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Global Macroevolution and Macroecology of Passerine Song

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Abstract

Studying the macroevolution of the songs of Passeriformes (perching birds) has proved challenging. The complexity of the task stems not just from the macroevolutionary and macroecological challenge of modelling so many species, but also from the difficulty in collecting and quantifying birdsong itself. Using machine learning techniques, we extracted songs from a large citizen science dataset, and then analysed the evolution, and biotic and abiotic predictors of variation in birdsong across 578 passerine species. Contrary to expectations, we found few links between life-history traits (monogamy and sexual dimorphism) and the evolution of song pitch (peak frequency) or song complexity (standard deviation of frequency). However, we found significant support for morphological constraints on birdsong, as reflected in a negative correlation between bird size and song pitch. We also found that broad-scale biogeographical and climate factors such as net primary productivity, temperature, and regional species richness were significantly associated with both the evolution and present-day distribution of bird song features. Our analysis integrates comparative and spatial modelling with newly developed data cleaning and curation tools, and suggests that evolutionary history, morphology, and present-day ecological processes shape the distribution of song diversity in these charismatic and important birds.

Introduction

Bird song is one of the most attractive dimensions of bird biodiversity, shaping our ecological soundscape (Pijanowski et al. 2011) and providing a tangible link between the evolutionary past and the ecological present. Recent methodological and empirical advances have provided new insights into the early diversification of birds (*e.g.*, Jetz et al. 2012; Jarvis et al. 2014) and the (at least) two separate origins of learned bird song (Zhang et al. 2014), yet understanding the evolution of song structure itself has proven challenging (Read and Weary 1992; Brenowitz 1997; Slabbekoorn and Smith 2002a; but see Greig et al. 2013; Gonzalez-Voyer et al. 2013; Mason et al. 2014; Tietz et al. 2015; Tubaro and Mahler 1998; Weir et al. 2011, 2012). Several studies have modelled bird song within restricted clades (*e.g.*, Ryan and Brenowitz 1985; Read and Weary 1992; Grant and Grant 1996; Price and Lanyon 2002), and proposed links between patterns of song diversity across temporal and spatial scales (Baker 2001), but there are remarkably few broad-scale empirical studies (notable exceptions include Weir *et al.* 2011; Tobias *et al.* 2014; Mason & Burns 2015). Understanding broad patterns of song evolution and diversity could provide insights into the evolution of language, and complement the expanding literature on songbird neurobiology (*e.g.*, Doupe and Kuhl 1999; Brainard and Doupe 2002).

Male song is critical for successful mating, and so is likely under strong sexual selection (Nowicki and Searcy 2004; Wilkins et al 2013; but see Price 2015). For example, in oscines, song complexity may be an honest signal of mate quality (Mountjoy and Lemon 1996; Nowicki et al. 1998; Nowicki and Searcy 2004; Spencer et al. 2005; Leitão et al. 2006).

Variation in bird song has the potential to serve as a form of prezygotic mating barrier (*e.g.*, Haavie et al. 2004; Edwards et al. 2005; reviewed in Podos and Warren 2007) and thus could also drive diversification (Slabbekoorn and Smith 2002b; Forschler and Kalko 2007). For example, white crowned sparrows respond less to historically and geographically distant songs (Derryberry 2007, 2011), and songs of closely related species in sympatry are more dissimilar

(Seddon 2005), highlighting the importance of birdsong in mate recognition and in maintaining reproductive cohesion. However, the evolution and diversity of birdsong is likely constrained by both bird ecology and physiology.

Selection on species' traits such as the morphology of the vocal tract (trachea, larynx, and syrinx; Podos et al. 2004), beak morphology (Herrel et al. 2005; Huber and Podos 2006; Derryberry et al. 2012), and body size (Seddon 2005; Cardoso 2010) could limit potential for song production. In addition, noisy or densely-vegetated environments may strongly affect song characteristics (Morton 1975; Hansen 1979; Ryan and Brenowitz 1985), although meta-analytical evidence for such effects is weak (Boncoraglio and Saino 2007). Potential environmental drivers of song features are often highly predictable and conserved across habitat-types (*e.g.*, Tobias et al. 2010; Francis et al. 2012). For example, dense vegetation limits the transmission of high frequencies, while the background noise in urban areas masks lower frequencies, selecting for songs with lower (*e.g.*, Tobias et al. 2010) and higher (Slabbekoorn et al. 2007; Brumm and Naguib 2009; Luther and Derryberry 2012; Luther et al. 2015) frequencies, respectively. Thus birdsong evolution is a product of complex interactions between multiple pressures on breeding system, morphology, and the physical habitat characteristics.

We focus here on passerines, the perching birds. The passerines are an excellent study system for exploring the evolution of vocal communication due to their diversity, wide geographical distribution, and song complexity. Moreover, the two major sub-clades of passerines, the oscines and suboscines, differ in their song acquisition. Songs in oscines are typically learnt, whereas songs in suboscines are more often innate (Kroodsma and Miller 1996; Beecher and Brenowitz 2005; Touchton *et al.* 2014), potentially making the oscine clade more sensitive to rapidly changing ecological influences on song production (Rios-Chelen et al. 2012). In

addition, the anatomy and neurology of the song system is known to differ between these clades, which could also lead to differential constraints on song evolution (Amador et al. 2008; Gahr 2000).

A broad-scale analysis of passerine song requires simple metrics that can be quantified and compared among multiple and highly variable species. We examine the pitch of the loudest note in a song (the peak frequency) and the complexity of the song (measured as the standard deviation of the frequencies within a song). There are strong *a priori* expectations on how variation in these axes of song structure might capture the relative importance of bird physiology, life history and environment. For example, if morphological constraints shape song evolution, we might expect species that are smaller to have higher-pitched songs, and species in more complex habitats where sound transmission is more difficult (such as forests) to have lower-pitched songs. However, if song characteristics are driven primarily by sexual selection, we might expect life history traits such as mating system to be associated with greater male song complexity, as song is acting as a mechanism for female choice (*e.g.*, Loffredo and Borgia 1986). Larger repertoire sizes of songs, one common measure of song complexity, are often associated with increased female-preference (Beecher and Brenowitz 2005). However, female zebra finches, a species with single-song repertoires, prefer songs with lower variation in pitch (*i.e.*, a lesser coefficient of variation in pitch; Woolley and Doupe 2008), and there is evidence that sexual selection can also drive the evolution of simpler songs whose quality is therefore easier to assess (*e.g.*, Cardoso and Hu, 2011). Large, cross-species analyses with the same measure of complexity are thus necessary to unpick these contrasting, but not mutually exclusive, hypotheses about the role of life history traits and environment in determining bird song.

Making use of a worldwide citizen science database of bird recordings (Xeno Canto; <http://www.xeno-canto.org/>), and modern machine learning techniques (Giannakopoulos 2015), we present a synthetic analysis of broad evolutionary and spatial patterns of passerine birdsong. Using over 5,000 songs taken from 578 bird species, we find strong evidence for biogeographical constraint on the evolution and present-day distribution of birdsong, but limited evidence for influences of sexual selection or life-history traits.

