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Mechanisms shaping the acoustic structure of the song during cultural evolution in the Long-billed Hermit hummingbird (*Phaethornis longirostris*)

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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Dedicatoria

A mi madre, que siempre me alienta a brincar hacia un mejor futuro.
A mis queridos sobrinos Camila, Ezra y Yunuén, que me recuerdan qué es lo importante.
A mi hermana Pamela, a Florecita y a Sandra, que han sido un pilar en mi vida durante este proceso.
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Resumen

Comprender los mecanismos que moldean la evolución de la diversidad de los sistemas biológicos es un tema central en las ciencias naturales. Dentro de esta diversidad están los comportamientos aprendidos, los cuales, aunque comparten principios con la evolución genética, siguen dinámicas más flexibles. Estas variantes son denominadas cultura y representan la diversidad de los rasgos aprendidos y en especial en la comunicación animal. El estudio de acervos longitudinales de estos rasgos permite analizar su evolución con mayor detalle. Por ello en esta investigación, utilizamos un conjunto de datos único de cinco décadas de cantos del ermitaño Piquilargo (*Phaethornis longirostris*) para examinar dos mecanismos clave:1) si la prevalencia de estos rasgos en las poblaciones está determinada por su eficacia en la propagación dentro del ambiente, y 2) si las características del canto que tienen mayor labilidad evolutiva son aquellas menos restringidas por características físicas del sistema de emisión. Para probar estos mecanismos, realizamos experimentos de propagación con tipos de cantos de baja prevalencia (≤2 años en la población) y alta prevalencia (≥5 años en la población). Posteriormente, codificamos los tipos de cantos para llevar a cabo reconstrucciones filogenéticas y análisis macroevolutivos, incluyendo la evaluación de señal filogenética y tasa evolutiva. Nuestros resultados indican que, si bien la evolución cultural está vinculada a la variabilidad en las habilidades de propagación de los tipos de canto, la degradación de estos no se asocia directamente con su prevalencia. Esto sugiere que las principales presiones selectivas que determinan la prevalencia de los cantos no son de origen ecológico. Los análisis filogenéticos revelaron una fuerte señal filogenética, indicando una relación estrecha entre la estructura del tipo de canto y las características del canto. Aunado a esto, encontramos que la diferencia en la tasa evolutiva fue significativa entre características no tan restringidas y restringidas. Este estudio por primera vez prueba experimentalmente el efecto de dos mecanismos que restringen la evolución cultural y su patrón de cambio.

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Introducción

El estudio de los procesos evolutivos desde una perspectiva mecanistica ha sido fundamental para comprender la compleja y jerárquica naturaleza de los sistemas biológicos (Glennan & Illari, 2018). Este enfoque es especialmente relevante en el estudio del comportamiento, un rasgo moldeado por múltiples presiones selectivas y la interacción de diversos componentes biológicos (Stutchbury & Morton, 2022). Esta complejidad se incrementa cuando los comportamientos son aprendidos socialmente, permitiendo la existencia de un acervo cultural. Aunque la transmisión cultural comparte similitudes con la transmisión genética, es más dinámica, ya que no requiere parentesco entre individuos y permite la transferencia horizontal dentro de una misma generación (Mace & Holden, 2005; Perreault & Mesoudi, 2012). Este dinamismo facilita cambios direccionales en pocas generaciones, favoreciendo la adaptabilidad ante presiones ecológicas heterogéneas y permitiendo la acumulación e innovación de rasgos a través del aporte de múltiples individuos (Mesoudi *et al.,* 2016).

El estudio de la cultura y su evolución en animales es un área relativamente joven, con sus primeros trabajos hace aproximadamente 50 años (revisado en Boyd & Richerson, 2024). A pesar de ello, su relevancia es indiscutible. El estudio de la cultura en el comportamiento animal es fundamental para comprender los rasgos aprendidos, ya que el comportamiento aprendido rara vez opera de manera autónoma; en cambio, están frecuentemente moldeados por presiones sociales que influyen en su adecuación (Tchernichovski et al, 2017). Los mecanismos que regulan esta adecuación provienen de distintos tipos de selección. Por ejemplo, la selección sexual favorece características que aumentan el éxito reproductivo, mientras que la selección ecológica promueve rasgos que optimizan la comunicación, el forrajeo o la migración (Alem *et al.,* 2016; Danchin *et al.,* 2018; Jesmer *et al.,* 2018; Williams *et al.,* 2013).

La direccionalidad y patrón de la evolución no solo se basa en estas presiones directas. Existen fuerzas indirectas, como los sesgos cognitivos, que pueden surgir de la explotación sensorial, favoreciendo ciertas variantes culturales (Tobias *et al.,* 2010; Fuller & Endler, 2018). Estos sesgos pueden derivar de la selección sobre otros rasgos cognitivos o comportamentales, y así como de limitaciones físicas que afectan su expresión. Así, aunque el espacio teórico de posibles rasgos culturales es amplio, la capacidad de los individuos para aprenderlos y ejecutarlos también se ve restringida por su biología y desarrollo (Podos *et al.,* 2004; Podos *et al.,* 2009; Podos *et al.,* 2022).

Entre los comportamientos aprendidos, los cantos ocupan un papel central. Estas señales tienen un rol crucial en la adecuación de los organismos que las aprenden, para defender territorios y cortejar (Catchpole & Slater, 2008; Podos *et al.,* 2020). Este tipo de rasgos comportamentales pueden ser de gran complejidad al ser el resultado de la de variación de múltiples dimensiones (*i.e*., tiempo, energía y frecuencia). Esta complejidad tiene como consecuencia un espacio de rasgo teórico amplio, debido a la alta variabilidad de combinaciones posibles y la variabilidad producto del aprendizaje como errores o pequeñas innovaciones (Vernes *et al.,* 2021; Williams, 2021).

Este espacio de rasgo (o espacio acústico) teórico no es infinito, ya que diversos factores limitan la saturación y moldean su diversidad. Entre ellos, destacan las restricciones impuestas por la morfología del sistema de producción (*e.g*., tamaño corporal, forma y tamaño del pico), y las presiones derivadas de la comunicación efectiva. En este sentido, la teoría de impulso sensorial juega un papel crucial al favorecer variantes que exploten los sentidos del receptor, minimicen el riesgo de detección por depredadores y optimicen su propagación en el entorno local (Tobias *et al.,* 2010; Prather *et al.,* 2012; Fuller & Endler, 2018). Comprender cómo estos mecanismos moldean la diversidad de los rasgos culturales a lo largo de su evolución es fundamental, ya que aún no se ha determinado con precisión la magnitud de su influencia en los patrones de evolución cultural.

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Capítulo 1

The role of propagation of the song during cultural evolution in the Long-billed Hermit hummingbird

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Abstract

Cultural evolution has been considered an important driver promoting diversity in animal communication, yet the ecological mechanisms shaping this diversity remain poorly understood. By combining a longitudinal dataset of Long-billed Hermit (*Phaethornis longirostris*) song recordings spanning five decades with field experiments quantifying signal degradation, we tested two hypotheses: (1) cultural evolution generates variation in the propagation properties of song types, and (2) if such variation explains differences in persistence between low-persistence (persisting ≤2 years) and high-persistence (≥5 years) song types. To test these hypotheses, we conducted playback experiments, comparing the degradation of song types at different distances and heights. While cultural evolution produced significant acoustic variation affecting the fidelity and propagation range in the environment, we found no detectable link between degradation and song type persistence. Contrary to sensory drive predictions, song cultural evolution showed no significant evidence of selection by the environmental constraints. Low-persistence songs exhibited reduced temporal blurring compared to high-persistence songs, and overall degradation showed no association with persistence. Instead, we found a height-specific pattern of song degradation for the receiver, with songs propagating more effectively at the species' flight height, a behaviorally relevant height, as this is the height at which non-lekking individuals approach and assess lek members. These results demonstrate that cultural evolution creates acoustic diversity with consequences for signal transmission, but propagation efficiency does not directly predict cultural success. This decoupling challenges the assumption that environmental constraints drive cultural evolution and instead implicates non-ecological forces, such as social learning biases, sexual selection, or cultural drift, as key drivers of song type turnover. Our findings challenge the assumption that environmental constraints predictably shape cultural evolution and highlight the need to disentangle multiple selective pressures in that maintain vocal traditions.

Key Keywords

Cultural evolution,Sensory drive, Acoustic Adaptation Hypothesis, Hummingbird communication, and Song propagation, Learning biases

Introduction

Understanding the mechanisms shaping the evolution of diversity in biological systems is a central issue in natural sciences research. When studying the diversity of phenotypic traits, most attention has focused on evolutionary factors influencing their structure, such as sexual and ecological selection (Odom *et al.,* 2014). However, for behavioral traits with a substantial learning component in their acquisition, social learning seems to be one of the primary mechanisms generating diversity in their structure at ecological time scales (Williams, 2021). Social learning entails the modification of individual behavior, based on previous experiences, to resemble that of conspecifics, which can generate novel variants by the occurrence of copy imperfections, modification, rearrangement of trait components, or by the invention of new traits (Williams & Lachlan, 2022). The resulting pool of behavioral trait variants learned from related or unrelated individuals and maintained or transmitted over generations is usually seen as culture (Aplin, 2019). When the frequency of trait variants varies through time, cultures evolve in a process that resembles genetic evolution. Both evolutionary processes are able to interact in a gene-culture coevolution, allowing ecological and sexual selection to shape the traits, their expression, and associated cognitive and perceptual biases (Endler, 1992; Podos *et al.,* 2004; Whitehead *et al.,* 2019)

As previously mentioned, biases occurring during social learning may be associated with the structure of traits and the sensory capacity of the receivers. This idea has been proposed to explain some macroevolutionary patterns of genetic evolution in animal communication (the sensory drive hypothesis, Endler, 1992), although a similar process may shape signals during cultural evolution. Under this scenario, cultural evolution would tend to favor those signals with greater detectability or contrasts in a medium according to the receiver's sensory profile (Boughman, 2002; Law & Gold, 2008; Tobias *et al.,* 2010). However, despite being a theoretically sound process, the role that sensory drive has played in the processes of cultural evolution in animal species and learning biases is still poorly understood. While a sender might tune the conspicuousness of a signal to the selected range of perceptual tuning of the receiver for sensory exploitation (*e.g.,* the sight of the anole lizards evolved to detect prey movement, which is exploited by males in their "push-up" courtship display, Kirkpatrick & Ryan, 1991), it also must account for properties of the local environment affecting propagation (Tobias *et al.,* 2010). These environmental properties may improve propagation, but they may also degrade specific signal characteristics necessary for reception and discrimination by the receiver (Boughman, 2002; Tobias *et al.,* 2010; Fuller & Endler, 2018).

The selective process imposed by the environment on acoustic signals has been formalized as the acoustic adaptation hypothesis (AAH), a part of the framework of the sensory drive hypothesis, in which acoustic signals are expected to have optimal propagation in the environment where they have evolved. Conditions of the local environment, such as vegetation structure, temperature, and humidity, can alter signals during propagation. These alterations can result from attenuation, which involves the loss of energy by atmospheric absorption, reducing the intensity and affecting the acoustic features (*e.g.,* high frequencies) of the signal that the receivers can perceive. The presence of objects can also degrade acoustic signals (*e.g.,* vegetation, rocks, cliffs, etc.) in the environment if they scatter or deflect the sound waves, generating reverberations that can modify the structure of the signals (Boncoraglio & Saino, 2007; Tobias *et al.,* 2010; Sandoval *et al.,* 2015; Hardt & Benedict, 2020). Furthermore, adding a layer of complexity, vegetation is not uniform and can vary in its spatial composition and structure (de Conto *et al.,* 2024). Which pressures both emitter and receiver to select strategic positions where transmission windows allow fidelity and longer-range propagation of the message (Morton *et al.,* 1986; Nemeth *et al.,* 2001; Mathevon *et al.,* 2005).

Most of our knowledge on acoustic adaptation comes from a handful of avian groups that show extensive vocal production learning, where their vocal communication is used for multiple functions such as mate attraction, bonding, territory defense, disputes/aggression, and contact (Bitterbaum & Baptista, 1979; Podos *et al.,* 2004; Catchpole & Slater, 2008; Tobias *et al.,* 2010). For example, a few studies have found that the most frequent song variants (hereafter song types) in the repertoires of two species of passerines are those better transmitted in their native habitats (*e.g.,* Potvin & Parris, 2012; Potvin & Clegg, 2015; Benedict & Warning, 2017). In addition, research has shown that trait features are modified as a result of cultural evolution across several years (*e.g.,* Byers *et al.,* 2010; Williams *et al.,* 2013; Zimmerman *et al.,* 2016; Ju *et al.,* 2019; Garland *et al.,* 2022), but, it remains to be seen whether these features are linked to the propagation properties of the signals. It has also been found that juveniles prefer to copy less degraded songs (Morton *et al.,* 1986; Peters *et al.,* 2012), suggesting a copying bias that might provide a mechanistic link between sensory drive and non-random cultural evolution (Peters *et al.,* 2012; Lachlan *et al.,* 2014; Williams, 2021). However, to the best of our knowledge, not a single study has directly link the propagation properties of a signal to the probability of it being copied in a population, which would establish a more direct link between cultural evolution and sensory drive.

In the present study, we aim to understand the role of the propagation properties as one of the mechanisms shaping acoustic structure in the cultural evolution of songs in the lekking Long-billed Hermit hummingbird (*Phaethornis longirostris*) using a collection of recordings from a five-decade period from twelve leks. To examine the variation in transmission properties of song types affects their attractiveness as learning templates, thereby influencing their likelihood of being copied and their persistence in the population. As Long-billed hermits' songs are developed through learning song types that are shared by sub-groups of males within a lek (song neighborhood) (Araya-Salas & Wright, 2013). Therefore several song types can be found in a lek, suggesting a dynamic process of song type creation and change over time. In addition, Long-billed Hermits form leks in densely vegetated areas in tropical rainforests, exhibit strong fidelity to lek sites, and partition vertical space during both singing or flight. The second being relevant during first assessment by non-lekking individuals (females or male juveniles). Making the Long-billed Hermits an ideal candidate for investigating the role of habitat-based degradation during the cultural transmission of songs (Stiles & Wolf, 1979; Araya-Salas *et al.,* 2019).

Materials and methods

Song type categorization and persistence

We obtained Long-billed Hermit songs from a recording data set of a five-decade period from twelve leks in four sites of Costa Rica: La Selva Biological Station, La Tirimbina Biological Reserve, Las brisas, and Hitoy-Cerere National Park (Stiles & Wolf 1979, Araya-Salas & Wright 2013, Figure 1). All three sites consist of evergreen lowland tropical wet forest. We registered the time and frequency positions of songs in the recordings using the software Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2025). During this process, we categorized songs into song types by visual inspection of the spectrograms (Vargas-Castro *et al.,* 2012; Araya-Salas *et al.,* 2019). To determine persistence (defined as the duration of the period during which a song type was produced), we included only those song types recorded at leks that were also sampled both in the year prior to their first occurrence and in the year following their last occurrence. This ensured us that song types appeared and disappeared during the observed period. Using the persistence of these song types, we established a binary categorization for them: low-persistence song types that lasted no longer than two years, and high-persistence song types observed in a time range of at least five years.

Experiment site

The experiments were conducted at three of the twelve leks with the most extensive prior recording collection. These leks are found within La Selva Biological Station, on the Caribbean slope of Costa Rica (10°230N, 84°10W) (Figure 1). This reserve, owned by The Organization for Tropical Studies (OTS), has an elevation range of 30 to 150 m. and a temperature range from 24.7 to 27.1 °C with two periods that differ in amount of rainfall: high rainfall (June- December) and low rainfall (February-April) (Eklund *et al.,* 1997; Whitfield *et al.,* 2007). La Selva comprises 1615 hectares of evergreen tropical wet forest, where 53-73% is old-growth forest, and the remaining area consists of secondary succession vegetation originating from abandoned cocoa tree (Theobroma cacao) plantations (Whitfield *et al.,* 2007; Boyle & Sigel, 2015).

