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1 Evolution of vocal performance and song complexity in island birds

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25

26 **Abstract**

27 Oceanic islands share distinctive characteristics thought to underlie a set of parallel
28 evolutionary trends across islands and taxonomic groups – including life history traits,
29 morphology and visual signals. To which extent acoustic signals also change in parallel on
30 islands is less clear. Some important processes associated with insularity, such as founder
31 effects and reduced sexual selection, could lead to a decrease in vocal performance and
32 song complexity on islands. In a field-based study, we recorded 11 insular species and their
33 closest mainland relatives. Out of the 11 species pairs, 6 live in the tropics (São Tomé /
34 Mount Cameroon), and 5 in the temperate region (Madeira / southern France). For each
35 species we measured two proxies of vocal performance (song duration and syllable rate)
36 and one proxy of song complexity (syllable diversity). This study did not recover a clear
37 relationship between the island environment and song traits. If as expected, syllable rate
38 was lower in island species than in their mainland counterparts, the two other proxies
39 showed no clear island-mainland pattern of divergence. Several factors may explain the
40 absence of reduction for song duration and syllable diversity. Among those, relaxation of
41 interspecific competition on islands may have led to an increase in syllable diversity, or
42 correlations between song variables may have constrained song evolution. More studies on
43 island species are needed to draw a better picture of divergence patterns and go beyond
44 the confounding ecological factors that could explain peculiar song characteristics in
45 islands.

46 **Keywords:** Acoustic communication, Insularity, Sexual selection, Sexual signals, Tropics,
47 Vocal performance

48 **Introduction**

49 The small area and isolation of oceanic islands make them amenable natural laboratories
50 for the study of ecology and evolution (Whittaker et al. 2017). They share a set of ecological
51 conditions driving convergent evolution in insular species across the world (Grant 1998), as
52 documented for a wide range of traits including life-history traits (Adler & Levins 1994;
53 Covas 2012; Novosolov et al. 2013), body size (dwarfism and gigantism of animals and
54 plants: Lomolino 2005; Clegg & Owens 2002; but see Meiri et al. 2008), brain size (Sayol et
55 al. 2018) and ecological niche expansion (Grant 1998; Blondel 2000; Scott et al. 2003; Eloy
56 de Amorim et al. 2017). Such convergences across diverse traits under insular conditions
57 are grouped under the name “insularity syndrome” and could also include convergent
58 evolution in communication signals (e.g. Figuerola & Green 2000; Baker 2006; Morinay et
59 al. 2013; Doutrelant et al. 2016; Robert et al. 2021).

60 In insular birds, the evolution of acoustic signals remains poorly understood. In
61 particular, if some trends have been found for decreased song frequencies in islands
62 compared to mainland (Robert et al. 2021), it remains poorly known if vocal performance
63 and song complexity are affected by insularity. Even if this question has been investigated
64 for a long while (e.g., Lack & Southern, 1949), previous studies comparing bird songs on
65 islands versus the mainland have not been conclusive. In 15 studies reviewed by Price
66 (2008), only 8 showed a decrease of song complexity on islands. Similarly, Morinay and
67 coworkers (2013) did not find a significant pattern of parallel complexity or vocal
68 performance reduction in a study comparing online-libraries records of songs of 49 island
69 passerines and their closest mainland relatives. However, in that study, songs were
70 recorded in different habitats and recording conditions, and such uncontrolled variation may
71 have masked insular-mainland differences. Large scale studies controlling these variations
72 are thus needed to test whether vocal performance and song complexity are different on

73 islands compared to mainland.

74 Vocal performance reflects the degree of challenge to the motor system, the
75 respiratory system, or other physiological processes involved in singing (Cardoso 2017).
76 We chose syllable rate and song duration as two proxies of vocal performance. Trade-offs
77 between song parameters (e.g., “vocal deviation”, Podos 2001) are used as proxy of song
78 performance by some authors (Cardoso 2017) but are not used here because their strength
79 is thought to differ a lot between different families (Podos et al. 2004). Syllable rate is a
80 classic indicator of vocal performance (e.g., Morinay et al. 2013, Hill & Pawley 2019, but
81 see Kroodsma 2017 and associated replies: Cardoso 2017; Cardoso & Atwell 2017, Podos
82 2017; Vehrencamp et al. 2017). In the robin, *Erithacus rubecula*, Brémond (1968) showed
83 for instance that conspecifics reacted less to song artificially modified with increased silence
84 and thus reduced syllable rate. Song duration has been less used as a proxy for vocal
85 performance, but long songs are expected to constitute a challenge for the respiratory
86 system (Suthers & Zollinger, 2008). It has been used for this purpose in a study comparing
87 online-libraries records of songs of island and mainland passerines (Morinay et al. 2013).
88 Both acoustic components are probably involved in mate choice and male-male competition
89 in many species (Catchpole & Slater 1995; Gil & Gahr 2002). In relation to performance,
90 artificially increased syllable rates are preferred by females in canaries (*Serinus canaria*, a
91 Fringillidae as the chaffinch, *Fringilla coelebs*, we study in the present paper) (Drăgănoiu et
92 al. 2002), and simulated intrusions (playback experiments) increase syllable rates in
93 chiffchaffs (*Phylloscopus collybita*) (Linhart et al. 2013).

