



# Allopatric montane wren-babblers exhibit similar song notes but divergent vocal sequences

Abhinava Jagan Madabhushi<sup>1,2</sup> · Ananda Shikhara Bhat<sup>1</sup> · Anand Krishnan<sup>3,4</sup>

Received: 27 April 2023 / Revised: 4 September 2023 / Accepted: 9 September 2023  
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2023

## Abstract

The songs of many passerine birds consist of notes temporally arranged into vocal sequences following syntactic structures and function both in courtship and territorial defense. Geographic barriers are important drivers of avian speciation and also influence the divergence of song. However, there is relatively little quantitative study of the relationship between geographic barriers and the syntactic structure of vocal sequences. Here, we investigate interspecific divergence in song notes and syntax within the allopatric montane Asian wren-babblers (*Spelaeornis*). Employing a quantitative analysis of note transitions and co-occurrence using song recordings from publicly accessible databases, we find that *Spelaeornis* appears to have undergone diversification in song syntax without divergence in note parameters. Broadly, we find three different syntactic structures across the eight species in the genus, each occurring in a different geographic region in Asia, with two species apparently exhibiting intermediate syntax. Species within the genus appear to possess similar song notes, but subgroups confined to different geographic regions (e.g., hills south of the Brahmaputra river) arrange these notes according to different syntactic rules to construct songs. Our computational framework to examine the signal structure and diversification across multiple scales of signal organization may help further our understanding of speciation, signal evolution, and, more broadly, fields such as linguistic diversification.

## Significance statement

In a genus of birds that live in montane habitats with no geographic overlap, we find that the individual building blocks of song, or notes, have not diverged across species. Instead, we find that species in different geographic regions construct song according to different rules, or syntax. We show that gaps between mountains can thus result in divergence in song syntax independently of divergence in song notes.

**Keywords** Syntactic structure · Vocal sequences · Geographic barriers · Montane birds · Wren-babblers

---

Communicated by H. Brumm.

---

✉ Anand Krishnan  
anandk@jncasr.ac.in

<sup>1</sup> Department of Biology, Indian Institute of Science Education and Research (IISER) Pune, Pashan Road, Pune 411008, India

<sup>2</sup> Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA

<sup>3</sup> Department of Biological Sciences, Indian Institute of Science Education and Research (IISER) Bhopal, Bhauri 462066, Madhya Pradesh, India

<sup>4</sup> Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bengaluru 560064, Karnataka, India

## Introduction

Allopatric speciation, the process underlying the formation of new species by geographic isolation, has long been a subject of research interest (Price 2007). Geographic barriers such as rivers, mountains, oceans, or valleys can reproductively isolate populations of a species, thereby preventing gene flow. This, over time, results in the accumulation of genetic differences, such that the two species remain isolated from each other on secondary contact (Irwin et al. 2001). The initial reproductive isolation may be reinforced by pre-mating isolation mechanisms such as temporal separation of breeding periods (Hillis 1981; Marshall and Cooley 2000), divergent habitats (ecological isolation) (Egan and Funk 2009), morphological differences (mechanical isolation)

(Richmond et al. 2011), and behavioral differences (behavioral isolation) (Marler and Slabbekoorn 2004; Uy et al. 2018). Of these, the last is particularly relevant to organisms that learn behavioral traits because learned behaviors may diverge relatively rapidly over evolutionary time owing to natural selection, sexual selection, or through neutral evolutionary processes (Lachlan and Servedio 2004; Yeh and Servedio 2015). Understanding allopatric speciation thus requires a comprehensive understanding of how behaviors and sensory signals vary among close relatives and across geographic barriers.

Perhaps the best-studied learned behaviors in this regard are the complex, culturally transmitted songs of passerine birds. Learned songs exhibit complex structures that, among other communicative functions, support species recognition and minimize interspecific hybridization (Marler and Slabbekoorn 2004; Bradbury and Vehrencamp 2011). Each song consists of individual vocal units – notes or syllables – which are, in many species of passerine birds, ordered in complex temporal arrangements to form vocal sequences. This temporal arrangement is referred to as the syntax of the song, here referring specifically to how notes are arranged in a sequence and not to the meaning or context in which they are produced (Marler and Peters 1988; Kershenbaum et al. 2012; Fishbein et al. 2020). Syntax may follow a number of rules, including repetitive songs, repetitions of specific motifs, or highly complex songs consisting of a number of note types. Studies in diverse taxa (Searcy and Marler 1981; Searcy et al. 1981; Marler and Peters 1988; Isler et al. 1998; Briefer et al. 2013; Kershenbaum et al. 2016; Engesser and Townsend 2019) have suggested that both acoustic structure of individual notes and the syntactic structure of vocal sequences may play an important role in mate attraction, species recognition, and communication of context (Balaban 1988; Wanker and Fischer 2001; Charrier and Sturdy 2005; Dahlin and Wright 2012; Kershenbaum et al. 2012; Suzuki et al. 2018; Ciaburri and Williams 2019; Bhat et al. 2022). Thus, it is important to study acoustic signals at multiple hierarchical scales of organization to understand their evolution and function.

A number of studies have shown that geographic barriers exert potent influences on the structure of bird songs (Marler and Tamura 1962; Baker 2006; Baker et al. 2006; Podos and Warren 2007; Irwin et al. 2008; Kirschel et al. 2009; Grant and Grant 2010; Lachlan et al. 2013, 2016). In white-crowned sparrows, geographically separated populations exhibit different dialects (Marler and Tamura 1962), and the same pattern is observed in insular populations of birds separated from the mainland (Baker et al. 2006; Lachlan et al. 2013). Song structure could evolve by simple addition and deletion of new notes to the repertoire, through changes in the syntactic rules which dictate how songs are constructed (i.e., increased repetition of the same notes,

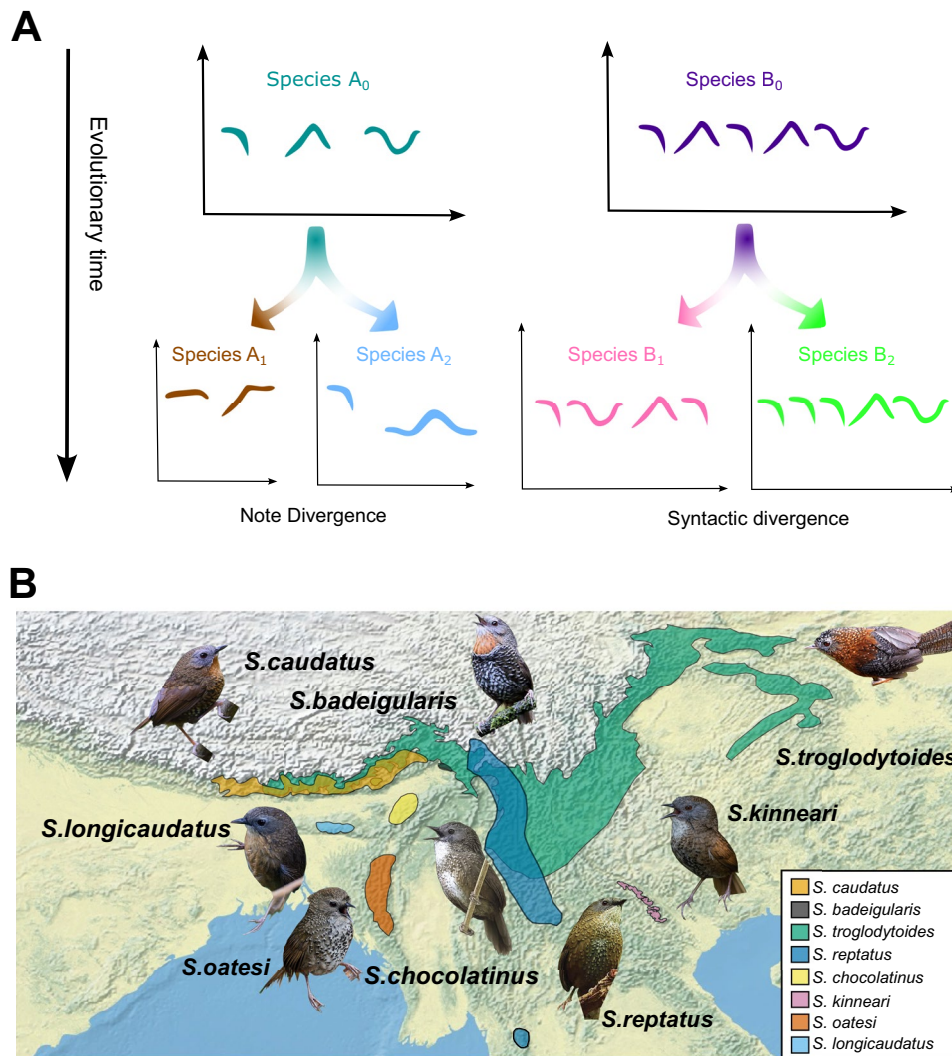
use of certain motifs), or through a combination of both these processes (Fig. 1A). Quantitative studies that examine both notes and syntactic structure of song in allopatric bird species are therefore needed to better understand the role of note change versus sequence change in the evolution of song. Such an approach would enable us to examine how syntax changes across geographic barriers in comparison to divergence in note structure. For example, do geographically proximate species exhibit similar syntactic rules but different notes, or different syntactic structures with or without note change? Given the parallels between bird song and human language (Hunt 1923; Doupe and Kuhl 1999; Salwiczek and Wickler 2004; Berwick et al. 2011; Miyagawa et al. 2013; Collier et al. 2014; Henry et al. 2015; Sainburg et al. 2019), such research provides insight into the influence of geography on human language evolution, specifically the role of cultural drift in trait change at shorter time scales (Lachlan and Servedio 2004).