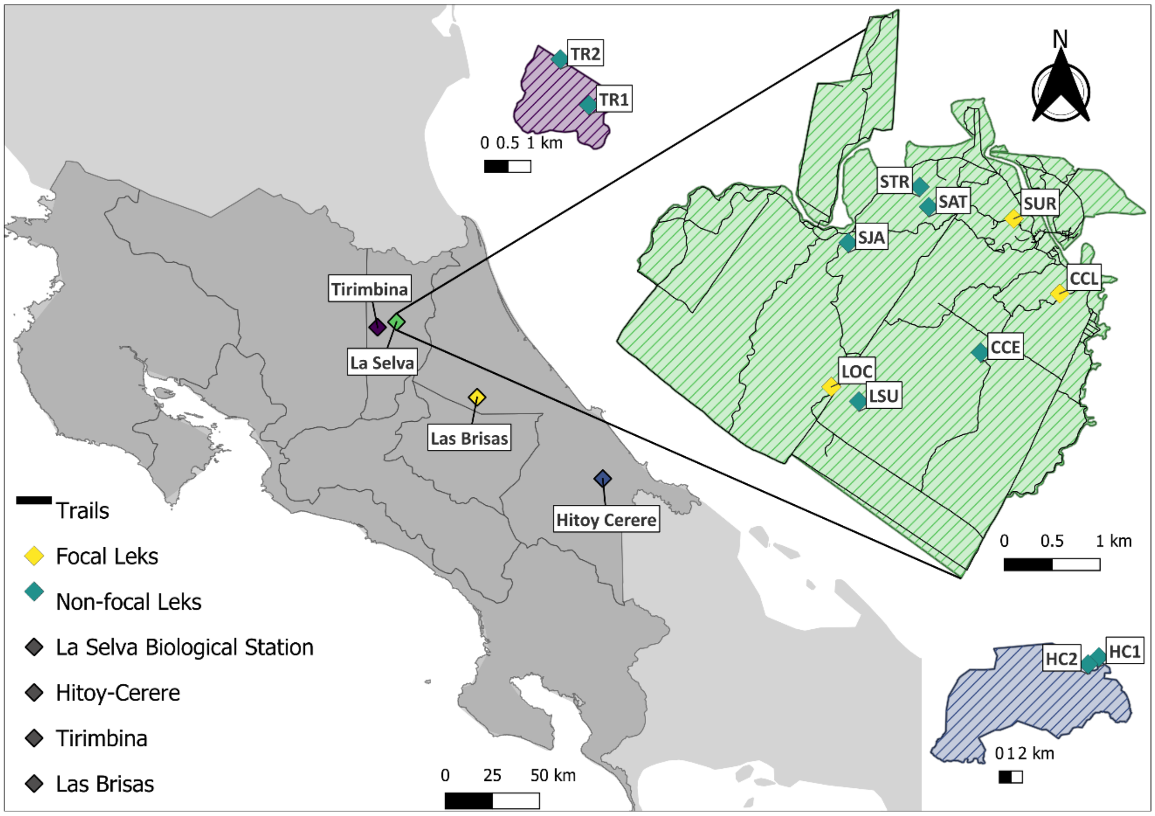

Figure 1. Map of Costa Rica, showing the locations with historical recordings of Long-Billed Hermit song types. The diamond-shape in the upper right corner highlights La Selva Biological Station, where historical recordings were made at eight leks. Experiments were conducted at three of these leks (marked in violet). The layer of La Selva Biological Station was provided by the OTS (Organization for Tropical Studies).

Propagation experiments

To conduct song type propagation experiments, we positioned a speaker (Bose Soundlink) at 2.29 m above the ground, the mean perching height of singing males at leks (± 1.40 m S.D., N = 32; present study). The speaker output volume for the master sound file was calibrated to be emitted at SPL 82 dB, the mean pressure of the song of P. longirostris (Talavera & Araya-Salas, in prep). The calibration was done using an Extech sound level meter 407750, with a C-weighting fast response, which was previously calibrated at 94 dBs utilizing a class one digital calibrator (BYQTEC model ND9B).

For the playback data set, we randomly chose 20 song types with the highest signal-to-noise ratio for each category (high and low persistence). The total number of song types was primarily based on the number of high-persistence song types, as our historical data set consists mainly of low-persistence song types. Whenever possible, we included three songs of each song type from different individuals and years to account for variation among individuals. We also aimed to include five copies of each song to further account for within individual variation. We kept only those songs with a signal-to-noise ratio above 3 dB (Figure 2). The selected songs were combined into a single master sound file, in which each song was separated by 0.1 seconds of silence, and their position was randomly determined. The master sound file was created using the R package baRulho (Araya-Salas *et al.,* 2025).

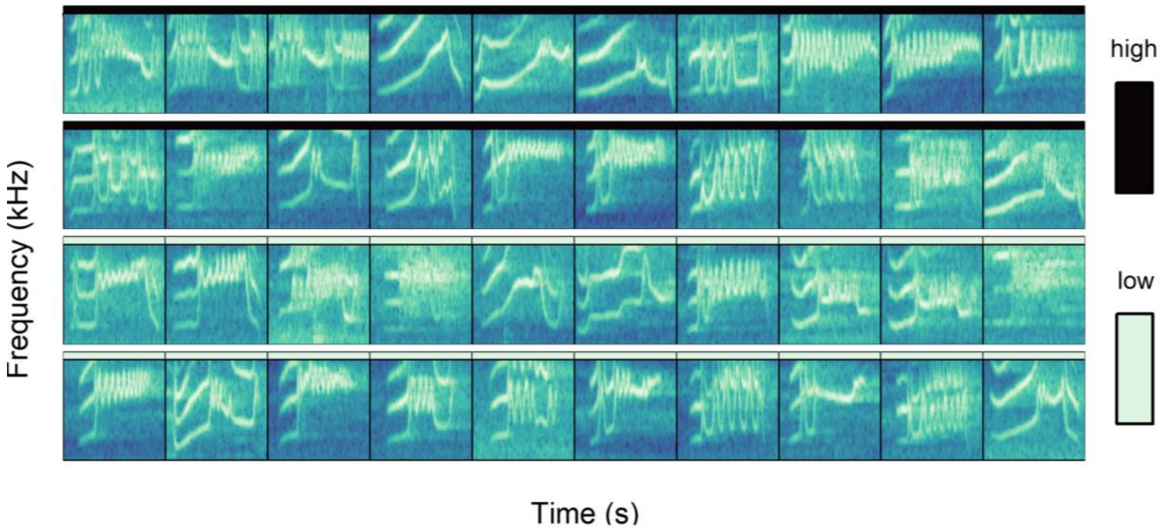

Figure 2. The 40 song types used in the propagation experiment. The categories are base on the persistence of the song types in the leks. Songs in the two top panels are high-persistence song types and those in the two bottom panels are low-persistence song types.

To re-record playback songs, we deployed a linear array of three microphones (Rode NTG4+ with a digital Zoom H6 recorder) positioned at a distance of 10, 20, and 40 m from the speaker. The selected distances are biologically relevant as they closely align with the mean distance between male perches within a lek (44.76 ± 31.29 meters S.D., N = 1248; unpublished data from Araya-Salas, M.). The array was set up at two different heights: 2.29 m, which is the mean height of singing perches (± 1.17 meters S.D., N = 32; present study), and 3.2 m, corresponding to the mean flight height of these hummingbirds (± 1.39 meters S.D., N = 74; present study). These heights were chosen to reflect the most likely vertical position of the intended audience for these signals.

We conducted propagation experiments at three leks within la Selva Biological Station. Trials were conducted at three locations within each lek, selected randomly from a pool of previously observed perch locations. The speaker was placed at the location of the selected perch, and four replicates of the experiment were conducted at each location, one in each of the four cardinal directions (Figure 3). Playbacks were conducted twice in each direction to generate sample duplicates that could be used in cases the re-recorded songs were masked by other sounds in the environment (Graham *et al.,* 2016; Phillips *et al.,* 2020). The only exception to this design was CCL, as only three replicates could be made in the limited space available due to a nearby river.

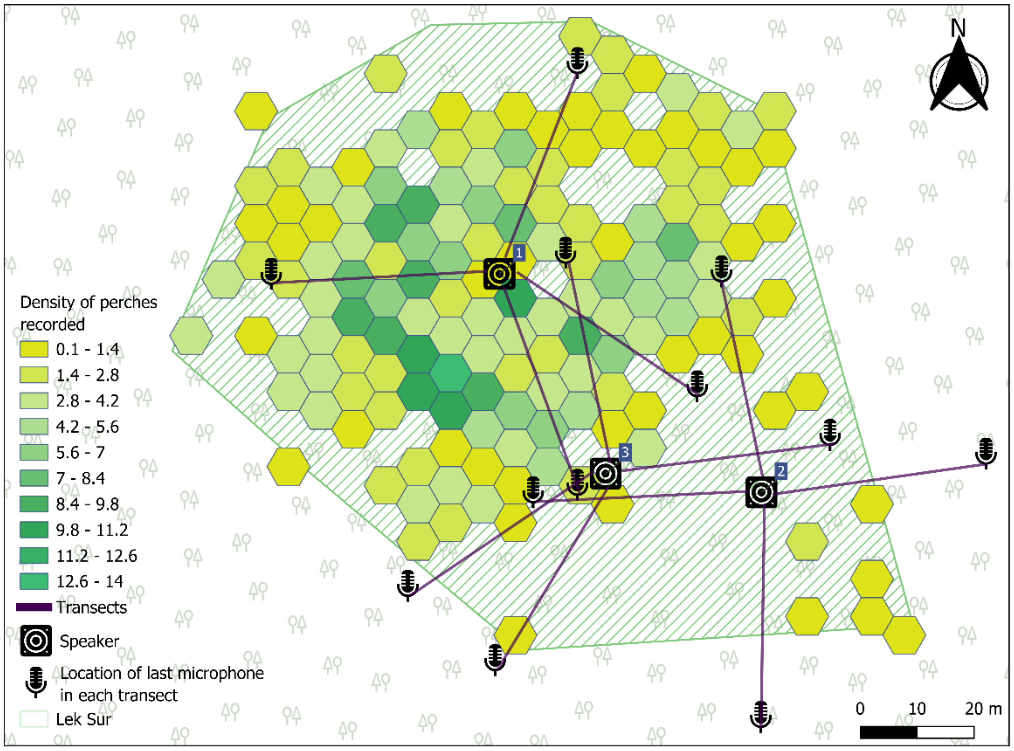

Figure 3. The minimum convex polygon is drawn with our perch locations in the lek SUR, where the hexagons show the density of the perches through the years (*i.e.,* 2010-2016). The figure includes our three trials (speaker icons) and their respective four replicates (microphone icons).

Propagation analysis

Changes in the acoustic structure during song propagation (*i.e.,* degradation) were quantified with the R package baRulho (Araya-Salas *et al.,* 2025). This involved comparing the reference songs against those re-recorded at various distances. Reference songs were made by re-recording the master sound file at 1m from the speaker in an open field near the lek to account for any potential effect introduced by the playback and recording equipment (cables, microphone, recorder, and speaker). Degradation was quantified using eight acoustic metrics: excess attenuation (EA); signal-to-noise ratio (SNR); blur ratio (BR); tail-to-signal ratio (TSR); cross-correlation; envelope correlation; spectrographic blur ratio; and spectrographic cross-correlation (Dabelsteen *et al.,* 1993; Hardt & Benedict, 2020; Araya-Salas, *et al.,* 2025; see additional information for detailed definitions). In brief, these metrics quantify degradation as changes in the distribution of power across time or frequency domains, alterations in their time-by-frequency representation (spectrograms), or attenuation relative to its theoretical expectation or relative to the stationary background noise level.

In some cases, re-recorded songs can be masked by co-occurring environmental sounds, which prevents accurate assessment of degradation. Therefore, we excluded from analyses. To identify masked re-recorded songs, we compared the intensity of noise adjacent to the songs with that of a segment in the recording where no masking sounds occurred. Cases where the adjacent noise was more intense than the unmasked noise segment suggested that masking noise occurred near the song, likely obscuring the song itself. To quantify this, we measured the signal-to-noise ratios (SNR) of the songs using both adjacent and unmasked background noise. We then estimated the best-fit line for the relationship between the two using a linear regression model. Masked songs were identified as cases where the observed 'adjacent' SNR was significantly lower than the expected value based on the linear regression fit. More precisely, masked songs were defined as those for which the residuals of the SNR regression model fell within the first quartile of their distribution (Figure S1). We defined our unmasked ambient noise as the lowest peak sound pressure level (SPL) in 0.5 seconds. We calculated these values in multiple segments located at the start or end of the recordings, and the segment used as reference was automatically selected using a custom R routine based on our definition of unmasked ambient noise. Adjacent noise was measured in the 0.05s segment immediately before the start of each song.

We used Bayesian regression models to evaluate the effect of the song type persistence and height of the receiver on the propagation metrics on nine degradation measures: 1) blur ratio; 2) excess attenuation; 3) tail-to-signal ratio; 4) signal-to-noise ratio; 5) cross-correlation; 6) envelope correlation; 7) spectrum correlation; 8) spectrum blur ratio; and 9) overall degradation (PC1). The overall degradation metric was based on all eight metrics of degradation, obtained through a principal component analysis on zero-mean, unit variance degradation measures (Jolliffe, 2002; Araya-Salas *et al.,* 2025). Each propagation metric was modeled separately with persistence and height as their predictor. Distance was modeled as a monotonic effect in which distance levels are not assumed to be equidistant with respect to their effect on the response variable, but they are rather estimated from the data (Bürkner & Charpentier, 2020). The SNR of the original song recording, the playback sites (leks), the transect, and replicate were included as a varying intercept effect to account for the environment of each lek and the non-independence of observations, respectively. Effects are presented as median posterior estimates and 95% credibility intervals as the highest posterior density interval. All models were run using the R package brms (Bürkner, 2021) on four chains for 3000 iterations, following a warm-up of 1000 iterations. Predictors whose credible intervals did not include zero were regarded as having an effect on the response variables. The potential scale reduction factor for model convergence was kept below 1.01 for all parameter estimates.

We also generated plots from posterior predictive samples to assess the adequacy of the models in describing the observed data. Previous to any modeling, the data were partitioned randomly into 75%-25% using the R package Caret (Kuhn, 2008). The largest subset of the data was allocated for training the regression, and the smaller was reserved for estimating posterior predictive checks. Lastly, to assess the variation in overall degradation (PC1) among song types, we ran a regression model including song type ID as a predictor in addition to persistence and height, and as varying intercept effect the lek and transect. We performed posterior post-hoc pairwise comparison on the marginal effects on the marginal effects of song types. The use of a Principal Component Regression (overall degradation), represents an overall robust way to englobe a multidimensional phenomenon, we followed the advices and general thresholds used for this analysis (Nakazato *et al.,* 2020; Anish *et al.,* 2021).

Results

From the initial 255,296 re-recorded songs, 190,792 remained after excluding songs likely to be masked. The filtered dataset was then divided into two parts: 75% of the data (147,116 songs) for modeling, and the remaining 25% (43,676 songs) for posterior predictive checks, which provide an estimation of the model fit to the observed data (Figure S12).

The first component from our PCA summarizing degradation metrics accounted for 57% of the variation in the data (Figure S2). Not a single metric, including overall degradation (PC1), showed the expected pattern of higher degradation in low persistence song types (Figure 4). On the contrary, the only detected effect showed the inverse pattern, with a lower amount of blurring in the time domain (blur ratio) in low persistence song types (Table S1). The significant pattern observed in all our models was increased degradation with increased distance as expected by the propagation physics fundamentals and inverse square law.