94 Song complexity may be linked to mate quality (Nowicki et al. 1998; Nowicki and
95 Searcy 2004; Mennill et al. 2006; Byers & Kroodsma 2009). For instance, playback
96 experiments in whitethroat *Sylvia communis* (a close relative of *Sylvia atricapilla*) and
97 chaffinch, showed that conspecifics gave stronger responses to longer songs with more

98 elements (respectively : Balsby & Dabelsteen 2001, and Leitão et al. 2006). Also house
99 wren (*Troglodytes aedon*) males sing less complex songs with lower syllable rates at lower
100 latitudes (Kaluthota et al. 2016), generally associated with weaker sexual selection
101 presumably due to lower seasonality or greater food availability (Read & Weary 1992;
102 Martin et al. 2010; Weir & Wheatcroft 2011; Najar & Benedict 2019). There are several song
103 complexity metrics; here we used the within-song syllable diversity following Morinay et al.
104 (2013), who used it also in island-mainland song comparisons.

105 On islands, vocal performance and song complexity may diverge for several reasons
106 in a predictable or unpredictable way. Changes could be unpredictable due to drift (Parker
107 et al. 2012; Potvin & Clegg 2014), or follow convergent evolutionary directions (island
108 syndrome: Morinay et al. 2013) due to either founder effects, linked to the colonisation
109 process, or to adaptation to the peculiar ecological conditions of islands. In oscine
110 passerines, song has to be learned (Catchpole & Slater 1995), and founder events have
111 been shown to disturb the learning process (Lachlan et al. 2014). On islands the acoustic
112 space is less saturated due to the reduced species diversity, which is expected to reduce
113 the need for species recognition (Robert et al. 2019). Finally, competition for mating is also
114 expected to be weaker (Griffith 2000). Overall, this means that some components of the
115 vocal repertoire could be lost at the time of island colonisation because of the reduced and
116 random sampling associated with founder events, and that selective pressures on song
117 evolution (species recognition and sexual selection) could be weaker on islands. Thus,
118 vocal performance and song complexity are both expected to decrease in insular
119 populations.

120 Here, we tested these predictions by conducting controlled recordings (in similar
121 habitats, during the breeding period, with consistent recording apparatus and with
122 equivalent sampling efforts) of the songs of 11 insular species (5 from a temperate island

123 and 6 from a tropical island). We investigated how these 11 species differ from those of
124 their closest mainland relatives. Morphology imposes evolutionary constraints on song (Gil
125 & Gahr, 2002) and, as such, island-mainland differences in body mass (Lomolino 2005;
126 Clegg & Owens 2002; but see Meiri et al. 2008) could lead to peculiar song features in
127 island populations (Potvin, 2013). Thus, we also controlled for differences in body mass
128 between insular and continental species in our statistical analyses. The song of some of
129 these focal species is already known as differing in terms of frequency ranges (Robert et al.
130 2021). Yet, insular characteristics of the others features of their songs have not been
131 studied. We measured vocal performance (song duration and syllable delivery rate) and
132 song complexity (syllable diversity), and predicted lower values on islands compared to the
133 mainland, especially for vocal performance.

134

135 **Methods**

136 ***Study site and species pairs***

137 Our study was based on the comparison of vocal performance and song complexity proxies
138 of insular and continental related species pairs. We focused on two pairs of insular and
139 continental acoustic communities. The tropical pair comprised São Tomé Island, hereafter
140 referred to as ‘tropical island’, and Mount Cameroon, hereafter referred to as ‘tropical
141 mainland’. The temperate pair comprised Madeira Island, hereafter referred to as
142 ‘temperate island’, and southern France, hereafter referred to as ‘temperate mainland’. São
143 Tomé and Madeira are located 250 km and 657 km away from the mainland, respectively.
144 We worked on comparable mature or primary forests (mature laurel and evergreen oak
145 forests in the temperate zone, and primary rainforests in the tropics) with similar
146 propagation properties (Robert et al. 2019). For each community (tropical island, tropical

147 mainland, temperate island and temperate mainland), we worked on three sites (separated
148 by at least 3 km, Appendix 1 in Supporting Information).

149 On the islands we recorded the common vocalising species. We then recorded their
150 closest vocalising relative on the mainland (see Appendix 2 in Supporting Information for an
151 example of each typical song). In the tropics, AR, TL, MM & CD recorded the vocalisations
152 of the following six pairs of species: one non-oscine, the African emerald cuckoo
153 (*Chrysococcyx cupreus insularum* versus *Chrysococcyx c. cupreus*); and five oscines: a
154 pair of orioles (São Tomé oriole *Oriolus crassirostris* versus Western black-headed oriole
155 *Oriolus brachyrhynchus*), a pair of paradise-flycatchers (São Tomé paradise-flycatcher
156 *Terpsiphone atrochalybeia* versus red-bellied paradise-flycatcher *Terpsiphone rufiventer*), a
157 pair of prinias (São Tomé prinia *Prinia molleri* versus green longtail *Urolais epichlorus*), a
158 pair of speiropses (Black-capped Speirops *Zosterops lugubris* versus Mount Cameroon
159 Speirops *Zosterops melanocephalus*), and a pair of sunbirds (Newton's sunbird *Anabathmis*
160 *newtonii* versus Northern double-collared sunbird *Cinnyris reichenowi*). In the temperate
161 region, AR and CD recorded the vocalisations of five pairs of oscines species: a pair of
162 European robins (*Erithacus rubecula* in Madeira and Southern France), a pair of Eurasian
163 blackbirds (*Turdus merula cabrerae* and *Turdus m. merula*), a pair of Eurasian blackcaps
164 (*Sylvia atricapilla heineken* and *Sylvia a. atricapilla*), a pair of firecrests (Madeira firecrest
165 *Regulus madeirensis* and common firecrest *Regulus ignicapilla*), and a pair of common
166 chaffinches (*Fringilla coelebs madeirensis* and *Fringilla c. coelebs*). These pairs were
167 chosen based on molecular phylogenies or on taxonomy as a proxy for relatedness (see
168 Covas 2012; Morinay et al. 2015; Doutrelant et al. 2016). Although the sunbird pair is made
169 up of two species currently placed in two distinct genera, ongoing molecular analyses have
170 recovered them as sister species (Rauri Bowie, Martim Melo & Luis Valente, unpublished
171 data). If several continental species were good candidates (it was the case for 2 out the 11

