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Title: Patterns of bird song evolution on islands support the character release hypothesis in tropical but not in temperate latitudes

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Abstract

The character release hypothesis—which predicts that a decline in interspecific competition leads to the expansion of trait expression—remains to be tested for communication signals. Taking advantage of the fact that oceanic islands host fewer species than the mainland, we tested whether island birds show an increase in frequency bandwidth of acoustic signals compared with mainland birds. Given the higher animal diversity and more saturated acoustic space in the tropics, we expected acoustic character release, if any, to be stronger in the tropics than in the temperate zone. We field recorded 22 bird species (11 pairs consisting of an endemic island species and its closest mainland relative) breeding at similar latitudes and in similar habitats: six tropical pairs (São Tomé Island/Mount Cameroon) and five temperate pairs (Madeira Island/southern France). For each species, we measured the degree of acoustic interference experienced when vocalizing and the spectral characteristics of its song (minimum and maximum frequencies, bandwidth). As expected, island species spent more time vocalizing alone, and any overlap in vocalizations involved fewer species. The vocalizations of island species spanned broader frequency bandwidths than their mainland counterparts in the tropics (true for all six pairs), but this pattern was less evident in the temperate region (2/5 pairs with no marked differences and 1/5 with opposite pattern). Overall, the character release of communication signals only occurred where the differential in number of species was large (tropics). We discuss latitude differences and the potential factors driving the observed differences.

1 INTRODUCTION

Ecological opportunity, defined as the availability of ecologically accessible resources that may be exploited (Stroud and Losos, [2016](#)), is a crucial driver of trait diversification and radiation (Schluter, [2000](#)). It can arise when a species loses one or more close competitors, which allows it to expand its niche into areas previously occupied by the competitor(s), in a process labelled as *character release* (Grant, [1972](#); Herrmann et al., [2020](#)). Oceanic islands, characterized by species-poor communities with low levels of interspecific competition (Whittaker et al., [2007](#)), offer an ideal setting for the study of character release. Character release has been well documented on islands in relation to diet, with island species being on average more generalist than their mainland counterparts (e.g. Cox & Ricklefs, [1977](#); Diamond, [1970](#); Lister, [1976](#)). Animal communication strategies, that are expected to be affected by the level of species interference, could also show signs of character release (Naugler & Ratcliffe, [1994](#)). In particular, species interference is expected to affect acoustic signals that transmit over long distances and, thus, can easily mask each other (Wilkins et al., [2013](#)). Hence, acoustic signals are good candidates for character release (Wollerman & Wiley, [2002](#)).

Acoustic signalling is a widespread type of communication for many organisms including insects, frogs, mammals and birds (Catchpole & Slater, [2008](#); Bradbury & Verhencamp, [2011](#)). Specific acoustic signals may facilitate species recognition, avoid costly interbreeding (Kirschel et al., [2009](#); Pfennig & Pfennig, [2009](#); Seddon, [2005](#)) and decrease aggressiveness

(Doutrelant et al., [2000](#); Seehausen & Schluter, [2004](#)). Acoustic signals have two physical dimensions: one corresponding to the energy distribution in the temporal domain (how the signal changes over time) and the other to the frequency domain (how much of the signal lies within each given frequency band over a range of frequencies). The frequency domain is likely an appropriate target for character release when competition is reduced. In particular, the frequency bandwidth (the difference between maximal and minimal frequency) is expected to be related to the diversity of singing species in a given community (Wilkins et al., [2013](#)). Indeed, increasing competition for acoustic space is expected to lead to increased partitioning of its use (Robert et al., [2019](#); Slabbekoorn & Planqué, [2008](#); Weir et al., [2012](#)) and, symmetrically through the principle of character release, a decrease in interspecific acoustic competition is expected to allow each species to expand its bandwidth into spectral areas previously occupied by others (Weir et al., [2012](#)). Yet, few studies have been conducted because opportunities to test this hypothesis are scarce.

Oceanic islands provide an ideal setting to determine to which extent character release affects acoustic signals. Small isolated oceanic islands present simplified biotas regarding the mainland, with less species and lower competition (Whittaker et al., [2017](#)). The reduced species richness on islands translates in fewer vocalizing species, resulting in less saturated soundscapes (Robert et al., [2019](#)). Hence, acoustic interference is also expected to decrease on islands. Acoustic interference mask signal frequencies, reducing signal perception and discrimination (Lohr et al., [2003](#)). Even if species are able to improve their capacity to extract important information in noisy environments (Aubin & Jouventin, [1998](#); Lengagne et al., [1999](#); Benney & Braaten, [2000](#)), their signals are also expected to minimize interference and rapidly change when constraints are increased or relaxed (Derryberry et al., [2020](#); Luther & Gentry, [2013](#)). Although some song traits, such as syllable diversity, are probably unaffected by the selective pressure to avoid interference, it has been shown that song frequency range was inversely related to the complexity of the acoustic environment (Grant & Grant, [2010](#); Naugler & Ratcliffe, [1994](#); Weir et al., [2012](#)).

To date, the large majority of work comparing bird song on islands *versus* mainland has focused on the temporal domain, that is syntax or note composition (reviewed in Lachlan et al., [2013](#); Parker et al., [2012](#); Potvin & Clegg, [2014](#); Price, [2008](#)). For frequency bandwidth, one study testing the character release hypothesis found that species with fewer same-family sympatric species used wider frequency bandwidths and detected a non-significant trend of insularity on this trait (Morinay et al., [2013](#)). One possible reason for this non-significant result is that the authors used songs from public libraries that were recorded in different habitats and conditions and with different material. This uncontrolled variation in song recordings may have masked island–mainland differences. Only a carefully designed field-based study can control these variations and thus test whether frequency bandwidth is different on islands compared to the mainland.

To determine whether changes occur in the frequency bandwidth of island birds, we conducted controlled recordings in the field (in similar habitats and using the same recording equipment) of bird species vocalizing on two oceanic islands and their closest relatives on the mainland. We obtained sound recordings for 11 pairs of bird species belonging to four communities situated in a tropical zone—rainforests of São Tomé Island and Mount Cameroon—and in a temperate zone—laurel forests of Madeira Island and evergreen oak forests of Southern France. These four communities have been previously studied, and sound propagation experiments showed similar environmental filtering for each island/mainland habitat pair (Robert et al., [2019](#)). The four communities presented a gradient of acoustic

constraints linked to the diversity of bird and insect species, with both mainland communities containing more vocalizing species than island communities (Robert et al., [2019](#)). On Madeira Island, 13 species breed in the habitat we sampled (Romano et al., [2010](#)), whereas c. 50 species breed in the temperate mainland habitat (Dubois et al., [2008](#)). On São Tomé Island, 25 land bird species are forest breeding residents (Jones & Tye, [2006](#)) in contrast to the c. 350 species breeding on Mount Cameroon (Njabo, [2015](#)). A previous study comparing island and mainland soundscapes showed that higher species richness of the mainland communities translated in a more saturated acoustic space, especially in the species-rich tropics (Robert et al., [2019](#)).

First, to evaluate the level of acoustic interference that each focal species has to cope with, and thus the potential role for interspecific interactions in the observed frequency bandwidth on islands, we compared the proportion of time each focal species vocalized alone (without temporal overlap) and the number of species co-vocalizing with each song of the focal species in relation to latitude and insularity. We expected the proportion of time each focal species vocalized alone to be lower on the mainland than on the islands and, hence, a higher degree of acoustic interference among species in the mainland communities. Secondly, we tested whether species living in habitats with less acoustic interference (islands) exhibited vocalizations with broader frequency bandwidths than their mainland counterparts. Such a difference would support the hypothesis of character release for island birds compared with the mainland community from which they originated. Because acoustic interference among species is potentially higher in the species-rich tropics, we further expected character release to be more prevalent on the tropics than on the temperate island, as the difference in species richness between islands and mainland is smaller in the latter. Thirdly, we determined whether differences in frequency bandwidths were triggered by a change in lower and/or higher frequencies of bird vocalizations. Inside the frequency range limited by hearing capacity (Dooling, [1982](#); Okanoya & Dooling, [1988](#)), the upper limit of the frequency bandwidth of bird vocalization is mostly determined by extrinsic factors, such as insect noise (Kirschel et al., [2009](#)) and environmental filtering (Marten & Marler, [1977](#)), whereas the lower limit of vocalization frequencies is mostly constrained by intrinsic factors linked to the vocal cord length (Ryan & Brenowitz, [1985](#)). Hence, we predicted that differences between mainland and island birds should occur more in high than low frequencies, when controlling for body size (as a proxy of vocal cord length).

2 MATERIAL AND METHODS

2.1 Species pairs and study area

We worked on two pairs of island and mainland acoustic communities. The tropical pair comprised São Tomé Island, hereafter referred to as tropical island, and Mount Cameroon, hereafter referred to as tropical mainland. The temperate pair comprised Madeira Island, hereafter referred to as temperate island, and southern France, hereafter referred to as temperate mainland. São Tomé (859 km²) and Madeira (801 km²) are two oceanic islands that were never connected to the mainland from which they are separated by c. 250 and 657 km, respectively. We worked on comparable mature laurel and evergreen oak forests in the temperate zone, and on primary rainforests in the tropics. For each of the four communities (*tropical island*, *tropical mainland*, *temperate island* and *temperate mainland*), we worked at three sites (separated by at least 3 km, Appendix [S1](#)).

On islands, we recorded the common vocalizing species. We then recorded their closest vocalizing relatives on the mainland in order to test the hypothesis that bird song is a trait affected by character release after colonization of islands (Appendix S2). In the tropics, AR, TL, MM and CD recorded the vocalizations of six species pairs, including two non-oscines (pigeons and cuckoos) and four oscines. On the temperate mainland, AR, SJ and CD recorded the vocalizations of five pairs of oscines species. The pairs were chosen in order to maximize evolutionary relatedness (as we aimed to investigate how species songs diverge on islands relatively to the song of their mainland counterparts) based on molecular phylogenies or on current taxonomy (as in Covas, 2012; Doutrelant et al., 2016; Morinay et al., 2013). Although the sunbird pair is made up of two species currently placed in two distinct genera, ongoing molecular analyses have recovered them as sister species (Rauri Bowie, Martim Melo & Luis Valente, unpublished data). If several mainland species were good candidates (it was the case for 1 out of the 11 pairs, the flycatcher pair), we chose the one living in the same habitat. All 11 island taxa have been described as either a different species or a differentiated subspecies from mainland populations, except for the robin which was formerly described as an endemic subspecies in Macaronesia (Hounsome, 1993) but is now classified within the nominate *Erithacus r. rubecula* (Clements et al., 2019; Garcia-del-Rey, 2011; Billerman et al., 2020). Except for the cuckoo pair, all tropical pairs are made of well-differentiated species. By contrast, in the temperate region, all pairs represent conspecific populations or a very recent speciation event in the case of the firecrests (whose island population was treated as conspecific with the mainland species until recently, Päckert et al., 2001). Hence, tropical pairs are derived from older divergence events (most having occurred in the Plio-Pleistocene border, c. 2–3 mya: Melo et al., 2011) than temperate pairs.