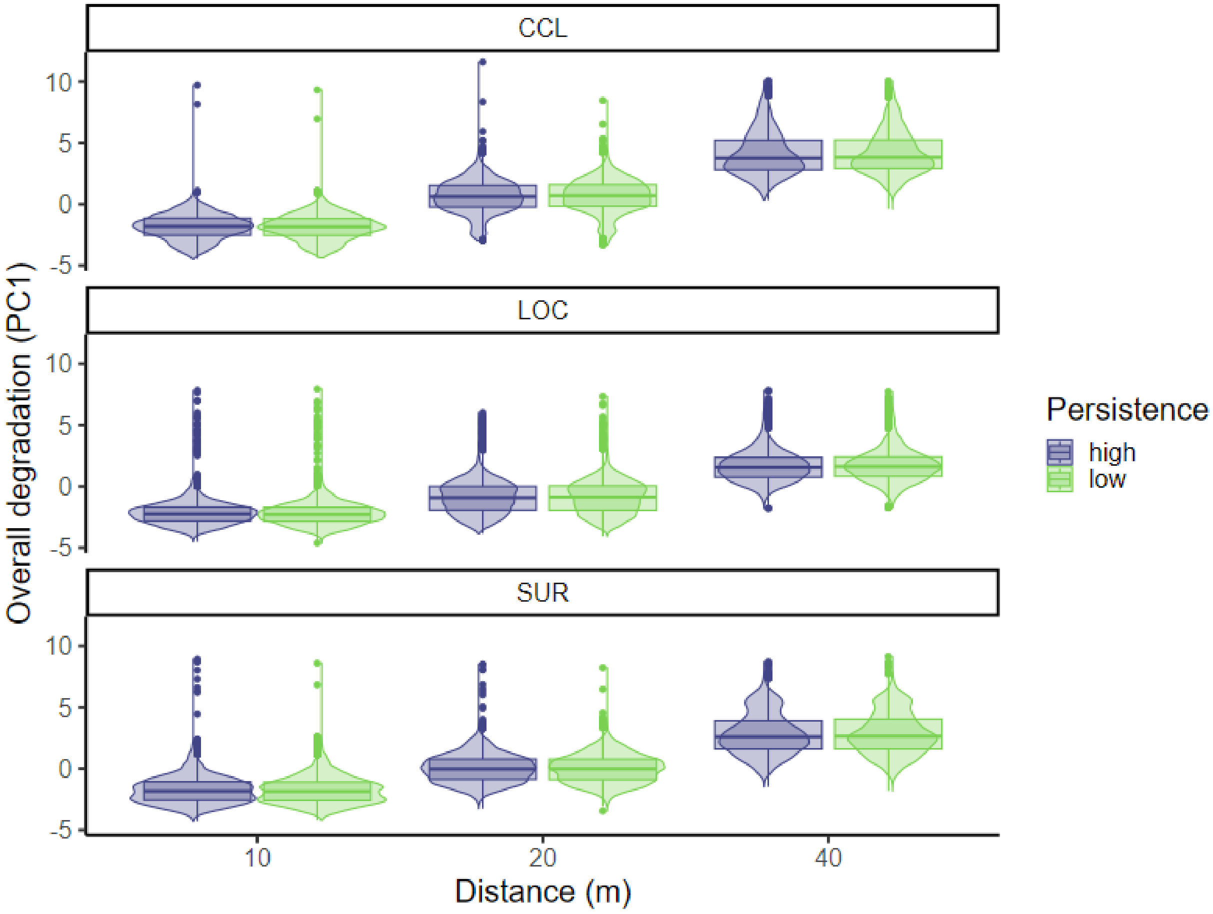

Figure 4. Overlaid violin and box plot showing the density, median, and interquartile range of the distribution of the overall degradation (PC1) across leks colored by persistence category.

We found better propagation at the highest receiver height: overall degradation (PC1), signal-to-noise ratio, tail-to-signal ratio, envelope correlation, spectrum blur ratio, and spectrum correlation all quantified lower degradation at this height (Figure 5; Table S1).

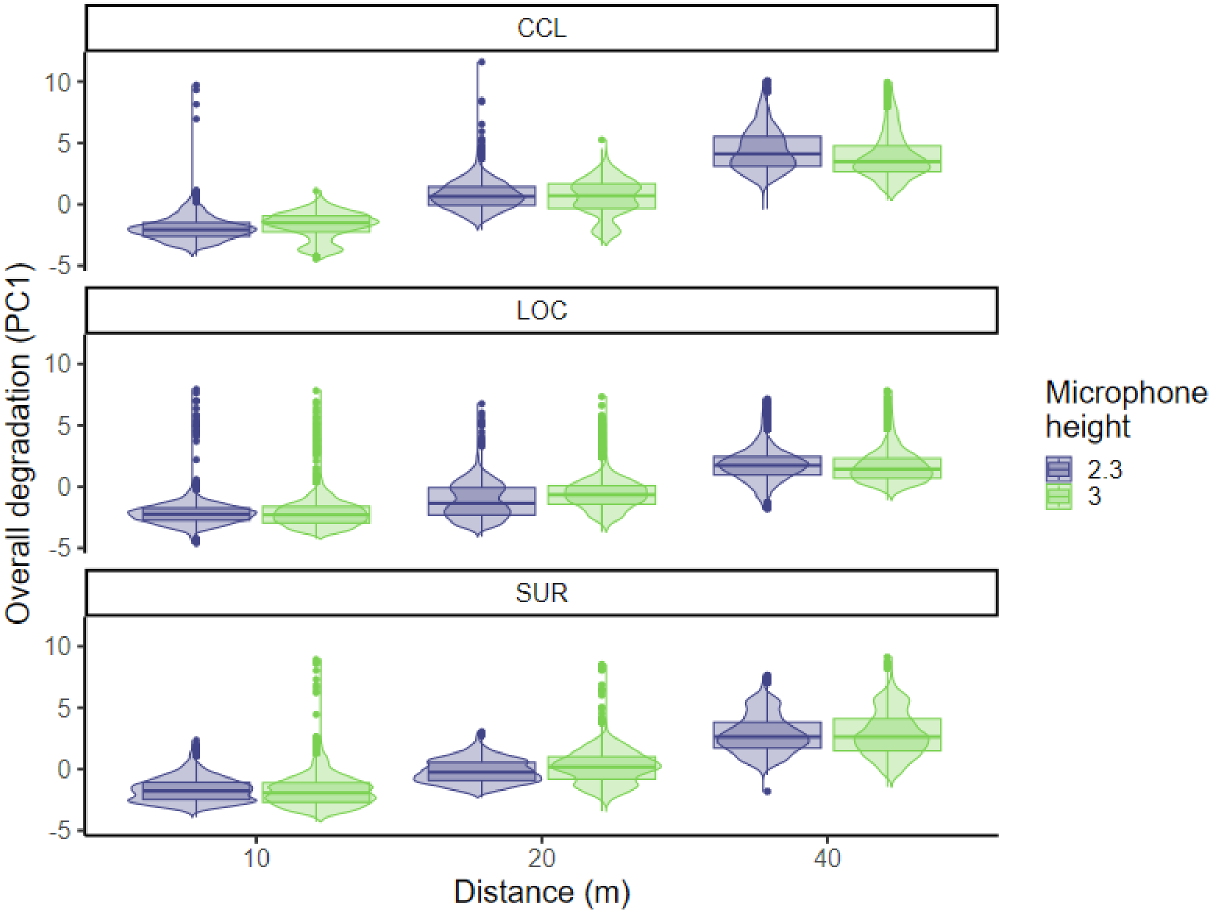

Figure 5. Overlaid violin and box plot graphs show the density, median, and interquartile range of the distribution of the overall degradation (PC1) across leks colored by height.

The song types have a significant difference in their propagation degradation among them, with no clear pattern related to their persistence. The only trend observed is that the better-propagated song types show sufficiently large differences to yield statistically significant in a pairwise comparison (Figure 6).

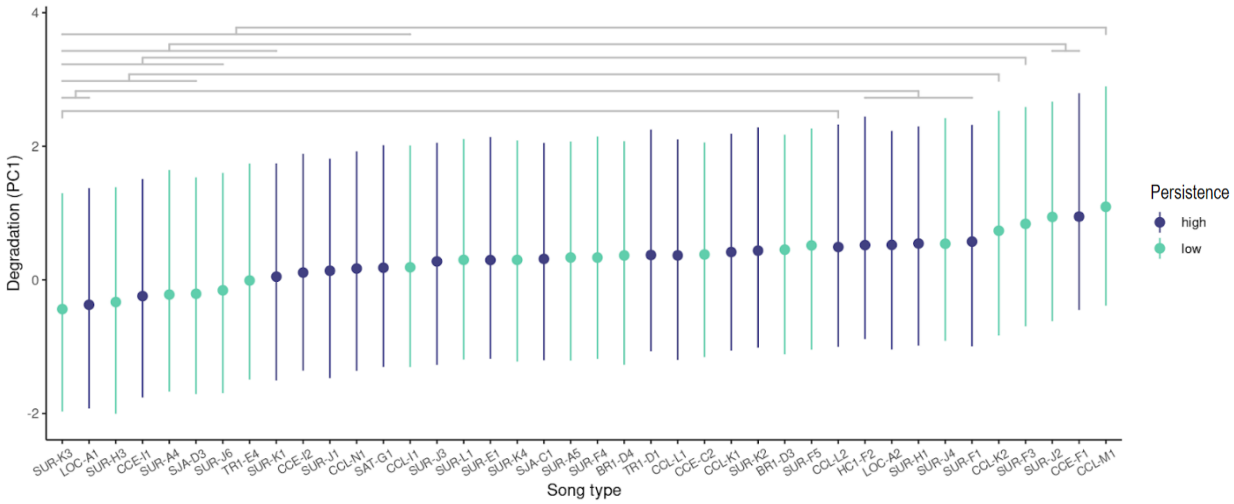

Figure 6. Estimated marginal predicted posterior means (with 95% confidence intervals) of overall degradation (PC1) across different song types. Brackets connecting song types indicate that the difference between posteriors means did not include zero.

Discussion

In this study, we investigated the role of signal propagation in shaping the cultural evolution of songs in the Long-billed Hermit (*Phaethornis longirostris*). Specifically, we tested the hypothesis that sensory drive mediated by environmental propagation properties of the songs influences the cultural evolution of these signals by examining whether low-persistence songs were associated with higher levels of acoustic degradation. We found significant differences among song types (*i.e.,* low and high persistence) in their acoustic degradation, which may indicate that cultural evolution in Long-billed Hermits affects the propagation properties of their signals. However, our findings are not consistent with a role of sensory drive, as none of the degradation metrics analyzed showed the predicted association with song persistence. We did, however, find that receiver height alters the fidelity of the received signal, as the sound propagated with less degradation at flying height, providing higher quality signals to the key non-lek individuals.

Cultural evolution and the dynamics of cultural transmission create fertile ground for selection to act upon, as avian song types differ substantially in their ability to propagate through the environment. While we hypothesized that ecological selection pressures played a key role, this was not the case. Nevertheless, these propagation abilities still exert effects, and they manifest through two forms of degradation. The first influences how far a sound can travel, affecting the chance to be heard by naive males trying to join a lek and females seeking mates (Dabelsteen *et al.,* 1993). The second explains how accurately the sound structure is perceived, a factor with more subtle but critical consequences (Dabelsteen *et al.,* 1993; Hardt & Benedict, 2020). The latter form of degradation may influence the codification of individuality, and fitness, potentially making certain song types more distinct within the lek. Such distinctiveness, in turn, could affect the learning process of songs to subsequent generations of lekking (McComb *et al.,* 2003; Ritschard *et al.,* 2023).

Previous studies have suggested that ecological selection does not necessarily link song type popularity with local adaptations for propagation (Cueva *et al.,* 2024). This link has only gotten support in longitudinal studies where environmental pressures such as rising urban noise and heterogeneity in the environment have favored song types that propagate better (Kopuchian *et al.,* 2004; Luther & Baptista, 2010; Cueva *et al.,* 2024). However, in our 50-year dataset, we found no evidence of a linking ecological selection with song propagation and song type persistence. The only significant difference was found in blur ratio, in which low persistence song types were less degraded than their counterpart, contradicting our hypothesis.

The lack of evidence of a strong selection on song propagation might come from the fact that, in the evolution process of these songs, maximizing propagation distance does not increase fitness. Two different factors might compensate for the lack of distance optimization. First, as is common in lekking hummingbirds, Long-billed Hermits are highly mobile, often traveling distances greater than those separating some leks, making possible for receivers to approach a potential signal source. Second, because lek territories exhibit high fidelity spatial and temporal, the cumulative acoustic output by the lek can be detected from longer than any individual territory. This persistent cumulative signal may lead other males and females, whether foraging, searching for a lek or seeking mates, towards the lek.

The pattern of cultural evolution of song types may be the result of multiple selective forces acting in tandem or synergistically (Kokko *et al.,* 2003). Song type persistence may be influenced by factors such as learning biases, enforced by sexual selection through mate choice and male-to-male competition. Additionally, natural selection also imposes constraints on the variance in propagation of song types, as song conspicuousness might increase predation risk of the individuals producing those song types (Lachlan *et al.,* 2004; Williams *et al.,* 2013; Mougeot & Bretagnolle, 2000). Alternatively, the observed pattern may be a by-product of the lack of strong directionality (directional selection), allowing variation without filtering (Bentley *et al.,* 2004; Podos *et al.,* 2004). In this case, the observed levels of variation in song propagation generated by cultural evolution would not impact the chance of a song being detected and/or copied.

Biases may play a role in song type persistence dynamics within cultural evolution. These biases could be content-based, exploiting females' sensory and cognitive biases, or frequency-dependent, favoring certain song types according to their popularity in the lek (Lachlan *et al.,* 2004; Williams *et al.,* 2013). These biases are not mutually exclusive: novel songs are easily extinguished if they are not adopted by the lek, as males tend to choose those already in use. Conversely, high persistence songs may be maintained to reinforce lek cohesion and identity. Moreover, multiple males singing the same song types may provide a means for females to assess learning abilities (Lachlan *et al.,* 2004). In Indigo Buntings (*Passerina cyanea*), first-year males singing established song types were more successful than those with novel song types. Similarly, in Swamp Sparrow (*Melospiza georgiana*), both sexes responded more strongly to typical song types (Payne *et al.,* 1998; Lachlan *et al.,* 2014). Although cultural conformity can drive song persistence, its evolution does not necessarily follow a uniform process; instead, different signal types within the same species may be subject to independent patterns of selection depending on the underlying selection forces (Podos *et al.,* 2004; Byers *et al.,* 2010).

Lastly, our results indicate height-specific pattern of acoustic degradation, in concordance with the general consensus, that receivers tending to choose higher positions to improve signals fidelity (Nemeth *et al.,* 2001; Mathevon *et al.,* 2005).

This pattern is likely due to the decreasing density of vegetation with height, and the diminishing ground effect (Embleton, 1996; Nemeth *et al.,* 2001; Padgham, 2004). Notably, the height with better propagation fidelity corresponds to typical flight height, providing a hint of the importance role for signal assessment during flight. When key receivers (females and juvenile males) enter the lek, they need to evaluate male vocalizations and make decisions “on the fly” on which male copulate or which male take as a tutor (Snow, 1974; Stiles & Wolf 1979).

Our study found that variation in the acoustic structure of learned songs, generated during cultural evolution, does influence the propagation of song types. However, this variation does not correlate with differential persistence of song types promoted by cultural evolution. In addition, we observed that songs are received better at the height of flight height, targeting key non-lek individuals. These findings contribute to the ongoing discussion on the role of propagation properties in the selection of signals, as is postulated by Acoustic Adaptation Hypothesis (Boncoraglio & Saino, 2007; Ey & Fischer, 2009; Hardt & Benedict, 2020) and the mechanism involved in this selective process. Our results suggest that cultural evolution may not consistently select for improved propagation efficiency, challenging the assumptions about the strength and directionality of selection on song propagation qualities.

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Supplementary material

Our definitions to describe the vocal components are adapted from Catchpole and Slater (2008) to fit the patterns observed in P. longirostris:

1) Element: a solid, continuous line on the spectrogram.
2) Song: a short and complex vocalization made of a single element without silent intervals.
3) Song type: a variant of the song of an individual; we classify songs into the same category by visually comparing the acoustic structural characteristics.

