of sympatric species (black  
535 dots) and the arrows represent the colour divergence between those species. The two polygons  
536 (2-D in the figure but 3-D in analyses) represent our prediction for when a few species occur in  
537 sympatry ( $N = 4$ ) versus several species ( $N = 10$ ) and depicts how the number of sympatric  
538 species should increase the sympatric signal volume but will also decrease sympatric signal  
539 divergence.

540

541



542

543 **Figure 2.** Degree of sympatric overlap predicts colour divergence in both male and female

544 wood-warblers and song convergence in male wood-warblers, among sympatric species pairs

545 only. As the degree of sympatric overlap between species increases, (A) male whole-body colour

546 distance increases, (B) female whole-body colour distance increases, (C) male song bandwidth

547 distance (square root transformed) decreases, and (D) male song syllable rate distance (log

548 transformed) decreases. Individual points (shaded gray circles) represent species pairs and the

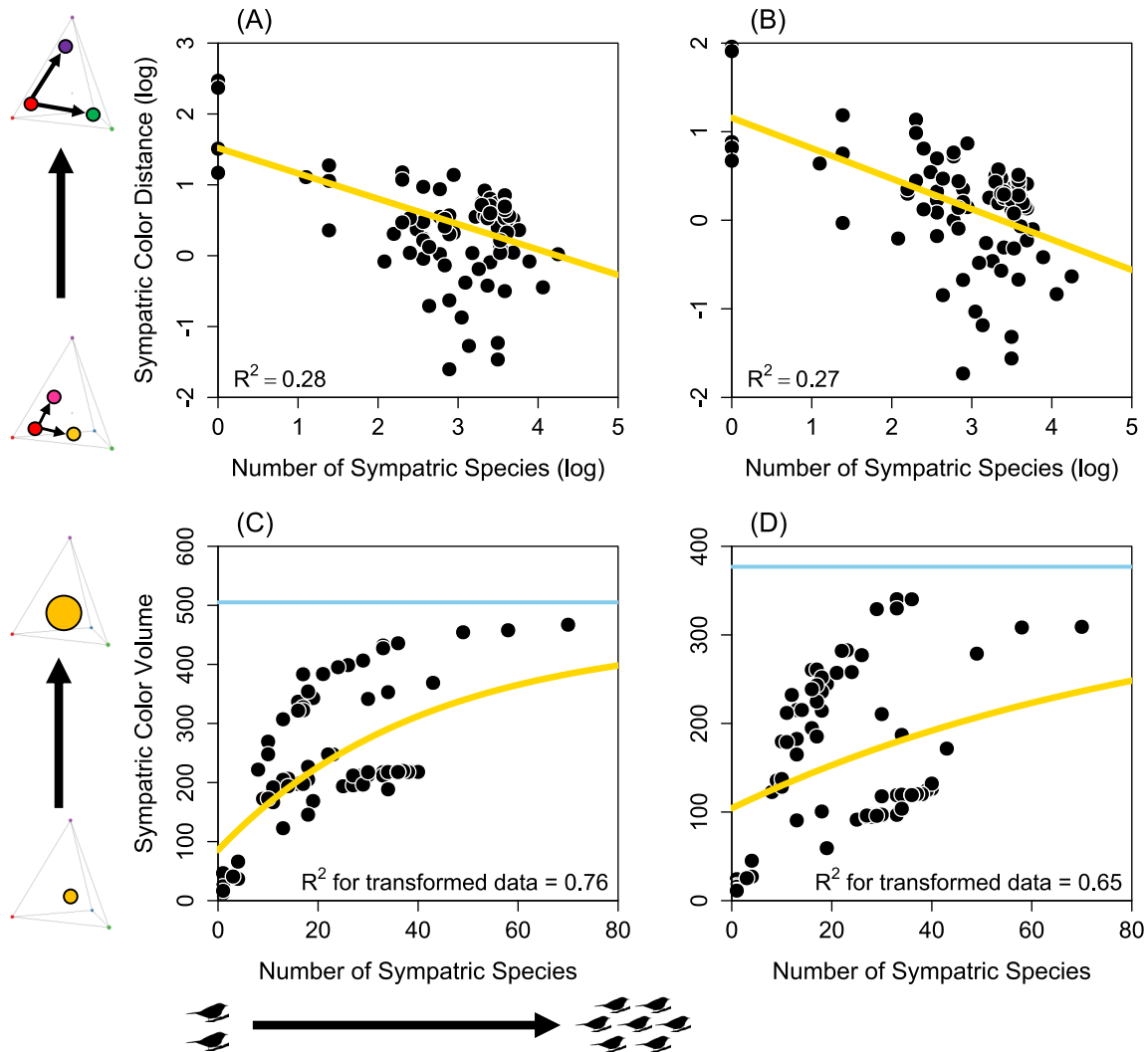
549 trendlines (gold lines) depict results from linear mixed models (Table S6-7). Increasing colour

550 distances are depicted in avian JND-colour space along the y-axis in panel A, and example song

551 differences are illustrated via pairs of sonograms that are increasingly different along the y-axis

552 in panel C. Finally, depictions of increasing sympatric overlap is under the x-axis in panel C,  
553 showing two ranges (in yellow and blue) and their overlap (in green).