2.2 Morphological data

We obtained the body mass for each of the 22 focal taxa. We found body mass data in the literature for tropical mainland and all temperate taxa (*Regulus madeirensis*: Billerman et al., 2020; Madeiran robin and blackbird: Hounsome, 1993; Madeiran chaffinch: Grant, 1979; Madeiran blackcap: Dietzen et al., 2008). For São Tomé island taxa, body mass data were collected on the field by MM (available on SAFRING database, University of Cape Town). When only ranges were reported or when masses were reported separately for males and females, we assumed the midpoint median was the mean of the two values. Body mass did not differ significantly between island and mainland species (pairwise comparisons using Wilcoxon rank-sum test, $p > 0.35$).

2.3 Recordings and acoustic data

Sites, recording apparatus and audio materials used here were the same as in (Robert et al., 2019). Robert et al. (2019) analysed soundscape organization at the community level, whereas here, we focus on 11 island–mainland species pairs and analyse a distinct set of acoustic variables (related to expected responses to a relaxation of acoustic interference). Acoustic data were collected during the breeding season (*temperate mainland*: April 2017; *temperate island*: March 2017; *tropical mainland*: November 2016; *tropical island*: September 2016). Dates of fieldwork differ among the four communities but are equivalent in terms of timing of the breeding season (Christy & Clarke, 1998; Jones & Tye, 2006; Garcia-del-Rey, 2011; Serle, 1981; Vokurková et al., 2018; Billerman et al., 2020). The recording apparatus consisted of four unidirectional microphones ME66/K6 [Sennheiser] (flat frequency response between 40 Hz and 20 kHz) coupled with a FR2 recorder [Fostex] and three Song Meter SM3 recorders [Wildlife Acoustics] equipped with omnidirectional microphones. The sampling

frequency was 44.1 Hz, and 16-bit recordings were saved in *wav* format on 32GB SDHC cards.

2.3.1 Omnidirectional recordings and species temporal interference

In each of the three sites of each of the four communities, we sampled dawn choruses with omnidirectional Song Meters. Dawn chorus concentrates the strongest vocal activity for most bird species (Dabelsteen & Mathevon, 2002; Henwood & Fabrick, 1979) and thus corresponds to the strongest acoustic competition period. Each morning, the three microphones were set at least 200 m apart to ensure acoustic independency (Hart et al., 2015). They were positioned on trees at 2 m height and configured to record continuously for 2 h30 (1 h before sunrise, 1 h30 after sunrise). Each studied community was recorded for 9 days, 3 days at each site. Each day, we realized three simultaneous passive recordings (with our three Song Meters), resulting in a total of 27 recordings of dawn chorus per studied community. We then analysed the eight highest-quality omnidirectional recordings (e.g. those without rain or human disturbance); if more than eight high-quality recordings were available, eight were selected at random from all high-quality recordings. These recordings represented at least six different days and each of the three distinct sites for each community.

For each recording, we analysed ten periods of 3 min each. These ten 3-min periods were taken at the beginning of each quarter of an hour for the 2 h30 period of recording. Overall, we analysed 30 min for each song meter record and 240 min for each community (we analysed eight recordings per community). Focusing on the 22 species we studied, and in order to assess temporal interference, we determined the start and end times of each identified vocalization during the 3-min periods of each recording by using cursor placement in Avisoft-SASLAB Pro software. We defined silence as any period of time without vocalization for more than 1 s. We identified each species of vocalizing bird, but we were unable to do the same for insects whose vocalizations were classified into distinct ‘types’. To assess the extent to which other vocal bird species and insects interfere temporally with the vocalization of each focal species, we measured two proxies for each of them: i) the proportion of time the species vocalized alone (without any other bird species or type of insect calls temporally overlapping) during the ten 3-min periods and ii) the number of other species co-vocalizing with each vocalization produced by the focal species during these ten 3-min periods.

2.3.2 Unidirectional recordings and frequency bandwidth

To investigate changes in vocalization frequency within species pairs, we performed unidirectional recordings of the vocalizations of the focal species in the three sites of each of the four communities described above. For the two non-oscines pairs (pigeon and cuckoo), we recorded vocalizations recognized as ‘song’ by the ornithologist community, based on our own experience, and on Xeno-canto (<http://www.xeno-canto.org>) and Macaulay (Cornell Lab of Ornithology, <http://macaulaylibrary.org>) online libraries. Observers always stood at least 200 m apart to ensure that vocalizations would be acoustically independent and would come from distinct individuals. Frequency parameters are only accurate if they are calculated from recordings obtained at short distances (high frequencies fade with distance) and against a low background noise. For this reason, even if we often recorded more than 25 individuals per species, we restricted signal analysis to the highest-quality recordings performed at a distance lower than 30 m, mostly between 5 and 20 m from the recorded bird. Overall, we analysed on average 8.75 ± 1.77 (mean \pm se) individuals per species (1352 songs and 194 individuals analysed in total, 8.82 ± 1.84 songs per individuals, and 61.5 ± 34.04 songs per species;

Appendix [S3](#) for sample sizes per species and raw data). We did not use songs from online libraries because they were obtained with a variety of recording methods and sourced from different habitats, factors that can affect song frequency (Smith et al., [2013](#)).

Using high-resolution power spectra and amplitude thresholds, we determined the minimum frequency and the maximum frequency for each song (Zollinger et al., [2012](#)) with Avisoft-SASLAB Pro software [Avisoft Bioacoustics] (Appendix [S4](#)). Amplitude thresholds were always included between 13 and 18 dB below the song peak amplitude (amplitude of the loudest frequency). We checked the correctness of measurements visually on spectrograms (Appendix [S4](#); FFT, 1024; Frame, 50%; Window, Hamming; Overlap, 50%). We then computed frequency bandwidth as the log (maximum frequency)-log (minimum frequency) for each song. Using this ratio scale is more biologically meaningful because birds, as other terrestrial vertebrates, perceive frequency on a logarithmic scale (Cardoso, [2013](#); Levitin & Rogers, [2005](#)). Comparison of frequency differences on a linear scale could bias the results by overestimating the importance of the higher-frequency relative to the lower-frequency domain (Cardoso, [2013](#)). It was not possible to analyse data blind to location (island/mainland) because, for most of the species pairs, songs differed between island species and their mainland counterparts.

We computed accumulation curves for frequency bandwidths of each studied species separately (Appendix [S5](#)). Accumulation curves allow us to see whether we had recorded enough individuals to characterize species song bandwidths in an accurate way. For all of the focal species, accumulation curves of the average frequency bandwidth against sampling effort reached a plateau indicating that sampling sizes were adequate.

2.4 Statistical analyses

2.4.1 Do species have greater temporal overlap on the mainland?

We assessed whether temporal interference differed between island and mainland by analysing two dependent variables separately: (1) the proportion of time during which a focal species vocalized alone and (2) the number of species co-vocalizing. We used a generalized linear mixed-effects model (GLMM) with R package lme4 (Bates et al., [2015](#)). For both variables, we only retained the 3-min periods during which the focal species was detected. We used a binomial error distribution (species vocalizing alone or not) and a Poisson error distribution (number of species co-vocalizing) for the dependent variables (1) and (2), respectively, and weighted analyses by the total duration each species vocalized. We tested insularity (island/mainland), latitude (tropical/temperate) and their interaction as fixed effects and conducted pairwise post hoc analysis. We also included time of the quarter as a continuous variable since the vocal activity of birds is expected to decrease as the morning progresses (Dabelsteen & Mathevon, [2002](#)). We included ‘species’ nested in ‘pair’ nested in ‘family’ as random factors to account for taxonomic structure of the data. For each dependent variable, we selected the best model by minimizing the Akaike criterion AIC (Akaike, [1987](#)), and considered that models differing by less than 2 AIC units were equivalent. *p*-values and degree of freedom were approximated with the Kenward–Roger approach in *pbkrtest* package (Halekoh & Højsgaard, [2014](#)).

2.4.2 Does song frequency bandwidth increase on islands?

We assessed how song frequencies differed between islands and the mainland by analysing three dependent variables separately: (i) frequency bandwidth, (ii) minimum frequency and (iii) maximum frequency. We compared these variables between mainland and island using linear mixed-effects models (LMM, using a Gaussian error distribution) with the lme4 R package (Bates et al., 2015). We included ‘individual’ nested in ‘species’ nested in ‘pair’ nested in ‘family’ as random factors to account for the phylogenetic structure of the data (Beauchamp, 2004; Covas, 2012; Doutrelant et al., 2016; Griffith, 2000; Morinay et al., 2013). We tested insularity (island/mainland), latitude (tropical/temperate) and their interaction as fixed effects, as these factors are both linked to the level of community complexity. We included bird mass as a proxy for vocal cord length, as this primarily determines the minimum frequency that a bird can achieve (Naugler & Ratcliffe, 1994; Potvin, 2013). Best model selection was done as described for temporal overlap. In order to test homogeneity of individual variance in frequency bandwidth between island and mainland species, we performed Bartlett tests. Details of the analyses are presented in the Appendix S6. Even if we predicted different patterns of frequencies on islands and mainland, we were also interested in assessing which species in particular could drive these trends. For this, we conducted a comparison of frequency bandwidth at species level, that is for each of the 11 mainland–island pairs of species using *t*-tests. As these repeated tests lead to multiple comparisons risk, we used Benjamini and Hochberg (1995) method of false discovery rate in order to adjust *p*-values and control the expected proportion of false discoveries among the rejected hypotheses. All statistical analyses were conducted in R v.3.05.1 (R Development Core Team 2017).

2.4.3 Do phylogenetic relationships affect the results?

In order to investigate how phylogenetic relationships among species could influence the results, we analysed the same variables (minimum frequency, maximum frequency, frequency bandwidth and number of overlapping species) using a Bayesian phylogenetic mixed model (BPMM) approach. We did not model the proportion of time each species spent vocalizing alone because binomial distributions are not supported by these analyses. Details of the analyses are presented in the Appendix S7.

3 RESULTS

3.1 Species interference

We detected 65 bird species (from 29 families) and 25 different types of insect calls in the tropical mainland, 16 bird species (from 13 families) and 11 different types of insect calls on the tropical island, 21 bird species (from 13 families) in the temperate mainland and eight bird species (from six families) on the temperate island. We detected no insect calls in the recordings of the temperate zone.