*Spelaeorinis* is a genus of montane understory birds from Asia (del Hoyo et al. 2014) occurring from the Himalayas to Southeast Asia (see “Materials and methods,” Fig. 1B) (IUCN 2019). They thus present a good system to comparatively examine how the vocal sequences evolve across geographic barriers between hill ranges. Here, we quantitatively examine the syntactic structure of vocal sequences as well as the parameters of song notes in this genus. Specifically, we first ask whether individual song notes vary between species. Secondly, we quantitatively analyze the syntactic structure (here, we refer to the temporal arrangement of notes within a song, or the structure of a vocal sequence) of *Spelaeorinis* songs to address whether different allopatric species exhibit distinct vocal sequences, arranged according to different rules. We also hypothesized that geographically proximate species possess similarities in their syntactic structure and vocal sequence content. Our study thus examines how geographic barriers influence diversification in complex learned signals across multiple organizational scales.

## Materials and methods

### Study species

The genus *Spelaeorinis* consists of eight species of allopatric montane wren-babblers – *S. caudatus*, endemic to the Eastern Himalayas, *S. badeigularis* of the Mishmi Hills in India, *S. troglodytoides* that replaces other *Spelaeorinis* species at higher elevations, *S. chocolatinus*, *S. oatesi*, and *S. longicaudatus* of hill ranges south of the Brahmaputra river, and *S. kinneari* and *S. reptatus* from Southeast Asia (Fig. 1B). These allopatric species are endemic to restricted ranges, replacing each other in wet montane forests (Rasmussen and Anderton 2005; Collar 2006; King and Donahue 2006; del



**Fig. 1** **A** Acoustic signal divergence may involve a divergence in the frequency-time parameters (acoustic structure) of individual notes (note divergence, left), and the rules followed to order these individual notes into a song (syntactic divergence, right). **(B)** Geographical ranges of the genus *Spelaeorinis*. The images of *Spelaeorinis* were sourced with permission from the Macaulay library (Cornell Laboratory of Ornithology, Ithaca, NY, USA) (ML101191261- Jon Irvine,

ML379201951- Anupam Nahardeka, ML379618361-Lakpa Tenzing Sherpa, ML378245821- Pranjal J. Saikia, ML213328961- Xiwen Chen, ML269988921- Ngoc Sam Thuong Dang, ML205760231-James Eaton, ML378358871- Firoz Hussain). Species ranges were sourced from the International Union for Conservation of Nature (IUCN 2019), and the figure was created in QGIS (Quantum GIS Development Team 2013; <http://qgis.osgeo.org>)

Hoyo et al. 2014). Many of these species are only known from a very small geographic area. Therefore, intraspecific variation is likely to be low, and our study focused primarily on interspecific variation and variation across geographic regions.

## Recordings

We sourced song recordings of the genus *Spelaeorinis* from multiple online song databases: the Macaulay library (<https://www.macaulaylibrary.org/>), Xeno-Canto (<https://xeno-canto.org/>), and AVoCet ([<https://xeno-canto.org/>\) \(see Supplementary information 1 for a full list of recordings, including recordist and location\). This dataset was curated to include recordings that were longer than 10 s in duration with relatively low background noise, and also to ensure that none of the recordings were duplicates from different databases \(i.e., recordings from the same person collected on the same date at the same location\). For purposes of sample size, we considered a “recording” as being all audio database files recorded by the same recordist on the same day. There were only 4 cases in our dataset where the same recordist recorded songs on different dates, and the vast majority of our dataset consisted of recordings](https://avocet.integrativebiol</a></p>
</div>
<div data-bbox=)

made at different times and by different people. Thus, although it is not possible to identify the number of individuals recorded from database recordings, our method was conservative in that it did not assume that each recording came from a separate individual. The recordings, as listed in the Supplementary information, also broadly represented a large part of each species' range, especially those with larger distributions. For many species with highly restricted ranges, we analyzed recordings from multiple locations within the small known geographic area occupied by each species. These locations are listed in Supplementary Data 1. Although there are limitations inherent in data sourced from online databases, we took care to maximize geographic coverage and to minimize the possibility of overrepresentation of certain recordings in our dataset. Our total sample for analysis was thus as follows: *S. caudatus*: 1864 notes, 244 songs analyzed from 28 recordings; *S. badeigularis*: 1358 notes, 253 songs from 14 recordings; *S. troglodytoides*: 1574 notes, 213 songs from 19 recordings; *S. chocolatinus*: 759 notes, 135 songs from 12 recordings; *S. reptatus*: 622 notes, 50 songs from 4 recordings; *S. kinneari*: 904 notes, 62 songs from 8 recordings; *S. oatesi*: 1561 notes, 219 songs from 14 recordings; *S. longicaudatus*: 940 notes, 156 songs from 11 recordings. Although our sample size for *S. reptatus* was small, it consisted of recordings from different parts of the species' range; however, we consider our analysis for this species as preliminary. As a whole, however, our sample sizes were in line with other studies that use similar datasets to examine geographic and interspecific variation (Searfoss et al. 2020; Soma and Brumm 2020), especially given the restricted geographic ranges of *Spelaeornis* wren-babblers.

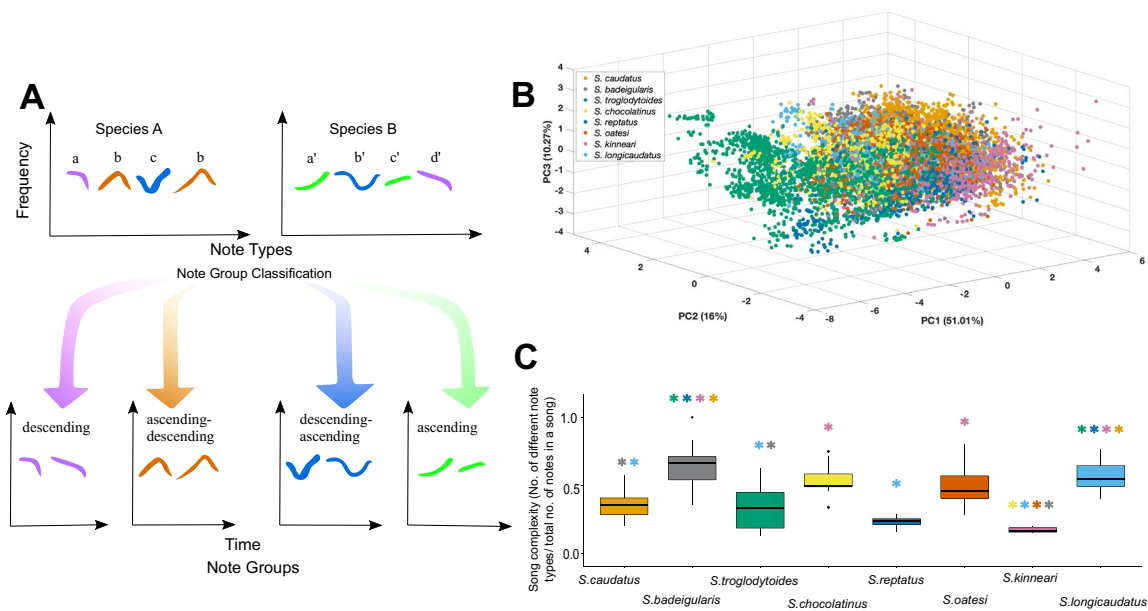
### Comparison of note parameters

Using Raven Pro Version 1.6 (Cornell Laboratory of Ornithology, Ithaca, NY, USA), we first digitized individual notes of each species and calculated 10 parameters that described the properties of each note: note duration, 90% bandwidth (difference between the frequencies containing 90% of energy in the power spectrum), peak frequency, minimum and maximum frequencies of the peak frequency contour, start and end frequencies of the peak frequency contour (these combined giving parameters of note shape), center frequency (frequency of 50% energy in the power spectrum), average entropy, and the time of maximum energy relative to the start of the note (peak time relative). Because of the potential for variation in database recordings, we selected peak frequency parameters as they do not vary as much according to the equipment used or the distance from the bird and are thus relatively robust. We then performed a principal component analysis (PCA) on the correlation matrix of these parameters to examine interspecific note overlap of *Spelaeornis* in signal space (the