554



555

556 **Figure 3.** As the number of sympatric species increases, (A) male sympatric colour divergence

557 decreases and (B) female sympatric colour divergence decreases. Additionally, (C) male

558 sympatric colour volume and (D) female sympatric colour volume are positively related to the

559 number of sympatric species. For panels A and B, gold lines represent the trendline from PGLS

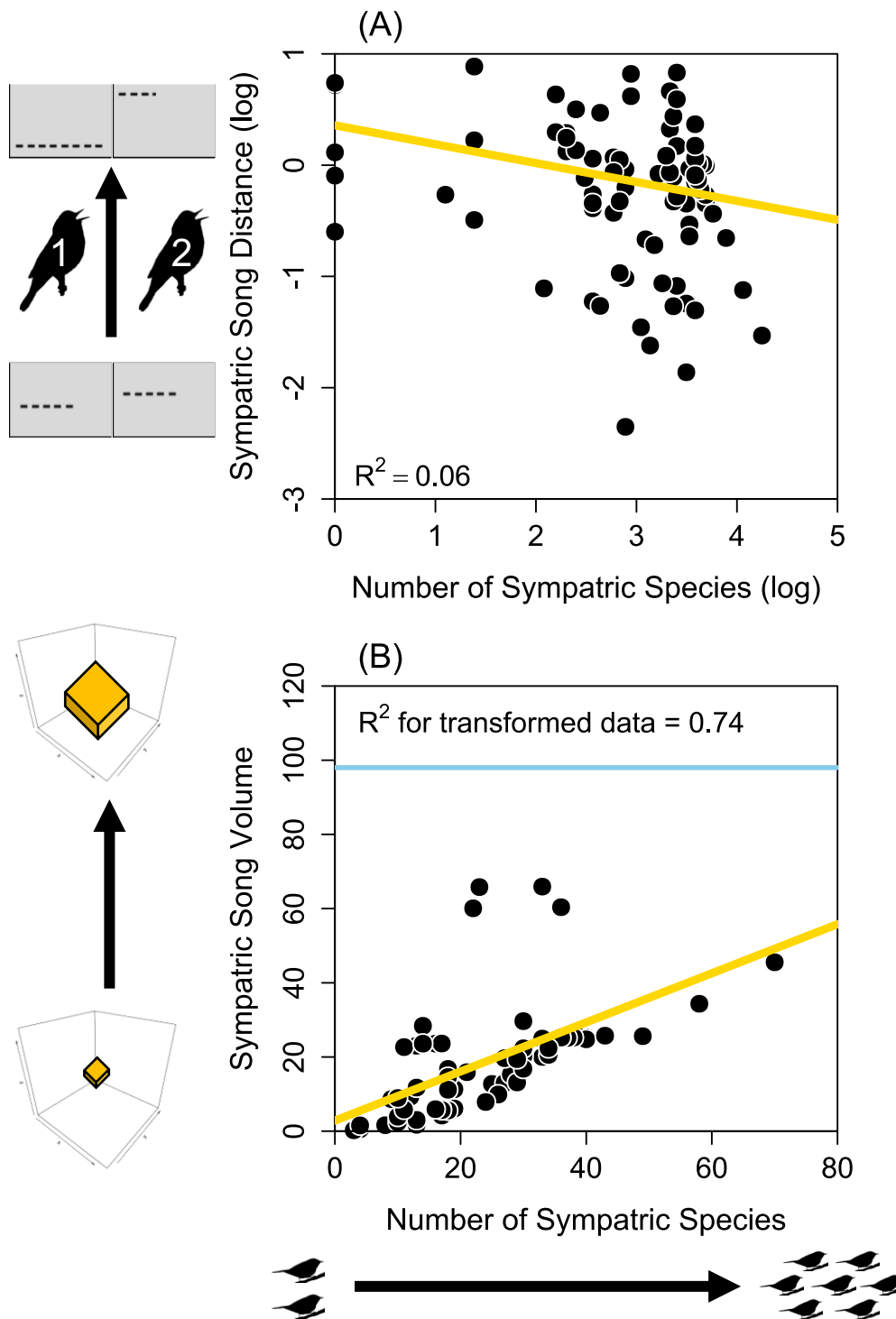
560 analyses. The relationships between (C) male and (D) female sympatric colour volume and

561 number of sympatric species (estimated by gold lines) depict the raw data to illustrate how as

562 sympatric colour volume approaches the maximum warbler colour volume per sex (blue line),

563 the relationship plateaus. The data were log transformed for PGLS analyses. Each point in panels

564 A and B represents a sympatric colour distance (Figure S1a), while each point in panels C and D  
565 represents a sympatric colour volume (Figure S1c). The same example colour distances from  
566 Figure 2a are depicted along the y-axis in panel A. Increasing colour volumes depicted along the  
567 y-axis of panel C. Number of sympatric species depicted by warbler silhouettes along x-axis of  
568 panel C.  
569



570

571 **Figure 4.** As the number of sympatric species increases, (A) male song divergence decreases.