For the degradation measurements, we will followed the definitions of Araya-Salas *et al.,* 2025:

1) Blur-Ratio (BR): the distortion in the time dimension between the model and the observation sound taking into account the attenuation. Higher values indicate more degradation.
2) Excess attenuation (EA): the extra amount of attenuation from the predicted loss of amplitude by distance as a result of spherical spreading and atmospheric absorption. Higher values indicate more degradation by energy loss.
3) Signal-to-Noise-Ratio (SNR): This ratio evaluates how much the energy from the source signal stands out from the energy of the background noise.
4) Tail-to-Signal-Ratio (TSR): the amount of energy in the reverberations after the time frame of the source signal. Higher values indicate more degradation.
5) Spectrum correlation: compares the power spectrum, lower values indicate more degradation. Lower values indicate less similarity, thus more degradation.
6) Envelope correlation: compares the amplitude envelopes constructed using a Hilbert transformation. Lower values indicate less similarity, thus more degradation.
7) Spectrum blur Ratio: the distortion in the frequency dimension between the model and the observation sound taking into account the attenuation. Higher values indicate more degradation.
8) Cross-correlation: using a cross-correlation determines the differences in the spectrograms caused by distortion. Lower values indicate less similarity, thus more degradation.

For our criteria of filtering the noisy song example, that may be overlapped by a sudden vocalization of another noise, we removed the lowest quantile of our model of adjacent snr, using the song signal to noise ratio of the song example. The coefficients of the intercept was 0.4120, and the song signal to noise ratio was 0.7267 (Figure S1).

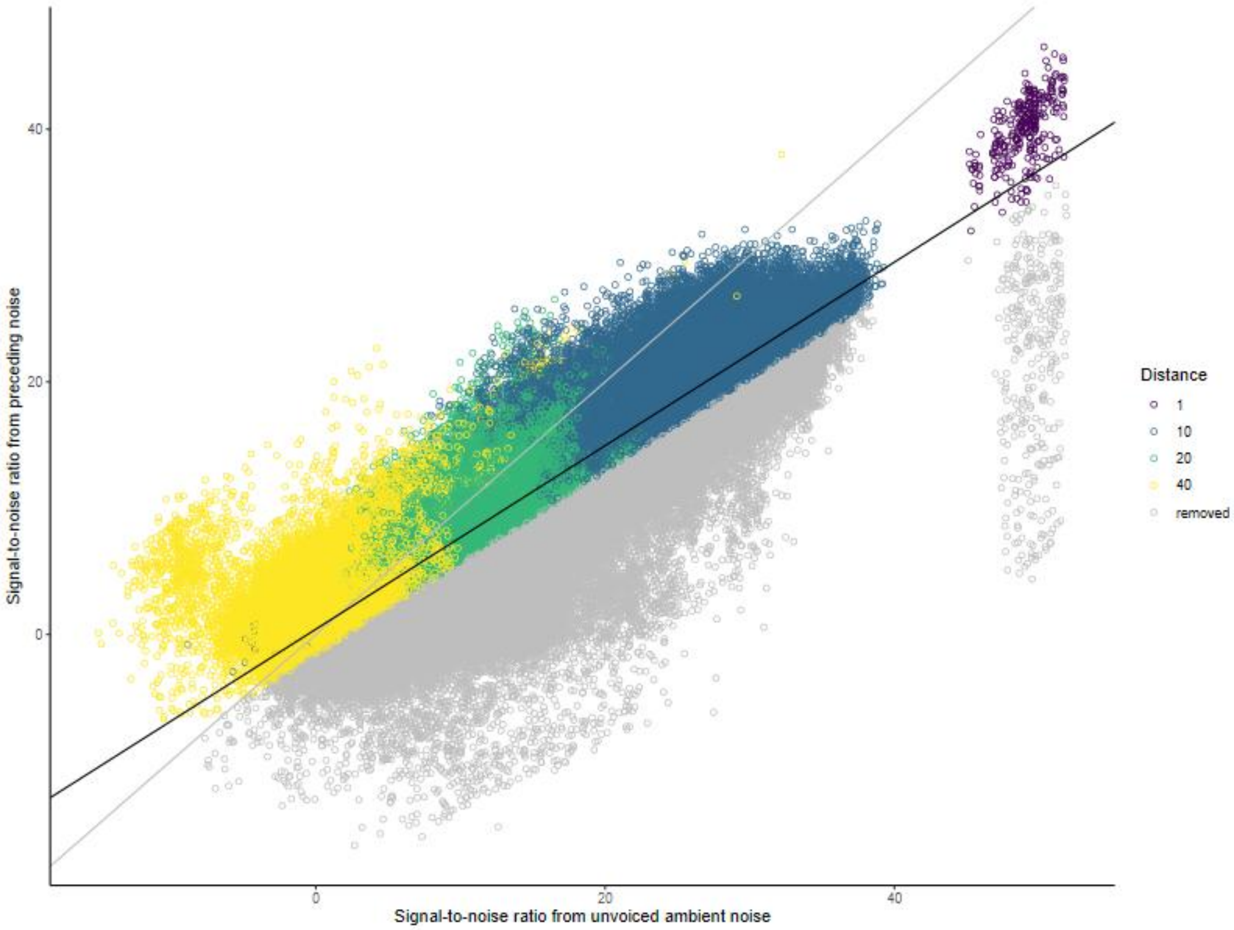

Figure S1. The distribution of all Signal-to-noise values calculated using the unvoiced ambient noise (unmasked ambient noise) and preceding noise (adjacent SNR). The colors represent the re-recorded distance. The grey line represents the identity line (x = y), and the black line is the slope of the model of SNR. The grey dots in the right graph show the abnormal values of SNR excluded by belonging lowest quantile.

The Principal Component Analysis captures over 90% of the total variance of the data, with the first principal component explaining more than 50%. This indicates a strong summarization of the variance of the data. The rotation of the PCA provides a comprehensive summary of the overall degradation as all the metrics have similar patterns, where they will increase with the degradation (Figure S2).

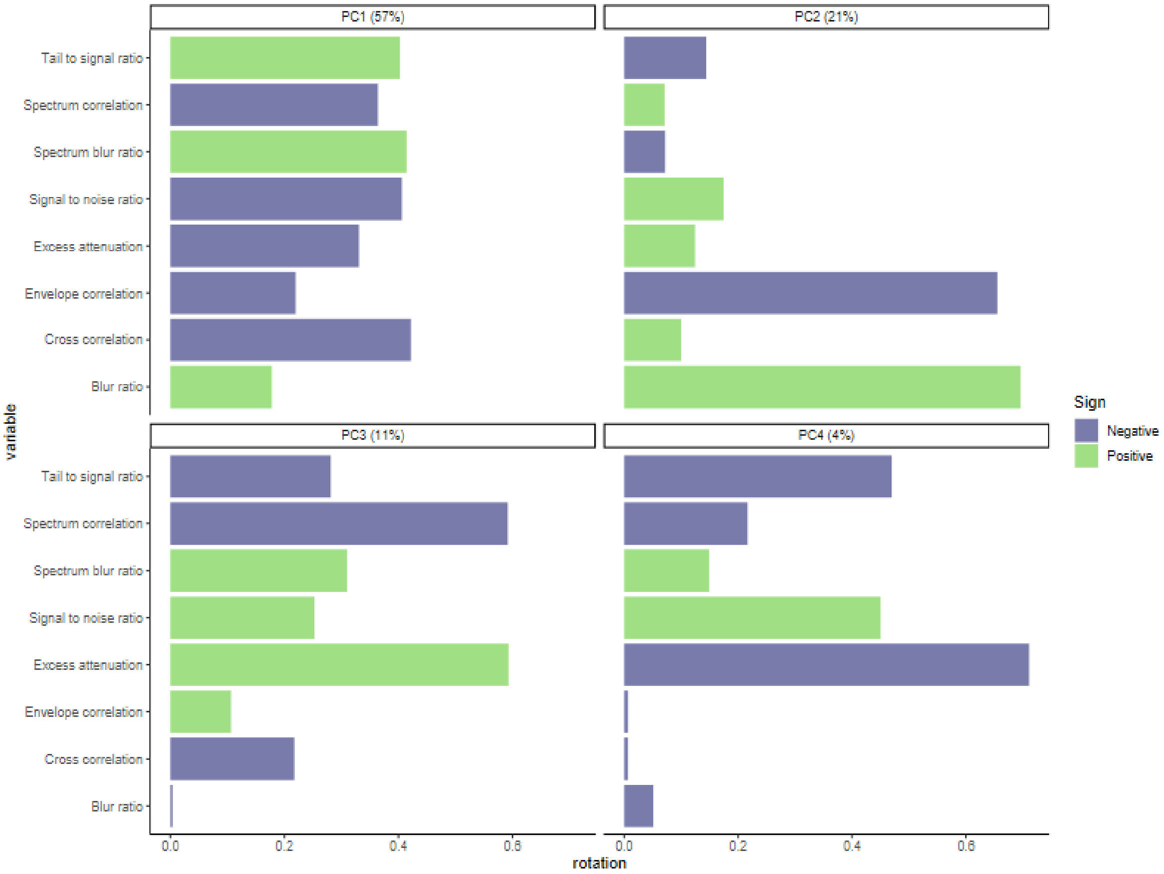

Figure S2. The result loadings of the principal component analysis for each of the different components was obtained.

For our understanding of the persistence and height relationship with degradation, we developed nine models, whose results are summarized in Table S1. Utilizing the credible interval, we inferred that in persistence only one measure of degradation had a significant relationship, while height had six in the models (Figure S4-11). The posterior predictive checks graphs showcased our small partition fitted accordingly in the model, giving us confidence that the model values are not overfitted. The only distinct difference in data representation occurred in spectrum correlation (Figure S12). Lastly, we annexed a summarization of all degradation metrics for all song types and the total to showcase the variance in the data set (Table. S2)

Table S1. Resume of the effect size and credible interval for each model and each parameter, if the 95% credible interval included zero in the interval is non-significant, the significant values are indicated by bold letters. Lastly the Effect size measures the strength of the relationship.

Independent variable	**Direction of degradation**	**Predictor**	**Effect Size**	**95% Credible Interval**
PCA	Higher (+)	Persistence	-0.009	-0.299 – 0.286
Blur ratio	Higher (+)	**Persistence**	**0.006**	**0 – 0.012**
Excess attenuation	Higher (+)	Persistence	-0.024	-0.355 – 0.316
Signal-to-noise ratio	Higher (-)	Persistence	0.248	-0.750 – 1.180
Tail-to-signal ratio	Higher (+)	Persistence	-0.052	-0.500 – 0.379
Cross-correlation	Higher (-)	Persistence	0.009	-0.028 – 0.046
Envelope correlation	Higher (-)	Persistence	-0.015	-0.038 – 0.006
Spectrum blur ratio	Higher (+)	Persistence	-0.004	-0.016 – 0.009
Spectrum correlation	Higher (-)	Persistence	0.006	-0.026 – 0.038
PCA	Higher (+)	**Height**	**0.036**	**0.028 – 0.044**
Blur ratio	Higher (+)	Height	0	0 – 0
Excess attenuation	Higher (+)	Height	0.010	-0.022 – 0.042
Signal-to-noise ratio	Higher (-)	**Height**	**-0.411**	**-0.442 – -0.379**
Tail-to-signal ratio	Higher (+)	**Height**	**0.168**	**0.145 – 0.190**
Cross-correlation	Higher (-)	Height	0	-0.001 – 0.001
Envelope correlation	Higher (-)	**Height**	**0.002**	**0.001 – 0.003**
Spectrum blur ratio	Higher (+)	**Height**	**0.002**	**0.001 – 0.002**
Spectrum correlation	Higher (-)	**Height**	**-0.002**	**-0.003 – 0**

PCA

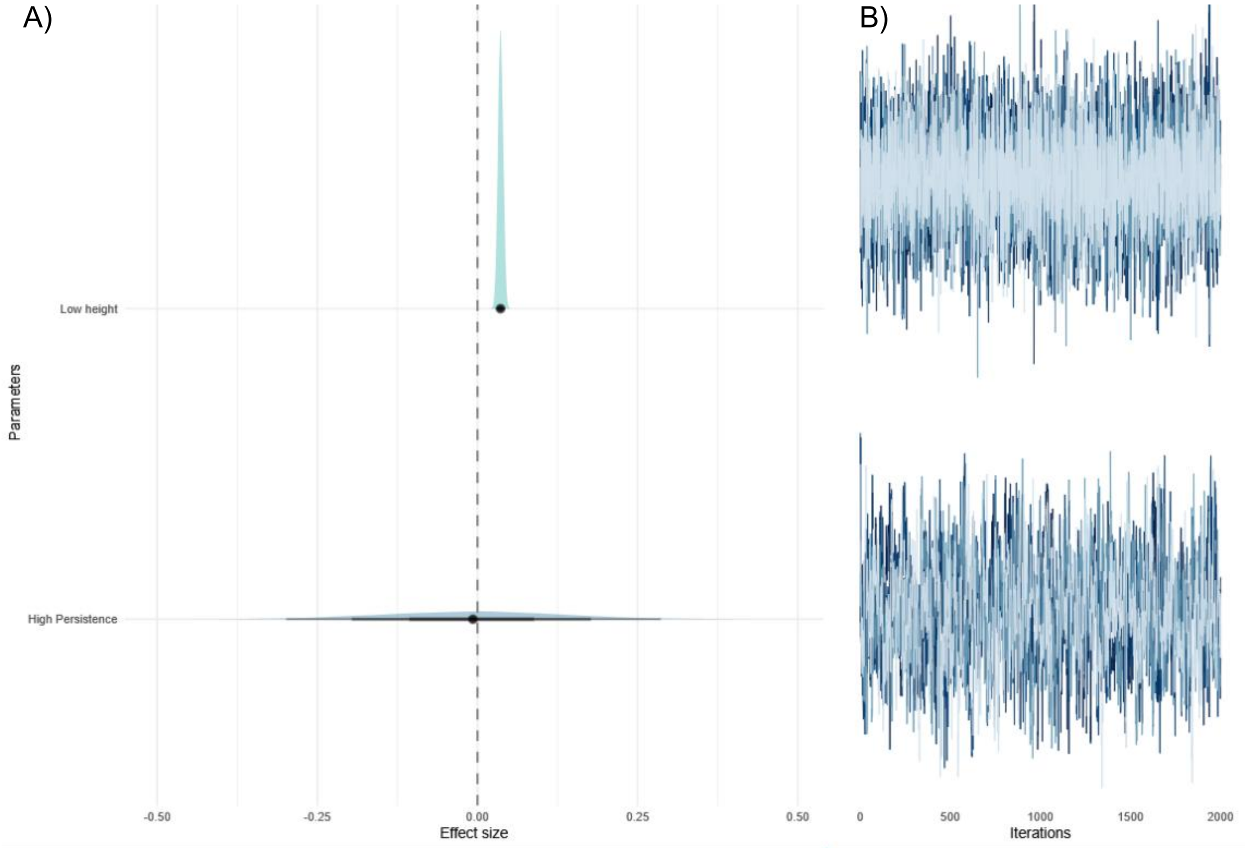

Figure S3. The overall degradation (PC1) model shows only significant results in height, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher PC1 scores mean greater degradation. Therefore, lower heights are more degraded overall as they have a positive effect size.