The proportion of time that a focal species vocalized alone varied in relation to insularity and latitude: tropical species vocalized less often alone than temperate species, and mainland species vocalized less often alone than island species (Table 1, Figure 1). Moreover, post hoc analyses showed that the island–mainland difference was higher in the tropical zone (difference = -0.17 ± 0.03 for the temperate zone and -1.55 ± 0.42 for the tropics, $p < 0.01$ in both cases). As expected, species that vocalized earlier in the morning were less likely to vocalize alone (Table 2).

The number of species co-vocalizing with the focal species is affected by the interaction between insularity and latitude (Table 1, Figure 2). On the mainland, species vocalizations overlapped with the vocalizations of more species than on islands (Table 1, Figure 2). The overlap included more species in the tropical than in the temperate zone (Table 1, Figure 2). Post hoc analyses showed that the island–mainland difference was greater in the temperate ($p < 0.001$ and estimate = -0.74 ± 0.02) than in the tropical zone ($p < 0.001$ and estimate = -0.47 ± 0.03). Finally, focal species overlapped with more species when vocalizing earlier (during the dawn chorus) than later in the morning (Table 1). Results of BPMM were the same (Appendix S7).

3.2 Frequencies

Our analyses of frequency bandwidth variation showed a significant interaction between insularity and latitude (Table 2). Frequency bandwidth was broader on the tropical island than on the tropical mainland, but no significant difference was found in the temperate area (Figure 3). Bird mass had no significant effect and was not retained in the best model (Table 2 and Appendix S8).

Our prediction that maximum frequencies should be higher on islands compared with the mainland held strongly for the tropics but not for the temperate zone (Table 2, Figure 3 and Appendixes S9 and S10). Finally, minimum frequencies were not significantly different on islands (Table 2, Figure 3 and Appendixes S9 and S10). As expected, mass was negatively correlated to minimum and maximum frequencies (Table 1).

Results of Bayesian phylogenetic mixed models (BPMM) corrected for phylogenetic relatedness were equivalent in terms of significance and relative strength of estimates (Appendix S7). In particular, results of BPMM indicated broader frequency bandwidths on the islands compared with the mainland, and stronger island–mainland differences in the tropics compared with the temperate zone. We found the same significant interaction between latitude and insularity in the variations of maximum frequencies. However, BPMM recovered a significant diminution of minimum frequencies in islands.

When looking at each species independently (*t*-tests, Figure 3), we found that in the tropics three of the six species pairs showed broader frequency bandwidths on the island (cuckoos: $p < 0.001$, orioles: $p < 0.001$ and flycatchers: $p < 0.001$). The three other pairs—speirops, sunbirds and pigeons—showed trends in the same direction, but the differences were not significant. In the temperate region, the effect of insularity was only present in the robins and firecrests that had a broader bandwidth on the island ($p = 0.048$ and $p < 0.001$ respectively). The chaffinches, on the contrary, had a narrower bandwidth on the island ($p < 0.001$). The blackbird and blackcap pairs showed no significant differences in bandwidth between island and mainland.

Among the pairs with broader frequency bandwidth on islands, broader bandwidth was achieved by all individuals (individuals with the lowest bandwidths on the island population had higher-frequency bandwidths than individuals with the lowest bandwidths in the mainland population; Appendix S6). This was also the case for the flycatcher, the only species that had a significantly different (greater) variance among individuals on the island than the on the mainland (Appendix S6).

4 DISCUSSION

This study showed that, on islands, birds vocalize more often alone and co-vocalize with a lower number of species than on the mainland. As such, island species face less acoustic interference from sympatric species, the necessary condition for the occurrence of character release of acoustic signals. Evidence for character release was detected, but, as predicted, it was much more prevalent on the tropical rather than the temperate island: i) the proportion of time each species vocalized alone was greater in the temperate than in the tropical region and ii) all tropical island birds tended to sing with a broader frequency bandwidth than mainland species, a result only replicated in two of the five temperate species. This broader bandwidth did not reflect higher inter-individual variance among island birds, but was achieved by all individuals in the island population. Broader frequency bandwidths were mostly the result of an increase in maximal frequencies rather than a decrease in minimal frequencies, in accordance with being a response to changes in the environmental soundscape on islands (decrease in acoustic interference).

4.1 Character release: the central role of competition

The association between lower acoustic interference and broader bandwidths of bird songs observed on islands, relatively to the mainland, suggests that the relaxation of interspecific competition may have played a role in the evolution of acoustic signals on islands, as predicted by the character release hypothesis. Community composition is considered as one of the major constraints affecting signal evolution (Wilkins et al., [2013](#)). For instance, many studies recorded frequency partitioning at the community level in insects (Shieh et al., [2015](#); Sueur, [2002](#)), fish (Ruppé et al., [2015](#)), (Duellman & Pyles, [1983](#); Sinsch et al., [2012](#)) and birds (Luther, [2009](#); Robert et al., [2019](#); but see Slabbekoorn & Planqué, [2008](#); Seddon & Tobias, [2010](#), Tobias et al., [2014](#)).

Character release could be due to a change in two non-exclusive factors. First, interspecific competition between closely related species, using the same song features and frequency windows (Kroodsma, [1977](#); Luther, [2009](#); Weir et al., [2012](#)), is likely to lead to high signal overlap and hence to an increase in communication errors. These misdirected interactions are expected to lead to reproductive or agonistic character displacement (Grant & Grant, [2010](#); Kirschel et al., [2009](#)). Secondly, frequency interference from other biotic sources can mask the signal produced and harm its integrity (Lohr et al., [2003](#)) and, under the sensory drive hypothesis (Endler, [1992](#)), changes in biotic constraints should lead to rapid changes to minimize signal degradation and maximize discrimination (Luther & Gentry, [2013](#); Tobias et al., [2010](#)). Such changes in signal design should occur when biotic constraints are either increased or relaxed.

Here, the importance of the acoustic community saturation on the change in frequency range is supported by two findings. First, the effect of insularity was much stronger in the tropics, in accordance with the much stronger decrease in species richness between island and the mainland. In our study systems, bird species diversity on the tropical island was c. 14 times lower than on the mainland, whereas in the temperate region, it was only c. four times lower. Secondly, we found that, in the tropics, the frequency bandwidth widened mostly by increasing the maximum frequency, which is more often associated with environmental constraints, including the sounds of insects. Insects are the primary source of noise in tropical rainforest (Luther & Gentry, [2013](#)). Insects have been shown to change the way green hylia (*Hylia prasina*) vocalizes in Cameroon (Kirschel et al., [2009](#)), and they are invoked as a reason why species breeding in tropical forests vocalize across narrower bandwidths than at high latitudes (Weir et al., [2012](#)). Nevertheless, this interference effect does not exclude the

effect of reduced competition among closely related species. To disentangle the role of each process, studies controlling for the sound propagation properties of the habitat, such as ours, must be extended to different communities where the number of closely related sympatric species varies. It will then be possible to assess the relative roles of acoustic competition with close relatives and ambient noise in shaping the evolution of song frequencies.

4.2 Character release: less prevalent on temperate islands

The wider frequency bandwidth of island species is observed for most of the tropical species, but only for two of the temperate species (*Erithacus rubecula* and *Regulus madeirensis*). This may be explained by the fact that temperate mainland species already (i) exhibit a very wide frequency bandwidth compared with tropical mainland species (Figure 3; Weir et al., 2012) ii) spend a larger proportion of time vocalizing alone (Figure 1) and (iii) co-vocalize with fewer species (in average only one, Figure 2). Under these conditions, the frequency bandwidth of some temperate mainland species may have already reached its maximum value and may be constrained on islands because of limiting factors such as physical features of habitat or species morphology. Additionally, a greater island–mainland distance (Madeira is located 657 km away from the mainland while São Tomé is at 250 km) is expected to increase the susceptibility of the island to founder effects and decrease the complexity of vocalizations (reviewed in Price, 2008). This may explain the narrowing of the frequency range of the song of the chaffinch from Madeira Island (*Fringilla coelebs madeirensis*), which is associated with the loss of the terminal ‘flourish’—the part of the song with the highest frequency (present in some individual songs in the mainland population, Figure S3 in Appendix 6). Alternatively, or in combination, because this flourish is the intrasexual element of the chaffinch song (Leitão & Riebel, 2003), its loss may have been caused by a release of sexual selection in the island population.

4.3 Can other factors affect song observed spectral characteristics?

Predation, sexual selection, territoriality and sociality are four factors expected to be relaxed on islands (Beauchamp, 2004; Griffith, 2000; Stamps & Buechner, 1985). Could any of these factors concur to explain the differences we observed here? Predation is known to affect call frequency bandwidth, which can be widened to facilitate heterospecific communication in mobbing for nestling predators and narrowed down to be less detectable (Dutour et al., 2017; Marler, 1955). Predation has been shown to lead to the evolution of low-amplitude songs (Searcy & Nowicki, 2006), changes in signalling locations (Møller et al., 2008) or in signalling rates (Akçay et al., 2016; Schmidt & Belinsky, 2013), but never to date to changes in song frequency bandwidth. Hence, at this stage, inferring a role of predation in the observed differences would be too speculative. A relaxation of sexual selection or territoriality is predicted to decrease song complexity (Kaluthota et al., 2016), which can lead to a reduction in frequency bandwidth—and may explain what we observed for the chaffinch pair (*Fringilla coelebs*) as discussed above. Population density is known to increase on islands (MacArthur et al., 1972), leading to increased sociality (Stamps & Buechner, 1985). Increased sociality could result in an increased need for individual recognition (Chaine et al., 2018) and thus in higher signal variability (Dale et al., 2001). This mechanism would result in increased frequency bandwidth at the island population level, but not to wider frequency bandwidths at the individual level as we also documented here.

Habitat structure is often presented as one of the most important selective forces for acoustic signal evolution. The acoustic adaptation hypothesis predicts that acoustic signals should

evolve towards minimizing the attenuation and degradation of the signal in relation to the structure of each habitat (Morton, [1975](#)). Yet, disentangling the role of environmental filtering from the role of acoustic interference can be challenging. For example, Morton ([1975](#)) compared the frequency bandwidth of 85 Neotropical bird species and found that species from lower elevations, that is living in closed habitats—but also in species-rich communities—had significantly narrower song frequency bandwidths than species from higher elevations living in open habitats—but also in species-poor communities. Hence, the observed changes in frequency bandwidth equally fitted predictions arising from differential sound transmission properties in open/close habitats and predictions made for species-poor/species-rich communities. In our study, we controlled for sound propagation properties by recording songs in habitats presenting a similar profile of sound degradation (Robert et al., [2019](#)); therefore, the changes we observe in frequency bandwidths cannot be attributed to habitat differences.