Material and Methods

We evaluated the pitch and complexity of birdsong across passerines using one of the largest databases of birdsongs currently available and data on passerine biology, life history and geographical distribution. First, we constructed a series of phylogenetic regressions to examine correlations with key life history traits and environment, accounting for phylogenetic uncertainty by running models across the Bayesian posterior distribution of the bird tree of life. Second, we contrasted our phylogenetic regressions with a spatial analysis using the same suite of variables, but evaluating correlations across space. To account for unequal sampling of birdsong in Europe and the Neotropics, we repeated all analyses across all species (global), and separately for Old and New World species. We conduct separate analyses for life history traits and environmental variables to account for unequal distributions of data among species; we were able to find much less data for our life-history variables. The exception to this is body mass, for which data were readily available across most species and so, as a significant predictor of variation in birdsong metrics, was used in all models.

Song download, cleaning, and measurement

All available song data for passerines was downloaded from the Xeno-Canto database of birdsongs from around the world (<http://www.xeno-canto.org/>) with search criteria specifying the type of vocalization as “song”, quality “A” (*i.e.*, the highest recording quality as rated by users), songs from males, confirmed visualization of the bird, and with no other bird species in the recording. While we cannot be certain that each recorder defined “song” in the same fashion, here our intention is to study the evolution of male bird vocalizations that advertise territory and/or for mates. We further emphasise that, while the meta-data entries for each song indicated they were sung by a male, we cannot guarantee that some of these recordings were not from females as females are also known to sing (see Tobias et al. 2016). When several

recordings were available for the same species, we downloaded multiple files per species. *R* (version 3.1.3; R Core Team 2015; Supplementary Materials 1) and *Ruby* (<https://www.ruby-lang.org/>; Supplementary Materials 2 and 3) code to download songs from Xeno Canto is available in the Supplementary Materials and online (<https://github.com/willpearse/Xena>). As reported in the results in more detail below, we downloaded an average of 10.26 songs per species. In the Supplementary Materials, we release the data on all songs we downloaded (Supplementary Materials 4), the subset of data we manually checked (see below; Supplementary Materials 5), and the meta-data for all downloads (Supplementary Materials 6).

A bout of singing from an individual bird can consist of multiple songs. We assessed each song separately, splitting sound recordings using the *pyAudioAnalysis* Support Vector Machine (SVM) approach (Giannakopoulos, 2015) trained on background noise within the sound files. Briefly, this approach uses the highest- and lowest- energy 10% segments of the recordings to train an SVM to detect regions of the recordings that contain birdsong, and then segment and extract them from the rest of the recording. This approach is commonly used to detect human speech on smartphones (*e.g.*, “OK Google”, “Hey Siri”, or “Hey Cortana”), but to our knowledge this is the first time this approach has been applied to birdsong. Of the resulting song files, only those with a duration greater than one second were retained, removing calls or exceptionally short songs from the analysis. Once separated, individual song files were digitally filtered (removing sounds outside the range 0.3-8 kHz) and then analyzed using the *seewave* package (Sueur et al. 2008) in *R*. In total, we processed and segmented 5,933 recordings.

There are many potential sources of uncertainty that could affect any global analysis of birdsong, particularly one relying on an automated detection algorithm. These potential challenges include background noise, different recording standards, difficulty isolating the

start/end of a song, and differentiating between a song and a call. To verify that our pipeline was not biasing our results, we manually examined a subset of our data and report repeats of all spatial and PGLS analyses conducted across this subset (see below and Supplementary Materials 7 and 8, respectively). To do this, a random song segment was selected from each species and manually verified: if any excessive or variable background noise, such as another bird species, was detected, the file was discarded and a new random sample was analyzed. We performed manual verification by listening to the song segment and examining its spectrogram by eye, and (as with the results we present here) used the *seewave* package (Sueur et al. 2008) to analyse the songs themselves. For 21 species (4.2%), we were unable to find a clean exemplar, usually due to having only one recording for the species.

There are additional sources of error in our machine learning pipeline that we do not explicitly address. First, the meta-data on Xeno-Canto, like all data, is imperfect, and we cannot guarantee that a bird's song was not misclassified as a call by its recorder. Second, the pipeline may merge songs and calls within a single recording. Those wishing to replicate our approach should be mindful of these limitations, which may be mitigated by careful manual curation of recordings. In all science there is a trade-off between sample size and sample quality. Each investigator must decide for themselves whether the increase in sample size possible with automated approaches outweighs the potential decrease in sample quality in comparison with manual curation.

To characterise song spectral structure, we used two measures of the central tendency of pitch: mean frequency (kHz) and peak frequency (the frequency at which the amplitude was highest). Mean and peak frequency were highly correlated ($r = 0.906$; $p < 0.001$); as mean frequency is more sensitive to varying frequency bands of background noise, we retained only peak frequency for further analysis. To assess song complexity, we evaluated seven alternative

metrics: standard deviation of the frequency, inter-quartile range of the frequency, Renyi entropy, Shannon entropy, temporal entropy, spectrotemporal entropy, and total entropy (the product of the Shannon, Renyi, and temporal entropy). Measures of entropy calculate the information theoretic randomness of the spectral structure, with 0 being a pure tone and 1 being random noise, which is quantitatively similar to measuring the spread of the frequency, and thus it is unsurprising that all seven features measured are highly correlated (mean $r = 0.457$). We selected the standard deviation of the frequency as our proxy of song complexity for further analysis, again due to this measure's robustness to varying frequency bands of background noise, and because the peak and standard deviation of frequency demonstrated the lowest correlation coefficients in the dataset ($r_{5931}=0.0015$, $p=0.91$), and as such represent independent axes of song diversity. Having more unique notes and/or elements in a song would increase the standard deviation of frequency, making this an intuitive measure of biological complexity that is directly comparable across different bird songs. Further, since these metrics of song structure resemble those used widely in the birdsong research community (e.g., Deregnaucourt et al. 2005; Kirschel et al. 2009; Morton 1975), we were able to make strong *a priori* predictions on their expected variation across species in different environments. Other metrics of birdsong exist, and there is a wide variety of metrics that assess diversity, but peak and standard deviation of frequency are well suited to a study such as this as they are calculable, and directly comparable, across taxa.

Figure 1 gives two examples of how the two song metrics we focus on here (peak and standard deviation of frequency) quantify song character. A critical component of our metrics is that, while we suggest they do measure pitch and complexity reasonably well, they do not measure *information content* directly. For example, were a bird to produce a song that was entirely random white noise, it could have a reasonably high standard deviation of frequency but, by virtue of being random, would communicate essentially no information (see Shannon 1948).

We acknowledge this limitation of our study, and alternative metrics that capture information content (such as Shannon's entropy, which, in our data, was correlated with the standard deviation of the frequency) could reveal different patterns.

We averaged each metric across all songs for a species, providing a single estimate of peak and standard deviation of frequency per species. A variance decomposition analysis (following Crawley 2007) revealed that 68.8% and 58.5% of the variance in the peak and standard deviation of frequencies, respectively, is contained within these species-level aggregates. Thus these averages are fair representations of the underlying data.

Life History Comparative Analyses

To investigate the influence of morphological and life history traits on bird song, we aggregated data on body mass (using Wilman et al. 2014), sexual dimorphism and mating system (using Lislevand et al. 2007), and higher taxonomic membership (oscine vs suboscine). Sexual dimorphism was calculated as the ratio between male body mass (g) and female body mass (g). Mating system was coded as a binary variable with cooperative breeders and occasionally polygynous species ($\leq 15\%$ polygyny) considered monogamous, and mostly polygynous ($>15\%$ polygyny), polyandrous, and lek or promiscuous species considered non-monogamous. Sexual dimorphism and mating system represent two independent proxies for the strength of sexual selection across species. Of the species for which we had song data, we obtained estimates of body mass for 537 species, sexual dimorphism for 209 species, and degree of monogamy for 129 species. We fit models across only those species for which we had complete data (103 species).