572 Additionally, (B) sympatric song volume for males is positively related to the number of



573 sympatric species. For panel A, gold lines represent the trendline from PGLS analyses. The  
574 relationship between sympatric song volume and number of sympatric species depicts the raw  
575 data and demonstrates how the relationship (estimated by the gold line) does not change as the  
576 sympatric song volume approaches the total warbler song volume (blue line). The data were log  
577 transformed for PGLS analyses. Each point in panel A represents a sympatric song distance  
578 (Figure S1b), while each point in panel B represents a sympatric song volume (Figure S1d).  
579 Example song differences are illustrated via pairs of sonograms that are increasingly different  
580 along the y-axis in panel C. Increasing song volumes depicted along the y-axis of panel B.  
581 Number of sympatric species depicted by warbler silhouettes along x-axis of panel C.  
582

583

584 Supplemental Information for: **Sympatry drives colour and song divergence in**  
585 **wood-warblers (Parulidae)**

586

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595

596 3 supplemental texts; 11 supplemental tables; 1 supplemental figure

597

## 598 SUPPLEMENTAL TEXT

599 **Text S1: Plumage reflectance methods details**

600 We obtained specimens from the University of Michigan Museum of Zoology, the American  
601 Museum of Natural History, and the Royal Ontario Museum. We excluded specimens that were captured  
602 outside the breeding season, did not exhibit breeding plumage, or were molting. In total, we had 91  
603 species with reflectance data for at least one male and 90 species with data for at least one female. If a  
604 body region contained multiple colours, we measured the reflectance of the colour with the largest surface  
605 area. To measure plumage reflectance, we used a spectrometer (USB4000 spectrometer with PX-2 pulsed  
606 xenon lamp; Ocean Optics, Inc., Dunedin, FL, U.S.A) with the reflectance probe mounted in a matte  
607 black rubber holder that excluded all external light and maintained the probe at a fixed distance from (~5  
608 mm), and perpendicular to, the measured surface. We collected five reflectance measurements per body  
609 region and calculated an average of the five reflectance measurements per body region per individual.

610

611 **Text S2: Song variable descriptions**

612 Duration is the time between the onset and offset of the song, as measured from the waveform.  
613 Syllable rate is the number of syllables divided by duration, with a syllable defined as a continuous trace  
614 on the spectrogram. Minimum frequency is the frequency below which 5% of the signal's energy is  
615 contained, and maximum frequency is the frequency below which 95% of the signal's energy is contained,  
616 as measured from the spectrogram (512-point fast Fourier transform [FFT], Hamming window, 93%  
617 overlap, 1 ms temporal resolution, 86 Hz frequency resolution). Frequency range is the difference  
618 between minimum and maximum frequency. Entropy is a measure of the randomness of energy  
619 dispersion in the frequency domain, with pure tones having low entropy and white noise having high  
620 entropy.

621 In Raven Pro (v. 1.4; Cornell Lab of Ornithology, Ithaca, NY, USA; 512-point FFT, Hamming  
622 window, 87.5% overlap, 1.1-kHz high-pass filter), song cross-correlations are calculated based on  
623 comparing the amplitude values at each frequency-by-time bin in the spectrograms of two songs. One  
624 spectrogram is “slid” past the other in time steps equal to the temporal resolution of the spectrograms  
625 (1.45 ms). At each step, the two spectrograms are unpacked into vectors of amplitude values in the same  
626 order of frequency and time and then those vectors are correlated between the two songs. The step with  
627 the highest correlation value is selected, and represents how similar the two songs are, given the  
628 difference in time between them.

629

630 **Text S3: Testing for potential pseudoreplication issues in sympatric distance and sympatric volume**  
631 **analyses**

632 Our sympatric signal distance and sympatric signal volume analyses have possible issues with  
633 pseudoreplication. Each sympatric distance and sympatric volume data point represents an average of  
634 between 2 to 71 species. Further, some species, such as the yellow warbler (*Setophaga petechia*), overlap  
635 with many species, and their colour and song data were used to calculate sympatric distances and  
636 sympatric volumes for each of those species they overlap with. We therefore ran additional analyses that  
637 mitigate the effect of pseudoreplication. Instead of calculating sympatric signal (color and song) distance  
638 or sympatric signal volume using all sympatric species for each focal species, which ranged from 1 to 70  
639 species, we randomly selected up to five sympatric species and used only those species to calculate  
640 sympatric signal distance or sympatric signal volume, as described above. We then used PGLS analyses  
641 to test how these alternative sympatric signal distances or sympatric signal volumes were related to the  
642 number of sympatric species. This process was repeated 10,000 times. The results of these alternative  
643 analyses (Table S10) mirrored those presented in the main text. While the relationship between number of  
644 sympatric species and sympatric song distance and volume were  $p > 0.05$ , they still trended in the same  
645 direction as our original analyses. Therefore, we find that these alternative analyses revealed a negligible

646 effect of pseudoreplication on our results.