Finally, divergence in frequency bandwidth is often a by-product of morphological divergence (Krishnan & Tamma, [2016](#); Podos, [2001](#)). For instance, wider frequency bandwidths are often found at higher-pitched peak frequencies, which have been shown to be associated with lighter body mass (Ryan & Brenowitz, [1985](#)), and wide frequency ranges are more easily produced by shorter bills (Palacios & Tubaro, [2000](#); Podos et al., [2004](#)). In our models, we controlled for body size and found a significant and expected link between minimum, maximum frequencies and mass but not between bandwidth and mass. Therefore, the documented increase in frequency bandwidth on islands is unlikely driven by differences in body mass. For bill length, island birds—at least in passerines—have usually longer bills (Clegg & Owens, [2002](#); Grant, [1968](#)) and thus should have lower-pitched dominant frequencies (Palacios & Tubaro, [2000](#)), but no consequences on bandwidth are predicted.

5 CONCLUSION

Our results showed that 1) island species face more acoustic interference than their mainland closest relatives and that 2) in the tropics, island birds had a wider frequency bandwidth than their mainland closest relatives. Understanding the reasons for these changes is important to understand processes of species diversification given the central role of signals in pre-mating isolation in birds. Here, we propose that the increase in frequency bandwidth in the song of tropical island birds could be caused by character release after mainland species colonize islands where acoustic space is less saturated. The importance of competition for acoustic space in driving song evolution was underscored by the fact that the widening of the frequency bandwidth of island birds songs was mostly limited to the tropics, where the reduction in interspecific competition and overall acoustic interference upon island colonization is much more extreme than in the temperate region. This suggests that the impact of the ‘island environment’ on convergent evolution (the ‘island syndrome’: Baeckens & Van Damme, [2020](#)) can be idiosyncratic, as island traits can vary with latitude, with some being more marked in the tropics (e.g. competition differential as shown here) and others in the temperate region (e.g. environmental stability differential: Covas, [2012](#)).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

C.D., M.M, D.G., T.L. and A.R. designed this study. C.D., M.M, S.J., T.L. and A.R. recorded songs on the field. A.R. measured acoustic variables and interference scores. A.R. performed analyses. A.R. wrote the first draft. All authors contributed to revisions of the manuscript, approved its final version and accept to be held accountable for its content.

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FIGURES AND TABLES

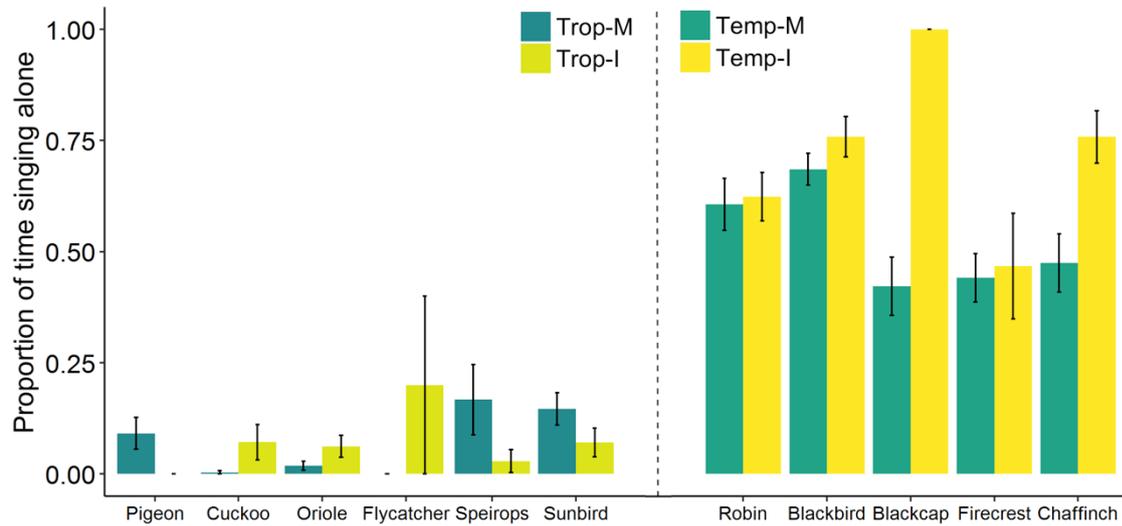


Figure 1: Proportion of time (mean \pm standard error of the mean) the species is vocalizing alone (without other bird species or type of insect calls) on Song Meter recordings. Tropical pairs are on the left of the dashed line while temperate are on the right. Mainland species (M) are in green while island species (I) are in yellow.

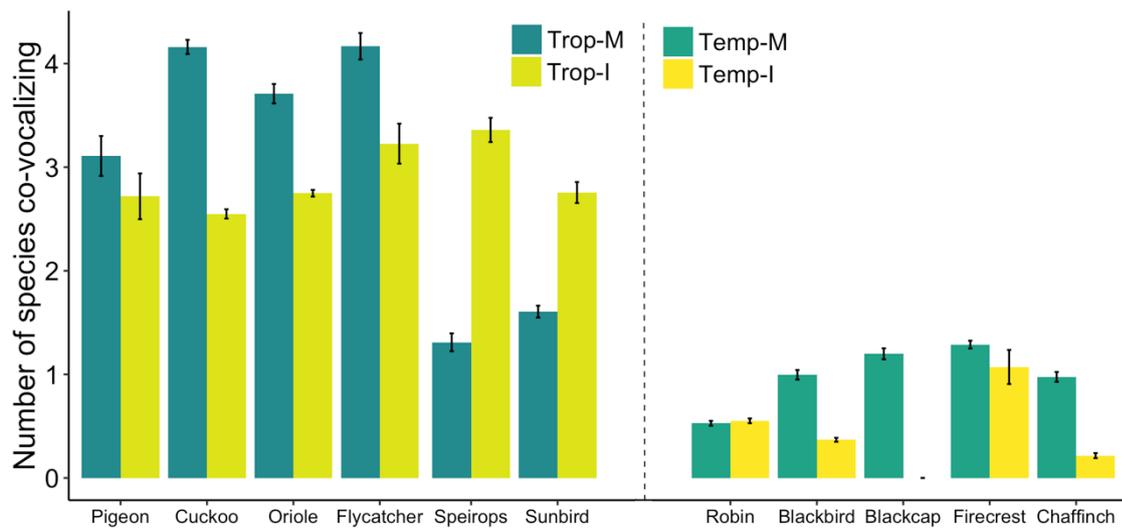


Figure 2: Number (mean \pm standard error of the mean) of other bird species and type of insect calls co-vocalizing with each song produced by the focal species on Song Meter recordings. Tropical pairs are on the left of the dashed line while temperate are on the right. Mainland species (M) are in green while island species (I) are in yellow.

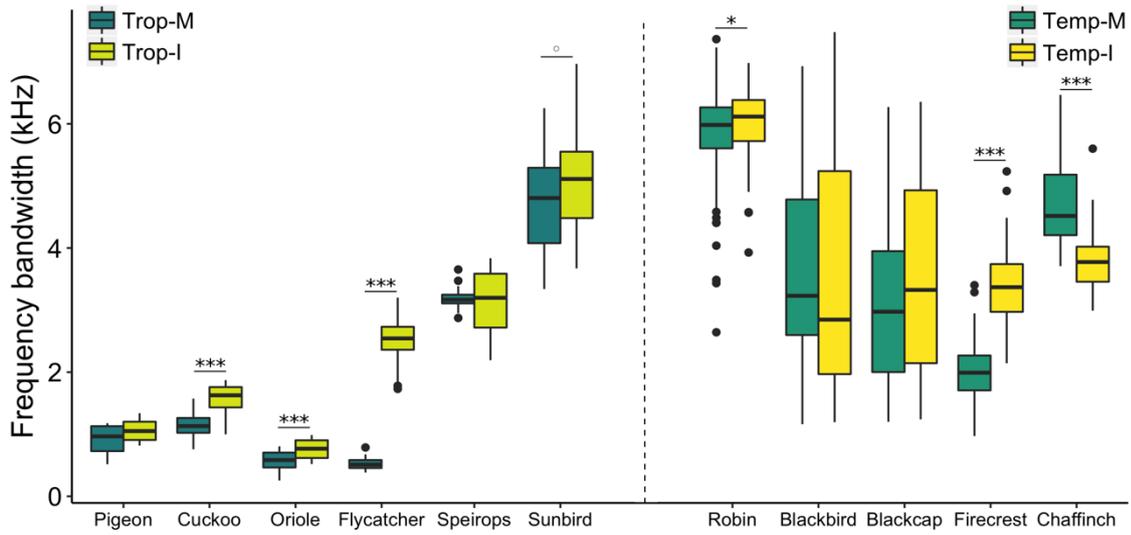


Figure 3: Frequency bandwidth for each of the 11 island species and their mainland counterparts, for the tropical (left) and the temperate (right) zone. Mainland species (M) are in green while island species (I) are in yellow. Each point is a single song measurement. Symbols associated with p-values for paired t-tests: no symbol: non-significant, ° < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Table 1: Results of the best models for the two proxies of acoustic interference: proportion of time each focal species is vocalizing alone (GLMM, binomial distribution) and number of species (birds and insects) temporally co-vocalizing with each song of the focal species (GLMM, Poisson distribution)

	Proportion of time vocalizing alone				Number of species co-vocalizing			
	Z	df	Estimate	P-value	Z	df	Estimate	P-value
Intercept	-0.74	-	-0.50 ± 0.68	-	3.67	-	0.44 ± 0.12	-
Time after sunrise	17.21	554	0.10 ± 0.006	<0.001	-15.81	7718	-0.03 ± 0.002	<0.001
Insularity: “island” ¹	4.85	613	0.17 ± 0.04	<0.001	-49.61	7719	-0.74 ± 0.01	<0.001
Latitude: “tropic” ²	-4.69	16	-4.21 ± 0.90	<0.001	6.02	76	0.27 ± 0.03	<0.001
Insularity*latitude (“island” ¹ *“tropic” ²)	3.24	52	1.38 ± 0.43	<0.01	8.68	7232	-0.07	<0.001

1. Reference category is “mainland”
2. Reference category is “temperate”

Table 2: Results of the best linear-mixed models for frequency bandwidth, minimum frequency and maximum frequency. Variables were considered on a logarithmic scale.