Phylogenetic Generalized Least Squares (PGLS) regressions (Freckleton et al. 2002) were performed using the *pgls* function in *caper* version 0.5.2 for *R* (Orme 2013) with either peak frequency or standard deviation of the frequency as the response. Body mass, and sexual

dimorphism were natural-log transformed prior to analysis. In all cases, the maximum likelihood estimate of Pagel's λ (Pagel 1999) was used to correct for phylogenetic non-independence during model-fitting. To account for uncertainty in the phylogeny (Bollback 2005), each model was run over a random sample of 100 phylogenetic trees taken from the posterior distribution of the "Ericson All Species" bird phylogeny (Jetz et al. 2012). We report the mean (and standard deviation) values of all model coefficients across these phylogenies in the main text. Latin binomials were standardized to the Jetz et al. (2012) phylogeny. In the supplementary materials (8), we present qualitatively identical results from analyses using Pagel's δ (Pagel 1999), which tests for accelerating rates of trait evolution and is equivalent to an Ornstein-Uhlenbeck model of constrained evolution with a single optimum (Uyeda *et al.* 2015). We additionally repeated all analyses for the oscines and suboscines separately (also presented in Supplementary Materials 8).

Biogeographic Comparative Analyses

Ecological variation in geographic or environmental space can be explored using different, but comparable, methods that differ in the units of analysis (Gaston et al. 2008; Olalla-Tárraga et al. 2010). The first, referred to as a 'cross-species' or often 'comparative' approach, uses species as units of analysis and summarises environmental predictor information by averaging values within the geographic range of each species. The second, sometimes referred to as an 'assemblage' approach, uses spatial cells as units of analysis, and ecological or trait information is summarised by averaging the values across the species found within each cell. While these approaches have specific advantages and disadvantages (for discussion see Adams and Church 2011; Morales-Castilla et al. 2013), both need to account for autocorrelation, either among species (phylogenetic non-independence in the 'cross-species' approach) or among spatial units (spatial non-independence in the 'assemblage' approach). Here we employ both

methods as they can offer complementary perspectives. To take into consideration phylogenetic non-independence we used PGLS models (see above for details). To account for spatial non-independence we use spatial statistics. First, we inspected the significance of univariate relationships between the response variables (peak frequency and standard deviation of frequency) and predictors (mean annual temperature, net primary productivity, and species richness), adjusting the effective number of degrees of freedom following Dutilleul et al. (1993). We then checked for spatial autocorrelation in the residuals using Moran's *I*; in the absence of residual autocorrelation, OLS regression model coefficients can be considered reliable (Bini et al. 2009). If significant spatial autocorrelation in the residuals was detected, we re-examined the regression coefficients assuming spatially explicit simultaneous autoregressive model (SAR, Cliff & Ord 1981) to ensure that models were not misspecified.

Data on species' continental breeding ranges were obtained for 496 species from Hawkins et al. (2007) and overlaid onto a global Behrmann equal-area grid, comprising 12,639 cells of ca. 10,000 km². Environmental data were obtained from several sources: mean annual temperature was extracted from WorldClim (BIO1; Hijmans et al. 2005), values of annual Net Primary Productivity (NPP) were extracted from Imhoff et al. (2004), and elevation was computed from GTOPO at the 30 arc-seconds resolution (data available at http://www.ngdc.noaa.gov/seg/cdroms/ged_iiia/datasets/a13/fnoc.htm). In addition, we generated a separate layer representing total passerine species richness per cell (globally, not just those species retained in this analysis) as a proxy for biotic complexity/intensity. These environmental variables were either averaged across the geographic range of each species for the 'cross-species' analyses, or within each grid cell for the 'assemblage' analyses (for elevation, the 97.5th quantile was used as a proxy for the highest elevations within each grid cell, and the mean of these values across each species range was used for the cross-species analyses). Body size and the oscine/suboscine distinction were included as additional co-

variates to account for the influence of morphology on birdsong characteristics, as preliminary results showed it was an important driver of birdsong and body size shows strong phylogenetic and geographic biases. All biogeographic data processing and analyses were performed with R package *raster* version 2.5-2 for R (Hijmans and van Etten 2015). We also repeated all analyses on the oscine and suboscine clades separately, and present those results in the Supplement (Supplementary Materials 8).

We included net primary productivity (NPP) as a proxy of habitat complexity under the assumption that high primary production represents areas with increasingly dense and complex vegetation. Due to significant collinearity between NPP and mean species richness within species ranges, we ran separate PGLS models which included only one of these predictors at a time. However, because we believed species richness, independent of NPP, may increase competition for acoustic space, imposing selective pressure on birds to produce increasingly complex songs to prevent signal interference from other species (Wilkins et al. 2013), we included both richness and NPP as separate predictors in our assemblage-based models, where problems of collinearity were less. We included temperature in both cross-species and assemblage-based models as it is also thought important in structuring ecological relationships (Currie et al. 2004; Hawkins et al. 2003; Brown et al. 2004) and it demonstrates a strong latitudinal gradient.

Results

Of the ca. 5,100 passerine bird species for which we found phylogenetic data, we were able to download and extract song data for 578 (mean number of songs per species: 10.26, standard deviation: 16). We emphasise that the distribution of songs per species is right-skewed; our human-checked analyses of a single song per species suggest this unequal sampling does not bias our results. As described in the methods, our life history analyses are based on 103 species, while our biogeographic analyses are based on 497 species. In total, we analysed data from 5,933 songs (details of the songs analysed are given in Supplementary Materials 6); their general distribution on the phylogeny is shown in Figure 2. We emphasise that our results are on a limited subset of the passerines (~10%; see also Supplementary Materials 10), and as such our analysis is far from a definitive analysis of the evolution of birdsong in this clade. To demonstrate robustness of our results we have fit multiple statistical models to each response variable, and highlight confidence intervals around each parameter in all results tables. We report tests for spatial auto-correlation within the assemblage-based models in Supplementary Materials 11.

In the supplementary materials, we present two additional sets of analyses to examine the validity of our models. In the first (assemblage models in Supplementary Materials 7, PGLS models in Supplementary Materials 8,), we report models fit to a set of manually checked birdsongs (one per species). That these results are qualitatively identical to the results reported here suggests that (1) our machine learning pipeline has not biased our results and (2) variation in numbers of songs per species (see above) have not unduly affected our results. In the second set of analyses (PGLS models in Supplementary Materials 8, assemblage models in 8), we fit models to the oscine and sub-oscine passerines separately. As with the models we present here, these models support variation among the clades and, bar body mass (which varies between the clades), show qualitatively identical results to those we present here.

Comparative (PGLS) analyses

Results of the PGLS analyses using life history traits identified body mass as the single significant predictor of pitch (peak frequency), with larger bodied species having lower pitch (Table 1 and Figure 3). Pagel's lambda was estimated at $\lambda=0.024 \pm 0.046$, which indicates little phylogenetic signal in the residuals of the model. For models predicting song complexity (standard deviation of frequency), none of the included life-history trait predictors were significant (including body mass), although Pagel's lambda was estimated as $\lambda=0.772 \pm 0.045$ indicating moderate to high phylogenetic signal in the residuals.