172 pairs: the prinia species and the paradise-flycatcher species), we matched the pairs by
173 habitat (species inhabiting same habitat were selected). All 11 insular taxa have been
174 described as, at least, differentiated subspecies from mainland populations, except for the
175 robin which was formerly described as an endemic subspecies of Macaronesia (Hounscome
176 1993) but is now included in the nominate subspecies (Clements 2000; Garcia del Rey
177 2011; Billerman et al. 2020). Except for the cuckoo pair, all tropical pairs are made of well
178 differentiated species, whereas in the temperate region all pairs represent conspecific
179 populations or a very recent speciation event in the case of the firecrests (whose insular
180 population was treated as conspecific with the mainland species until recently, Päckert et
181 al. 2001). Hence tropical pairs represent older divergence events (although still considered
182 recent as they occurred in the Plio-Pleistocene border, c. 2-3 mya: Melo 2007) than those
183 of the temperate pairs.

184

185 ***Morphological data***

186 We obtained the body mass for each of the 22 focal taxa. We found body mass data in the
187 literature for tropical mainland and all temperate taxa (*Regulus madeirensis*: Del Hoyo et al.
188 2019; Madeiran robin and blackbird: Hounscome 1993; Madeiran chaffinch: Grant 1979;
189 Madeiran blackcap: Dietzen et al. 2008). For São Tomé island taxa, body mass data were
190 collected on the field by MM (available on SAFRING database, University of Cape Town).
191 When only ranges were reported or when masses were reported separately for males and
192 females, we assumed the midpoint median was the mean of the two values. Body mass did
193 not differ significantly between island and mainland species (pairwise comparisons using
194 Wilcoxon rank-sum test, $P > 0.35$).

195

196 ***Recordings***

197 We made recordings of each of the study species by using Fostex FR2 recorders [Fostex,
198 Tokyo] coupled with unidirectional microphones Sennheiser ME66/K6 [Sennheiser,
199 Hanover] (flat frequency response between 20Hz and 20kHz). The signal was sampled at
200 44.1 kHz with a 16 bits digitisation and files were saved in .wav format. Data were collected
201 during the breeding season in 2016 and 2017 (*temperate mainland*: Apr 2017; *temperate*
202 *island*: Mar 2017; *tropical mainland*: Nov 2016; *tropical island*: Sept 2016). Each recording
203 was selected from different locations: in each of the four communities, recordings were
204 obtained in three distinct sites; within each site recordings were obtained at least 200 m
205 apart to ensure they came from different individuals. We recorded the typical vocalisations
206 usually recognised as “song” by the ornithologist community based on our own experience
207 and on xeno-canto (<http://www.xeno-canto.org/>) and Macaulay (Cornell Lab of Ornithology,
208 <https://www.macaulaylibrary.org/>) online-libraries. We restricted the analyses to the highest
209 quality files and, on average, we measured 7.04 (± 3.02) songs per individual, 10.27 (\pm
210 2.19) individuals per species, and 72.32 (± 29.46) songs per species (1591 songs analysed
211 in total; sample sizes are presented in Appendix 3 in Supporting Information). These
212 recordings were obtained at less than 30 m (mostly between 5 and 20 m) from the focal
213 bird.

214 Using Avisoft software [Avisoft Bioacoustics, Berlin], we computed spectrograms and
215 oscillograms with Fast Fourier transforms (FFT 1024 points; Frame 50%; Hamming
216 window; Overlap 75%). We determined song duration using cursor placement on
217 oscillograms. On oscillograms and spectrograms we visually identified the number of
218 different syllables (short repeated units as defined by Catchpole & Slater 1995) within each
219 song as a measure of syllable diversity. We divided the number of syllables per song by the
220 song duration to obtain syllable rate (Appendix 4 in Supporting Information). Duration and
221 syllable diversity were significantly and positively correlated ($r=0.45$, $P<0.001$, Appendix 5

222 in Supporting Information). Syllable rate was significantly but moderately correlated to both
223 syllable diversity ($r = 0.13$, $P < 0.001$) and duration ($r = -0.058$, $P < 0.05$).

224 To assess whether we had recorded enough individuals to characterise species song
225 characteristics in an accurate way, we computed accumulation curves of the means of song
226 duration and maximum sampled syllable rate (Appendix 6 in Supporting Information). This
227 was not done for syllable diversity, as this would require labelling all syllables from all songs
228 to see whether adding a new song would add to an existing accumulated syllable diversity,
229 which was technically unfeasible with our means.