	Frequency bandwidth (logged ratio)				Minimum frequency (logged)				Maximum frequency (logged)			
	<i>T</i>	df	Estimate	P-value	<i>T</i>	df	Estimate	P-value	<i>T</i>	df	Estimate	P-value
Intercept	6.10	-	0.94 ± 0.15	-	35.97	-	8.05 ± 0.22	-	40.43	-	8.99 ± 0.22	-
Mass	-	-	-	-	-5.88	173	-0.007 ± 0.001	<0.001	-4.75	173	-0.007 ± 0.001	<0.001
Insularity: “island” ¹	-1.06	174	-0.03 ± 0.03	0.29	-0.90	173	-0.02 ± 0.02	0.37	-1.56	173	-0.05 ± 0.03	0.12
Latitude: “tropic” ²	-1.33	8	-0.27 ± 0.1	0.41	-1.02	8	-0.29 ± 0.29	0.34	-1.96	8	-0.56 ± 0.29	0.09
Insularity*latitude (“island” ¹ *“tropic” ²)	3.28	174	0.19 ± 0.06	<0.01	-0.91	173	-0.03 ± 0.04	0.36	2.78	173	0.15 ± 0.05	<0.01

1. Reference category is “mainland”
2. Reference category is “temperate”

SUPPORTING INFORMATION

Appendix 1 – Site localizations and altitudes

Table S1. Gazetteer with altitude above sea level (ASL) of the twelve localities (four communities) for which samples were collected. Soundscape was characterized in two localities of each region and are described in Robert et al (2019).

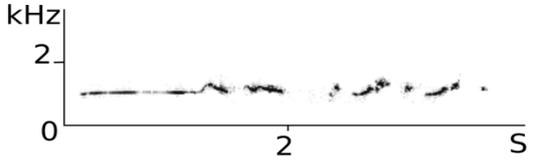
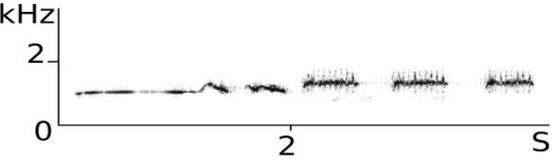
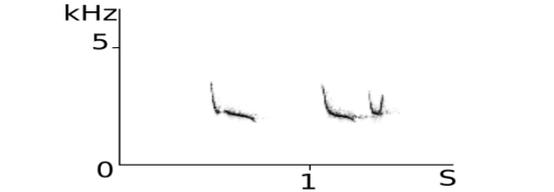
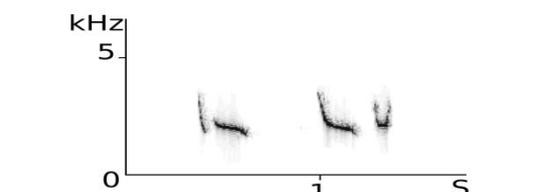
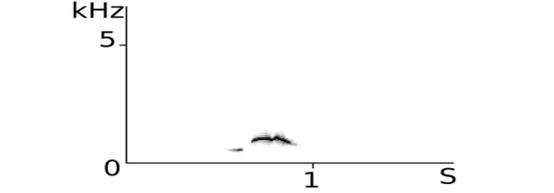
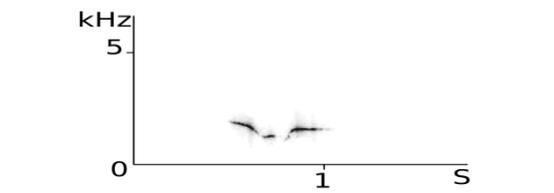
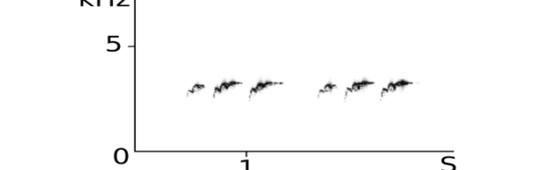
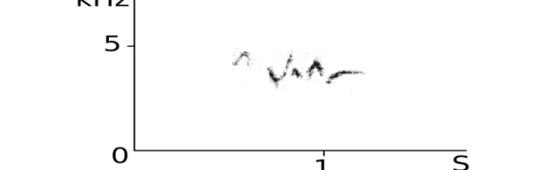
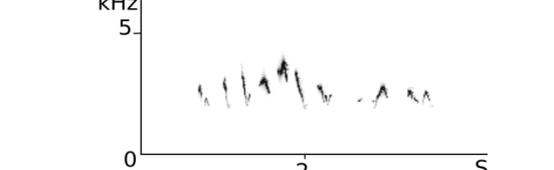
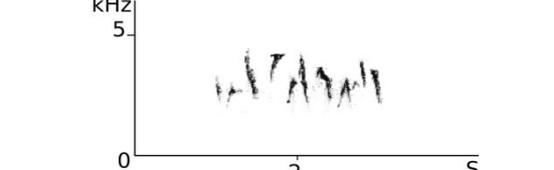
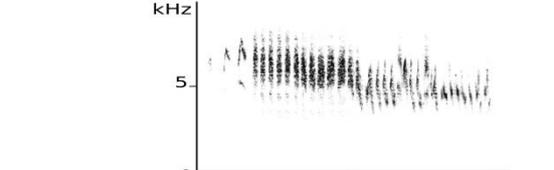
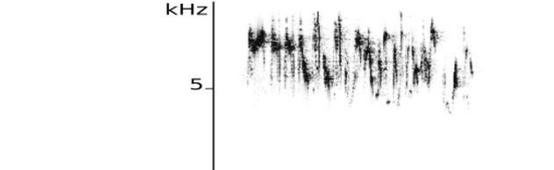
REGION	LOCALITY	LATITUDE	LONGITUDE	ASL
Madeira Island	Seixal	32°48'55.56"N	17°06'51.46"O	400
Madeira Island	Achada	32°50'19.19"N	17°11'35.70"O	700
Madeira Island	Portela	32°45'09.81"N	16°48'13.91"O	500
Mediterranean basin	la Rouvière	43°39'28.23"N	03°40'42.60"E	290
Mediterranean basin	La Verne	43°16'40.98"N	06°16'54.78"E	650
Mediterranean basin	Maruèjols	43°50'07.97"N	04°11'25.69"E	200
São Tomé Island	Chamiço	00°19'04.54"N	06°35'56.90"E	600
São Tomé Island	Macambrará	00°16'30.85"N	06°36'20.37"E	1200
São Tomé Island	Morro Esperança	00°17'38.68"N	06°36'39.86"E	1000
Cameroon	Mapia	04°10'23.46"N	09°11'57.91"E	1950
Cameroon	Bakingili Forest	04°05'27.30"N	09°02'39.25"E	300
Cameroon	Etome Forest	04°03'17.09"N	09°06'23.04"E	400

Literature cited:

Robert A, Lengagne T, Melo M et al. 2019. The theory of island biogeography and soundscapes: Species diversity and the organization of acoustic communities. *J Biogeogr*, 00:1–11. doi:10.1111/jbi.13611.

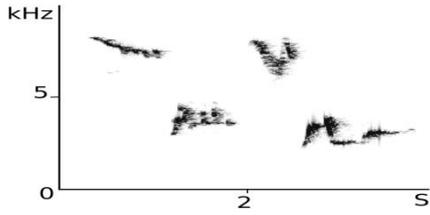
Appendix 2 – Typical songs of focal species

Table S2. Spectrograms of the songtypes of the study species

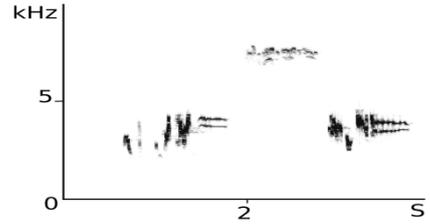
Tropical mainland	Tropical island
<p><i>Treron calvus</i></p> 	<p><i>Treron sanctithomae</i></p> 
<p><i>Chrysococcyx chrysococcyx cupreus</i></p> 	<p><i>Chrysococcyx chrysococcyx insularum</i></p> 
<p><i>Oriolus brachyrhynchus</i></p> 	<p><i>Oriolus crassirostris</i></p> 
<p><i>Terpsiphone rufiventer</i></p> 	<p><i>Terpsiphone atrochalybeia</i></p> 
<p><i>Zosterops melanocephalus</i></p> 	<p><i>Zosterops lugubris</i></p> 
<p><i>Cinnyris reichenowi</i></p> 	<p><i>Anabathmis newtonii</i></p> 

Temperate mainland	Temperate island
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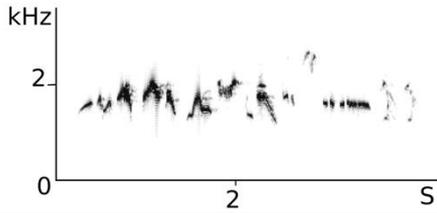
Erithacus rubecula



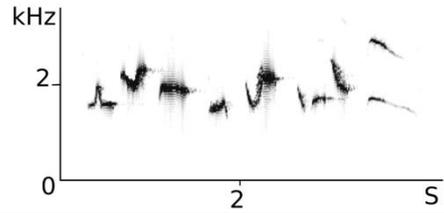
Erithacus rubecula



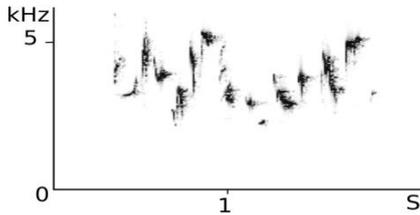
Turdus merula merula



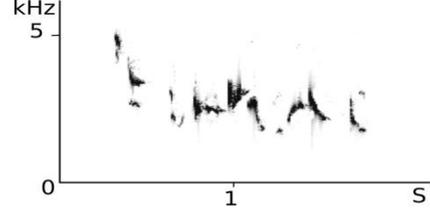
Turdus merula cabrerai



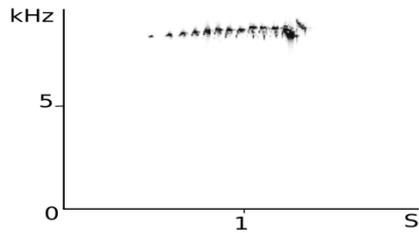
Sylvia atricapilla atricapilla



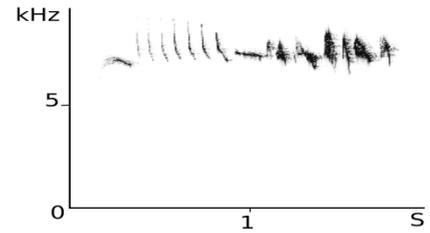
Sylvia atricapilla heineken



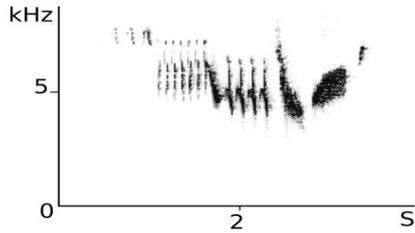
Regulus ignicapillus



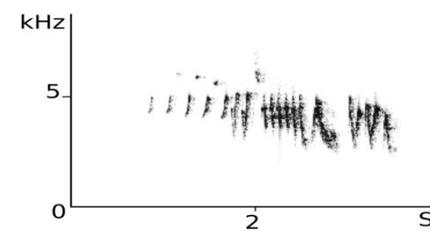
Regulus madeirensis



Fringilla coelebs coelebs



Fringilla coelebs madeirensis



Appendix 3 – Sample sizes and raw data

Table 1: Bird species pairs (island-mainland), sample sizes, and measured frequency parameters