Kaiser-Meyer-Olkin measure for this PCA was 0.78, which was adequate to proceed with this analysis). To quantify this overlap, we trained a Linear Discriminant classifier on the note parameters described above, using the Classification Learner app in MATLAB (Mathworks Inc., Natick, MA, USA) with 10-fold cross-validation, and assessed the accuracy with which notes were correctly assigned to the different species. We additionally performed a statistical randomization test of whether species overlapped more or less than expected by chance. For this, we randomly reshuffled data points across species, maintaining the sample size for each individual species (Chek et al. 2003; Luther 2009; Schmidt et al. 2013; Krishnan 2019; Chitnis et al. 2020). For each of the 1000 such randomized datasets, we calculated the average interspecific Euclidean distance (for the first three principal components) in signal space. Finally, we compared the observed average interspecific distance to the distribution obtained from the randomized datasets by computing a *Z*-score. If the song notes of *Spelaeornis* overlapped in signal space, the observed interspecific distance in the signal space should be less than that expected by chance alone, thus resulting in a negative *Z*-score.

### Classifying note types and note groups

Before analyses of song syntactic structure, we constructed sequences illustrating the temporal structure of each song. This required us to first classify song note types for each species based on differences in spectral structure and the parameters we measured (Fig. 2A). We verified these note type classifications in two ways: first, by measuring classification accuracy using a linear discriminant classifier as detailed above, and secondly, by cross-verifying the note classifications using a second observer in a double-blind paradigm. In a small number of cases, the classifier incorrectly assigned visually dissimilar notes to the same group, and we manually defined the notes as subclasses of the same note type in these cases. However, this was rare (three instances), and the combination of methods generally enabled us to reliably classify note types. We used these note types to calculate measures of song complexity (see below). However, note type classifications did not permit interspecific comparisons of syntax as the note types and diversity were not statistically comparable across species (subsequent analyses required that all species be compared within the same state space). We, therefore, also grouped notes into "note groups," which were consistent across species, based on their spectral shape (Fig. 2A). This enabled direct interspecific comparison of song syntax, as notes with minor variations in spectral structure or frequency were pooled into the same note group. As before, we verified note group classifications in a double-blind paradigm (i.e., a second author also scored note groups). Because this classification paradigm was used to examine



**Fig. 2** **A** Schematic representation of the framework followed to classify notes from different species into note types and note groups (see “Materials and methods”). Different note types of species A and species B are depicted by alphabets (top), and different note groups in each species are represented by different colors. **(B)** Three-dimensional signal space of *Spelaeornis* constructed using the first three principal components (PC 1–3) of the correlation matrix of 10 measured note parameters. *Spelaeornis* exhibits overlap in note param-

eter space. **(C)** Box plot depicting the song complexity metric across species in *Spelaeornis*. Boxes represent the interquartile range, the whiskers extend to 1.5 times this range, and the central line represents the median. Outliers are shown as black dots. Colored asterisks above each box represent the colors of the species that differed significantly from the species represented in the box. Further details are given in Supplementary Table S2

sequences in further analyses, we calculated Cohen’s kappa comparing the observed probability of agreement with the average expected probability of agreement (calculated as an average across 20 songs scored in a double-blind analysis). Across species, we thus hierarchically grouped notes, eventually resulting in nine note groups, abbreviated as letters in the relevant figures and tables. These were as follows: ascending (a), descending (b), ascending-descending (c), descending-ascending (d), ascending-descending-ascending (e), descending-ascending-descending (f), notes with constant frequency (k), complex notes with more than two inflection points and a total duration of less than 200 ms (g), and long complex notes with more than two inflection points and a total duration of more than 200 ms (l). To ensure that we had adequately sampled all the note types/note groups, we computed note accumulation curves for each species by randomizing the order of digitized notes for all songs.

**Syntactic analyses**

To examine and compare vocal sequences and syntactic structures, we employed a series of metrics calculated using both note types and note groups. Using the note type classifications, we first calculated a metric of song complexity (the number of different note types in a song divided by the total

number of notes in the same song). For each song (sample sizes above) for each species, we computed and compared the average values of song complexity for each recording (the unit “recording” defined above) using a Kruskal-Wallis test with a post-hoc Dunn test. Because further syntactic comparisons relied on species having similar sample spaces (i.e., the set of all possible notes that the species could emit), we used note groups as a unit in subsequent analyses for direct interspecific comparison. To examine song syntax in *Spelaeornis*, we constructed note group sequences for each song, for each species. We first modeled *Spelaeornis* song structure as a first-order Markov chain and constructed a transition probability matrix (*N*) for each species, where the *i*-*j*th entry of the matrix, *N*<sub>*ij*</sub>, represents the probability of transition from note group *i* to note group *j*. To further validate our analysis, we employed a co-occurrence metric which is free of Markovian assumptions (Bhat et al. 2022). This analysis is based on the premise that not all vocal sequences in animals may be Markovian (Kershenbaum et al. 2014), and it is thus important to cross-verify results without making underlying assumptions about the processes involved. Here, for a given set of note group sequences, we define <sup>*d*</sup>*C*<sub>*ij*</sub> as the probability that the note group *j* occurs within *d*-1 notes of note group *i*. We computed <sup>*d*</sup>*C*<sub>*ij*</sub> for song sequences for each species. Next, we constructed artificial

sequences where notes were randomly distributed following a stationary uniform distribution. Because we used a uniform distribution, the probability of a note occurring in an artificially constructed sequence was given by the proportion of occurrence of that note in the species' song (obtained from real data). We generated 50 such artificial sequences to compute a robust estimate of expected co-occurrence  ${}^dE_{ij}$ . Following this, we calculated the ratio of observed to expected co-occurrence,  ${}^dR_{ij}$ , defined as the ratio of  ${}^dC_{ij}$  to  ${}^dE_{ij}$  for each species.  ${}^dR_{ij}$  is a measure of whether note group  $j$  occurs within  $d-1$  notes of note group  $i$  more or less often than expected by chance alone.  ${}^dR_{ij} > 1$  suggests note group  $j$  occurs within  $d-1$  notes of note group  $i$  more often than expected by chance alone, and  ${}^dR_{ij} < 1$  suggests that  $j$  occurs within  $d-1$  notes of  $i$  less often than expected by chance alone. For the analysis reported in the "Results," we used a  $d$ -value of 4, but also repeated our analysis for  $d$ -values of 2 and 6 to ensure that our choice of  $d$  did not influence the observed patterns; previous studies also indicate that the choice of  $d$  does not change co-occurrence patterns in vocal sequences (Bhat et al. 2022). We chose to report results for a  $d$ -value of 4 because, on average, songs of *Spelaeornis* consist of 4–8 notes and a distance of 4 thus captures biologically meaningful note co-occurrence patterns.