647

## 648 SUPPLEMENTAL TABLES

649

650 **Table S1.** Correlation coefficients among our six song variables.

	<b>Duration</b>	<b>Min. Frequency</b>	<b>Max. Frequency</b>	<b>Bandwidth</b>	<b>Entropy</b>
Duration					
Min. Frequency	-0.07				
Max. Frequency	-0.07	0.80			
Bandwidth	-0.01	-0.02	0.58		
Entropy	0.02	0.18	0.39	0.42	
Syllable Rate	-0.14	0.24	0.29	0.14	0.50

651

652 **Table S2.** Principal components analysis results for our song space. Only three principal components had  
 653 an eigen value greater than 1.0, and we only interpreted variables for a given principal component if they  
 654 had a loading greater than |0.4|, which are in bold.

	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>
Duration	-0.08	0.25	<b>0.75</b>
Minimum Frequency	<b>0.43</b>	<b>-0.65</b>	0.15
Maximum Frequency	<b>0.58</b>	-0.25	0.27
Bandwidth	0.38	<b>0.48</b>	0.25
Entropy	<b>0.44</b>	<b>0.45</b>	-0.13
Syllable Rate	0.38	0.16	<b>-0.51</b>
Eigen Value	2.47	1.17	1.05
Variance Explained	41.2%	19.5%	17.6%

655

656 **Table S3.** Wood-warblers have high numbers of allopatric species pairs within each multi-species genus  
 657 and within each large geographic area. These data illustrate that the result of allopatric species exhibiting  
 658 higher phylogenetic distances is not solely explained by deep phylogenetic relationships (i.e. *Myioborus*  
 659 vs. *Vermivora*) or biogeographic isolation (i.e. a North American species not overlapping with a South  
 660 American species), as there is high levels of allopatry within each genus and geographic area.

	<b>Number of species</b>	<b>Number of total species pairs</b>	<b>Number of allopatric species pairs</b>	<b>Percent of allopatric species pairs</b>
Basileuterus	8	28	16	57%
Cardellina	5	10	8	80%
Geothlypis	12	66	47	71%
Myioborus	10	45	35	76%
Myiothlypis	15	105	64	61%
Oreothlypis	8	28	20	71%
Parkesia	2	1	1	100%
Setophaga	34	561	374	67%
Vermivora	3	3	0	0%
North America	45	990	794	80%
Central America	18	153	125	79%
Caribbean	10	45	35	78%
South America	29	406	295	73%

661



662 **Table S4.** The results from our linear mixed models for how sympatric categorization (i.e. sympatry vs.  
663 allopatry) and phylogenetic distance predict male and female plumage colour distances. Each model  
664 contained the two species for a given pairwise value as separate random effects. Allopatry was the  
665 reference level for the sympatric categorization variable in all analyses. The marginal  $R^2$  value, which  
666 represents how much variation is explained by the fixed effects alone, is below each model name, while  
667 the statistics for each predictor variable are in the right-most three columns. P-values < 0.05 in bold.  
668 Asterisk indicates p-values < 0.05 when p-values were adjusted for a false discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male whole-body colour distance</b> $R_m^2 = 0.04$	<b>Intercept</b>	<b>2.94</b>	<b>23.58</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>22.09</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.14</b>	<b>-4.81</b>	<b>&lt;0.001*</b>
<b>Male head colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>5.31</b>	<b>23.83</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>8.69</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.15</b>	<b>-2.82</b>	<b>0.005*</b>
<b>Male upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.48</b>	<b>16.46</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>12.59</b>	<b>&lt;0.001*</b>
	Sympatry vs Allopatry	0.06	1.79	0.074
<b>Male under-body colour distance</b> $R_m^2 = 0.04$	<b>Intercept</b>	<b>3.33</b>	<b>18.03</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.02</b>	<b>15.89</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.49</b>	<b>-7.93</b>	<b>&lt;0.001*</b>
<b>Male flight feather colour distance</b> $R_m^2 = 0.10$	<b>Intercept</b>	<b>0.59</b>	<b>7.28</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>33.49</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>0.05</b>	<b>2.26</b>	<b>0.023*</b>
<b>Female whole-body colour distance</b> $R_m^2 = 0.05$	<b>Intercept</b>	<b>2.68</b>	<b>26.32</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>22.07</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.23</b>	<b>-9.23</b>	<b>&lt;0.001*</b>
<b>Female head colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>4.44</b>	<b>23.64</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>10.21</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.27</b>	<b>-6.32</b>	<b>&lt;0.001*</b>
<b>Female upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.37</b>	<b>21.89</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>9.46</b>	<b>&lt;0.001*</b>
	Sympatry vs Allopatry	-0.03	-1.13	0.260
<b>Female under-body colour distance</b> $R_m^2 = 0.05$	<b>Intercept</b>	<b>3.17</b>	<b>17.84</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.02</b>	<b>15.54</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.61</b>	<b>-11.05</b>	<b>&lt;0.001*</b>
<b>Female flight feather colour distance</b> $R_m^2 = 0.10$	<b>Intercept</b>	<b>0.71</b>	<b>10.56</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>30.73</b>	<b>&lt;0.001*</b>
	Sympatry vs Allopatry	0.02	1.07	0.284