230

231 ***Statistical analyses***

232 All three dependent variables (song duration, syllable rate and syllable diversity) were log-
233 transformed to ensure their normality (based on graphical assessment of residuals). We
234 used linear mixed-effects models (LMM) using the *R* package nlme (Bates & Pinheiro 2011)
235 to explore patterns of variation. For each of the three response variables, we ran a model
236 testing insularity (island/mainland), latitude (tropical/temperate), the interaction between
237 latitude and insularity, body mass, and altitude as fixed effects. We included bird mass
238 (from HBW, Billerman et al. 2019) as a proxy for syrinx mass, long recognized as
239 influencing the timing of sound production (e.g., Brackenbury 1978; Gaunt 1987). Syrinx
240 mass primarily determines the minimum frequency that a bird can achieve (Ryan &
241 Brenowitz 1985; Potvin 2013), but it may also affect other variables such as syllable rate as
242 a result of trade-offs between rate and frequency bandwidth (Podos 1996, 1997). We
243 included altitude because of its negative correlation with temperature and species number,
244 which has been found to influence song properties such as frequency (Morton 1975;
245 Kirschel et al. 2009). Finally, we included “species” nested in “pair” nested in “family” as a
246 random factor to account for the phylogenetic structure of the data (Griffith 2000;

247 Beauchamp 2004; Covas 2012; Morinay et al. 2013; Doutrelant et al. 2016). We weighted
248 the analyses by sample size, i.e., by the number of recordings per individual. We selected
249 the best model by minimising the Akaike Information Criterion (AIC: Akaike 1987), and
250 considered that models differing by less than 2 AIC units were equivalent.

251 We were also interested in assessing which particular species could be driving
252 potential song differences between islands and mainland. For this, we compared song
253 duration, syllable rate, and song complexity for each of the 11 island-mainland species
254 pairs, by conducting t-tests. All statistical analyses were conducted in R v.3.05.1 (R
255 Development Core Team 2017).

256 In order to investigate how phylogenetic relationships among species could influence
257 our results, we also analysed the same variables (song duration, syllable rate and syllable
258 diversity) using a Bayesian phylogenetic mixed model (BPMM) approach (Appendix 7 in
259 Supporting Information).

260

261 **Results**

262 All three song variables were affected by the interaction between latitude and insularity in
263 different ways (Table 1).

264 **Syllable rate** – As predicted, syllable rate was lower on islands (Table 1; Figure 2).
265 Syllable rate was not affected by altitude but it was significantly influenced by body mass,
266 with lighter species singing faster (Table 1). When we looked at each species
267 independently, four tropical pairs (cuckoo, oriole, speirops, and sunbird) out of six showed
268 lower syllable rates on the island, thereby driving the insularity x latitude effect (the
269 paradise-flycatcher and the prinia showing higher syllable rate on the island). Three
270 temperate pairs (robin, firecrest, and chaffinch) out of five showed lower syllable rate on the
271 island (the blackcap showing higher syllable rate and the blackbird showing no change,

272 Figure 1). Accumulation curves of the mean of maximum sampled syllable rate (Appendix 6
273 in Supporting Information) showed that a plateau was reached for 9 out of 11 pairs, except for
274 the paradise-flycatcher and the blackcap, for which increasing the sampling effort would
275 have increased their already higher syllable rate on the island, which would have been
276 conservative for our results.

277 **Song duration** – Contrary to our expectation, song duration was longer in the
278 tropical island than in the tropical mainland and it did not differ between the temperate
279 island and the mainland (latitude by insularity interaction Table 1; Figure 2). It was not
280 affected by altitude but it was significantly influenced by body mass, heavier species
281 producing longer songs (Table 1). When looking at each species independently, we found
282 that four tropical pairs (cuckoo, oriole, paradise-flycatcher, and sunbird) out of six showed
283 longer songs on the island, thereby driving the island x latitude effect (the speirops showed
284 a significantly lower song duration, and the prinia did not show any significant variation).
285 The absence of difference in song duration between island and mainland in the temperate
286 area is due to the fact that only two pairs (firecrest, chaffinch) out of five showed longer
287 songs on the island (the blackbird and the blackcap showed shorter songs and the robin did
288 not show any change, Figure 2). Accumulation curves of mean of song duration maxima
289 (Appendix 6 in Supporting Information) showed that all species were sufficiently sampled,
290 except the insular speirops and blackbird. Since both species presented shorter songs on
291 islands, increasing sampling effort could have shown no variation between island and
292 mainland, or could have reinforced the insularity effect.

293 **Syllable diversity** – As expected, syllable diversity was lower on the temperate
294 island than on the temperate mainland but, in contrast, it was higher on the tropical island
295 than on the tropical mainland. Syllable diversity was not affected by body mass but it was
296 significantly negatively correlated to altitude (Table 1). The general increase we found in the

297 tropical island was driven by three species pairs (paradise-flycatcher, prinia, and sunbird)
298 out of six (the speirops showed lower values and the cuckoo and oriole did not show any
299 variation). The lower syllable diversity found in the temperate island was driven by three
300 species pairs (blackbird, blackcap, and chaffinch) out of five (the firecrest showed a
301 significant increase and the Robin did not change, Figure 3).