To statistically compare transition probability matrices between species, it is necessary that all the Markov chains being compared share the same state space. Therefore, we added a pseudocount of 0.0001 to each entry of the  $9 \times 9$  transition matrix of each species (thus ensuring that all pairwise transition probabilities were non-zero, and the state space of every species comprised the nine possible note groups defined earlier; for visualizations of transition probabilities, we used the original matrices). We then computed the frequency of occurrence for each transition  $ij$  in each species' songs and added this to the pseudocount. This gave us a  $9 \times 9$  transition probability matrix for each species. Next, we employed a homogeneity test that computes a minimum discrimination information statistic (mdis) (Bhat et al. 2022). This statistic tests for differences in the distributions of transition probabilities between samples (in our case species) based on the Kullback-Leibler divergence (Kullback et al. 1962). The test statistic is asymptotically distributed as a  $\chi^2$  distribution with  $S(S-1)(r-1)$  degrees of freedom where  $S$  is the number of states of the Markov chain (in our case, the number of note groups, i.e., 9) and  $r$  is the number of different samples to be compared (in our case, number of species). We computed this statistic for a comparison of all 8 species, as well as pairwise between any two species.

Finally, to test for sequence similarity between species across geographic regions, we computed the pairwise Levenshtein distances between the vocal sequences of each species pair. We then computed a median Levenshtein distance for each species pair and constructed a distance matrix  $D$ , where

$D_{ab}$  represents the median Levenshtein distance between the song sequences of species  $a$  and  $b$ . Using this matrix, we constructed a distance dendrogram using the unweighted pair group method with arithmetic mean (UPGMA). Species closer together on this dendrogram possessed similar vocal sequence structures.

## Results

### *Spelaeornis* does not exhibit interspecific note parameter divergence

The first three principal components of 10 note parameters explained more than 77% of the variation in the notes of *Spelaeornis* (Supplementary Table S1). PC1 loaded moderately positively on all frequency parameters, whereas PC2 loaded positively on note duration and negatively on minimum peak frequency, and PC3 loaded positively on peak time and exhibited weak negative loading on average entropy.

Broadly, *S. caudatus* and *S. troglodytoides* occupy opposite ends of the three-dimensional signal space, encompassing all the note parameters of *Spelaeornis*. All other species of *Spelaeornis* heavily overlap with each other in between these extremes (Fig. 2B). This assertion was also supported by a randomization test (see "Materials and methods"). We found that the average interspecific distance in the note parameter space of *Spelaeornis* is much lower ( $Z$ -score =  $-40.248$ ,  $p < 0.001$ ) than expected by chance, as calculated from 1000 randomized datasets (see "Materials and methods"). Linear Discriminant Analysis further supports an overlap of notes in signal space. The LDA classifier correctly assigned notes to different species with an accuracy of only 55.8% (Supplementary Fig. S1). The notes of the species listed above, occupying opposite edges in *Spelaeornis*' signal space, were correctly classified at rates of 81.8% and 89.0%, respectively. However, these were the only two species with high classification rates: The classification accuracies for all other species were less than 60% (range: 11.6% for *S. reptatus* – 55.2% for *S. oatesi*) (Supplementary Fig. S1). Taken together, these statistical and quantitative analyses suggest that the song notes of *Spelaeornis* have not diverged in allopatry and that their songs have thus retained similar building blocks across their range, with notes overlapping in signal space more than expected by chance.

### Note types and note groups in *Spelaeornis*

We identified multiple note types in each species and verified these classifications using both linear discriminant classifiers and independent cross-verification by a second author with an average inter-observer agreement of 76.33%. The number of note types identified ranged from 6 to 21

across species (Supplementary Fig. S2), with classification accuracies ranging from 71.5% (*S. caudatus*) to 85.6% (*S. badeigularis*).

Because different species of *Spelaeornis* possess similar note parameters, as evinced by heavy overlap in signal space, we grouped notes into note groups for interspecific comparison based on spectral shape (see “Materials and methods”). The average inter-observer agreement in a double-blind note group classification paradigm was 77.75% (Cohen’s Kappa was 0.627, indicating substantial agreement between observers). Many note groups are shared across species, consistent with our interpretation of the interspecific overlap in signal space. The I note group, however, was unique to *S. troglodytoides* and was not observed in other species. Accumulation curves for all species for both note types and note groups were characterized by early saturation, providing evidence that our dataset reliably sampled the note repertoires in *Spelaeornis* (Supplementary Figs. S3 and S4).

### **Spelaeornis species differ in song complexity**

The song complexity of *Spelaeornis* exhibited significant interspecific differences (Kruskal-Wallis test,  $H = 57.05$ ,  $df = 7$ ,  $p < 0.001$ ). Qualitatively, we observed two groups, one consisting of species possessing lower song complexity (fewer note types as a proportion of song length) and the other comprising species with higher song complexity (higher number of note types as a proportion of song length) (Fig. 2C). We performed post-hoc pairwise comparisons using Dunn’s test, and 10 out of 28 species pairs exhibited statistically significant differences in song complexity (Supplementary Table S2). These differences are represented using colored asterisks in Fig. 2C. Thus, in spite of using similar building blocks (i.e., notes) in their songs, species of *Spelaeornis* differ in the complexity of these songs. This suggests that the temporal sequence or syntax of the songs varies between species, a possibility we next investigated using computational analyses of vocal sequence structure.

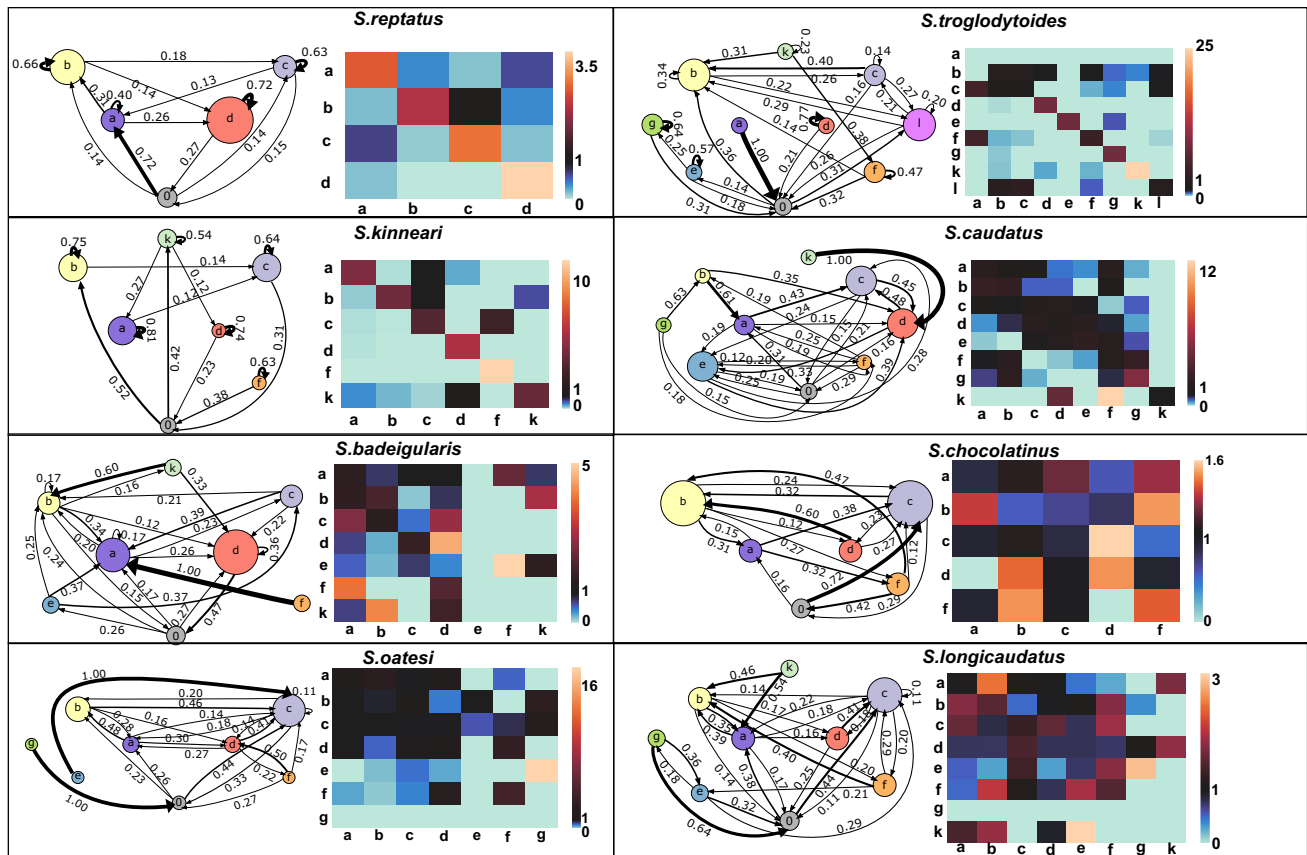
### **Syntactic divergence in the songs of Spelaeornis**