PGLS models including biogeographic predictors again identified body mass as a significant predictor of pitch and additionally revealed suboscines as having, on average, significantly lower pitch than oscines (Table 1). However, none of the environmental variables were significant predictors of pitch either at the global scale or within Old or New World species when analyzed separately (Table 1). For song complexity, NPP was a significant positive predictor globally, and among both Old and New World species when analyzed separately. Body mass was a positive significant predictor of song complexity for New World species, but non-significant at the global scale and when Old world species were analyzed separately. When swapping NPP for estimates of mean number of species across the range (both of which were strongly correlated; see methods), we found similar trends, with more complex songs in environments characterised by higher species richness.

Spatial (assemblage) analyses

Results of analyses conducted at the assemblage level were not compromised by the effects of spatial autocorrelation (see online Supporting Information S3). Pitch and complexity showed clear geographical gradients, with higher pitch towards the poles and in mountainous regions, and with lower pitch in tropical regions, Africa, the Arabian Peninsula, and Australia (Fig. 3C).

In contrast, while song complexity is greater in the tropics it did not show such a clear latitudinal trend within temperate regions (Fig. 3D).

Species richness, together with two environmental variables (temperature and productivity) and body mass, explained ca. 50% variation in pitch both globally and for the Old World, and as much as 66% within the New World (Table 2). Temperature and productivity were consistently negatively associated with pitch, regardless of geographic context (Table 2), with lower pitch found in warm and productive environments (Fig. 4A-C). The relationship between pitch and species richness was more variable, showing a significant negative correlation only in the New World. This Old and New World difference is likely driven by patterns across Europe, where species tend to have moderate to high pitch and passerine richness is also high (see Fig. 3A). Assemblage-based models for song complexity had similar goodness-of-fit as the equivalent models for pitch, explaining over 40% of the variation in song complexity, but revealed a significant positive relationship with both NPP and temperature (Table 2; Fig. 4D-F), consistent with our cross-species analyses. Species richness was negatively correlated with song complexity at the global scale and within the Old World, but positively correlated within the New World (Table 2).

We note that the subset of species we analysed is biased towards European and Neotropical passerine species, and thus does not capture well the geographic distribution of all passerines (Figs. 3A & B). However, we found no indication that either pitch or complexity varied with sampling completeness (compare Figs 3A & B with Figs 3C & D).

Sensitivity analysis

Re-analyses conducted on data subsetting to account for recording quality revealed qualitatively similar relationships (see online Supporting Information S3), and additionally suggest that

biases in the spatial sampling of songs did not influence our results – for the assemblage level analyses results for both datasets were virtually identical.

Discussion

We explored the diversity of birdsong in passerines using one of the largest comparative datasets available, encompassing over 500 species in two major clades, the oscines and suboscines. There has been much interest in the evolution of bird song and song complexity, both within and across species (reviewed in Slabbekoorn and Smith 2002a; Podos et al. 2004; Podos and Warren 2007; Wilkins et al. 2013). Here we bring together data on key life history traits related to breeding systems (sexual dimorphism and mating system), body size, and species distributions, to examine evolutionary and spatial patterns in song pitch (peak frequency) and complexity (standard deviation in frequency). We find that body size alone can explain almost a third of the variation in pitch across passerines, irrespective of their geographic distribution (Old World versus New World). However, traits related to breeding system were not significant. In the New World, pitch was also negatively correlated with temperature: birds in colder regions had a higher pitch in their songs. When analysed separately, song complexity was independent of body size and traits related to breeding systems, but when taking into account environmental context we found that song complexity increased with environmental axes related to habitat complexity and with body size. Our results therefore indicate that birds with more complex songs tend to be larger and found within more complex landscapes.

The relationships between body size and pitch, and the importance of habitat complexity in the evolution of bird song have been discussed previously (Wiley and Richards 1978; Ryan and Brenowitz 1985; Boncaraglio and Saino 2007; Derryberry et al. 2012); however, we are aware of only a few studies that have attempted to address these relationships across such broad geographic and taxonomic scales (see e.g. Cardoso 2010; Weir and Wheatcroft 2011; Weir et al. 2012). We additionally demonstrate the importance of phylogenetic history in shaping

present day patterns of birdsong diversity, and thus the importance of controlling for phylogenetic non-independence when performing cross species comparisons. Significant phylogenetic structure in bird song has been alluded to previously, but again direct tests are sparse and often restricted to smaller clades (*e.g.*, Price and Lanyon 2002; Cardoso and Mota 2007; Seddon *et al.* 2008). Overall, our results provide further empirical evidence that aspects of passerine song are strongly subjected to evolutionary constraints. We emphasise, however, that we were only able to include approximately 10% of global passerines in our analyses; it is possible that patterns may change in the face of more data and, below, we argue that more data is required to truly disentangle differences between New and Old World passerines.

Perhaps most surprising in our results is the lack of a significant difference between suboscine and oscine song complexity (Table 1). Oscines are songbirds, and so one would imagine their songs would be more complex. There are a number of life history and biogeographic factors that affect birdsong and which vary across these two clades, by including these variables in our model, we may have thus explained much of the variation in song that otherwise distinguishes them. Ultimately, however, (P)GLS analyses such as ours may not be sensitive to ‘phylogenetic natural history’ questions of the kind that contrast the evolution of large clades (see Uyeda *et al.*, 2017). Equally, as discussed in the methods, our analyses focus on *complexity* and not *information content*. Perhaps oscines’ more musical vocalizations are not much more variable, but are more melodic – a component of song we do not assess here.

Life history and body size

Birdsong is often linked to sexual dimorphism (Nottebohm and Arnold 1976; Arnold 1992; Gil and Gahr 2002; Seddon *et al.* 2013, Price 2015), and so it is surprising to see no link between size-dimorphism and pitch or song complexity. However, size-dimorphism does not solely reflect sexual selection or female choice (Blondel *et al.* 2002; Székely *et al.* 2007); and while

size-dimorphism can be associated with mating system and parental care, plumage-colour dimorphism often better reflects female choice (Owens and Hartley 1998). While our data also does not support a link between monogamy and birdsong, it is possible that variation among individuals within species confounds results. For example, polygyny, while represented in our data as obligate, is often facultative (Lislevand et al. 2007), and we are ignorant of the mating syndromes of our sampled individuals. Perhaps most critically, it is possible that mating system and environmental conditions could interact; males may be sexually selected for clearer, less complex signals within dense vegetation, which we were not able to address due to a lack of data overlap between life history and biogeographic data. It also remains possible that the standard deviation of frequencies did not adequately capture variation in song complexity; if so, more work is needed to define metrics that are comparable and definable across diverse taxa and song types.

Contrasting with the null relationships found with mating system, we show a strong negative correlation between body mass and pitch (peak frequency). Across many species the lowest possible frequency for vocalisation reflects fundamental biomechanical limitations of body size (Fletcher 2004; Huber and Podos 2006); our results supporting this relationship are therefore reassuring, if not unexpected. That we found mixed relationships between body size and song complexity (standard deviation of frequency) is perhaps more surprising; birds with larger beaks (beak size is strongly correlated with body size; Benkman 1991; Symonds and Tattersall, 2010) have a lower song pace (Derryberry et al. 2012), although slower song pace does not necessarily imply a less complex song. The lack of a significant association between body mass and song complexity in the Old World perhaps reflects a better sampling of New World birds in our analyses.