Pair name	Area	Species	Number of individuals	Number of songs	Minimum frequency (Hz)	Maximum frequency (Hz)
Pigeon	Tropical mainland	<i>Treron calvus</i>	6	6	703 ±186	1613 ±117
	Tropical island	<i>Treron sanctithomae</i>	6	6	645 ±214	1706 ±94
Cuckoo	Tropical mainland	<i>Chrysococcyx chrysococcyx. cupreus</i>	9	72	1656 ±53	2794 ±163
	Tropical island	<i>Chrysococcyx chrysococcyx insularum</i>	9	72	1630 ±52	3211 ±211
Oriole	Tropical mainland	<i>Oriolus brachyrynchus</i>	10	87	818 ±75	1382 ±212
	Tropical island	<i>Oriolus crassirostris</i>	10	80	788 ±59	1551 ±144
Flycatcher	Tropical mainland	<i>Terpsiphone rufiventer</i>	5	26	2672 ±87	3206 ±76
	Tropical island	<i>Terpsiphone atrochalybeia</i>	5	28	2435 ±231	4941 ±301
Speirops	Tropical mainland	<i>Zosterops melanocephalus</i>	7	26	1800 ±142	4981 ±187
	Tropical island	<i>Zosterops lugubris</i>	7	23	1752 ±224	4896 ±410
Sunbird	Tropical mainland	<i>Cinnyris reichenowi</i>	10	26	3411 ±513	8130 ±528
Robin	Tropical island	<i>Anabathmis newtonii</i>	10	21	3833 ±418	8940 ±493
	Temperate mainland	<i>Erithacus rubecula</i>	10	100	2496 ±425	8315 ±655
Blackbird	Temperate island	<i>Erithacus rubecula</i>	10	100	2565 ±345	8601 ±470
	Temperate mainland	<i>Turdus merula merula</i>	10	100	1471 ±143	5109 ±1405
Warbler	Temperate island	<i>Turdus merula cabrerai</i>	10	100	1503 ±177	4974 ±1718
	Temperate mainland	<i>Sylvia atricapilla atricapilla</i>	10	54	2231 ±233	5306 ±1046
Firecrest	Temperate island	<i>Sylvia atricapilla heineken</i>	10	55	2120 ±319	5637 ±1602
	Temperate mainland	<i>Regulus ignicapilla</i>	10	96	6258 ±477	8235 ±266
Chaffinch	Temperate island	<i>Regulus madeirensis</i>	10	82	5580 ±450	8965 ±431
	Temperate mainland	<i>Fringilla coelebs coelebs</i>	10	98	1858 ±193	6548 ±697
	Temperate island	<i>Fringilla coelebs madeirensis</i>	10	95	1654 ±204	5453 ±453

Appendix 4 – Measure of frequency parameters

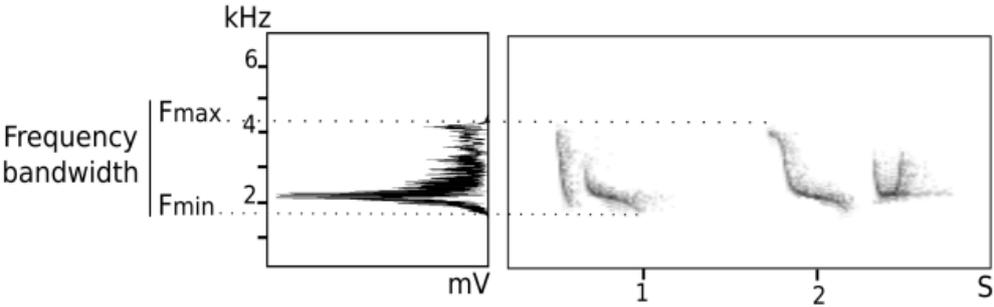


Figure S1: Amplitude spectrum and sonogram for a song type from a São Tomé emerald cuckoo (*Chrysococcyx cupreus insularum*).

Appendix 5 – Accumulation curves

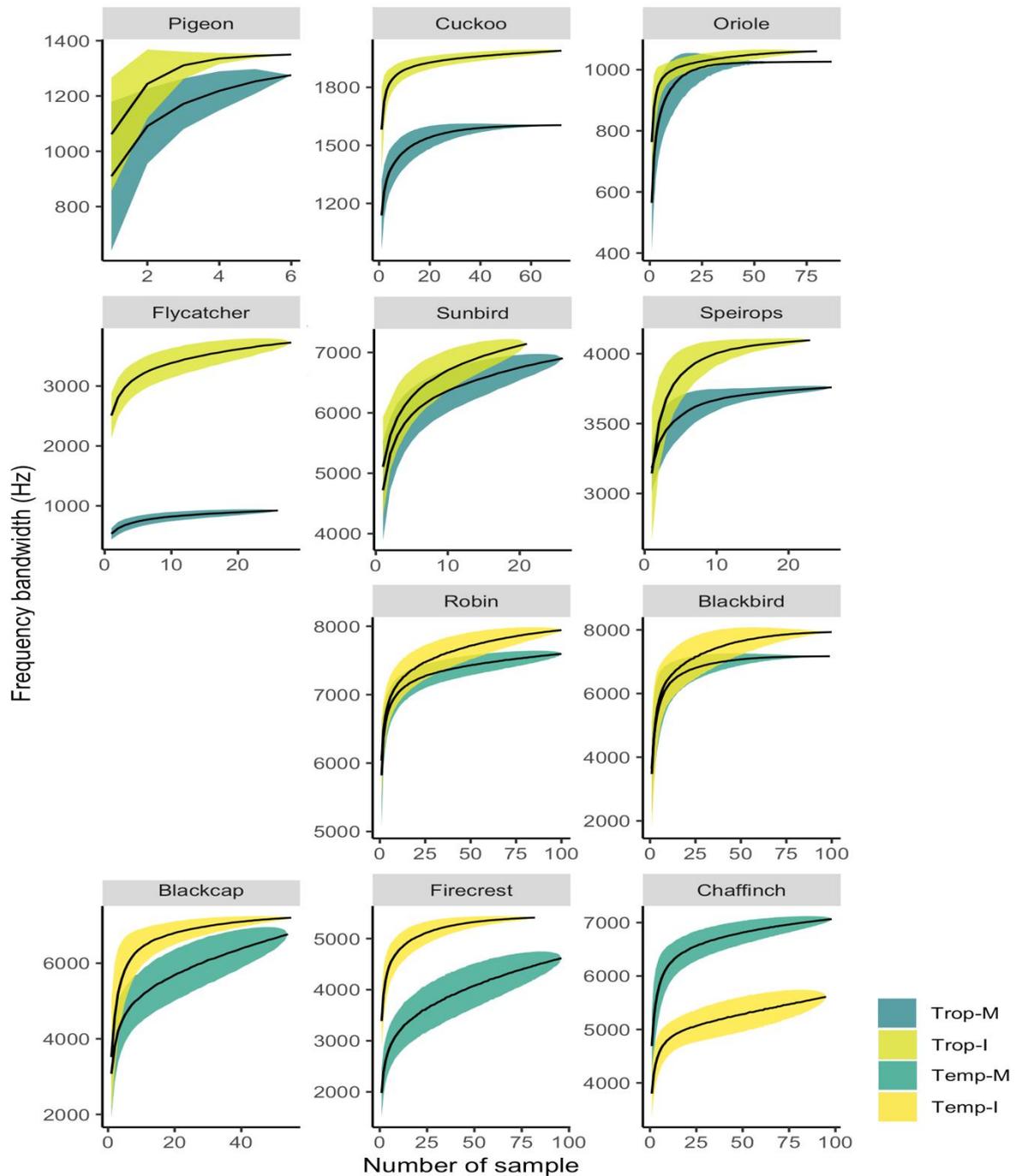


Figure S2: Accumulation curves of mean (line) \pm standard deviation of frequency bandwidth along the sampling of each focal species songs. For each species and each different number of samples, we calculated the mean of all frequency bandwidths calculated taking all possible combinations of this number of samples (when number of combinations was higher than 10000 we took 10000)

Appendix 6 – Homogeneity of frequency bandwidth within-species

We compared within-species variance in frequency bandwidth between island and mainland species of each pair by using Levene’s tests (Levene 1960). Results are presented in Table S3 and data are presented in Figure S3.

Among the pairs with significantly broader frequency bandwidth on islands (cuckoo, oriole, flycatcher, robin and firecrest), only the flycatcher pair had a significantly different (greater) variance among individuals on the island and for this species, all island individuals had broader frequency bandwidth than mainland individuals (Figure S3). Thus, when a broader bandwidth was detected on island it was achieved by all individuals in the island population (individuals with lowest bandwidths in the island population had higher frequency bandwidths than individuals with lowest bandwidths in the mainland population) and not only by a specialization of some island individuals towards high frequency bandwidths.