We employed a combination of first-order Markov chain analysis and a note co-occurrence analysis that does not assume a Markovian sequence structure (see “Materials and methods”) to examine the syntactic structure of *Spelaeornis* songs. As hinted at by the results of the song complexity analysis, we found that different species fell into three broad syntactic groups. *S. kinneari* and *S. reptatus*, both occurring in Southeast Asia, exhibited songs with relatively sparse inter-note transitions, with notes instead exhibiting a high tendency to repeat themselves. This was also borne out by the note co-occurrence analysis, where high probabilities of co-occurrence ( ${}^dR_{ij}$ ) were primarily along the diagonal

of the matrix, indicating that notes tended to co-occur with themselves more than other notes (Fig. 3). We defined this sequence structure as repetitive syntax. On the other hand, the songs of *S. caudatus* from the Eastern Himalayas consisted of 2 or 3 notes alternating with each other. This is represented by the reciprocating arrows between different nodes in Fig. 3, as well as the note co-occurrence matrix. Here, higher probabilities occurred both along the diagonal and with 1–2 other notes, indicating that each note type co-occurred with itself and one or two other notes. We defined this second syntactic type as alternating syntax. Finally, we also observed songs with complex syntax, primarily exhibited by *S. oatesi*, *S. longicaudatus*, and *S. chocolatinus* which occur in the hills south of the Brahmaputra River. In these species’ songs, each note group exhibited transitions to many different note groups, manifested as many arrows originating from each node in Fig. 3. In the co-occurrence matrices, probabilities were generally low and did not show any pattern of higher values either on- or off-diagonal, indicating that each note could generally co-occur with many other note types.

Two of the eight species (*S. badeigularis* and *S. troglodytoides*) in the genus exhibited evidence of intermediate syntactic types, employing a combination of the syntactic rules outlined above to order notes. *S. badeigularis* songs suggested an intermediate between repetitive and complex syntax, with high probabilities of transition to many different note groups in addition to having a relatively high probability of self-transitions (i.e., repetitions). An examination of the song sequences (Supplementary information) demonstrates multiple note groups in a single song, some of them repeating (unlike the other species with complex syntax). On the other hand, *S. troglodytoides* appears to use a combination of alternating and repetitive syntax, with some note groups tending to repeat and others alternating between each other. This species apparently uses either alternating or repetitive syntax in a song and not a combination of both (Supplementary information). The patterns described above are broadly consistent across different values of  $d$  (Supplementary Figs. S5 and S6), in keeping with the findings of other studies that have used the same analysis (Bhat et al. 2022). Similar patterns were also observed when considering note types instead of note groups (Supplementary Fig. S7). Our note group classification thus represents a valid means of interspecific comparison.

Using the aforementioned homogeneity test for Markov chains, we found that the transition probability matrices for different species of *Spelaeornis* differ significantly from each other ( $X^2 = 8061.23$ ,  $df = 504$ ,  $p < 0.001$ ). Pairwise species comparisons found that transition probability matrices differ for all species pairs (Supplementary Fig. S8). Furthermore, we also found that species exhibiting similar syntactic structure generally tend to have a smaller value of the test



**a- ascending; b- descending; c- ascending-descending; d- descending-ascending; e- ascending-descending ascending; f- descending- ascending-descending; g- complex; k- constant frequency; l- long complex**

**Fig. 3** Transition probabilities obtained by modeling note group sequences of *Spelaeorinis* as first-order Markov chains (left side on all the panels). Different colors represent different note groups (see key below the figure), and the size of the node is proportional to the frequency of occurrence in our dataset. The thickness of each arrow scales with increasing transition probabilities between note groups. The right side of all panels represents the ratio of observed to expected probability of co-occurrences for note groups for a value of  $d = 4$ . Warmer colors in the  $ij$ -th square on the matrix depict that note group  $i$  occurs with note group  $j$  more often than by chance. *S. kin-*

*neari* and *S. reptatus* exhibit repetitive syntax (more self-transitions and warmer colors along the diagonal in the co-occurrence matrix). In *S. caudatus*, we find alternating syntax (each note transitions into or co-occurs with 1–2 other note groups). *S. troglodytoides* exhibits some note groups with a higher propensity for self-transition and others showing alternation. *S. longicaudatus*, *S. oatesi*, and *S. chocolatinus* exhibit complex syntax, where each group can transition to many others with no discernible structure in the co-occurrence matrix. *S. badeigularis*, on the other hand, exhibits an intermediate between complex and repetitive syntax

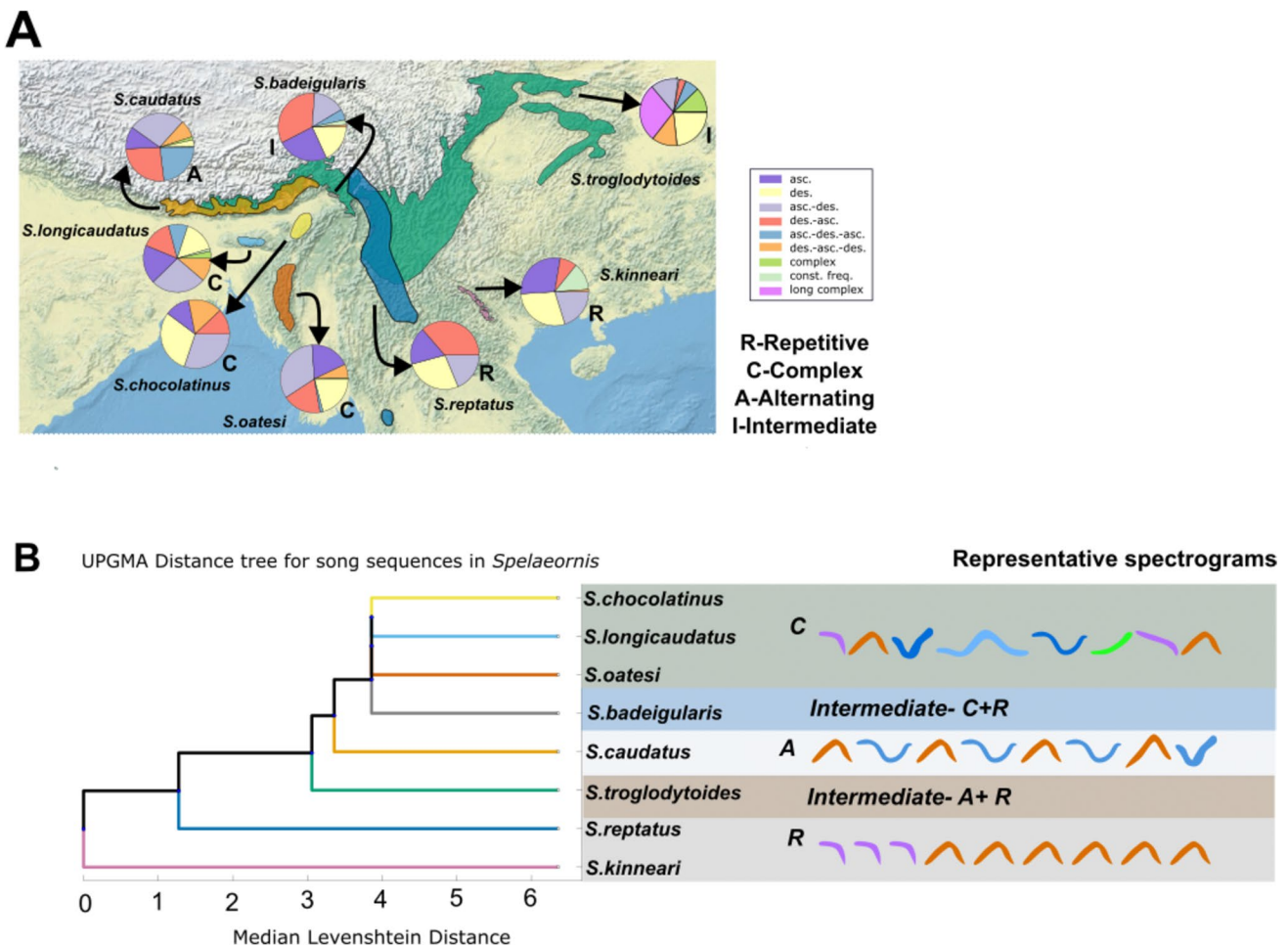
statistic when compared to species with different syntactic rules (Supplementary Fig. S8). Our analyses suggested that species of *Spelaeorinis* existing geographically closer to each other possess similar syntactic structure in their songs. Although the proportions of different note groups in the sequences analyzed differed across geographically proximate species (Fig. 4A), the syntactic rules employed to construct songs were conserved within each sub-region. We thus predicted that the vocal sequences of geographically proximate species should group together, i.e., exhibit greater similarity than those from different geographic regions. To further quantitatively examine sequence similarity across species, we calculated sequence similarity using the median interspecific Levenshtein Distance and constructed a distance

dendrogram using the UPGMA method (see “[Materials and methods](#)”). We observed that species geographically closer to each other are also closer to each other on the distance dendrogram (Fig. 4B), with intermediate species occupying more or less intermediate positions. This is consistent with syntactic diversification across geographic barriers in the absence of note divergence.