302 **Effects of phylogenetic relationships** – Results of Bayesian phylogenetic mixed
303 model are presented in Appendix 7 (Supporting Information). Broadly, results of BPMM
304 were equivalent to the LMM ones in terms of fixed-effect structure of the final models. In
305 particular, BPMM found a positive effect of insularity on syllable rate which was lower on
306 islands. As in LMM, syllable rate was significantly affected by mass, lighter species
307 producing faster songs. Contrasting with LMM, altitude had a significant and positive
308 (although very weak) effect on syllable rate. Song duration was not affected by altitude but
309 it was significantly influenced by body mass, lighter species producing longer songs.
310 Results of BPMM indicated a significant effect of interaction between “insularity” and
311 “latitude” on song duration: song duration was higher in the tropical island than in the
312 tropical mainland but it did not differ between the temperate island and mainland. Overall,
313 effects of the interaction “latitude x insularity” were weaker in the BPMMs than in LMMs.
314 This indicates that phylogenetic relationships explain a part of the significant link between
315 our three variables and the interaction between “latitude x insularity”. The temperate pairs
316 represent more recent colonisation and divergence events than the tropical pairs (except for
317 the cuckoo pair) which probably enhanced the effect of latitude. As in LMM, BPMM
318 indicated that syllable diversity changed with latitude and insularity (significant latitude by
319 insularity interaction). It was lower on the temperate island than the temperate mainland but
320 it was higher on the tropical island than the tropical mainland. As in LMM, syllable diversity

321 was not affected by body mass but it was significantly positively (not negatively) correlated
322 to altitude.

323

324 **Discussion**

325 A clear relationship between the island environment and song did not emerge from this
326 study. The only supported pattern was a decrease in syllable rate both in the tropical and
327 temperate islands. However, on islands, song duration was not lower (it even increased on
328 the tropical island), and although syllable diversity was lower in the temperate island, this
329 pattern did not hold in the tropics.

330 ***Syllable rate in island species***

331 The most consistent result across latitudes was the lower syllable rates shown by insular
332 species in comparison to their mainland counterparts. As mentioned in the introduction,
333 syllable rate is probably the song feature for which sexual selection towards exaggeration
334 has been better established (Drăgănoiu et al. 2002, Catchpole & Slater 2008, Byers et al.,
335 2015, Podos & Sung, 2020).

336 Patterns of lower vocal performance on islands are thus susceptible to be driven by
337 reduced intersexual selection on islands which could be due to three factors. First, insular
338 populations are of small size and are created stochastically from small subsets (individuals
339 colonising the island) of mainland populations. As such, they have lower levels of genetic
340 diversity than mainland populations, relatedness levels being a priori higher (Frankham
341 1997). Secondly, parasite pressure is lower on islands (e.g., see Pérez-Rodríguez et al.,
342 2013 for an example in Macaronesian blackcaps *Sylvia atricapilla*, and Loiseau et al., 2017
343 for bird communities in the Gulf of Guinea). Both lower genetic diversity and reduced
344 parasite pressure should reduce the indirect benefits of mate choice (benefits of passing
345 “good genes” to offspring) on islands and thus the strength of sexual selection. For instance

346 Petrie et al. (1998) showed that when males are genetically similar, levels of extra-pair
347 paternity (EPP) – which maximize the probabilities of passing genes to the next generation
348 – are lower, and such patterns have indeed been found in island passerines (Griffith 2000),
349 further supporting reduced sexual selection in insular communities. A third process could
350 lead to less stringent mate choice on islands. Insular species have higher survival and
351 probably higher longevity than mainland species (Covas 2012; Novosolov et al. 2013). This
352 could be associated with lower divorce rate, longer pair bonds (Botero & Rubenstein 2012)
353 and, hence, lower sexual selection because of reduced variance in mating success
354 (Figueroles & Green 2000).

355 Besides reduced intersexual selection, life history trade-offs could also explain the
356 lower syllable rate in island species. Parental care and investment in offspring survival are
357 higher in island species than in their mainland relatives (Covas 2012). A trade-off between
358 sexually secondary traits (and thus mate attraction) and parental care has been shown in
359 bird coloration (Figueroles & Green 2000) and bird song (at least between male song and
360 paternal care; Smith 1995; Rytkonen et al 1997). In relation to song, these trade-offs are
361 susceptible to impact all sexually selected features such as syllable rate.

362 Evolutionary trade-offs could also occur between song features and concur to
363 explain the documented change. In particular, Podos (1996, 1997) identified a negative link
364 between frequency bandwidth and trill rate in Emberizidae. In the two species that sing trills
365 in our data set (chaffinch and sunbird), syllable rate may be equivalent to trill rate.
366 Aforementioned trade-off is, however, unlikely to explain the observed decrease, as the
367 frequency range of the chaffinch song decreases, rather than increases, on the island,
368 whereas it does not change for the sunbirds (Robert et al. 2021). Moreover, we show a
369 global decrease of syllable rate in insular species even for species pairs with the same
370 frequency bandwidths on islands.

371 Finally, beak size and shape are known to directly influence song characteristics
372 and, in particular, vocal performance. For instance, larger beaks are associated with songs
373 produced at a slower pace in Darwin finches (Podos 2001) or in Meliphagidae (Friedman et
374 al. 2019). Here, we do not have data on beak morphologies but because beak size has
375 been shown to change in insular environments (Grant 1998; Blondel 2000; Scott et al.
376 2003; Eloy de Amorim et al. 2017), it will be a factor to explore by future studies trying to
377 understand changes observed on islands. Similarly, body size measures were not taken on
378 the recorded birds, but rather from species means, which could obscure any possible
379 effects of morphology on the song parameters analysed.