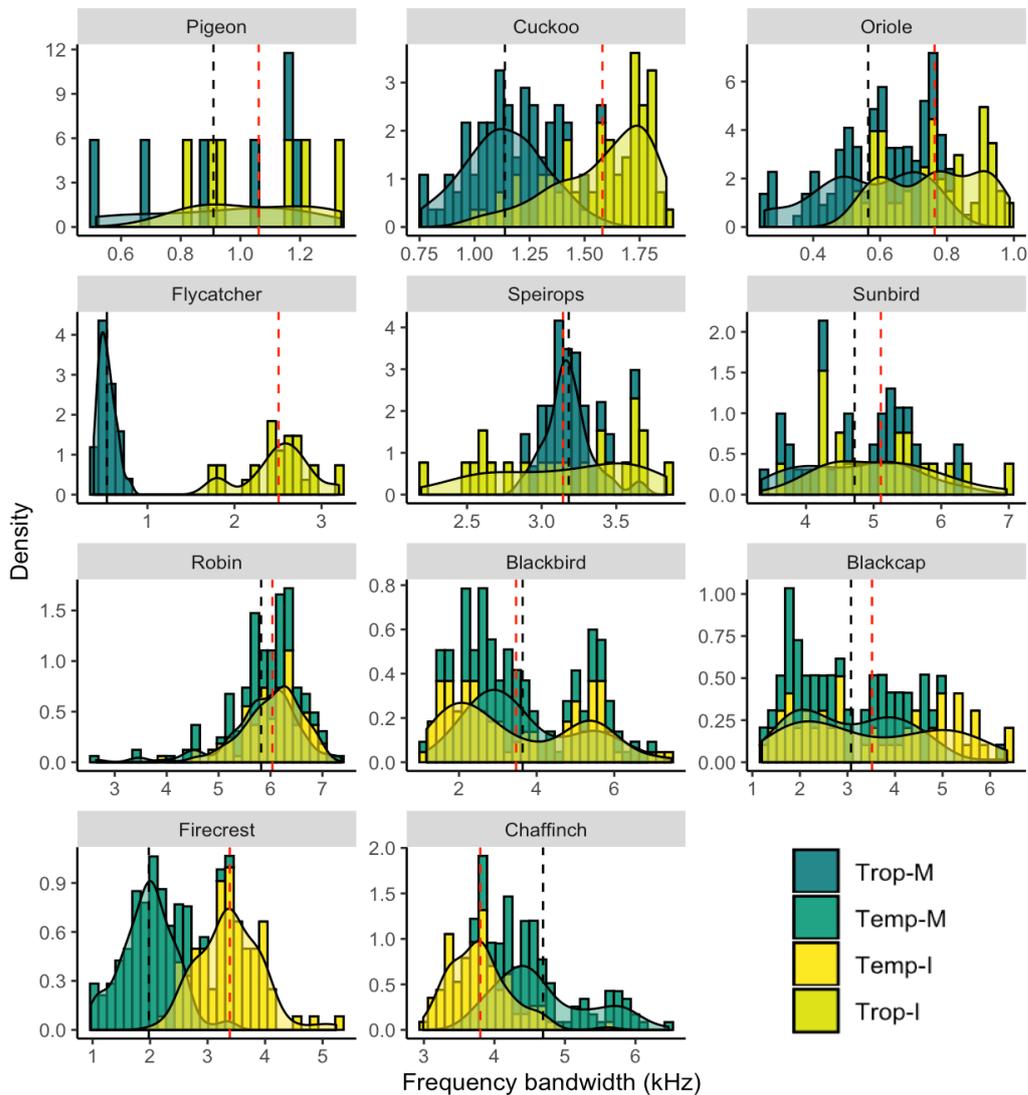


Figure S3: Histograms of frequency bandwidth (kHz) for each focal species with a smooth of the distribution under a generalized linear model. Each point is a single song measurement (see Table 1 in the main text for sample sizes). Population means of frequency bandwidths are indicated by vertical bars (red for island population and black for mainland population). Mainland species (M) are in green while island species (I) are in yellow. Population

Table S3: Results of Levene’s test for each species pair.

Species pair	F values	P-values
Robin	2.15	0.1439
Blackbird	6.62	0.0108
Blackcap	8.54	0.004
Chaffinch	11.69	<0.001
Firecrest	1.47	0.227
Pigeon	0.45	0.5177
Cuckoo	1.76	0.1862
Oriole	2.11	0.1484
Flycatcher	16.93	<0.001
Speirops	29.12	<0.001
Sunbird	0.07	0.788

Literature cited:

Howard Levene, *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*, Stanford University Press, 1960, 278–292 p.,

Appendix 7 - Bayesian phylogenetic mixed models

In order to investigate how phylogenetic relationships among species could influence our results, we also used Bayesian phylogenetic mixed models (BPMM), using the “*MCMCglmm*” R package (Hadfield 2010; Hadfield & Nakagawa 2010).

We performed four different BPMMs on the following variables: frequency bandwidth, minimum frequency, maximum frequency and number of overlapping species (we did not model the proportion of time each species spent vocalizing alone because binomial distributions are not supported by MCMCglmm). Similarly as for LMMs, frequency bandwidth, minimum frequency and maximum frequency were analysed on a logarithmic scale. As our data consisted of repeated samples per individual, we included « individual » as a random effect. Proceedings as for LMMs, we tested insularity (island/mainland), latitude (tropical/temperate) and their interaction as fixed effects. We also included body mass and altitude as fixed effects. Concerning the numbers of overlapping species, we used a Poisson error distribution. As in GLMMs, we tested insularity (island/mainland), latitude (tropical/temperate) and their interaction as fixed effects. We also included time of the quarter as a continuous fixed effect.

We downloaded 10000 alternative trees from Jetz and coworkers (2012) comprehensive bird phylogeny (downloaded from the BirdTree database: <https://birdtree.org>). We calculated posterior node probabilities in *PAUP** (Swofford 2003). All trees were identical (Figure S3) and therefore we only used one tree for the BPMM. As BirdTree phylogeny is restricted at the species level, we manually added the five island subspecies (*Chrysococcyx cupreus insularum*, *Sylvia atricapilla heineken*, *Fringilla coelebs madeirensis*, *Erithacus rubecula rubecula* and *Turdus merula cabrerai*) on this tree by arbitrary fixing phylogenetic distances with closest mainland relatives at 0.001 (distance from tips to root is 86 in this ultrametric tree). For each analysis, we ran the model using 2 chains for 800000 iterations and saved posterior samples after a burn-in period of 50000, thinning every 300 iterations, resulting in an effective sample size of at least 1000. Uninformative priors were used (inverse-Wishart with belief parameters set to 0.002 and variances set to 1) for both random effect and residual variances. We assessed model convergence using the ‘coda’ R package (Plummer et al. 2006). For each dependent variable, we selected the best model by minimizing the deviance information criterion DIC and considered that models differing by less than 2 DIC units were equivalent.

For all of the four models, results of BPMM were equivalent to those presented in the main text (LMM and GLMM) in terms of significance and relative strength of estimates (Table S4:S7). In particular, results of BPMM indicated broader frequency bandwidths on the islands compared to the mainland, and stronger island-mainland differences in the tropics compared to the temperate zone. Additionally, BPMM also highlighted the diminution of minimum frequencies in islands and we found the same significant interaction between latitude and insularity in the variations of maximum frequencies. Additionally, mainland species were overlapped by more species than were island species and the overlap included more species in the tropical than in the temperate zone.

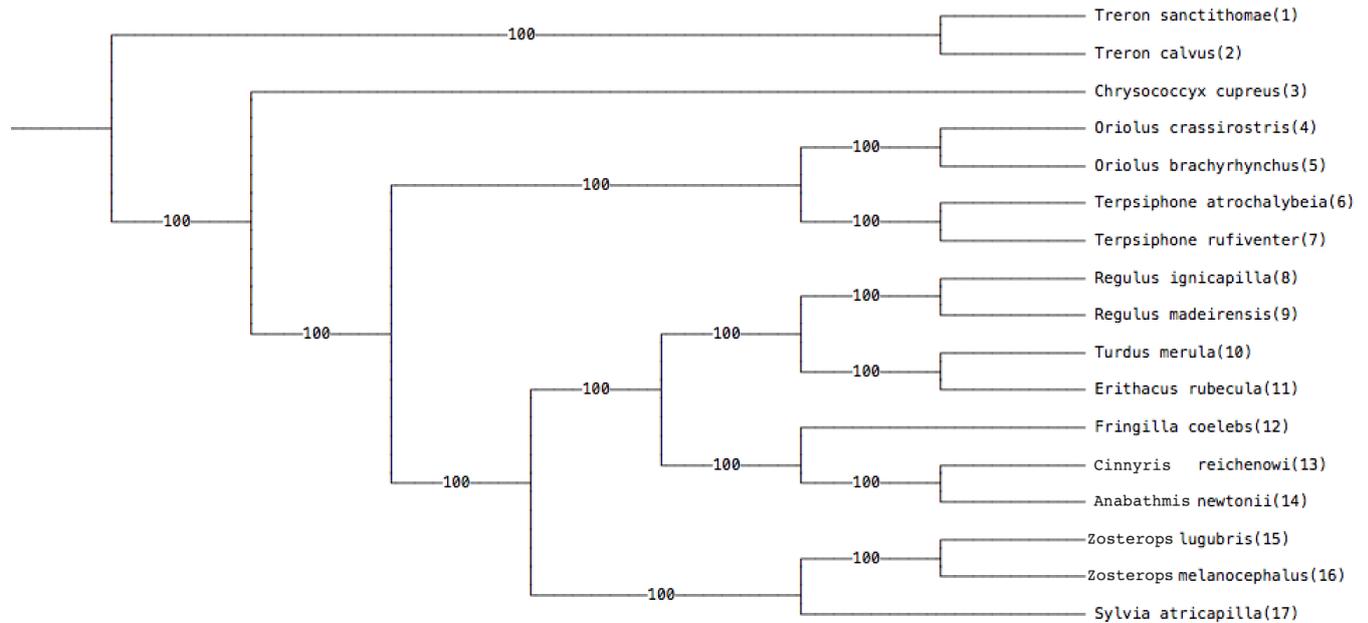


Figure S4: consensus phylogenetic tree generated from 10000 alternative trees from Jetz and coworkers (2012) with posterior probabilities.

Table S4: Results of the best BPMM for frequency bandwidth. Terms for which the 95% credible interval did not span 0 are presented in bold characters. A probability that the posteriors encompass zero (pMCMC) is provided as a statistical test.

	Frequency bandwidth (logged ratio)			pMCMC
	Estimate	95% Credible Intervals Lower 2.5%CI Upper 2.5%CI		
Intercept	0.88	0.28 1.41		-
Insularity: "island" ¹	-0.0008	-0.05 0.06		0.98
Latitude: "tropic" ²	0.04	-0.42 0.33		0.82
Insularity*latitude ("island"¹*"tropic"²)	-0.14	-0.25 -0.02		0.025

1. Reference category is "mainland"
2. Reference category is "temperate"

Table S5: Results of the best BPMM for minimum frequency. Terms for which the 95% credible interval did not span 0 are presented in bold characters. A probability that the posteriors encompass zero (pMCMC) is provided as a statistical test.

	Minimum frequency (logged)			pMCMC
	Estimate	95% Credible Intervals Lower 2.5%CI Upper 2.5%CI		
Intercept	8.17	7.36 8.99		-
Mass	-0.01	-0.02 -0.005		<0.01
Insularity: "island"¹	-0.06	-0.10 -0.02		<0.01
Latitude: "tropic" ²	-0.24	-0.78 0.24		0.30
Insularity*latitude ("island"¹*"tropic"²)	-0.003	-0.08 0.10		0.94

1. Reference category is "mainland"
2. Reference category is "temperate"

Table S6: Results of the best BPMM for maximum frequency. Terms for which the 95% credible interval did not span 0 are presented in bold characters. A probability that the posteriors encompass zero (pMCMC) is provided as a statistical test.