670 **Table S5.** The results from our linear mixed models for how sympatric categorization (i.e. sympatry vs.  
 671 allopatry) and phylogenetic distance predict male song distances and the song cross-correlation values.  
 672 Each model contained the two species for a given pairwise value as separate random effects. Allopatry  
 673 was the reference level for the sympatric categorization variable in all analyses. The marginal  $R^2$  value,  
 674 which represents how much variation is explained by the fixed effects alone, is below each model name,  
 675 while the statistics for each predictor variable are in the right-most three columns. P-values < 0.05 in  
 676 bold. Asterisk indicates p-values < 0.05 when p-values were adjusted for a false discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male song duration distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>-0.51</b>	<b>-4.28</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.20</b>	<b>0.028*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.26</b>	<b>-10.22</b>	<b>&lt;0.001*</b>
<b>Male song minimum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>25.68</b>	<b>22.25</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>9.20</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>-0.61</b>	<b>-2.23</b>	<b>0.026*</b>
<b>Male song maximum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>30.30</b>	<b>26.36</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>7.79</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	-0.46	-1.42	0.155
<b>Male song bandwidth distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>25.04</b>	<b>24.21</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<0.01	0.88	0.380
	<b>Sympatry vs Allopatry</b>	0.21	0.98	0.326
<b>Male song entropy distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>0.70</b>	<b>15.19</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.03</b>	<b>0.042*</b>
	<b>Sympatry vs Allopatry</b>	0.01	0.72	0.473
<b>Male song syllable rate distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>0.60</b>	<b>5.67</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>3.35</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>0.06</b>	<b>2.27</b>	<b>0.023*</b>
<b>Male song cross-correlation value</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>0.28</b>	<b>35.15</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&gt;-0.01</b>	<b>-9.44</b>	<b>&lt;0.001*</b>
	<b>Sympatry vs Allopatry</b>	<b>0.01</b>	<b>4.51</b>	<b>&lt;0.001*</b>

678 **Table S6.** The results from our linear mixed models for how degree of sympatric overlap and  
 679 phylogenetic distance predict male and female plumage colour distances for sympatric species pairs only.  
 680 Each model contained the two species for a given pairwise value as separate random effects. The  
 681 marginal  $R^2$  value, which represents how much variation is explained by the fixed effects alone, is below  
 682 each model name, while the statistics for each predictor variable are in the right-most three columns. P-  
 683 values < 0.05 in bold. Asterisk indicates p-values < 0.05 when p-values were adjusted for a false  
 684 discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male whole-body colour distance</b> $R_m^2 = 0.02$	<b>Intercept</b>	<b>3.33</b>	<b>20.03</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>6.00</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>0.20</b>	<b>2.13</b>	<b>0.033*</b>
<b>Male head colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>5.23</b>	<b>17.59</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>2.91</b>	<b>0.003*</b>
	<b>Degree of sympatry</b>	<b>0.48</b>	<b>2.72</b>	<b>0.007*</b>
<b>Male upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.93</b>	<b>14.70</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>3.70</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.12	-1.05	0.294
<b>Male under-body colour distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>4.18</b>	<b>16.25</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.38</b>	<b>0.017*</b>
	Degree of sympatry	0.28	1.70	0.089
<b>Male flight feather colour distance</b> $R_m^2 = 0.06$	<b>Intercept</b>	<b>0.98</b>	<b>8.97</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>11.74</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.06	0.92	0.360
<b>Female whole-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>3.03</b>	<b>24.74</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>5.34</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>0.16</b>	<b>2.27</b>	<b>0.023*</b>
<b>Female head colour distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>4.75</b>	<b>20.84</b>	<b>&lt;0.001*</b>
	Phylogenetic distance	<0.01	1.25	0.213
	Degree of sympatry	0.11	0.85	0.393
<b>Female upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.45</b>	<b>17.40</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>3.54</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.06	0.76	0.45
<b>Female under-body colour distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>3.77</b>	<b>18.01</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.07</b>	<b>0.038</b>
	<b>Degree of sympatry</b>	<b>0.28</b>	<b>2.05</b>	<b>0.041</b>
<b>Female flight feather colour distance</b> $R_m^2 = 0.07$	<b>Intercept</b>	<b>0.97</b>	<b>10.58</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>11.75</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.11	1.91	0.06