380

381 ***Song duration in islands species***

382 Contrary to our expectation, relatively to the mainland, songs were longer on the tropical
383 island but were similar in length on the temperate one. As explained above, trade-offs or
384 correlations between acoustic traits may counterbalance the predicted effect of insularity on
385 song and explain why we did not find the expected results. Trade-offs between frequency
386 ranges and trill rate (Podos 1997) and between amplitude (loudness) and syllable diversity
387 (Mota & Cardoso 2009) are documented in the literature. Yet, to the best of our knowledge,
388 there is no evidence of a trade-off between frequency range or syllable rate and song
389 duration. By contrast, our data showed that song duration is partly correlated to syllable
390 diversity ($r = 0.45$, $p < 0.001$) probably simply because of structural reasons as in longer
391 songs there should be more opportunity to include more syllables. Thus, selective
392 pressures towards greater syllable diversity on tropical islands may have driven the
393 increase in song duration that we documented in some tropical island species. Six out of 11
394 species showed similar patterns of island-mainland differences in song duration and
395 syllable diversity (both variables increased on the island for three species pairs (paradise-

396 flycatcher, sunbird and firecrest), and both variables decreased on the island for three
397 species pairs (speirops, blackbird and blackcap pairs).

398 As longer continuous singing may pose ventilation challenges (Suthers & Zollinger,
399 2008), song duration likely reflects a component of vocal performance. However,
400 physiological mechanisms of song production are not fully understood and it is a less-
401 established proxy of vocal performance than syllable rate. Morinay and coworkers (2013)
402 did not find any significant pattern of song duration reduction on islands in a study
403 comparing the online-library songs of 49 island passerines and of their closest mainland
404 relatives. Our documented difference in the tropics and lack thereof in the temperate region
405 is difficult to interpret without more evidence of the communication function of song duration
406 in each of the study species, especially as negative results could be due to the inadequacy
407 of the metric chosen for the study species (Cardoso 2017). As explained in the introduction,
408 past studies in the temperate region suggested that song duration is an adequate proxy for
409 song complexity due to its role in mate choice and male-male competition. This role was
410 demonstrated for most of the temperate species we studied here, but it remains to be
411 tested in tropical species.

412 Finally, contrasted results in vocal performance proxies could also be explained by
413 cultural drift during colonization that is susceptible to draw unpredictable island-mainland
414 differences.

415

416 ***Song complexity on islands***

417 We found that island syllable diversity was, as expected, lower in the temperate area but,
418 against our expectations, it was higher in the tropical area. Apart from the structural
419 correlation with song duration we discussed above, this pattern could be due to changes in
420 several selective factors that are expected to differ across latitudes, including distinct

421 biogeographic histories of different islands and/or different degrees of relaxation of sexual
422 selection on islands. Three explanations can be proposed to explain the lower song
423 complexity on the temperate island of Madeira contrasting with the higher song complexity
424 on the tropical island of São Tomé.

425 First, the character release hypothesis predicts an increase of song complexity in
426 communities encompassing fewer species, as is the case with island communities
427 (Kroodsma 1985; Naugler & Ratcliffe 1994). This hypothesis could explain the increase in
428 syllable diversity we observed on tropical islands. Character release is expected to lead to
429 an increase in song variability at the population level because, on the one hand, males are
430 less strongly selected to accurately reproduce species-specific songs and, on the other
431 hand, reduction in interspecific competition frees up acoustic space. Thus, in the future it
432 should be interesting to study changes in repertoire with different metrics such as among-
433 song repertoire size. Some authors have also argued that character release could lead to
434 more complex songs at the individual level (Morinay et al. 2013). If this is the case, an
435 increase of syllable diversity at the individual level could still lead to increased diversity at
436 the intra-individual level, at least in oscines learning their songs from conspecifics.
437 Character release is expected to be more pronounced at low latitudes where there are
438 greater differences in species numbers between mainland and islands (Robert et al. 2021);
439 this could explain why we found a higher syllable diversity on the tropical island compared
440 to the tropical mainland.

441 Secondly, two distinct consequences of founder events also predict reduced song
442 complexity in oscines, for which song is a learned behaviour (in our study, 10/11 species
443 pairs are oscines). Reduced complexity could be the consequence of (i) an interruption of
444 the learning period (Thielcke 1973; Baker 2006), which may occur when islands are
445 colonized by young birds that have not yet fully learned their song. In this case, individuals

446 perform songs that are similar to those of birds raised in laboratories in absence of singing
447 relatives. (ii) Cultural drift may occur because oceanic islands are colonised by small
448 numbers of individuals encompassing a small part of the song diversity of the continental
449 population (Parker et al. 2012; Potvin & Clegg 2014). In both cases, a reduced of
450 complexity is expected at the song level because, as previously noticed, a positive
451 correlation is expected in oscines between inter-individual level song diversity and song
452 complexity at the intra-individual level. Founder effects are expected to be stronger on more
453 remote islands (fewer colonisers), and are more strongly felt after recent colonization
454 events (Hill & Pawley 2019). In this study, the temperate island was more remote than the
455 tropical one and the temperate pairs represent more recent divergence events than the
456 tropical pairs. As such, the tropical pairs had time to rebuild any song diversity lost after
457 colonisation, in a similar process to the rapid recovery of genetic diversity after founder
458 events (Brekke et al. 2011). These two facts may explain why the reduced diversity has
459 only been found in Madeira, the temperate island. Our pattern of more recent divergence
460 events in temperate zone follows the pattern observed on the whole bird family. Sister
461 species are older in the tropics than in temperate region (Schluter & Pennel, 2017),
462 although rates of divergence in mating traits (e.g. body size, coloration and song) are often
463 slower in the tropics (Weir & Wheatcroft, 2011).