Biogeography: habitat complexity, temperature, and species richness

We found that environment was generally a stronger predictor of variation in bird song than our measures of bird morphology (excluding body size) and life history. Birdsong is often used for communication with conspecifics at long distances of 50 - 200 m (Wiley and Richards 1982), and there are obvious fitness advantages derived from effective transmission of vocal signals. To be heard by conspecifics, a song may therefore have to travel long distances with little attenuation, but also remain distinct from songs of other species to allow identification of conspecifics. In nature, environmental factors, such as habitat structure, competing noise, and atmospheric conditions, can have large influence on song transmission (Brumm and Naguib 2009). Sound attenuation depends predominantly on frequency, with lower frequencies propagating further distances due to decreased absorption by molecular vibrations (Wiley and Richards 1978, Wiley 2009). Different frequencies are absorbed, reflected, and refracted by different sized objects in their path (Wiley and Richards 1978). In a meta-analysis of bird song and habitat complexity, Boncoraglio and Saino (2007) reported that complex habitats select against higher frequencies, albeit weakly. We revisited these relationships in our data.

In our cross-species analyses we found that pitch was significantly predicted by body mass and membership of either the oscine or suboscine clade (as also found by Seddon 2005 and others). The oscine and suboscine clades can be distinguished on the basis of their vocal tract anatomy (Suthers, 2004), and so these results emphasise the potential importance of morphology in shaping the evolution of song. Equally, however, oscines generally learn their songs while suboscines do not (Touchton et al. 2014), and so it is possible that this pitch change is associated with song learning. Below we also discuss how differing environmental affinities might affect the clades' song pitch and complexity. We do not find important differences in the phylogenetic signal (phylogenetic signal is greater in the suboscines, but still greater than 0 in

both clades) of our song metrics in these clades (Supplementary Materials 8), which is consistent with (but does not prove) similar degrees of evolutionary constraint between the two clades. However, assemblage-based models identified robust negative relationships between pitch and both NPP and temperature. These results support similar findings at smaller scales suggesting that lower pitches are more often found in complex or closed environments—the Acoustic Adaptation Hypothesis—(Blumenrath and Dabelsteen 2004; Boncoraglio and Saino 2007, Tobias et al. 2010). Differences between cross-species and assemblage-based models might reflect either how data were aggregated in each method, or perhaps indicate species sorting across the landscape independent of evolutionary history, which we discuss further below.

We do find differences in the magnitude (and, in some cases, sign; see Supplementary Materials 7 and 8) of coefficients for life-history and biogeographic traits between oscines and suboscines. We are, however, reticent to ascribe too much importance to these differences. The suboscines are restricted to the New World, and as such apparent differences in response to environment may be artefacts of the environments to which they are exposed. For example, suboscines experience a more limited range of environmental conditions, and so we have less data to assess their responses to environmental gradients. Equally, true differences in habitat affinity (such as suboscines being more prevalent in dense forest) could lead to spurious clade-level differences by virtue of the impact of the drivers we have already identified on birdsong.

In both cross-species and assemblage-based analyses we showed song complexity increased with NPP and temperature (see Fig. 4). If NPP is positively associated with habitat complexity, as we suggest above, these results differ somewhat to previous work pointing towards lower song complexity in more complex environments. For example, Irwin (2000), found increased song complexity in more complex environments. For example, Irwin (2000), found increased song complexity at high latitudes, and Weir and Wheatcroft (2010) showed greater rates of

increase in syllable diversity (increased complexity) at high latitudes. This trend was also supported by the meta-analysis of Boncoraglio and Saino (2007), which provided some evidence that song complexity decreases with environmental heterogeneity and habitat complexity. It is possible, therefore, that our measure of NPP might be a better indicator of local species richness (*e.g.*, Rosenzweig 1995; Mittelbach et al. 2001), and that increased song complexity is driven more by increased competition for acoustic signal space (Nelson and Marler 1990; Brumm and Naguib 2009). Whilst we attempted to disentangle the effect of NPP from species richness in our assemblage analyses, results were sensitive to the data subset examined, and the resolution of our species richness data, which is derived from overlaying range-maps, may be insufficient to reliably differentiate between the two predictors. This, perhaps, explains the tendency of the sign of the association between our predictor variables and species richness to switch (positive or negative) when modelled in the Old and New World. Further, these switches could be related to a relative lack of tropical species within the Old World in our dataset (see Fig. 3A).

In keeping with our life history analyses, we also found that complexity was significantly positively correlated with body mass in the new world at the cross-species level, perhaps reflecting a link between increased neural capacity (larger birds tend to have larger brains) and greater song repertoires (Garamszegi et al. 2004). That a similar relationship was not apparent in the Old World might reflect differences in sampling or clade differences between oscines and suboscines, which differ in their mode of song acquisition (Kroodsma and Miller 1996; Beecher and Brenowitz 2005). Interestingly, song complexity increases with decreasing average body size at the assemblage level, both in the New and Old world (see Appendix S3 in Supporting Information). Nevertheless, we caution that body size and environmental conditions are often correlated in birds (*e.g.*, Bergmann's rule; Meriri & Dayan 2003), and we do not have the data to definitively disentangle these two potential drivers of birdsong.

Contrasting spatial and phylogenetic patterns and approaches

We explored two separate analytical frameworks, evaluating relationships across species whilst controlling for species evolutionary relationships, and across space taking into consideration spatial autocorrelation. By integrating over these frameworks it is possible to gain new insights that neither method alone is able to provide (Freckleton and Jetz 2009; Safi and Pettorelli 2010; Olalla-Tárraga et al. 2010; Adams and Church 2011). While consistent patterns in both approaches would suggest strong evidence for the underlying hypothesis, different patterns between ‘cross-species’ and ‘assemblage’ analyses can help identify new processes or potential biases. For example, both approaches identified negative associations between song pitch and environmental predictors (temperature and productivity) but they were only significant in the spatial approach. Both methods also detected a positive association between song complexity and productivity, but this was only significant for the New World in the cross-species analysis. That the two methods differed in significant predictors might, in part, reflect sampling biases in the taxonomic and spatial coverage of included passerine species: most of the Old World passerine species in our dataset are found in Europe; the tropical latitudes are under-sampled thus shortening both the temperature and productivity gradients in this geographic region.

Both approaches have strengths but also limitations. Cross-species analyses may, but need not necessarily (see Ives et al. 2007; Ives & Helmus 2011), over-simplify spatial data by summarizing them to a single measure for each species (Morales-Castilla et al. 2013). In turn, assemblage-based analyses can inflate effect sizes and overlook how the evolutionary relationships among species may have left an imprint on their spatial distributions (Freckleton et al. 2002; Freckleton and Jetz, 2009). We emphasise here how the two approaches may provide complementary information, and encourage their joint use: our assemblage-based results suggest that factors such as NPP and species richness are likely affecting birdsong, but

their lack of significance in the cross-species analysis suggests that more work is needed to both confirm this and disentangle the influence of these factors. Recent efforts suggest potential for combined approaches (*e.g.*, Freckleton and Jetz, 2009; Morales-Castilla et al. 2013; Kaldhusdal et al. 2015) that were, unfortunately, not computationally tractable in our case, but nonetheless offer exciting possibilities for the future.

Data quality and processing

Descriptions of species traits' and distributions across global scales offer powerful insight into the processes that shape diversity. By necessity, such macro-scale analyses are often based on noisy or coarse data; nonetheless, their synthesis across species and geographic scales can stimulate the formulation of novel hypotheses and theory. Our analyses used citizen science data on bird song from the Xeno-Canto database (<http://www.xeno-canto.org/>). This remarkable database represents one of the largest single sources of bird song globally. Working with data from Xeno-Canto is particularly challenging due to problems associated with: (1) species identification and the potential for intra-specific variation, and (2) recording conditions, but we believe our results are robust for the following reasons. (1) Our species-level estimates explain ~68% and ~58% of the total variance in peak and standard deviation of frequency, respectively. This suggests both that ignoring intra-specific variation is a reasonable simplification, and that species identifications are likely consistent (even if not always correct). (2) Local environmental conditions like weather and humidity affect sound recordings, which (despite our use of only the highest-quality of recordings) could confound our analyses. That we detect the expected relationship between body mass and frequency (see Figure 3 and Table 1; Fletcher 2004; Derryberry et al. 2012) suggests we retain the power to detect ecologically relevant signal in our data.