686 **Table S7.** The results from our linear mixed models for how degree of sympatric overlap and  
 687 phylogenetic distance predict male song distances and the song cross-correlation values for sympatric  
 688 species pairs only. Each model contained the two species for a given pairwise value as separate random  
 689 effects. The marginal  $R^2$  value, which represents how much variation is explained by the fixed effects  
 690 alone, is below each model name, while the statistics for each predictor variable are in the right-most  
 691 three columns. P-values  $< 0.05$  in bold. Asterisk indicates p-values  $< 0.05$  when p-values were adjusted  
 692 for a false discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male song duration distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>-0.75</b>	<b>-5.20</b>	<b>&lt;0.001*</b>
	Phylogenetic distance	<0.01	1.33	0.183
	Degree of sympatry	-0.09	-1.14	0.255
<b>Male song minimum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>25.04</b>	<b>17.06</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>5.06</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.27	0.31	0.759
<b>Male song maximum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>30.45</b>	<b>19.91</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>3.86</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.41	-0.41	0.685
<b>Male song bandwidth distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>23.33</b>	<b>19.81</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.02</b>	<b>2.15</b>	<b>0.032*</b>
	<b>Degree of sympatry</b>	<b>-1.67</b>	<b>-2.45</b>	<b>0.014*</b>
<b>Male song entropy distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>0.55</b>	<b>9.36</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>4.57</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.01	0.21	0.831
<b>Male song syllable rate distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>0.72</b>	<b>5.17</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.34</b>	<b>0.019*</b>
	<b>Degree of sympatry</b>	<b>-0.28</b>	<b>-3.46</b>	<b>0.001*</b>
<b>Male song cross-correlation value</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>0.29</b>	<b>28.01</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&gt;-0.01</b>	<b>5.46</b>	<b>&lt;0.001*</b>
	Degree of sympatry	<0.01	0.07	0.948

693

694 **Table S8.** The results from our linear mixed models for how degree of sympatric overlap and  
 695 phylogenetic distance predict male and female plumage colour distances for all species pairs. Each model  
 696 contained the two species for a given pairwise value as separate random effects. The marginal  $R^2$  value,  
 697 which represents how much variation is explained by the fixed effects alone, is below each model name,  
 698 while the statistics for each predictor variable are in the right-most three columns. P-values < 0.05 in  
 699 bold. Asterisk indicates p-values < 0.05 when p-values were adjusted for a false discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male whole-body colour distance</b> $R_m^2 = 0.04$	<b>Intercept</b>	<b>2.88</b>	<b>23.19</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>22.82</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.08	-1.29	0.198
<b>Male head colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>5.22</b>	<b>23.57</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>9.21</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.06	0.56	0.572
<b>Male upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.51</b>	<b>16.73</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>12.44</b>	<b>&lt;0.001*</b>
	Degree of sympatry	0.02	0.27	0.791
<b>Male under-body colour distance</b> $R_m^2 = 0.04$	<b>Intercept</b>	<b>3.14</b>	<b>17.14</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.02</b>	<b>16.77</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>-0.50</b>	<b>-4.05</b>	<b>&lt;0.001*</b>
<b>Male flight feather colour distance</b> $R_m^2 = 0.10$	<b>Intercept</b>	<b>0.59</b>	<b>7.37</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>33.67</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>0.12</b>	<b>3.00</b>	<b>0.003*</b>
<b>Female whole-body colour distance</b> $R_m^2 = 0.05$	<b>Intercept</b>	<b>2.60</b>	<b>25.39</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>23.02</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>-0.25</b>	<b>-5.03</b>	<b>&lt;0.001*</b>
<b>Female head colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>4.35</b>	<b>23.16</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>10.82</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>-0.34</b>	<b>-4.03</b>	<b>&lt;0.001*</b>
<b>Female upper-body colour distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>2.35</b>	<b>21.89</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>9.65</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.02	-0.42	0.673
<b>Female under-body colour distance</b> $R_m^2 = 0.04$	<b>Intercept</b>	<b>2.96</b>	<b>16.60</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.02</b>	<b>16.67</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>-0.71</b>	<b>-6.46</b>	<b>&lt;0.001*</b>
<b>Female flight feather colour distance</b> $R_m^2 = 0.10$	<b>Intercept</b>	<b>0.70</b>	<b>10.51</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.01</b>	<b>31.02</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>0.10</b>	<b>2.62</b>	<b>0.009*</b>

701 **Table S9.** The results from our linear mixed models for how degree of sympatric overlap and  
 702 phylogenetic distance predict male song distances and the song cross-correlation values for all species  
 703 pairs. Each model contained the two species for a given pairwise value as separate random effects. The  
 704 marginal  $R^2$  value, which represents how much variation is explained by the fixed effects alone, is below  
 705 each model name, while the statistics for each predictor variable are in the right-most three columns. P-  
 706 values < 0.05 in bold. Asterisk indicates p-values < 0.05 when p-values were adjusted for a false  
 707 discovery rate.