Blur ratio

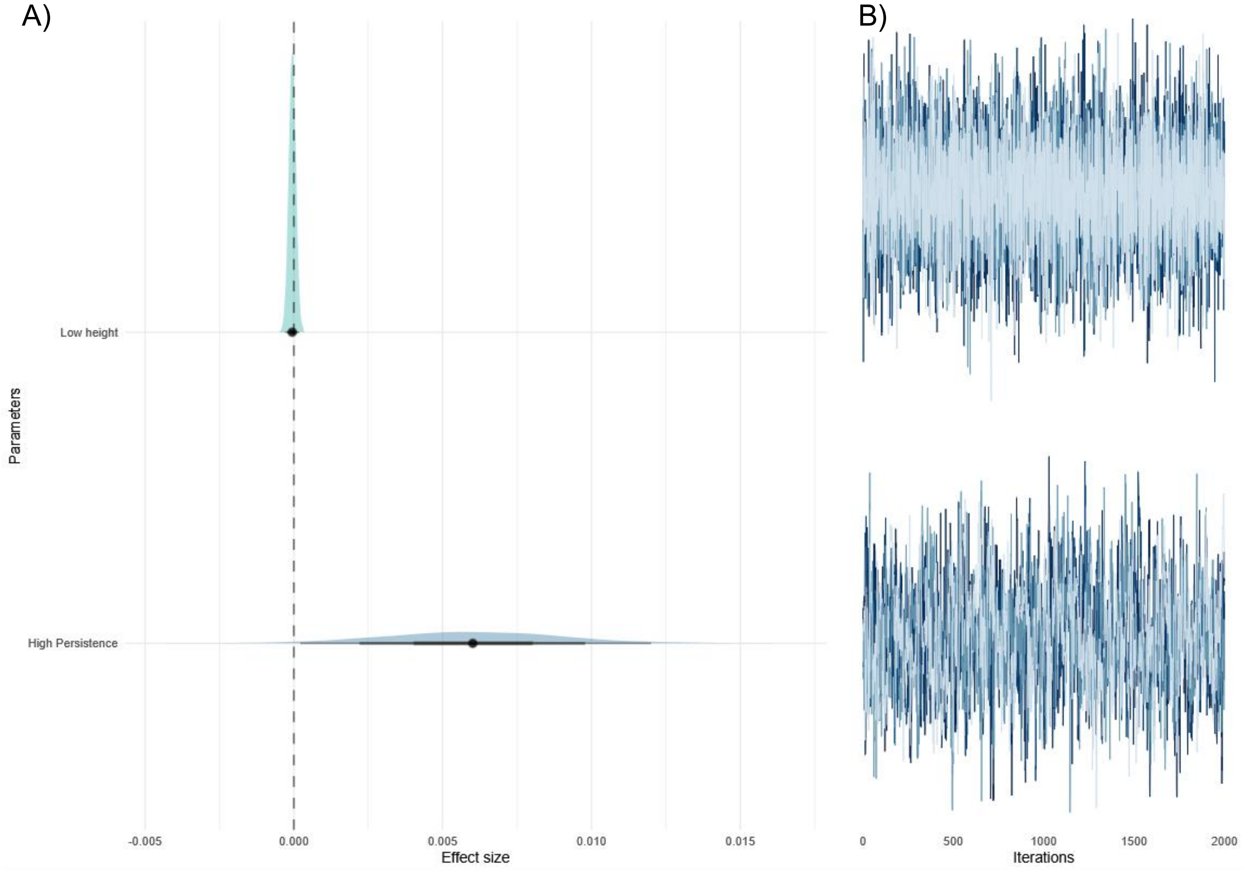

Figure S4. The blur ratio model shows only significant results in persistence, as is indicated in A), showing the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). The graphs on the right. B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher Blur-Ratio scores mean greater degradation. Therefore, high persistence songs are more blurred as they have a positive effect size.

Excess attenuation

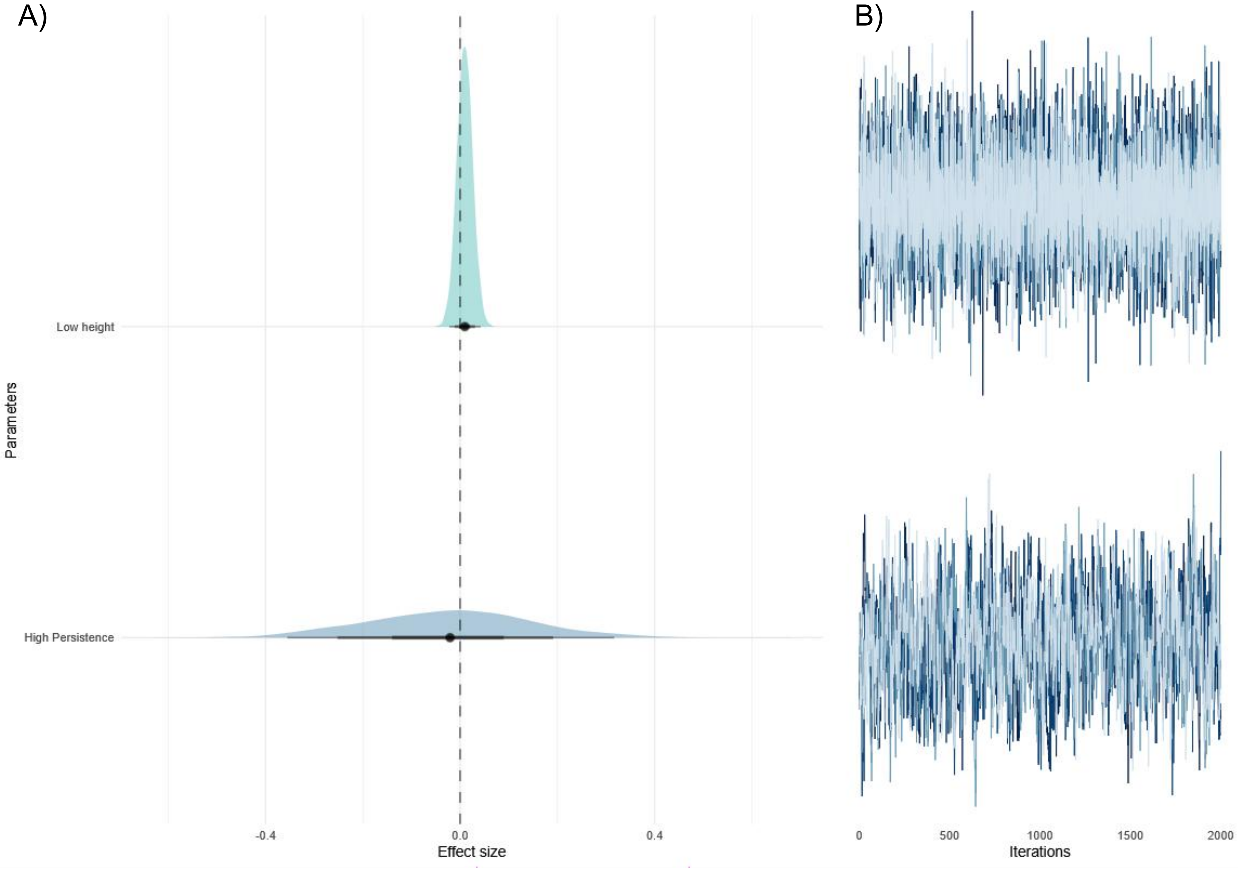

Figure S5. The excess attenuation model shows non-significant results, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter.

Signal-to-noise ratio

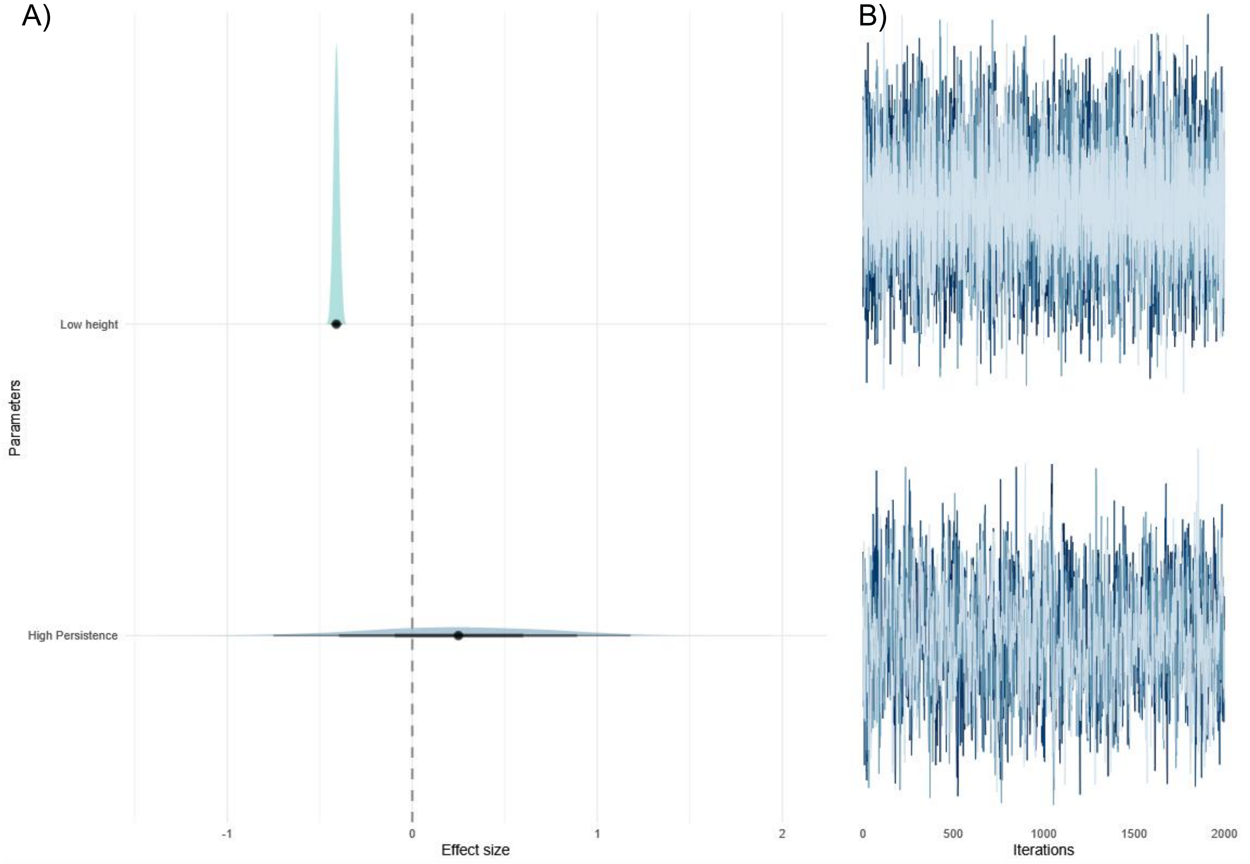

Figure S6. The Signal-to-noise ratio model only shows significant results for height, as is indicated in A) the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher Signal-to-Noise-Ratio scores mean less degradation. Therefore, lower heights are more degraded as they have a negative effect size.

Tail-to-signal ratio

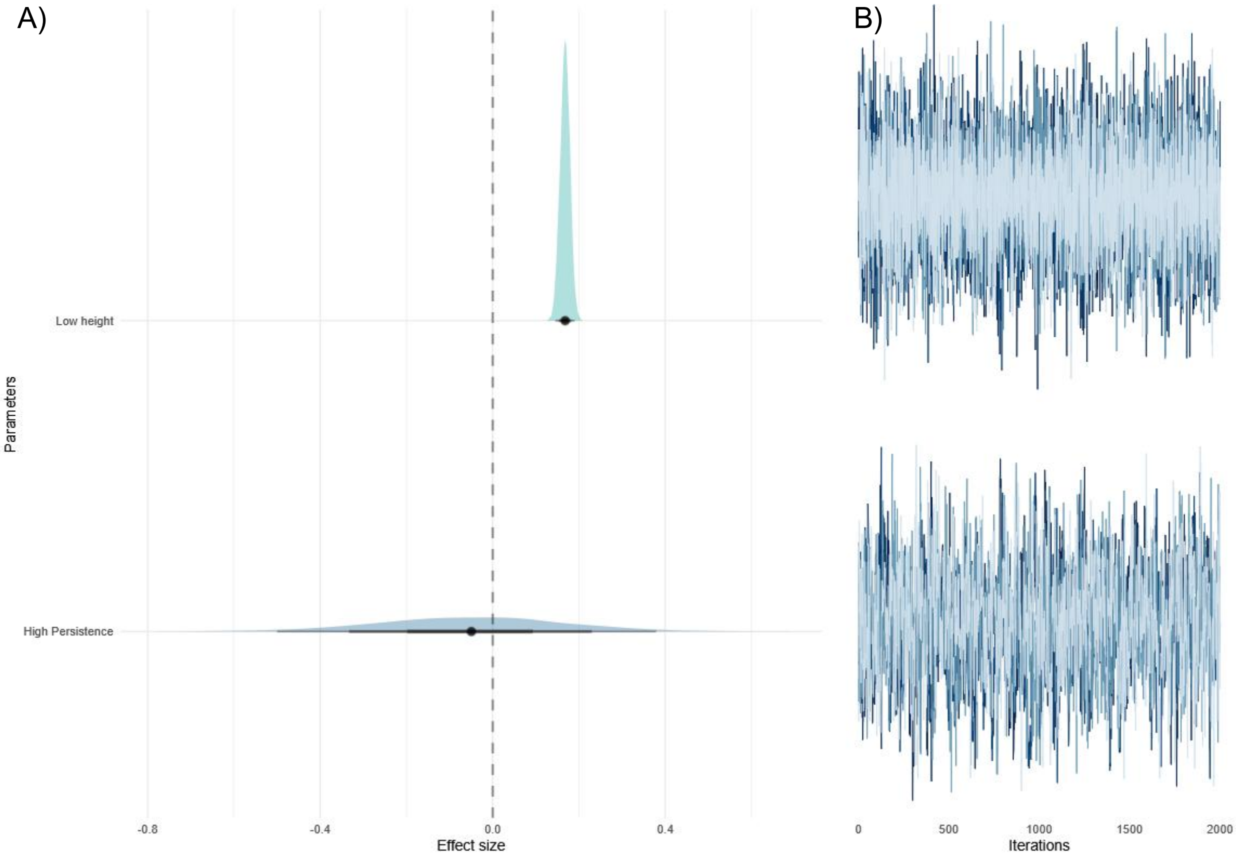

Figure S7. The Tail-to-Signal-Ratio model only shows significant results for height, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher Tail-to-Signal-Ratio scores mean more degradation. Therefore, lower heights are more degraded as they have a positive effect size.

Cross-Correlation

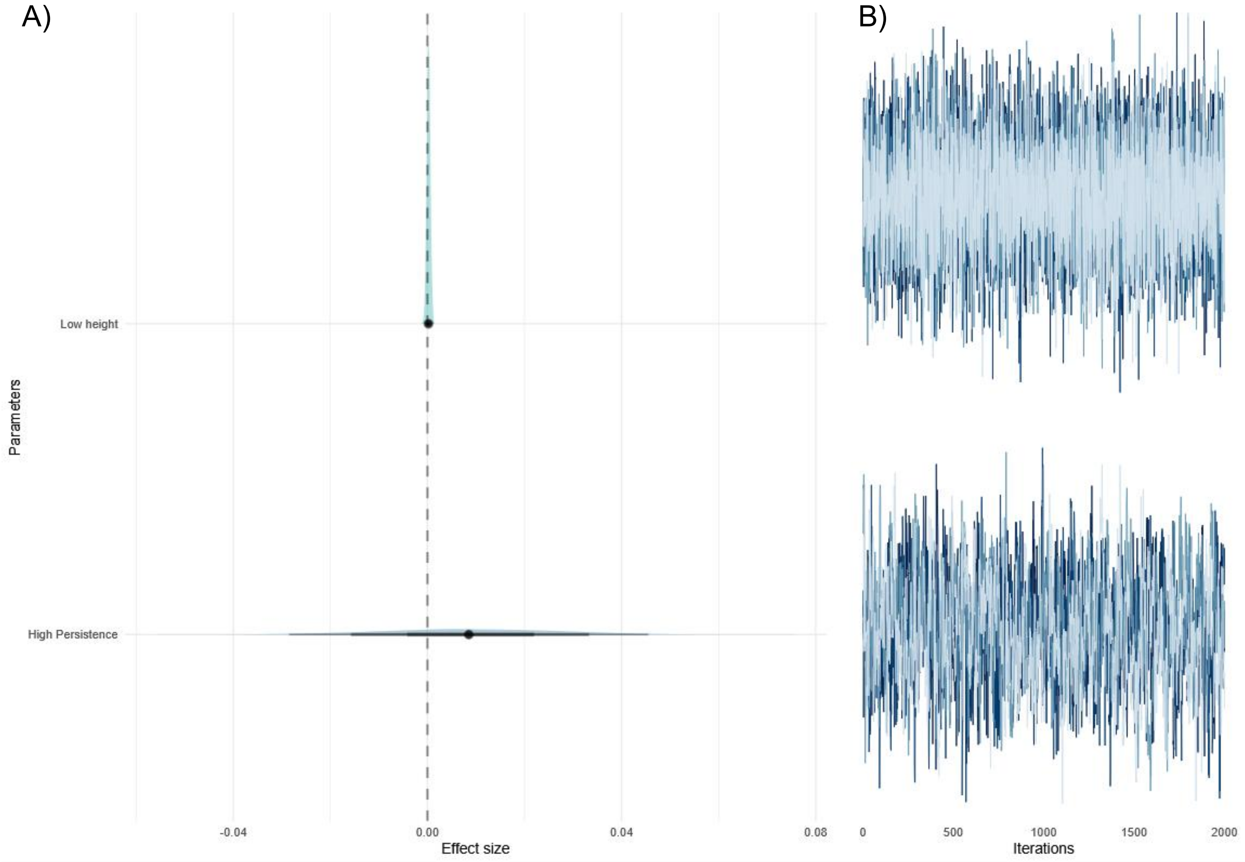

Figure S8. The cross-correlation model shows non-significant results, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter.