### Discussion

In summary, we found evidence that song notes in the genus *Spelaeorinis* remain more or less conserved across species, but are arranged into songs according to different





**Fig. 4** **A** Pie charts representing the proportions of different note groups across species in our dataset. Species geographically closer to each other exhibit similar syntactic structures (see alphabets), with changes across major geographic barriers. Note, in particular, the intermediate syntax of *S. badeigularis*, which occupies a junction between two major geographic regions. **(B)** UPGMA distance den-

drogram constructed using median Levenshtein distances between vocal sequences for each pair of species. Species with similar vocal sequences cluster together in this distance dendrogram and are also geographically proximate, as shown in the map. Also shown here are representative songs to indicate each syntactic type, schematics adapted from spectrograms of the actual recording for clarity

syntactic rules based on the presence of geographic barriers. We identified three broad syntactic groups, occupying the Eastern Himalayas, the hills south of the Brahmaputra river, and Southeast Asia, respectively. Within each of these regions, geographically proximate species exhibited similar syntactic structures in their songs, with only minor differences in the proportions of different note groups within their vocal sequences. Our analysis of note accumulation suggested that our sampling of the note group repertoires for each species is adequate, and therefore, we hypothesize that our results represent genuine interspecific changes in the syntactic structure of vocal sequences across geographic barriers. Because a variety of methods suggest that we have adequately sampled the note group repertoire in this genus, we believe that additional recordings will not significantly alter the pattern we observed,

particularly that of groups across biogeographic regions defined by vocal sequence structure.

Previous studies on interspecific song divergence have largely focused on differences in note parameters, or on broad, summarized metrics of song structure such as trill rate or song duration (Slabbekoorn and Smith 2002a, b; Haavie et al. 2004; Podos and Warren 2007; Irwin et al. 2008; Grant and Grant 2010; Tobias et al. 2010; Podos et al. 2013; Wilkins et al. 2013). Here, employing a combination of tools (Kershenbaum et al. 2012), including a robust computational analysis of note co-occurrence originally developed to study syntactic structure in anuran vocalizations (Bhat et al. 2022), we demonstrate syntactic diversification in the genus *Spelaeornis*. This implies that the rules by which notes are temporally arranged into songs have diversified across geographic barriers without significant change in the underlying notes

themselves. Our analytical framework enables us to compare temporal structure in diverse signals and thus investigate signal evolution from individual notes to syntax.

A potential caveat with database recordings is the geographical restriction in the obtained samples. This may be true in the case of *Spelaeornis*, especially given the restricted ranges of many species. However, the patterns we observe in the syntactic structure are consistent across species within a geographic region, suggesting that this method of sampling is adequate to address interspecific geographic variation in syntax. A second caveat is the possibility that certain recordings are overrepresented in the sequences as they are longer than others. This is likely the case for *S. reptatus*, which had the lowest sample size of all the species. However, patterns in syntax do not vary within a species (see Supplementary information 1 for example sequences), and each individual appears to produce relatively stereotyped songs. This consistency across recordings and locations suggests that our dataset is adequate for an interspecific comparison and that these caveats are unlikely to significantly alter our results. Finally, distinct song types with different syntactic structures may occur as rare songs in other species, particularly those such as *S. badeigularis* that occupy junctions between geographic regions (King and Donahue 2006; Praveen et al. 2022). However, the addition of rare song types is unlikely to significantly alter the salient pattern we observe, that of syntactic change across geographic regions without change in the underlying song notes. Therefore, the syntactic types we describe here likely represent the dominant forms within each geographic region.

Contrary to our initial predictions, we did not find any interspecific divergence in the note parameters in *Spelaeornis*. Instead, the overlap in signal space and a statistical randomization test suggest that *Spelaeornis* species use similar song notes. Taken together, our findings that species geographically closer to each other exhibit similar syntax, and also share note groups, point the way for future research to examine the behavioral role of notes versus syntax. *Spelaeornis* as a genus is very poorly studied, with some species going undetected for decades before being rediscovered (King and Donahue 2006). Phylogenetic studies did not include all species as there is relatively little material available. However, the most recent studies find that the Southeast Asian species and species South of the Brahmaputra (which were once considered a single species complex) (Collar 2006) all form a clade together (Cai et al. 2019), which is more or less consistent with the idea that syntactic groups and geographically proximate species also correspond broadly to phylogenetic groups. However, more research is required on this front, as well as on whether these species respond to each other's songs. Given the poor state of knowledge about these taxa, online song databases provide us with valuable data which, coupled with a rigorous

analytical framework, enables us to effectively examine questions about behavior and signal evolution. With so little known about the different hill ranges in the Himalayas and Southeast Asia, it is likely that undescribed species in this genus remain to be found (Praveen et al. 2022), and their songs may prove valuable in understanding the steps by which syntactic diversification of bird song has occurred.

The evolution and ontogeny of bird song exhibits many parallels to human languages (Doupe and Kuhl 1999; Salwiczek and Wickler 2004; Berwick et al. 2011; Miyagawa et al. 2013; Collier et al. 2014; Sainburg et al. 2019), and geography shapes the structure of human languages as well (Henry et al. 2015; Dunn 2019; Huisman et al. 2019; Urban 2021). In particular, bird song is also a culturally learned trait, with passerine species learning songs from their parents and local dialects (Marler and Tamura 1962, 1964). The presence of geographic barriers can, therefore, serve to isolate populations, and the presence of cultural transmission may result in rapid divergence and allopatric speciation (Lachlan and Servedio 2004; Yeh and Servedio 2015). Given these facts, it is, therefore, also interesting to note that the diversification of human languages in the region follows a similar geographic pattern of isolation across the same geographical barriers (Sagart et al. 2019). For example, there is an Indo-Chinese trail of language diversification north of the Brahmaputra River and the Burman language groups diversifying south of the Brahmaputra River. Other studies find geographic signatures of increasing linguistic diversity with distance, consistent with an influence of geographic isolation on the structure of languages (Huisman et al. 2019). Taken together, this suggests possible parallels in the evolution of diverse culturally transmitted traits and points to potential broad evolutionary insight from the study of both bird song and language.

Acoustic signals in general are shaped by various factors such as evolutionary history (McCracken and Sheldon 1997; Wilkins et al. 2013; Arato and Fitch 2021), geographic separation (Marler and Tamura 1962; Baker 2006; Baker et al. 2006; Podos and Warren 2007; Kirschel et al. 2009; Garland et al. 2013; Lachlan et al. 2013, 2016), and sexual selection (Seddon et al. 2013; Wilkins et al. 2013). By presenting evidence that (a) despite geographical isolation, *Spelaeornis* appears to possess similar song notes across species, and (b) syntactic structure of vocal sequences in *Spelaeornis* has diverged across geographical barriers, we shed light on the diverse paths through which signals evolve in allopatry (Kershenbaum et al. 2012). The Himalayas and Southeast Asia are regions with hyperdiverse ecological communities (Srinivasan et al. 2014; Mungee and Athreya 2021; Ashokan et al. 2022). Studies such as ours emphasize the importance of studying biodiversity, natural history, and behavior of taxa in these regions to understand the biogeography of communication strategies and signal evolution.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03385-9>.

**Acknowledgements** We are grateful to the many recordists (listed in the Supplementary information), whose recordings from public databases contributed to this project, as well as to Ramana Athreya, Umesh Srinivasan, Vaibhav Chhaya, Aurnab Ghose, and members of the Krishnan lab for useful feedback and discussions. Finally, we thank Seshadri KS for help with maps, Dr. Henrik Brumm, and two anonymous reviewers for their feedback.