<b>Model</b>	<b>Predictor Variable</b>	<b>Estimate</b>	<b>t-value</b>	<b>p-value</b>
<b>Male song duration distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>-0.59</b>	<b>-4.96</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>3.18</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>-0.33</b>	<b>-6.54</b>	<b>&lt;0.001*</b>
<b>Male song minimum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>25.40</b>	<b>22.12</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>9.57</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.27	-0.50	0.620
<b>Male song maximum frequency distance</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>30.12</b>	<b>26.37</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>0.05</b>	<b>8.01</b>	<b>&lt;0.001*</b>
	Degree of sympatry	-0.37	-0.58	0.565
<b>Male song bandwidth distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>25.20</b>	<b>24.46</b>	<b>&lt;0.001*</b>
	Phylogenetic distance	<0.01	0.68	0.500
	Degree of sympatry	-0.26	-0.60	0.550
<b>Male song entropy distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>0.70</b>	<b>15.34</b>	<b>&lt;0.001*</b>
	Phylogenetic distance	<0.01	1.95	0.05
	Degree of sympatry	<0.01	0.21	0.838
<b>Male song syllable rate distance</b> $R_m^2 < 0.01$	<b>Intercept</b>	<b>0.64</b>	<b>6.07</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&lt;0.01</b>	<b>2.96</b>	<b>0.003*</b>
	Degree of sympatry	-0.04	-0.68	0.50
<b>Male song cross-correlation value</b> $R_m^2 = 0.01$	<b>Intercept</b>	<b>0.28</b>	<b>35.73</b>	<b>&lt;0.001*</b>
	<b>Phylogenetic distance</b>	<b>&gt;-0.01</b>	<b>-10.00</b>	<b>&lt;0.001*</b>
	<b>Degree of sympatry</b>	<b>0.01</b>	<b>2.11</b>	<b>0.035*</b>

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709

710 **Table S10.** Results of phylogenetic generalized least squares (PGLS) models testing the relationships  
 711 between sympatric colour or song distance and number of sympatric species not weighted by degree of  
 712 sympatric overlap, as described in the Methods. The colour results mirror those in the main text. While  
 713 male sympatric song distance is not strongly related to number of sympatric species in this analysis, that  
 714 relationship using the weighted data was much weaker than the colour relationships, so these results are in  
 715 fact similar to the analyses using weighted data. P-values < 0.05 in bold.

<b>Model</b>	<b>Slope</b>	<b>Std. Err.</b>	<b>F<sub>1,83</sub></b>	<b>p-value</b>	<b>R<sup>2</sup></b>	<b>lambda</b>
<b>Male sympatric colour distance</b>	<b>-0.13</b>	<b>0.02</b>	<b>32.81</b>	<b>&lt;0.001</b>	<b>0.28</b>	<b>0.66</b>
<b>Female sympatric colour distance</b>	<b>-0.10</b>	<b>0.02</b>	<b>25.61</b>	<b>&lt;0.001</b>	<b>0.24</b>	<b>0.22</b>
Male sympatric song distance	0.05	0.04	1.74	0.191	0.02	0.61

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717 **Table S11.** The averaged results of 10,000 PGLS models comparing either sympatric signal distance or  
 718 sympatric signal volume to number of sympatric species. These analyses differ from those in the main  
 719 text in that we used only up to 5 randomly selected sympatric species for the signal distance and volume  
 720 calculations instead of all sympatric species for each focal species. P-values < 0.05 in bold.

<b>Model</b>	<b>Average <math>F_{1,83}</math></b>	<b>Average p</b>	<b>Average <math>R^2</math></b>	<b>Average lambda</b>
<b>Male sympatric colour distance</b>	<b>18.74</b>	<b>&lt;0.001</b>	<b>0.18</b>	<b>0.30</b>
<b>Female sympatric colour distance</b>	<b>17.87</b>	<b>&lt;0.001</b>	<b>0.18</b>	<b>0.07</b>
Male sympatric song distance	4.32	0.052	0.05	0.14
<b>Male sympatric colour volume</b>	<b>26.78</b>	<b>&lt;0.001</b>	<b>0.24</b>	<b>0.40</b>
<b>Female sympatric colour volume</b>	<b>9.00</b>	<b>0.008</b>	<b>0.10</b>	<b>0.60</b>
Male sympatric song volume	1.79	0.334	0.02	0.19