Envelope correlation

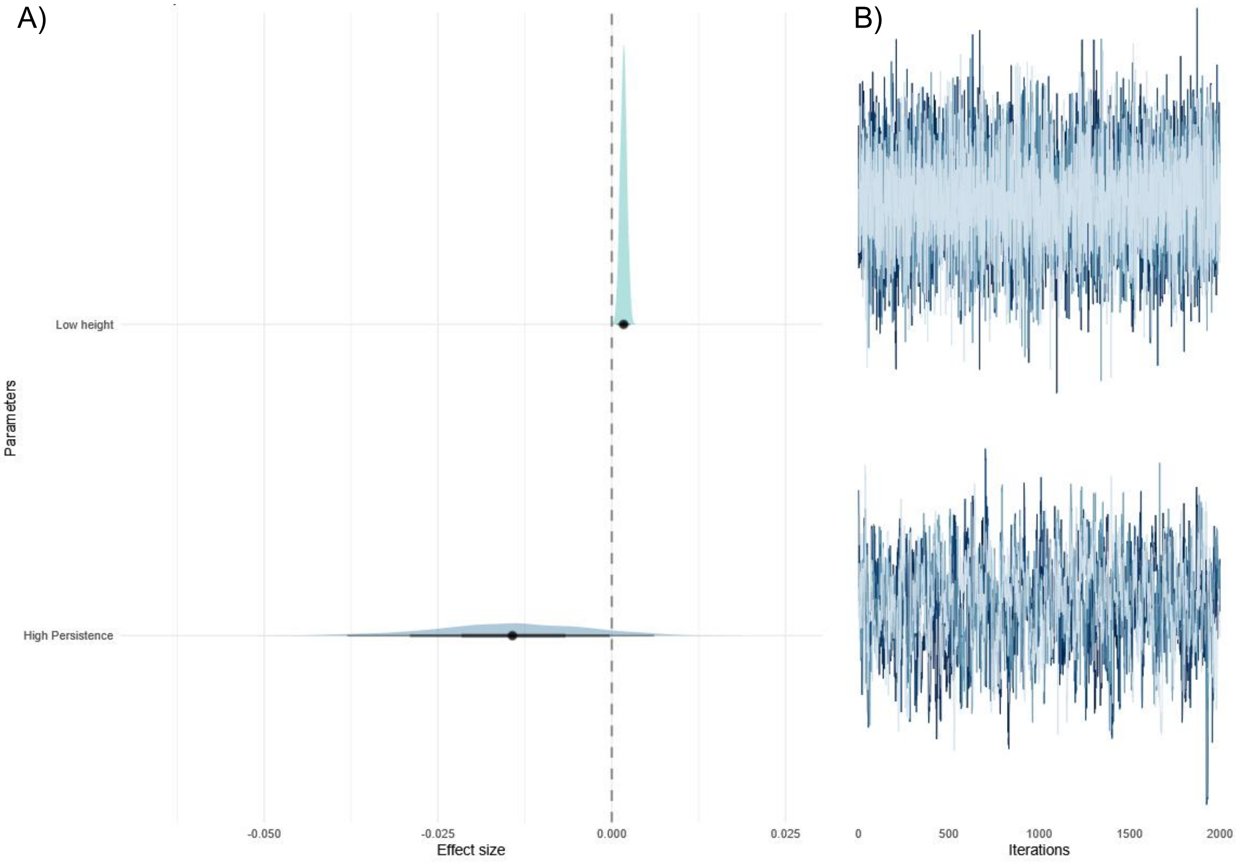

Figure S9. The envelope correlation model only shows significant results for height, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher envelope correlation scores mean less degradation. Therefore, lower heights are more degraded as they have a positive effect size

Spectrum blur ratio

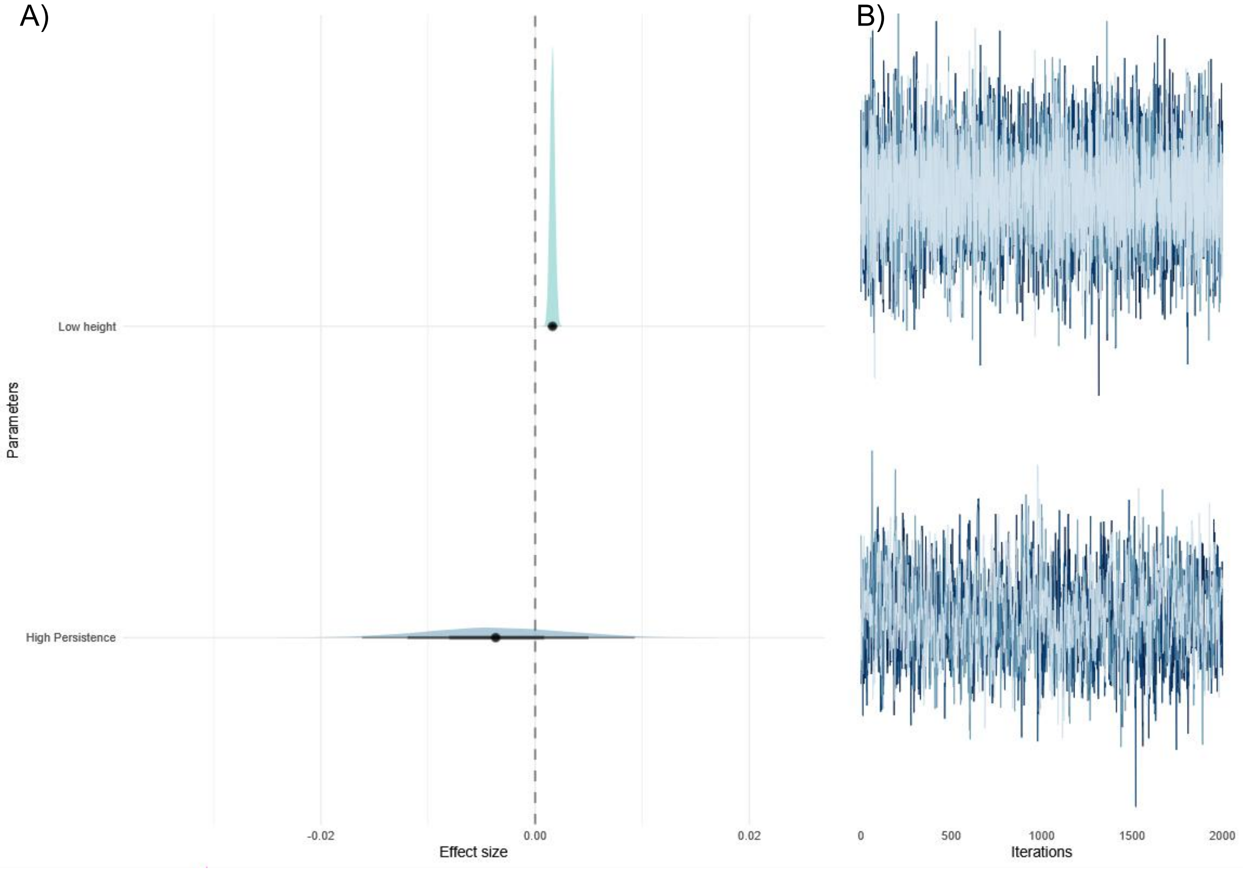

Figure S10. The spectrum blur ratio model only shows significant results for height, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) illustrate the overlap between the chains and mixing across iterations for each parameter. The reference level for height is low, and for persistence, it is high, and higher spectrum blur ratio scores mean more degradation. Therefore, lower heights are more degraded as they have a positive effect size.

Spectrum cross-correlation

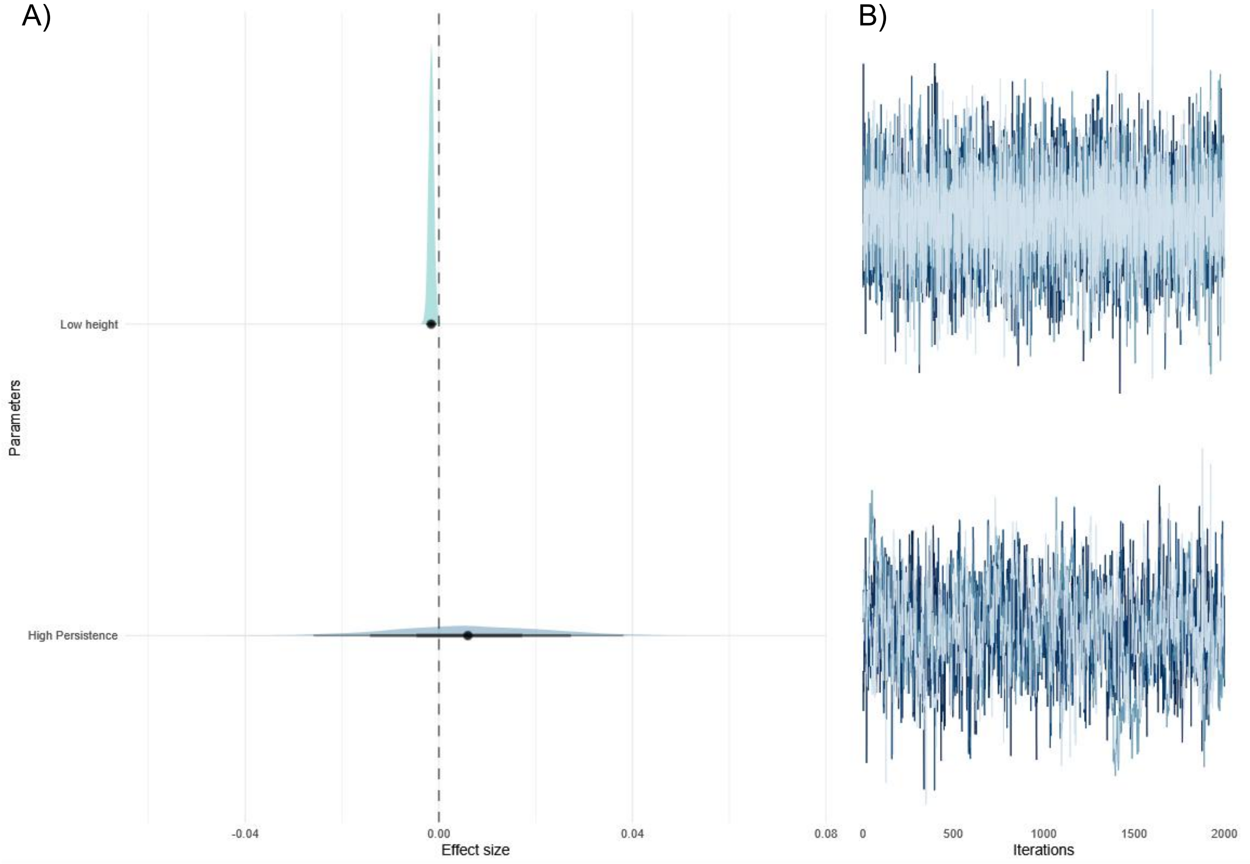

Figure S11. The spectrum correlation model only shows significant results for height, as is indicated in A), the posterior distribution of effect sizes and their credible intervals (50%, 80%, 95%). B) the overlap among the chains and mixing across iteration for each parameter. The reference level for height is low, and for persistence, it is high, and higher spectrum correlation scores mean less degradation. Therefore, lower heights are more degraded as they have a negative effect size

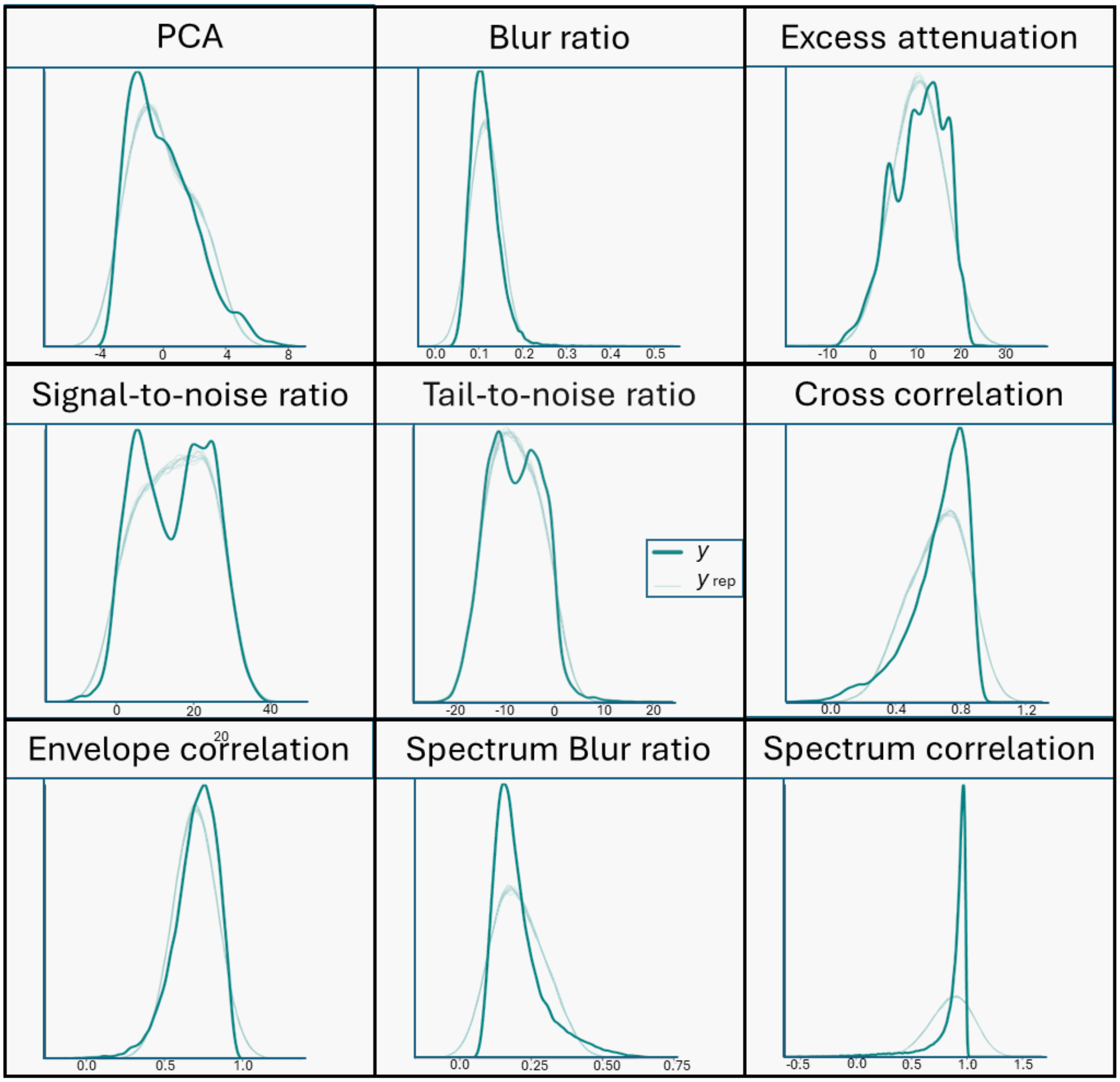

Figure S12. Posterior predictive check of each model, comparing the outcome (*y*), to the 25% remaining real data from the partitions (*yrep*), the closer the lines overlap the more accurately the model fits with the new data. The adjusting of the darker color (*y*) to (*yrep*), infers a overall good fit (PCA, Blur ratio, and Envelope correlation) overestimates variability (Cross correlation and Spectrum correlation), a slight lack multimodality (Excess attenuation, Signal- to noise-ratio and Tail-to noise ratio)

Table S2. A summary displaying the mean and standard deviation of each metric of degradation calculated for each song type and all together.