	Maximum frequency (logged)			
	Estimate	95% Credible Intervals		pMCMC
		Lower 2.5% CI	Upper 2.5% CI	
Intercept	8.96	8.11	9.78	-
Mass	-0.008	-0.01	-0.003	<0.01
Insularity: "island"¹	-0.06	-0.12	-0.002	0.04
Latitude: "tropic" ²	-0.29	-0.79	0.20	0.24
Insularity*latitude ("island"¹*"tropic"²)	0.14	0.02	0.26	0.02

1. Reference category is "mainland"
2. Reference category is "temperate"

Table S7: Results of the best BPMM for number of species overlapping. Terms for which the 95% credible interval did not span 0 are presented in bold characters. A probability that the posteriors encompass zero (pMCMC) is provided as a statistical test.

	Number of species overlapping			
	Estimate	95% Credible Intervals		pMCMC
		Lower 2,5% CI	Upper 2,5% CI	
Intercept	-0.70	-0.79	-0.63	-
Time after sunrise	-0.04	-0.05	-0.04	<0.001
Insularity: "island"¹	-0.85	-0.93	-0.75	<0.001
Latitude: "tropic"²	1.94	1.87	2.02	<0.001
Insularity*latitude ("island"¹*"tropic"²)	-0.68	-0.78	-0.59	<0.001

1. Reference category is "mainland"
2. Reference category is "temperate"

Literature cited:

- Hadfield, J. D. 2010. MCMCglmm: MCMC Methods for Multi-Response GLMMs in R. *Journal of Statistical Software* 33:1–22.
- Hadfield, J. D., and S. Nakagawa. 2010. General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* 23:494–508.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Plummer M, Best N, Cowles K, Vines K. 2006 CODA: convergence diagnosis and output analysis for MCMC. *RNews* 6, 7–11.
- Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Appendix 8 – Model selection

Table S8: Results of Akaike's Information Criteria (AIC) for model selection analysis for frequency variables, Δ AIC is the change in AIC relative to the best fit model

Model	Frequency bandwidth		Minimum Frequency		Maximum Frequency	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
~insularity*latitude+mass	-932.123	13.080	-2215.683	0.000	-1541.422	0.000
~insularity*latitude	-945.203	0.000	-2210.767	4.916	-1536.827	4.595

Table S9: Results of Akaike's Information Criteria (AIC) for model selection analysis for acoustic competition variables, Δ AIC is the change in AIC relative to the best fit model

Model	Proportion of time vocalizing alone		Number of species co-vocalizing	
	AIC	Δ AIC	AIC	Δ AIC
~insularity*latitude+time after sunrise	12096.2	0.000	64310.2	0.000
~insularity*latitude	12397.1	300.9	64509.9	199.7

Appendix 9 - Minimum, maximum frequency and frequency bandwidth of all studied species

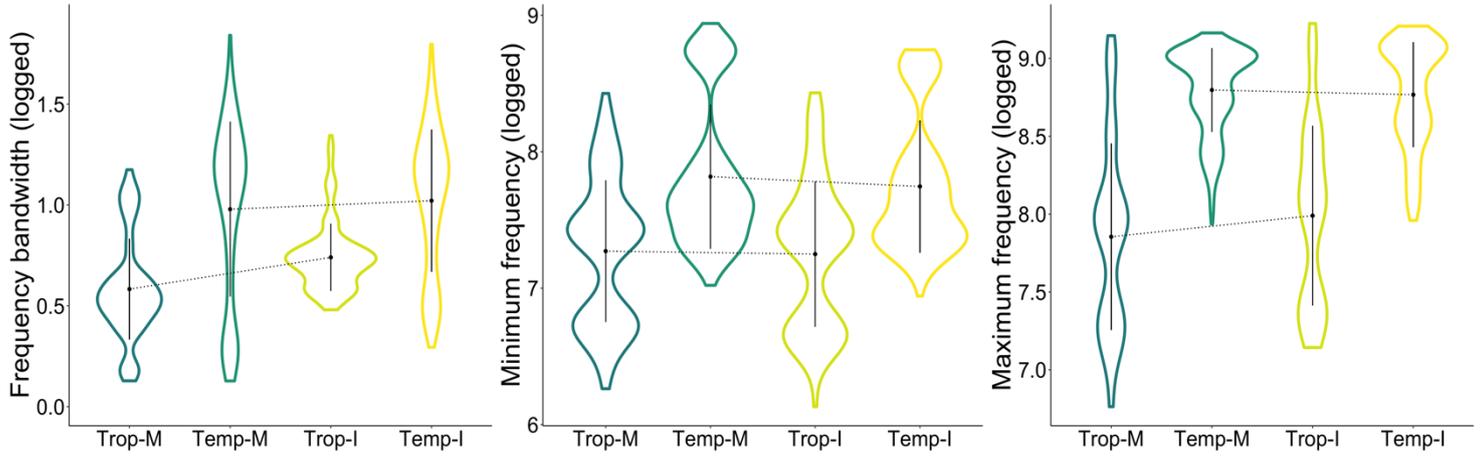


Figure S5: Mean and standard deviation of frequency bandwidth, minimum frequency and maximum frequency of all studied species in tropical mainland (Trop-M), temperate mainland (Temp-M), tropical island (Trop-I) and temperate island (Temp-I).

Appendix 10 – Maximum and minimum frequencies for each focal species

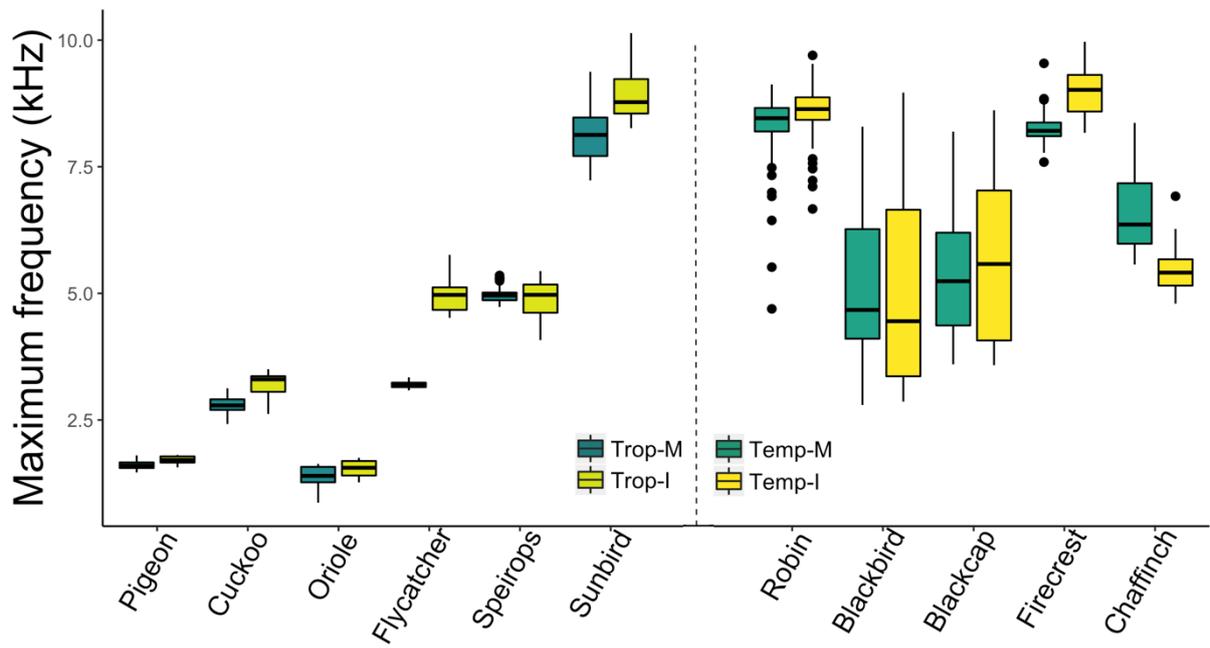


Figure S6: Maximum frequency for each of the 11 island species and their mainland counterparts, for the tropical (left) and the temperate (right) zone. Mainland species (M) are in green while island species (I) are in yellow.

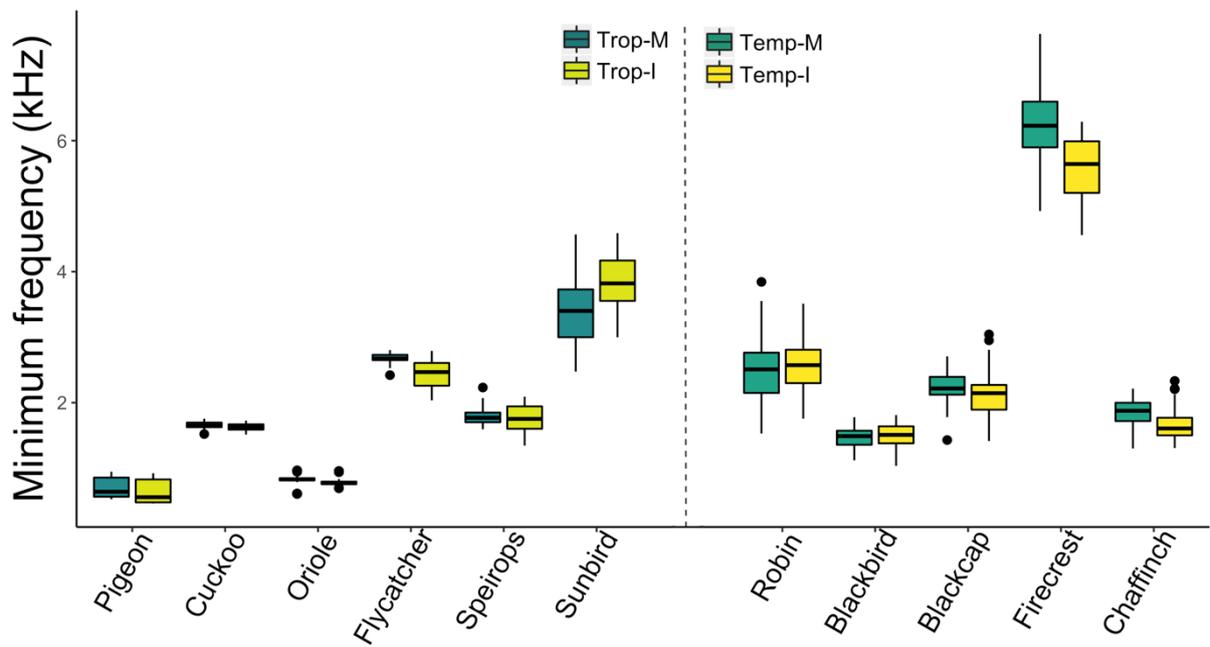


Figure S7: Minimum frequency for each of the 11 island species and their mainland counterparts, for the tropical (left) and the temperate (right) zone. Mainland species (M) are in green while island species (I) are in yellow.