**Funding** AK is funded by an INSPIRE Faculty Award from the Department of Science and Technology, Government of India, an Early Career Research Grant (ECR/2017/001527) and a Core Research Grant (CRG/2022/000187) from the Science and Engineering Research Board (SERB), Government of India. AJM and ASB are the recipients of the KVPY Fellowship from the Government of India.

**Data Availability** Data are included in the Supplementary information along with recording catalog numbers. Codes may be accessed at <https://github.com/ab-madabhushi>.

## Declarations

**Ethical approval** This research used recordings from existing databases, and thus, no research involving live animals was involved.

**Conflict of interest** The authors declare no competing interests.

## References

- Arato J, Fitch WT (2021) Phylogenetic signal in the vocalizations of vocal learning and vocal non-learning birds. *Phil Trans R Soc B* 376:20200241. <https://doi.org/10.1098/rstb.2020.0241>
- Ashokan A, Xavier A, Suksathan P, Ardiyani M, Leong-Skornickova J, Newman M, Kress WJ, Gowda V (2022) Himalayan orogeny and monsoon intensification explain species diversification in an endemic ginger (*Hedygium*: Zingiberaceae) from the Indo-Malayan Realm. *Mol Phylogenet Evol* 170:107440. <https://doi.org/10.1016/j.ympev.2022.107440>
- Baker MC (2006) Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection on songs. *Ethology* 112:757–771. <https://doi.org/10.1111/j.1439-0310.2006.01212.x>
- Baker MC, Baker MSA, Tilghman LM (2006) Differing effects of isolation on evolution of bird songs: examples from an island-mainland comparison of three species. *Biol J Linn Soc* 89:331–342. <https://doi.org/10.1111/j.1095-8312.2006.00677.x>
- Balaban E (1988) Bird song syntax: learned intraspecific variation is meaningful. *P Natl Acad Sci USA* 85:3657–3660. <https://doi.org/10.1073/pnas.85.10.3657>
- Berwick RC, Okanoya K, Beckers GJL, Bolhuis JJ (2011) Songs to syntax: the linguistics of birdsong. *Trends Cogn Sci* 15:113–121. <https://doi.org/10.1016/j.tics.2011.01.002>
- Bhat AS, Sane VA, Seshadri KS, Krishnan A (2022) Behavioural context shapes vocal sequences in two anuran species with different repertoire sizes. *Anim Behav* 184:111–129. <https://doi.org/10.1016/j.anbehav.2021.12.004>
- Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Associates, Sunderland, MA
- Briefer EF, Rybak F, Aubin T (2013) Does true syntax or simple auditory object support the role of skylark song dialect? *Anim Behav* 86:1131–1137. <https://doi.org/10.1016/j.anbehav.2013.09.019>
- Cai T, Cibois A, Alström P et al (2019) Near-complete phylogeny and taxonomic revision of the world's babblers (Aves: Passeriformes). *Mol Phylogenet Evol* 130:346–356. <https://doi.org/10.1016/j.ympev.2018.10.010>
- Charrier I, Sturdy CB (2005) Call-based species recognition in black-capped chickadees. *Behav Process* 70:271–281. <https://doi.org/10.1016/j.beproc.2005.07.007>
- Chek AA, Bogart JP, Loughheed SC (2003) Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecol Lett* 6:235–247. <https://doi.org/10.1046/j.1461-0248.2003.00420.x>
- Chitnis SS, Rajan S, Krishnan A (2020) Sympatric wren-warblers partition acoustic signal space and song perch height. *Behav Ecol* 31:559–567. <https://doi.org/10.1093/beheco/arz216>
- Ciaburri I, Williams H (2019) Context-dependent variation of house finch song syntax. *Anim Behav* 147:33–42. <https://doi.org/10.1016/j.anbehav.2018.11.001>
- Collar NJ (2006) A partial revision of the Asian babblers (Timaliidae). *Forktail* 22:85–112
- Collier K, Bickel B, van Schaik CP, Manser MB, Townsend SW (2014) Language evolution: syntax before phonology? *Proc R Soc B* 281:20140263. <https://doi.org/10.1098/rspb.2014.0263>
- Dahlin CR, Wright TF (2012) Does syntax contribute to the function of duets in a parrot, *Amazona auropalliata*? *Anim Cogn* 15:647–656. <https://doi.org/10.1007/s10071-012-0493-y>
- del Hoyo J, Collar NJ, Christie DA, Elliott A, Fishpool LDC (2014) HBW and BirdLife International Illustrated Checklist of the Birds of the World. Lynx Edicions BirdLife International, Barcelona
- Doupe AJ, Kuhl PK (1999) Birdsong and human speech: common themes and mechanisms. *Annu Rev Neurosci* 22:567–631. <https://doi.org/10.1146/annurev.neuro.22.1.567>
- Dunn J (2019) Global syntactic variation in seven languages: toward a computational dialectology. *Front Artif Intell* 2:15. <https://doi.org/10.3389/frai.2019.00015>
- Egan SP, Funk DJ (2009) Ecologically dependent postmating isolation between sympatric host forms of *Neochlamisus bebbianae* leaf beetles. *P Natl Acad Sci USA* 106:19426–19431. <https://doi.org/10.1073/pnas.0909424106>
- Engesser S, Townsend SW (2019) Combinatoriality in the vocal systems of nonhuman animals. *WIREs Cogn Sci* 10:1493. <https://doi.org/10.1002/wcs.1493>
- Fishbein AR, Idsardi WJ, Ball GF, Dooling RJ (2020) Sound sequences in birdsong: how much do birds really care? *Phil Trans R Soc B* 375:20190044. <https://doi.org/10.1098/rstb.2019.0044>
- Garland EC, Noad MJ, Goldizen AW et al (2013) Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale. *J Acoust Soc Am* 133:560–569. <https://doi.org/10.1121/1.4770232>
- Grant BR, Grant PR (2010) Songs of Darwin's finches diverge when a new species enters the community. *P Natl Acad Sci USA* 107:20156–20163
- Haavie J, Borge T, Bures S, Garamszegi LZ, Lampe HM, Moreno J, Qvarnström A, Torok J, Sætre G-P (2004) Flycatcher song in allopatry and sympatry - convergence, divergence and reinforcement. *J Evol Biol* 17:227–237. <https://doi.org/10.1111/j.1420-9101.2003.00682.x>
- Henry L, Barbu S, Lemasson A, Hausberger M (2015) Dialects in animals: evidence, development and potential functions. *Anim Behav Cogn* 2:132–155. <https://doi.org/10.12966/abc.05.03.2015>
- Hillis DM (1981) Premating isolating mechanisms among three species of the *Rana pipiens* complex in Texas and Southern Oklahoma. *Copeia* 1981:312–319. <https://doi.org/10.2307/1444220>
- Huisman JLA, Majid A, van Hout R (2019) The geographical configuration of a language area influences linguistic diversity. *PLoS ONE* 14:e0217363. <https://doi.org/10.1371/journal.pone.0217363>
- Hunt R (1923) The phonetics of bird-sound. *Condor* 25:202–208