To ensure that our machine learning pipeline did not introduce additional bias to our analysis, we repeated our analysis on a manually verified subset of the data, in which we found qualitatively identical relationships. Our use and release of open source software allows others to easily replicate our analyses and make different choices with regard to data quality and inclusion. We hope that, in the future, others will improve upon what we acknowledge is very much a first-pass attempt at automated recognition of birdsong from noisy but readily available data.

Summary

We find that environmental factors and body mass are stronger drivers of bird song pitch and complexity than life history traits representing sexual dimorphism or mating strategy. The ability for a song to be heard and recognized by conspecifics is shaped by the biotic and abiotic environment, and these constraints may therefore be more important in determining global patterns of bird song diversity, than mating strategy (Tobias et al. 2010). We suggest that songs increase in complexity with increasing intensity of biotic interactions and/or habitat complexity (measured through primary productivity) both across species and in space. It is our hope that, by providing tools to make use of citizen science data, our study will facilitate further analyses of bird song diversity and evolution.

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Tables

Table 1. Comparative analysis of bird song, controlling for phylogenetic non-independence using Phylogenetic Generalised Least Squares. All values are reported as mean value for each parameter (estimate, standard error, etc.) \pm the standard deviation of that parameter across all 100 bootstrap phylogenies. Note that all the suboscines in our analysis are restricted to the New World, thus we could not compare the oscine and suboscine clades in the Old World analyses.

	Frequency peak					Frequency std. dev.					
	Estimate	Std.	Pr(> t)	<i>R</i> ² <i>adj</i>	λ	Estimate	Std.	Pr(> t)	<i>R</i> ² <i>adj</i>	λ	
		Error		(%)			Error		(%)		
Life history traits: global	Intercept	6.606 \pm 0.077	0.858 \pm 0.039	0.000 \pm 0.000	4.291 \pm 0.0236	0.024 \pm 0.046	1072.071 \pm 21.519	156.764 \pm 6.189	0.000 \pm 0.000	22.591 \pm 0.772	0.772 \pm 0.045
	Log(body mass)	-0.831 \pm 0.012	0.161 \pm 0.002	0.000 \pm 0.000			29.429 \pm 0.819	43.09 \pm 0.239	0.496 \pm 0.009		
	Sexual dimorphism	1.311 \pm 0.107	0.915 \pm 0.009	0.158 \pm 0.034			501.405 \pm 3.096	297.497 \pm 0.343	0.095 \pm 0.002		
	Monogamy	0.487 \pm 0.021	0.276 \pm 0.003	0.081 \pm 0.013			62.173 \pm 9.609	86.936 \pm 0.116	0.479 \pm 0.071		
	Suboscine	-1.547 \pm 0.063	1.016 \pm 0.054	0.132 \pm 0.020			203.112 \pm 13.676	123.838 \pm 11.762	0.11 \pm 0.062		
	Biogeographic traits: global	6.312 \pm 0.066	0.585 \pm 0.024	0.000 \pm 0.000	3.000 \pm 0.122	0.122 \pm 0.050	1089.834 \pm 28.728	125.835 \pm 13.818	0.000 \pm 0.000	11.704 \pm 0.373	0.373 \pm 0.038
	Log(body mass)	-0.685 \pm 0.007	0.087 \pm 0.001	0.000 \pm 0.000			20.709 \pm 1.923	23.09 \pm 0.475	0.372 \pm 0.052		
	NPP	0.000 \pm 0.000	0.000 \pm 0.000	0.849 \pm 0.038			0.332 \pm 0.005	0.088 \pm 0.001	0.000 \pm 0.000		
	TEMP	0.000 \pm 0.000	0.001 \pm 0.000	0.837 \pm 0.045			0.164 \pm 0.024	0.214 \pm 0.001	0.447 \pm 0.062		
	Suboscine	-1.284 \pm 0.059	0.579 \pm 0.024	0.027 \pm 0.004			2.889 \pm 24.087	109.191 \pm 22.104	0.834 \pm 0.198		
Old World (contrast)	0.004 \pm 0.017	0.221 \pm 0.004	0.952 \pm 0.040			122.250 \pm 3.270	107.781 \pm 1.117	0.257 \pm 0.011			
New and Old (contrast)	0.452 \pm 0.013	0.384 \pm 0.002	0.240 \pm 0.014			140.879 \pm 4.802	55.946 \pm 3.31	0.014 \pm 0.006			

Biogeographic traits:		6.709 ±	0.631 ±	0.000 ±		1388.344	122.087	0.000 ±	
		0.065	0.027	0.000	0.122	± 15.766	± 6.889	0.000	0.607
Old World	Intercept				2.878 ±			17.589 ±	
					0.122	0.033		± 0.607	0.049
	Log(body mass)	-0.808 ±	0.118 ±	0.000 ±		-39.019 ±	29.486	0.188 ±	
		0.009	0.002	0.000		1.621	± 0.435	0.015	
	NPP	0.000 ±	0.001 ±	0.491 ±		0.344 ±	0.14 ±	0.015 ±	
		0.000	0.000	0.071		0.012	0.001	0.003	
	Temperature	0.000 ±	0.001 ±	0.618 ±		0.190 ±	0.251 ±	0.451 ±	
		0.000	0.000	0.056		0.025	0.001	0.053	
Biogeographic traits:		6.045 ±	0.447 ±	0.000 ±		891.853 ±	126.984	0.000 ±	
		0.004	0.023	0.000	0.002	5.898	± 3.039	0.000	0.003
New World	Intercept				7.066 ±			19.458 ±	
					0.002	0.011		± 0.003	0.028
	Log(body mass)	-0.550 ±	0.114 ±	0.000 ±		79.571 ±	32.337	0.015 ±	
		0.003	0.001	0.000		1.046	± 0.089	0.002	
	NPP	0.000 ±	0.000 ±	0.908 ±		0.254 ±	0.105 ±	0.017 ±	
		0.000	0.000	0.007		0.003	0.000	0.001	
	Temperature	-0.001 ±	0.001 ±	0.420 ±		0.194 ±	0.348 ±	0.579 ±	
		0.000	0.000	0.010		0.002	0.000	0.003	
	Suboscine	-1.111 ±	0.215 ±	0.001 ±		73.591 ±	61.688	0.232 ±	
		0.003	0.038	0.005		2.031	± 7.579	0.058	

Table 2. Assemblage-based analyses of bird song complexity (n=496). OLS models for species peak frequency and species standard deviation of frequency globally, and separately in the New World and the Old World.