Song type	Blur ratio	SNR	Tail-to-signal ratio	Excess attenuation	envelope correlation	cross-correlation	Spectrum blur ratio	Spectrum correlation
BR1-D3	0.11 ± 0.03	14.88 ± 9.27	-7.62 ± 4.78	10.68 ± 5.57	0.66 ± 0.13	0.67 ± 0.18	0.22 ± 0.10	0.85 ± 0.21
BR1-D4	0.11 ± 0.03	13.76 ± 9.32	-7.83 ± 5.82	10.39 ± 5.83	0.68 ± 0.12	0.67 ± 0.18	0.23 ± 0.12	0.88 ± 0.19
CCE-C2	0.1 ± 0.0	14.69 ± 9.45	-6.79 ± 4.55	10.72 ± 5.81	0.70 ± 0.12	0.69 ± 0.16	0.19 ± 0.07	0.84 ± 0.2
CCE-F1	0.13 ± 0.03	15.31 ± 9.29	-7.69 ± 4.89	11.09 ± 5.52	0.65 ± 0.15	0.63 ± 0.18	0.21 ± 0.08	0.81 ± 0.21
CCE-I1	0.11 ± 0.03	15.54 ± 9.66	-8.15 ± 5.29	10.38 ± 5.98	0.7 ± 0.13	0.66 ± 0.16	0.2 ± 0.09	0.89 ± 0.17
CCE-I2	0.11 ± 0.02	14.93 ± 9.71	-7.88 ± 5.30	10.05 ± 6.09	0.69 ± 0.12	0.68 ± 0.16	0.2 ± 0.09	0.90 ± 0.16
CCL-I1	0.09 ± 0.03	13.2 ± 9.25	-7.21 ± 5.22	9.73 ± 5.8	0.76 ± 0.12	0.58 ± 0.176	0.20 ± 0.08	0.85 ± 0.20
CCL-K1	0.12 ± 0.03	13.23 ± 9.5	-6.83 ± 5.41	10.42 ± 5.88	0.69 ± 0.13	0.59 ± 0.18	0.2 ± 0.07	0.83 ± 0.21
CCL-K2	0.11 ± 0.03	14.99 ± 9.75	-7.83 ± 5.28	10.12 ± 6.09	0.68 ± 0.13	0.57 ± 0.15	0.19 ± 0.08	0.88 ± 0.18
CCL-L1	0.13 ± 0.03	15.37 ± 9.56	-7.20 ± 5.49	10.63 ± 5.86	0.67 ± 0.16	0.63 ± 0.16	0.2 ± 0.07	0.87 ± 0.17
CCL-L2	0.11 ± 0.03	15.83 ± 9.48	-7.83 ± 4.85	10.79 ± 5.86	0.7 ± 0.11	0.64 ± 0.16	0.19 ± 0.07	0.84 ± 0.2
CCL-M1	0.12 ± 0.03	14.11 ± 9.29	-7.29 ± 5.37	10.60 ± 5.77	0.72 ± 0.13	0.5 ± 0.20	0.22 ± 0.08	0.83 ± 0.17
CCL-N1	0.12 ± 0.03	17.38 ± 9.39	-9.31 ± 4.86	11.07 ± 5.59	0.63 ± 0.14	0.63 ± 0.16	0.2 ± 0.08	0.86 ± 0.17
HC1-F2	0.12 ± 0.03	17.13 ± 9.74	-7.67 ± 4.94	10.71 ± 5.98	0.6 ± 0.13	0.75 ± 0.17	0.19 ± 0.09	0.9 ± 0.15
LOC-A1	0.10 ± 0.02	15.53 ± 9.82	-8.6 ± 5.46	10.19 ± 6.11	0.7 ± 0.11	0.75 ± 0.17	0.20 ± 0.1	0.89 ± 0.17
LOC-A2	0.1 ± 0.03	14.9 ± 9.67	-7.9 ± 5.36	10.29 ± 6	0.68 ± 0.13	0.69 ± 0.16	0.21 ± 0.1	0.89 ± 0.16
SAT-G1	0.12 ± 0.03	15.78 ± 9.8	-8.69 ± 5.6	10.15 ± 6.09	0.62 ± 0.15	0.71 ± 0.15	0.19 ± 0.09	0.9 ± 0.16
SJA-C1	0.12 ± 0.04	15.87 ± 9.49	-8.97 ± 5.46	10.5 ± 5.72	0.69 ± 0.15	0.67 ± 0.17	0.20 ± 0.09	0.86 ± 0.18
SJA-D3	0.11 ± 0.03	15.99 ± 9.6	-9.17 ± 5.69	10.46 ± 5.86	0.7 ± 0.15	0.71 ± 0.17	0.2 ± 0.09	0.87 ± 0.18
SUR-A4	0.11 ± 0.03	18.17 ± 9.59	-8.21 ± 4.63	11.41 ± 5.71	0.65 ± 0.12	0.74 ± 0.15	0.18 ± 0.09	0.88 ± 0.15
SUR-A5	0.11 ± 0.03	17.12 ± 9.53	-8.26 ± 4.96	10.88 ± 5.72	0.66 ± 0.12	0.7 ± 0.15	0.19 ± 0.09	0.87 ± 0.17
SUR-E1	0.1 ± 0.03	16.34 ± 9.52	-8.36 ± 5	10.67 ± 5.89	0.67 ± 0.13	0.7 ± 0.16	0.19 ± 0.07	0.87 ± 0.17

SUR-F1	0.11 ± 0.03	12.54 ± 9.58	-6.9 ± 5.33	10 ± 6.09	0.7 ± 0.13	0.62 ± 0.19	0.21 ± 0.09	0.85 ± 0.21
SUR-F3	0.09 ± 0.03	10.66 ± 9.06	-6.38 ± 5.23	10.37 ± 5.79	0.76 ± 0.11	0.51 ± 0.2	0.21 ± 0.08	0.75 ± 0.24
SUR-F4	0.1 ± 0.03	11.97 ± 9.2	-7.59 ± 5.95	9.81 ± 5.88	0.72 ± 0.12	0.65 ± 0.19	0.25 ± 0.12	0.83 ± 0.22
SUR-F5	0.09 ± 0.03	13.35 ± 9.78	-7.97 ± 5.64	9.85 ± 6.2	0.75 ± 0.1	0.66 ± 0.17	0.22 ± 0.11	0.86 ± 0.20
SUR-H1	0.12 ± 0.03	12.03 ± 9.18	-7.91 ± 5.76	10.19 ± 5.78	0.7 ± 0.15	0.56 ± 0.18	0.2 ± 0.07	0.79 ± 0.2
SUR-H3	0.1 ± 0.02	16.1 ± 9.39	-9.25 ± 5.56	11.1 ± 5.62	0.68 ± 0.13	0.64 ± 0.16	0.2 ± 0.07	0.84 ± 0.21
SUR-J1	0.11 ± 0.03	13.43 ± 9.71	-7.8 ± 5.41	10.14 ± 6.03	0.71 ± 0.14	0.58 ± 0.19	0.2 ± 0.08	0.82 ± 0.21
SUR-J2	0.11 ± 0.03	13.94 ± 9.14	-8.63 ± 4.74	10.89 ± 5.56	0.76 ± 0.15	0.61 ± 0.18	0.21 ± 0.07	0.76 ± 0.21
SUR-J3	0.12 ± 0.04	14.68 ± 9.75	-9.61 ± 5.83	10.48 ± 5.96	0.69 ± 0.17	0.67 ± 0.18	0.19 ± 0.08	0.85 ± 0.18
SUR-J4	0.11 ± 0.03	14.25 ± 9.54	-9.71 ± 6.14	10.27 ± 5.95	0.71 ± 0.16	0.63 ± 0.15	0.19 ± 0.07	0.85 ± 0.17
SUR-J6	0.13 ± 0.03	16.56 ± 9.67	-8.5 ± 5.1	10.36 ± 6	0.64 ± 0.18	0.73 ± 0.18	0.19 ± 0.08	0.9 ± 0.15
SUR-K1	0.1 ± 0.03	13.41 ± 9.73	-8.47 ± 6.07	9.83 ± 6.15	0.73 ± 0.11	0.68 ± 0.18	0.23 ± 0.12	0.87 ± 0.19
SUR-K2	0.09 ± 0.03	13.91 ± 9.49	-8.27 ± 5.79	10.13 ± 6.03	0.73 ± 0.13	0.69 ± 0.18	0.22 ± 0.11	0.87 ± 0.18
SUR-K3	0.09 ± 0.03	13.86 ± 9.72	-8.31 ± 5.98	9.95 ± 6.17	0.76 ± 0.09	0.7 ± 0.18	0.22 ± 0.11	0.89 ± 0.18
SUR-K4	0.11 ± 0.02	14.08 ± 9.77	-8.44 ± 6.12	9.72 ± 6.14	0.69 ± 0.11	0.67 ± 0.18	0.23 ± 0.12	0.89 ± 0.18
SUR-L1	0.12 ± 0.03	15.47 ± 9.65	-8.42 ± 5.53	10.35 ± 5.97	0.69 ± 0.14	0.69 ± 0.16	0.19 ± 0.09	0.90 ± 0.16
TR1-D1	0.09 ± 0.02	13.73 ± 9.26	-7.44 ± 5.3	10.26 ± 5.77	0.76 ± 0.11	0.62 ± 0.17	0.2 ± 0.08	0.82 ± 0.2
TR1-E4	0.11 ± 0.03	13.91 ± 9.57	-6.5 ± 4.95	10.2 ± 5.96	0.67 ± 0.13	0.64 ± 0.18	0.2 ± 0.07	0.85 ± 0.2
Total	**0.11 ± 0.03**	**14.75 ± 9.65**	**-8.04 ± 5.43**	**10.40 ± 5.91**	**0.69 ± 0.14**	**0.65 ± 0.18**	**0.20 ± 0.09**	**0.86 ± 0.19**

Capítulo 2

Physiological constraints affect the features of bird song during cultural evolution

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Abstract

Cultural evolution in non-primate species was once considered rare and largely stochastic, driven primarily by processes such as cultural drift. Social traits involved in cultural evolution can exhibit continuous change, with their transmission resembling genetic processes, but with greater dynamism as cultural transmission can occur in multiple directions and does not require genetic relatedness. This dynamic nature enables the use of phylogenetic tools to study cultural selection processes and uncover underlying patterns. This framework is particularly well-suited for exploring the complex and multidimensional behavioral traits, that emerge from the interaction of time, frequency, and energy, such as vocalizations, that characterize cultural evolution. We applied these methods to investigate the cultural evolution of song structure over a span of 50 years in five social units of the lekking Long-billed Hermit hummingbird (*Phaethornis longirostris*), focusing on how their evolution is constrained by vocal production mechanisms (*e.g.,* syrinx and beak). Using cultural trees and macroevolutionary techniques to analyze the evolutionary rate and patterns of selected song features revealed strong phylogenetic signal, indicating an important role of cultural evolution in shaping song types. Notably, we found that those song features less constrained by physiological limitations exhibited higher evolutionary rates. These findings offer new insights into the influence of mechanical production constraints on vocal culture, and the dynamics of cultural evolution among social units.

Keywords

Cultural trees, Physiological constraints, Continuous behavior traits, Macroevolutionary, Bias, Bioacoustics, Phylogenetic signal, Evolutionary rates, and Lekking behavior

Introduction

Social learning allows the organisms to produce and spread novel trait variants, in some cases even within a single generation as this process is not tied to genetic transmission. The cumulative variants of these traits inherited between individuals through generations are known as culture (Duboscq *et al.,* 2016; Aplin, 2019; Whiten, 2019; Williams, 2021). Evidence of this cultural process has been observed in a variety of animals and their behavioral traits such as food processing (*e.g.,* primates, bees, birds) (Kawai, 1965; Lefebvre, 1995; Alem *et al.,* 2016); migratory routes (*e.g.,* whales, sheep, and birds) (Valenzuela *et al.,* 2009; Palacín *et al.,* 2011; Jesmer *et al.,* 2018); vocal repertoires (*e.g.,* whales and songbirds) (Whiten *et al.,* 1999; Garland *et al.,* 2022); and mate choice (*e.g.,* fish and flies) (Dugatkin & Godin, 1993; Danchin *et al.,* 2018).

Culture follows evolutionary processes akin to genetics, where individual biases in learning and subsequent transmission via learning shape the trajectory of cultural evolution. This complex system of selection involving multiple individuals can make culture dynamic across time, not necessarily following a deterministic pattern (Podos *et al.,* 2004a; Byers *et al.,* 2010; Williams *et al.,* 2013; Whiten, 2019). The learning mechanism, inherently produces new variants through innovation, cumulative changes, errors in learning and the ability to modify learning traits (Podos *et al.,* 2004a; Mesoudi *et al.,* 2016; Mesoudi & Thornton, 2018; Williams, 2021; Williams & Lachlan, 2022). Simultaneously, the constraints imposed by learning and producing mechanisms determine the diversity of new variants generated through this process. As these trait variants persist over time, they allow selection can act upon them, favoring those that enhance fitness while remaining within the limits set by the constraints generating variants (Podos *et al.,* 2004a; Williams & Lachlan, 2022).

Vocal production learning is an interesting framework for studying cultural evolution in complex traits and their constraints. Acoustic signals forms arise from variations in energy across the frequency and time domains, making them inherently multidimensional. These multiple axes of variation coupled with culturally generated variation can produce a high diversity of behavioral variants with a high rate of macroevolutionary change (Medina-García *et al.,* 2015; Arato & Fitch, 2021; Vernes *et al.,* 2021; Williams & Lachlan, 2022). However, the expression of these traits is shaped and constrained by multiple anatomical and physiological mechanisms such as the vocal production system, neural learning capacity, motor control, and coordination (Podos *et al*., 2009; Hyland Bruno *et al.,* 2021). Among these, the vocal production system has been extensively studied, as it provides a clear physical basis for how sound is produced and may be limited (Podos *et al.,* 2004a; Podos *et al.,* 2009; Podos & Sung, 2020). However, our understanding of the role of such constraining mechanisms comes largely from comparative studies across species (Mason *et al.,* 2017; Derryberry *et al.,* 2018; Podos & Sung, 2020; Porzio *et al.,* 2024; Sagar *et al.,* 2024) and the effect of such constraints in shaping cultural evolution remains unclear.

There are two physiological components involved in the production of vocal sounds: 1) the sound production system (*e.g.,* larynx and syrinx); and 2) the filtering system (*e.g.,* tongue, lips, jaw, or beaks) (Podos *et al.,* 2004a; Podos *et al.,* 2009; Podos & Sung, 2020). Each component influences different dimensions of the sound, altering a number of features (Podos & Sung, 2020; Odom *et al.,* 2021; Vernes *et al.,* 2021; Friis *et al.,* 2021). In bird vocalizations, several physiological traits are closely linked to particular features of the vocalizations. For instance, beak size and body mass are both associated with minimum frequency (Podos *et al.,* 2004b; Mason *et al.,* 2017; Derryberry *et al.,* 2018; Porzio *et al.,* 2024; Sagar *et al.,* 2024) and beak size is also linked to element repetition rate (Hoese *et al*., 2000; Podos *et al*., 2009; Derryberry *et al.,* 2012). The shape of the spectral envelope (which represents the distribution of energy in the frequency domain) is also partly determined by the bird´s upper vocal tract and by the volume of the oropharyngeal-esophageal cavity (Podos & Sung, 2020). Additional physiological constraints have been suggested, such as the relationship of the signal duration which is limited by the air supply of the respiratory system, and the capacity to take short breaths along the silent intervals of the vocal output, particularly in whistles and continuous sounds this might play a bigger role (Plummer & Goller, 2008; Schmidt & Goller, 2016; Logue *et al.,* 2020). These physiological constraints likely influence the structure of acoustic signals, potentially limiting the extent of variation introduced through cultural evolution.