464 Finally, complex songs are expected to be a product of mate choice (Catchpole and
465 Slater 1995) and, as previously mentioned, intersexual selection is probably lower on
466 islands. A decrease of within-song complexity has been shown in some insular species
467 (e.g., common chaffinch, Baker & Jenkins 1987, reviewed in Price, 2008). Intersexual
468 selection is greater at high latitudes where the short breeding seasons increase the
469 importance of male song in mate attraction, whereas a burst of food availability decreases
470 the cost of singing (Irwin 2000). It has been shown that this leads to higher divergence rates

471 in song complexity at higher latitudes (Read & Weary 1992; Martin et al. 2010; Weir &
472 Wheatcroft 2011; Najar & Benedict 2019). Moreover some of the peculiar ecological
473 conditions of islands (such as lower seasonality or higher food availabilities) are more
474 marked at high latitudes, i.e., on temperate islands (Whittaker & Fernandez-Palacios 2007;
475 Covas 2012). Thus, if syllable diversity is affected by sexual selection, then decreased
476 syllable diversity is expected to be more pronounced on temperate islands than on tropical
477 ones. In our study, this latitude effect may be enhanced by the fact that Madeira is 10° to
478 the south of France while São Tomé is only 4° to the south of Cameroon. Reduction in
479 syllable diversity in the temperate island is well illustrated by the loss of the terminal
480 'flourish' syllable of the Common Chaffinch (see Appendix 2 in Supporting Information for a
481 spectrogram of typical song), which has both intersexual (Riebel & Slater 1998) and
482 intrasexual Leitão & Riebel (2003) functions.

483

484 **Conclusion**

485 Overall, this study confirms some of the predictions on the direction of song evolution on
486 islands but, more importantly, highlights how this process may be affected by several
487 mechanisms that can prevent convergent evolution of song traits on islands. To better
488 understand patterns of changes on islands for song performance and complexity, a larger
489 comparative study is needed. Field data are long to collect but are crucial to control both for
490 latitude and for time since island colonisation. Our study supported previous suggestions
491 that some aspects of the 'island effect' may be stronger on temperate regions. As with
492 genetic variation, studies on the evolution of song complexity on islands will need to
493 distinguish between short-term responses to founder events and long-term adaptations to
494 the island environment. In this respect, studies should sample species pairs across
495 latitudes and spanning a wide time range, from early colonisers to well-differentiated

496 endemic species. Also, it would be important to have more information about mechanisms
497 of vocal production in order to better understand trade-offs or structural correlations that
498 could involve proxies of song performance or song complexity. Overall, our study provides
499 additional elements to the debate regarding the predictability of evolutionary trends on
500 oceanic islands and the possibility of convergent evolution of acoustic signals within the
501 'insularity syndrome'.

502

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511

512

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748 **Table 1:** Variation of metrics of song performance and complexity proxies in island and mainland birds.
 749 Results of the best linear-mixed models for the two vocal performance variables: song duration, and syllable
 750 rate and one measure of song complexity – syllable diversity. Variables were considered on a logarithmic
 751 scale. Variables with a significant effect in bold.

Song Metrics	Independent variables	T	Df	Estimate	P-value
Syllable rate (logged)	Intercept	8.76		1.61	
	Altitude	-	-	-	-
	Mass	-3.42	1571	-0.29	<0.001
	Insularity (Island)	-4.85	1571	-0.10	<0.001
	Latitude (Tropics)	-0.64	8	-0.16	0.54
	Insularity*latitude (Island*tropics)	-1.58	1571	-0.05	0.11
Song duration (logged)	Intercept	1.99	-	0.86	-
	Altitude	-1.72	1570	-0.06	0.09
	Mass	2.94	1570	0.50	<0.01
	Insularity (Island)	0.88	1570	0.04	0.38
	Latitude (Tropics)	-0.58	8	-0.33	0.58
	Insularity*latitude (Island*tropics)	3.91	1570	0.26	<0.001
Syllable diversity (logged)	Intercept	4.43	-	1.74	-
	Altitude	-4.89	1571	-0.14	<0.001
	Mass	-	-	-	-
	Insularity (Island)	-4.37	1571	-0.12	<0.001
	Latitude (Tropics)	-0.88	8	-0.44	0.41
	Insularity*latitude (Island*tropics)	7.12	1571	0.40	<0.001