- Irwin DE, Irwin JH, Price TD (2001) Ring species as bridges between microevolution and speciation. *Genetica* 112–113:223–243. <https://doi.org/10.1023/A:1013319217703>
- Irwin DE, Thimban MP, Irwin JH (2008) Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): a strong role for stochasticity in signal evolution? *J Evol Biol* 21:435–448. <https://doi.org/10.1111/j.1420-9101.2007.01499.x>
- Isler ML, Isler PR, Whitney BM (1998) Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *Auk* 115:577–590. <https://doi.org/10.2307/4089407>
- IUCN (2019) The IUCN (International Union for Conservation of Nature) Red List of Threatened Species, version 2019-2. Accessed from <https://www.iucnredlist.org/>
- Kershenbaum A, Blumstein DT, Roch MA et al (2016) Acoustic sequences in non-human animals: a tutorial review and prospectus. *Biol Rev* 91:13–52. <https://doi.org/10.1111/brv.12160>
- Kershenbaum A, Bowles AE, Freeberg TM, Jin DZ, Lameira AR, Bohn K (2014) Animal vocal sequences: not the Markov chains we thought they were. *Proc R Soc B* 281:20141370. <https://doi.org/10.1098/rspb.2014.1370>
- Kershenbaum A, Ilany A, Blaustein L, Geffen E (2012) Syntactic structure and geographical dialects in the songs of male rock hyraxes. *Proc R Soc Lond B* 279:2974–2981. <https://doi.org/10.1098/rspb.2012.0322>
- King B, Donahue JP (2006) The rediscovery and song of the Rusty-throated Wren Babbler *Spelaeornis badeigularis*. *Forktail* 22:113–115
- Kirschel ANG, Blumstein DT, Smith TB (2009) Character displacement of song and morphology in African tinkerbirds. *P Natl Acad Sci USA* 106:8256–8261
- Krishnan A (2019) Acoustic community structure and seasonal turnover in tropical South Asian birds. *Behav Ecol* 30:1364–1374. <https://doi.org/10.1093/beheco/arz087>
- Kullback S, Kupperman M, Ku HH (1962) Tests for contingency tables and Markov chains. *Technometrics* 4:573–608
- Lachlan RF, Servedio MR (2004) Song learning accelerates allopatric speciation. *Evolution* 58:2049–2063
- Lachlan RF, van Heijningen CAA, ter Haar SM, ten Cate C (2016) Zebra finch song phonology and syntactical structure across populations and continents—a computational comparison. *Front Psychol* 7:980. <https://doi.org/10.3389/fpsyg.2016.00980>
- Lachlan RF, Verzijden MN, Bernard CS, Jonker P-P, Koese B, Jaarsma S, Spoor W, Slater PJB, ten Cate C (2013) The progressive loss of syntactical structure in bird song along an Island colonization chain. *Curr Biol* 23:1896–1901. <https://doi.org/10.1016/j.cub.2013.07.057>
- Luther D (2009) The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behav Ecol* 20:864–871. <https://doi.org/10.1093/beheco/arp074>
- Marler P, Peters S (1988) The role of song phonology and syntax in vocal learning preferences in the Song Sparrow, *Melospiza melodia*. *Ethology* 77:125–149
- Marler P, Slabbekoorn H (2004) *Nature's music: the science of bird-song*. Elsevier Academic Press, London, UK
- Marler P, Tamura M (1962) Song “dialects” in three populations of white-crowned sparrows. *Condor* 64:368–377. <https://doi.org/10.2307/1365545>
- Marler P, Tamura M (1964) Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146:1483–1486
- Marshall DC, Cooley JR (2000) Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicalcada neotredicim*. *Evolution* 54:1313–1325. <https://doi.org/10.1111/j.0014-3820.2000.tb00564.x>
- McCracken KG, Sheldon FH (1997) Avian vocalizations and phylogenetic signal. *P Natl Acad Sci USA* 94:3833–3836
- Miyagawa S, Berwick R, Okanoya K (2013) The emergence of hierarchical structure in human language. *Front Psychol* 4:71. <https://doi.org/10.3389/fpsyg.2013.00071>
- Mungee M, Athreya R (2021) Intraspecific trait variability and community assembly in hawkmoths (Lepidoptera: Sphingidae) across an elevational gradient in the eastern Himalayas, India. *Ecol Evol* 11:2471–2487. <https://doi.org/10.1002/ece3.7054>
- Podos J, Dybboe R, Ole Jensen M (2013) Ecological speciation in Darwin's finches: parsing the effects of magic traits. *Curr Zool* 59:8–19. <https://doi.org/10.1093/czoolo/59.1.8>
- Podos J, Warren PS (2007) The evolution of geographic variation in birdsong. *Adv Stud Behav* 37:403–458. [https://doi.org/10.1016/S0065-3454\(07\)37009-5](https://doi.org/10.1016/S0065-3454(07)37009-5)
- Praveen J, Karuthedathu D, Sankar S, Duraiswami H, Yobin Y, Baruah R (2022) What is the identity of the *Spelaeornis* wren-babbler that occurs on the slopes of Mugaphi Peak in south-eastern Arunachal Pradesh? *Indian Birds* 18:107–113
- Price T (2007) *Speciation in birds*. Roberts and Co., Publishers, Greenwood Village, CO, USA
- Rasmussen PC, Anderton JC (2005) *Birds of south Asia: the Ripley guide*. Lynx Edicions, Barcelona
- Richmond JQ, Jockusch EL, Latimer AM (2011) Mechanical reproductive isolation facilitates parallel speciation in western North American scincid lizards. *Am Nat* 178:320–332. <https://doi.org/10.1086/661240>
- Sagart L, Jacques G, Lai Y, Ryder RJ, Thouzeau V, Greenhill SJ, List J-M (2019) Dated language phylogenies shed light on the ancestry of Sino-Tibetan. *P Natl Acad Sci USA* 116:10317–10322. <https://doi.org/10.1073/pnas.1817972116>
- Sainburg T, Theilman B, Thielk M, Gentner TQ (2019) Parallels in the sequential organization of birdsong and human speech. *Nat Commun* 10:3636. <https://doi.org/10.1038/s41467-019-11605-y>
- Salwiczek LH, Wickler W (2004) Birdsong: an evolutionary parallel to human language. *Semiotica* 151:163–182. <https://doi.org/10.1515/semi.2004.066>
- Schmidt AKD, Römer H, Riede K (2013) Spectral niche segregation and community organization in a tropical cricket assemblage. *Behav Ecol* 24:470–480. <https://doi.org/10.1093/beheco/ars187>
- Searcy WA, Marler P (1981) A test for responsiveness to song structure and programming in female sparrows. *Science* 213:926–928
- Searcy WA, Marler P, Peters SS (1981) Species song discrimination in adult female song and swamp sparrows. *Anim Behav* 29:997–1003. [https://doi.org/10.1016/S0003-3472\(81\)80053-X](https://doi.org/10.1016/S0003-3472(81)80053-X)
- Searfoss AM, Liu W-C, Creanza N (2020) Geographically well-distributed citizen science data reveals range-wide variation in the chipping sparrow's simple song. *Anim Behav* 161:63–76. <https://doi.org/10.1016/j.anbehav.2019.12.012>
- Seddon N, Botero CA, Tobias JA et al (2013) Sexual selection accelerates signal evolution during speciation in birds. *Proc R Soc B* 280:20131065. <https://doi.org/10.1098/rspb.2013.1065>
- Slabbekoorn H, Smith TB (2002) Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution* 56:1849–1858. <https://doi.org/10.1111/j.0014-3820.2002.tb00199.x>
- Slabbekoorn H, Smith TB (2002) Bird song, ecology and speciation. *Phil Trans R Soc B* 357:493–503. <https://doi.org/10.1098/rstb.2001.1056>
- Soma M, Brumm H (2020) Group living facilitates the evolution of duets in barbets. *Biol Lett* 16:10–15. <https://doi.org/10.1098/rsbl.2020.0399>
- Srinivasan U, Tamma K, Ramakrishnan U (2014) Past climate and species ecology drive nested species richness patterns along an

- east-west axis in the Himalaya. *Glob Ecol Biogeogr* 23:52–60. <https://doi.org/10.1111/geb.12082>
- Suzuki TN, Wheatcroft D, Griesser M (2018) Call combinations in birds and the evolution of compositional syntax. *PLoS Biol* 16:e2006532. <https://doi.org/10.1371/journal.pbio.2006532>
- Tobias JA, Aben J, Brumfield RT, Derryberry EP, Halfwerk W, Slabekoor H, Seddon N (2010) Song divergence by sensory drive in Amazonian birds. *Evolution* 64:2820–2839
- Urban M (2021) The geography and development of language isolates. *R Soc Open Sci* 8:202232. <https://doi.org/10.1098/rsos.202232>
- Uy JAC, Irwin DE, Webster MS (2018) Behavioral isolation and incipient speciation in birds. *Annu Rev Ecol Evol S* 49:1–24. <https://doi.org/10.1146/annurev-ecolsys-110617-062646>
- Wanker R, Fischer J (2001) Intra- and interindividual variation in the contact calls of spectacled parrotlets (*Forpus conspicillatus*). *Behaviour* 138:709–726. <https://doi.org/10.1163/156853901752233361>
- Wilkins MR, Seddon N, Safran RJ (2013) Evolutionary divergence in acoustic signals: causes and consequences. *Trends Ecol Evol* 28:156–166. <https://doi.org/10.1016/j.tree.2012.10.002>
- Yeh DJ, Servedio MR (2015) Reproductive isolation with a learned trait in a structured population. *Evolution* 69:1938–1947. <https://doi.org/10.1111/evo.12688>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.