		Frequency peak				Frequency std. dev.			
		Estimate	Std. Error	Pr(> t)	R^2_{adj}	Estimate	Std. Error	Pr(> t)	R^2_{adj}
									0.439
Global	Intercept	0.029	0.006	0.000	0.514	0.040	0.005	0.000	
	Species richness	0.201	0.006	0.000		-0.241	0.006	0.000	
	Primary Productivity	-0.210	0.007	0.000		0.430	0.007	0.000	
	Annual Temperature	-0.451	0.007	0.000		0.064	0.007	0.000	
	Body mass	-0.123	0.006	0.000		-0.209	0.006	0.000	
<hr/>									
New World	Intercept	0.000	0.009	1.000	0.668	0.000	0.012	1.000	0.424
	Species richness	-0.067	0.015	0.000		0.140	0.020	0.000	
	Primary Productivity	-0.346	0.020	0.000		0.326	0.027	0.000	
	Annual Temperature	-0.574	0.017	0.000		0.188	0.022	0.000	
	Body mass	-0.302	0.011	0.000		-0.095	0.014	0.000	
<hr/>									
Old World	Intercept	0.040	0.007	0.000	0.495	0.050	0.006	0.000	0.500
	Species richness	-0.010	0.007	0.147		-0.092	0.006	0.000	
	Primary Productivity	-0.197	0.008	0.000		0.386	0.007	0.000	
	Annual Temperature	-0.487	0.008	0.000		0.144	0.007	0.000	
	Body mass	-0.131	0.007	0.000		-0.205	0.007	0.000	

Figure captions

Figure 1. Two example spectrograms from birds in the analysis. Time is on the horizontal axis, and frequency is on the vertical axis. Color indicates intensity, from blue (silence) to red (loudest). Arrows indicate the peak frequency (*i.e.*, the height of the darkest red location). White vertical bars indicate the SD of the frequency (*i.e.*, how much vertical spread there is in frequency across the song). The bird in the top row produces a song that covers a lower range of frequencies than the bird on the bottom row.

Figure 2. Peak frequency (kHz) and standard deviation of frequency mapped as continuous characters on a single posterior phylogeny from Jetz et al. (2012). Maximum likelihood estimation of the states at internal nodes was performed using the contrasts algorithm described by Felsenstein (1985) as implemented by the function *contMap* (Revell 2013) in the R package “*phytools*” (Revell 2012). Images from phylopic.org (under Creative Commons license). Note that estimates of phylogenetic signal (Pagel’s λ ; Pagel 1999) are given in Table 1 once body size, which we argue in the text and Table 1 is a driver of peak frequency, has been controlled for.

Figure 3. Scatterplot of peak frequency (kHz) as a function of body mass (g). Points are individual species estimates coloured by clade membership (Oscine or Sub-oscine). Regression lines are taken from the estimates in Table 1; the tendency for sub-oscines and larger-bodied birds to have a lower peak frequency of song can be seen.

Figure 4. Geographic patterns in species richness for the 496 passerine species included in the biogeographic analyses (A) in comparison with global species richness of 4150 species of

continental passerine species (B). Variation in our metrics of birdsong pitch (mean peak frequency) (C) and complexity (mean standard deviation of the frequency) (D) are also shown.

Figure 5. Scatterplots showing univariate assemblage-based relationships between mean peak frequency and mean annual temperature at the global scale with all explanatory variables in the spatial (assemblage) analyses. Lowess regression lines are shown in grey; points are semi-transparent to give an impression of density. Relationships between these variables in the Old and New World are shown in Supplementary Materials 9.