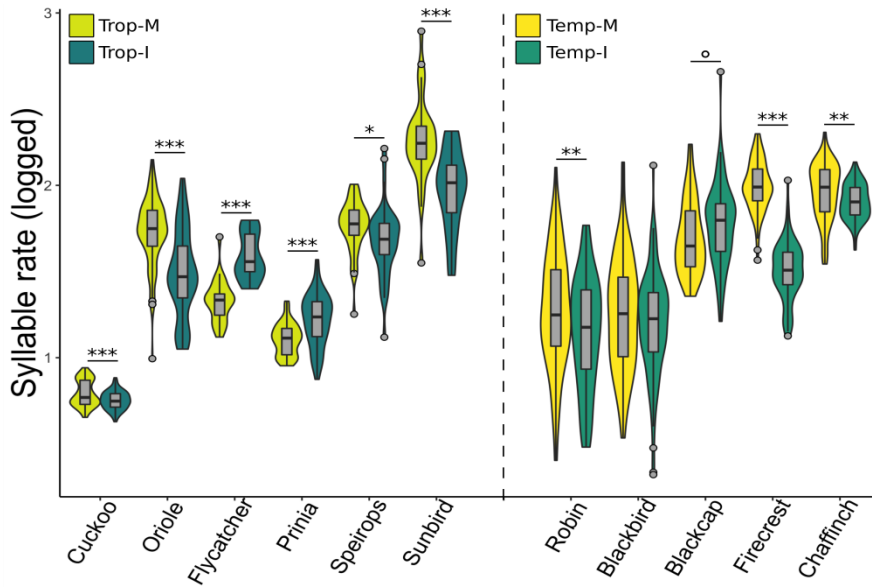
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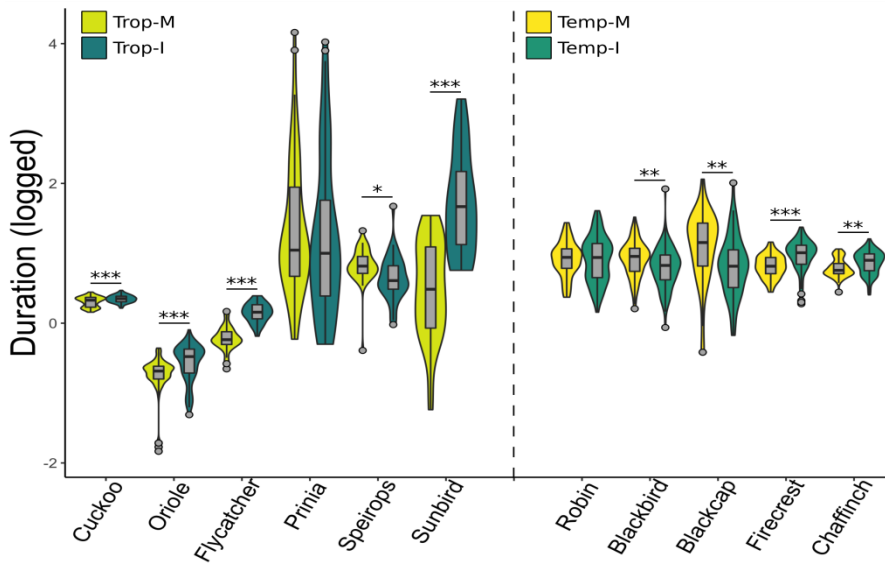


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760 **Figure 1:** Syllable rate (log) for 11 focal bird species, from tropical (Trop, left) and temperate (Temp, right) zones and
761 respective mainland (M) and islands (I). Symbols associated with p-values for paired t-tests: no symbol: non-significant,
762 °<0.1 , * < 0.05, ** < 0.01 ***<0.001. Shape of the violin plot show the probability density of the data at different values
763 and boxplot indicate quartiles of the distribution.

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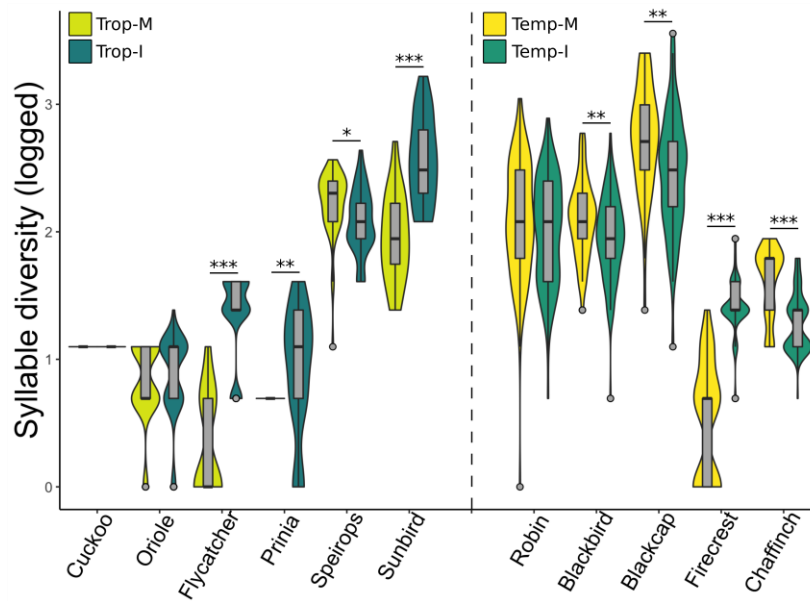
768 **Figure 2:** Duration (log) of the song of 11 focal bird species, from the tropical (Trop, left) and temperate (Temp, right)

769 zones and respective mainland (M) and islands (I) Symbols associated with p-values for paired t-tests: no symbol: non-

770 significant, ° <0.1 , * < 0.05 , ** < 0.01 *** <0.001 . Shape of the violin plot show the probability density of the data at

771 different values and boxplot indicate quartiles of the distribution.

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775 **Figure 3:** Syllable diversity (log) of the song of 11 focal bird species, from the tropical (Trop, left) and the temperate
 776 (Temp, right) zone and respective mainland (M) and islands (I). Symbols associated with p-values for paired t-tests: no
 777 symbol: non-significant, ° <0.1 , * < 0.05 , ** < 0.01 *** <0.001 . Shape of the violin plot show the probability density of
 778 the data at different values and boxplot indicate quartiles of the distribution.