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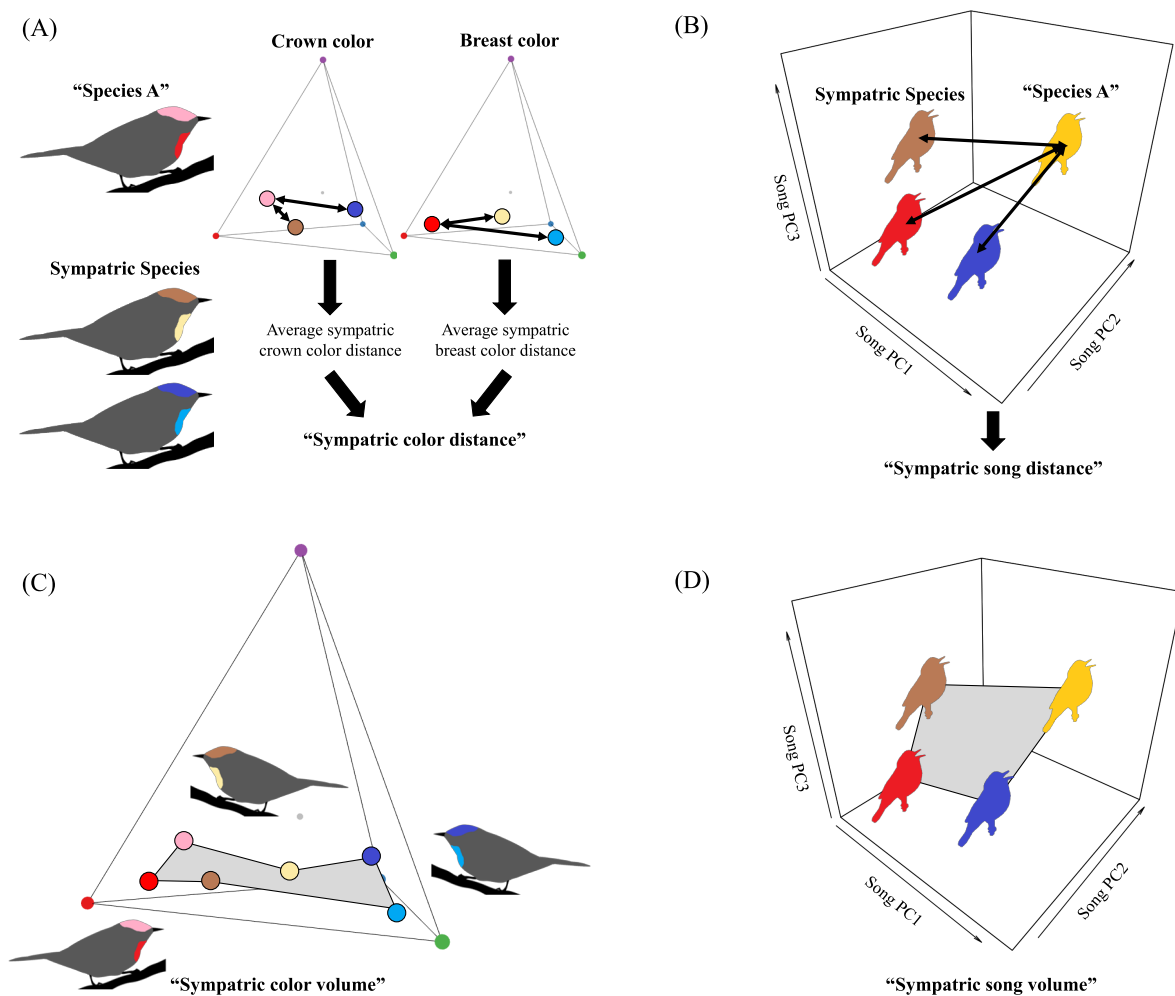
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## 723 SUPPLEMENTAL FIGURE

724 **Figure S1.** Illustrations depicting our methods for calculating sympatric colour and song distance and  
 725 sympatric colour or song volume. In each panel, the focal species is labeled “Species A” which is  
 726 sympatric with two species for our colour example and three for our song example. (A) We calculated  
 727 colour distances between “Species A” and its sympatric species for each body region (crown and breast  
 728 distances are depicted here, in avian JND-colour space). We averaged those colour distances, per body  
 729 region, and then we averaged again across body regions to create one sympatric colour distance for  
 730 “Species A”. (B) We calculated song distances between “Species A” and its sympatric species and  
 731 averaged those song distances to create one sympatric song distance for “Species A”. (C) For sympatric  
 732 colour diversity, we calculated the volume of the smallest geometric shape (shaded grey area) that  
 733 contained the colours of each body region for “Species A” and its sympatric species in avian JND-colour  
 734 space. (D) For sympatric song diversity, we calculated the volume of the smallest geometric shape  
 735 (shaded grey area) that contained the song of “Species A” and songs of its sympatric species  
 736 in our song space.

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