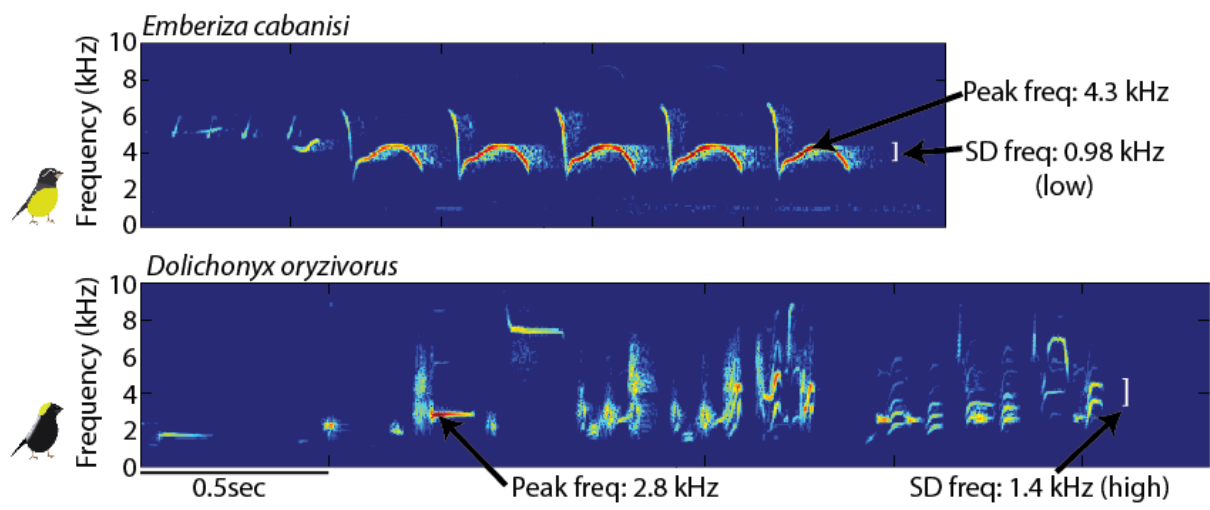


Figure 1

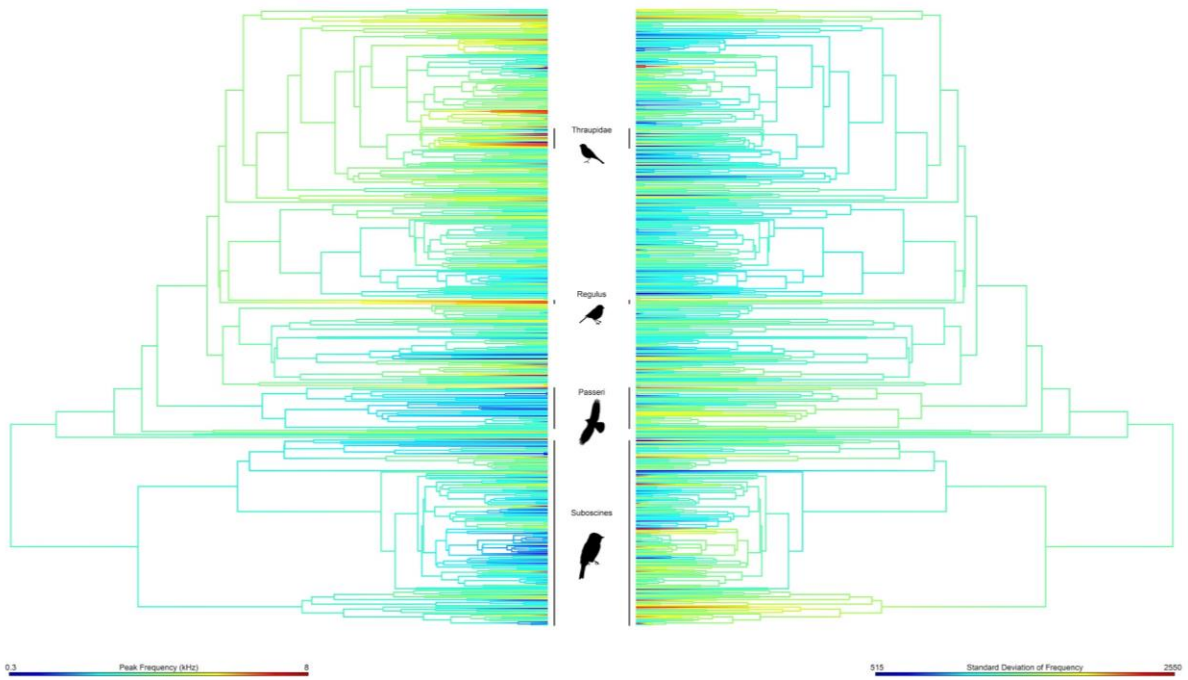


Figure 2

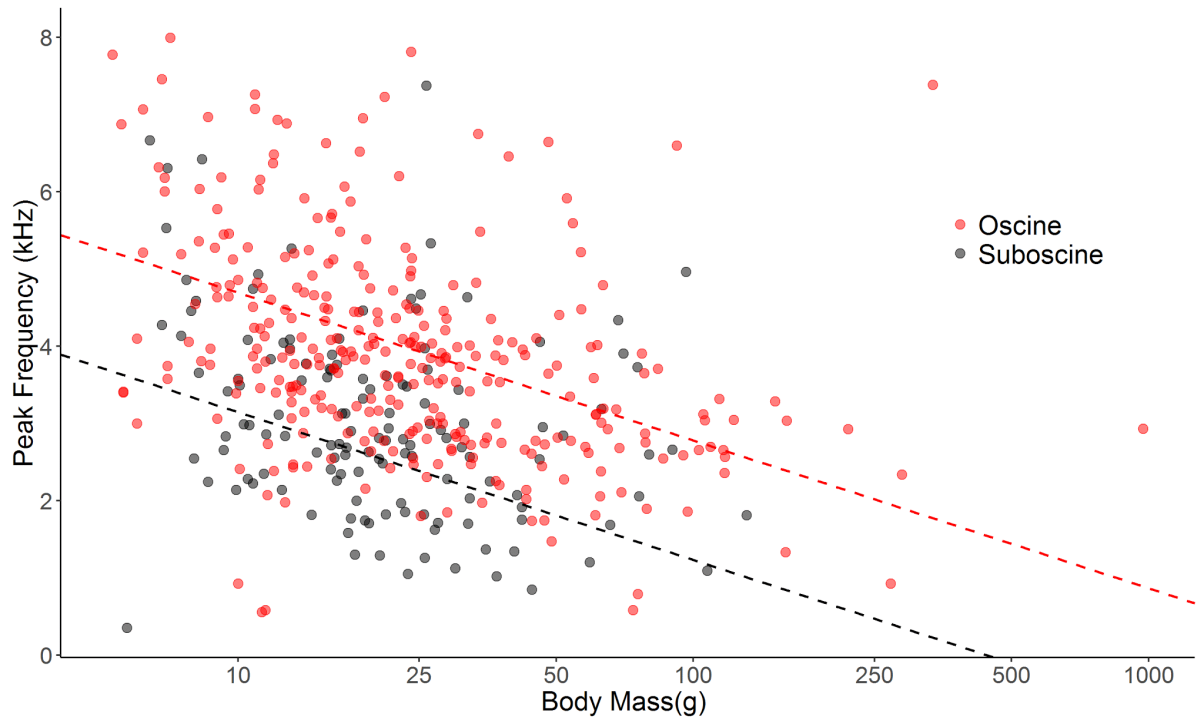
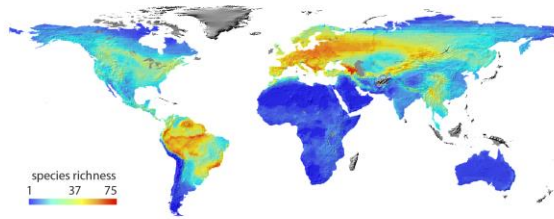
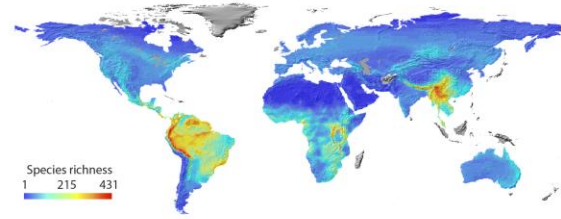


Figure 3

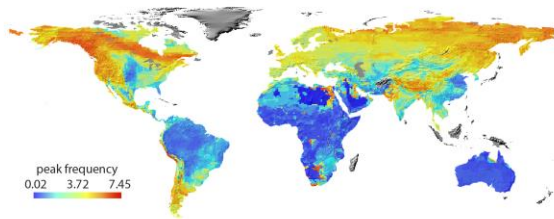
A) Passerine species richness in this study (n=496)



B) Continental passerine species richness (n=4150)



C) Mean peak frequency



D) Mean frequency standard deviation

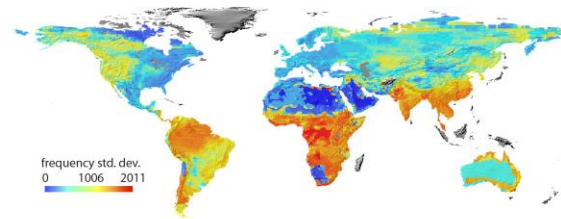


Figure 4

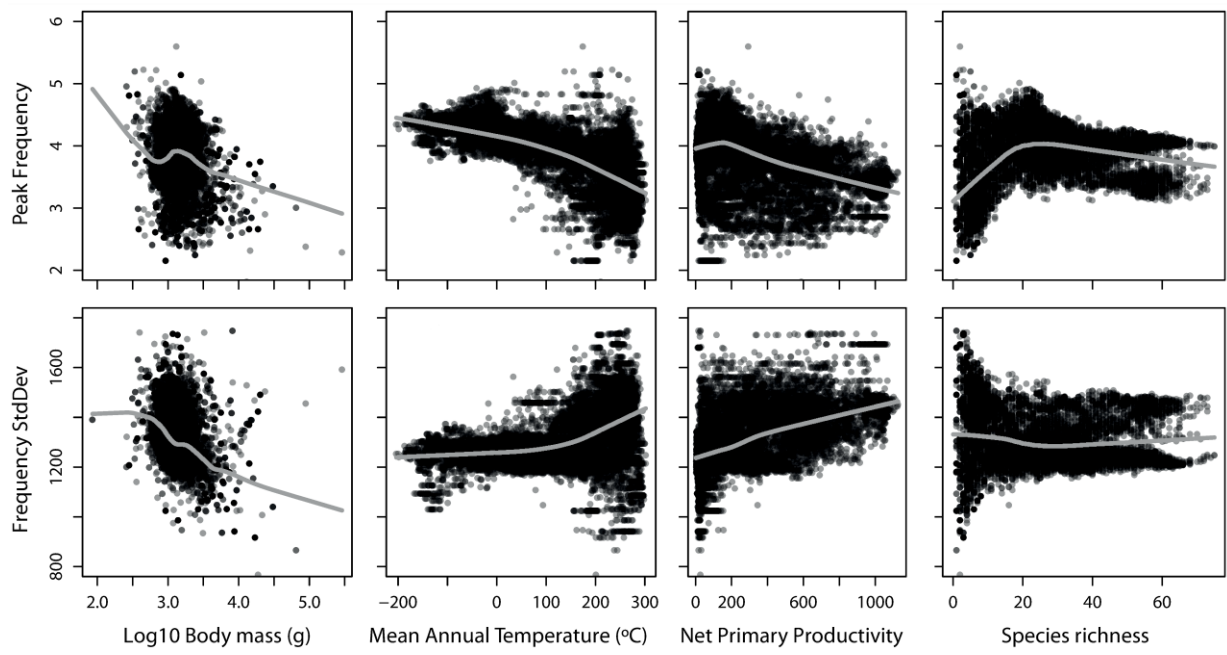


Figure 5