In this study, we investigate whether physiological constraints influence the evolutionary change of multiple structural features of a learned vocal trait during cultural evolution. Specifically, we evaluated whether the expected association between certain vocal features with physiological traits lowers the accumulation of change driven by cultural evolution in comparison to non-constrained vocal features. We use the lekking Long-billed Hermit hummingbird (*Phaethornis longirostris*) as our model species, as it has been confirming vocal learning of one song type and ability to substitute it through their adulthood (Araya-Salas & Wright, 2013; Araya-Salas *et al.,* 2019). Furthermore, vocal variants are shared among males within a lek, with some of these variants persisting for multiple years, suggesting a dynamic process of cultural evolution (Araya-Salas & Wright, 2013). This appears to be a broader cultural pattern in this understudied group of birds (Gaunt *et al.,* 1994; Gonzáles & Ornelas, 2009; Lara *et al.,* 2015; Gonzáles & Ornelas, 2019). Using the acoustic data from five leks spanning 50 years, we analyzed the changes in several acoustic features of the songs throughout time to estimate the evolutionary rate of change for each feature.

Methods

We characterized the structure of song types by annotating 12271 songs recorded from five leks over a 50-year sampling period in three sites in Costa Rica (Figure 1). Annotations were made using the software Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2024), setting the time and frequency positions of songs on the spectrograms. During this process, we cataloged the different song types by visual inspection of the spectrograms (Vargas-Castro *et al.,* 2012; Araya-Salas *et al.,* 2019; Figure 2).

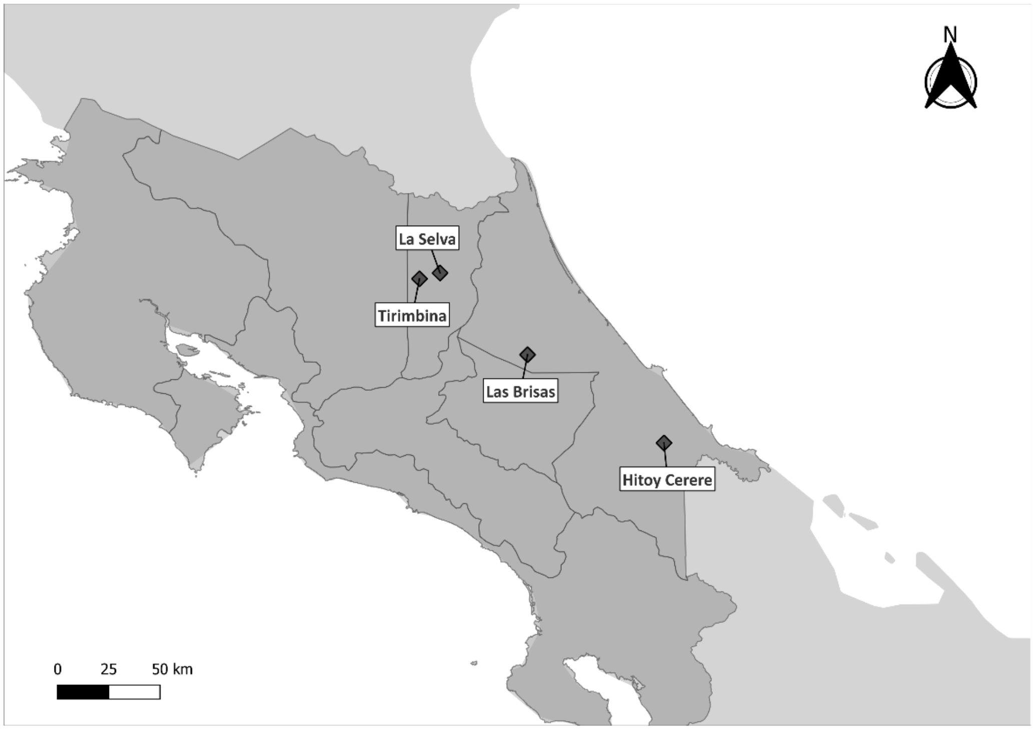

Figure 1. Map of the sites with leks studied in Costa Rica

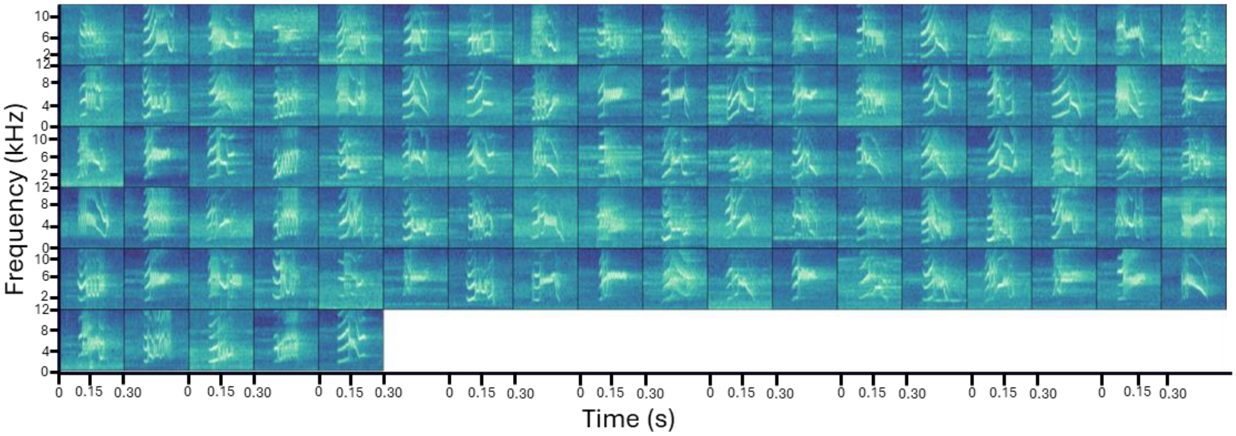

Figure 2. Example of the diversity of song types in the five leks, each square is a spectrogram from a different song type (95), and the axes illustrate the time and frequency values.

Annotations were exported into R (R Core Team, 2022) with the package Rraven (Araya-Salas, 2020). We then used the package warbleR (Araya-Salas & Smith Vidaurre, 2017) to automatically trace the contour of the fundamental frequency (*i.e.,* f0) for each annotated song. Precision of F0 tracking in the output contours was visually checked and manually tailored when required. For each annotated song we calculated the acoustic features for which we have an expectation of the degree of physiological constraint. Following our hypothesis, we separated the features into two categories: 1) Highly constrained, features that had been previously described in other bird species as constrained by the physiological mechanisms involved in song production; 2) Less constrained, features related to time and the distribution of energy in the time domain (Table 1). The expression of these features is due to their dependence on vocal motor control and behavioral flexibility rather than hard anatomical limits. To assess the extent to which acoustic features represent intrinsic characteristics of song types, we quantified their repeatability within song types using the package rptR (Stoffel *et al.,* 2017). Acoustic features with low repeatability were excluded from further analyses.

Table 1. Acoustic features, physiological constraint level, and associated citations.

Feature	Category	Support
Duration	Highly constrained	Schmidt & Goller, 2016; Teipel & Goller, 2025
Mean frequency	Highly constrained	Mason *et al.,* 2017; Friis *et al.,* 2022;
Maximum frequency	Highly constrained	Mason *et al.,* 2017
Minimum frequency	Highly constrained	Podos *et al.,* 2004b; Greig *et al.,* 2013; Mason *et al.,* 2017; Derryberry *et al.,* 2012
Frequency range	Highly constrained	Podos *et al.,* 2004b; Friis *et al.,* 2022
Mean peak frequency	Highly constrained	Elie & Theunissen, 2020
Modulation index	Highly constrained	Podos & Sung, 2020
Spectral entropy	Less constrained	
Skewness	Less constrained	
Kurtosis	Less constrained	
Time entropy	Less constrained	
Interquartile time range	Less constrained	

Peak time	Less constrained	

For the evolutionary analysis of these trait features, we used phylogenetic methods to build cultural trees constructed using the song types to represent the historical process of changes in song structure during cultural evolution. These cultural trees were used to evaluate the changes in song structure throughout the process of evolution and to identify the dimensions of the song that experienced greater variation (Mesoudi, 2017). The phylogenetic representation has already been constructed (Araya-Salas, in prep; Figure 3) using a fossilized birth-death process model in RevBayes v. 1.0.12 (Höhna *et al.,* 2018). To build the cultural trees, each song type contour was encoded as sequence, and aligned using the prank algorithm (Löytynoja, 2013).

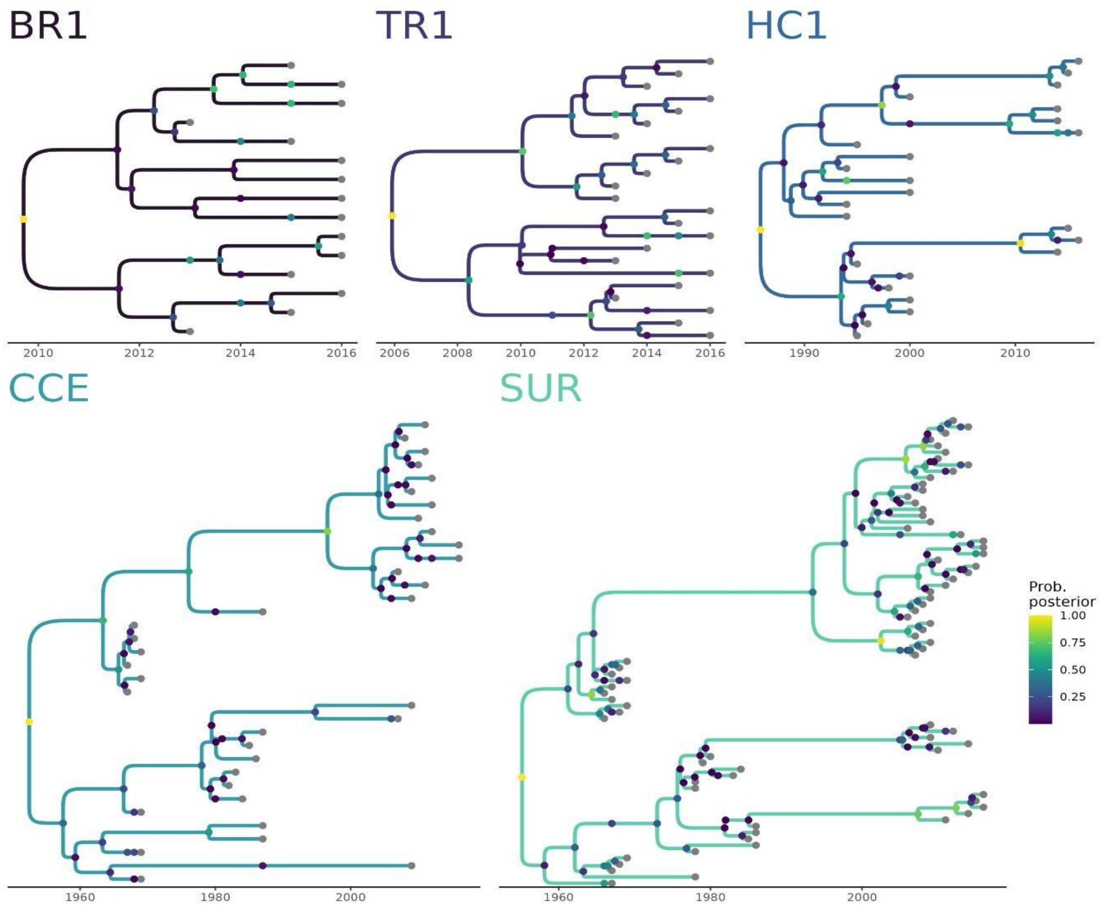

Figure 3. The five cultural trees detailing the song type evolution in each lek studied, each tree node is a song type and the color scheme in is based on its value of posterior distribution. The trees at the bottom contain more data, reflecting differences in site sampling effort.

To accomplish this, each song type was split into 20 segments of equal length. Each segment was classified into one of six categories of pure tones and trills: (1) slow trill, (2) medium-paced trill, (3) fast trill, (4) downward pure tone, (5) upward pure tone, and (6) flat pure tone (Figure 4, Araya-Salas, in prep).

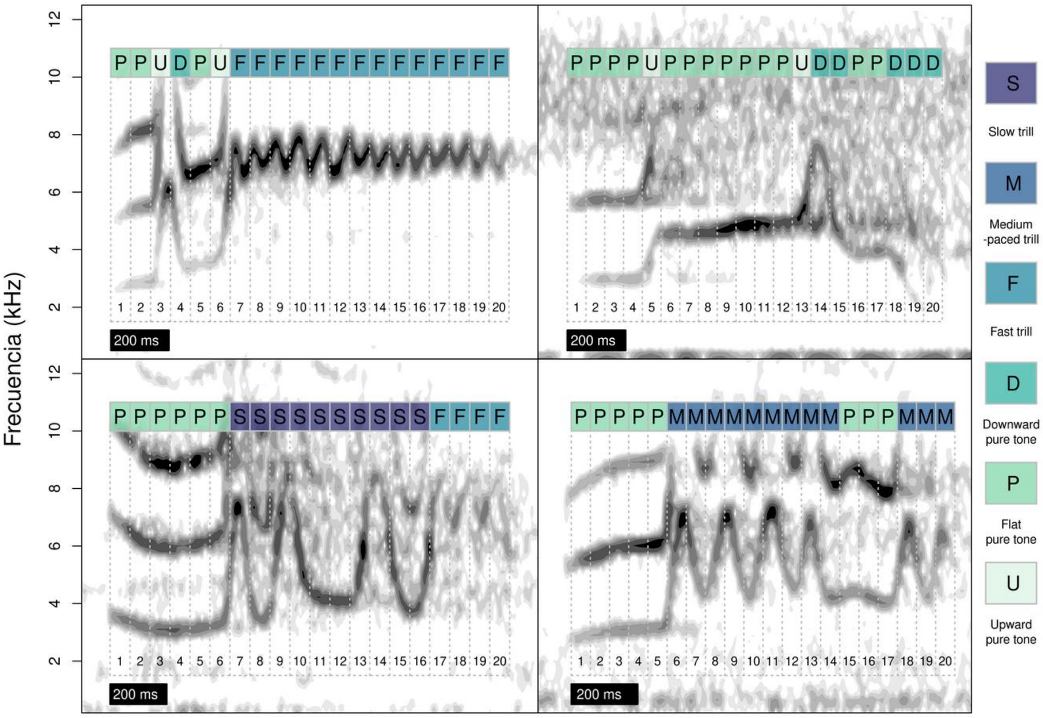

Figure 4. Four song-type examples detailing the segmentation and classification of each segment with the 6 unique categories.

These cultural trees were combined into a single supertree for further analysis (Figure 5). We first measured the phylogenetic signal of single acoustic features, using the R package phytools (Revell, 2024), as well as the overall phylogenetic signal of songs using acoustic features as dimensions of a multivariate trait with the R package geomorph (Adams *et al.,* 2025). This analysis allowed us to estimate whether closed related song types had similar feature values, with it inferring if the features are also transmitted during the cultural evolution process of song structure. Then, we compare the multivariate evolutionary rate of highly constrained features against that from less constrained features with the R package geomorph (Adams 2013; Adams & Otárola-Castillo, 2013; Revell, 2024; Table S3). For all three tests, multivariate analyses involved log-transforming all variables to account for differences in magnitude (Adams, 2013; Medina-García *et al.,* 2015).

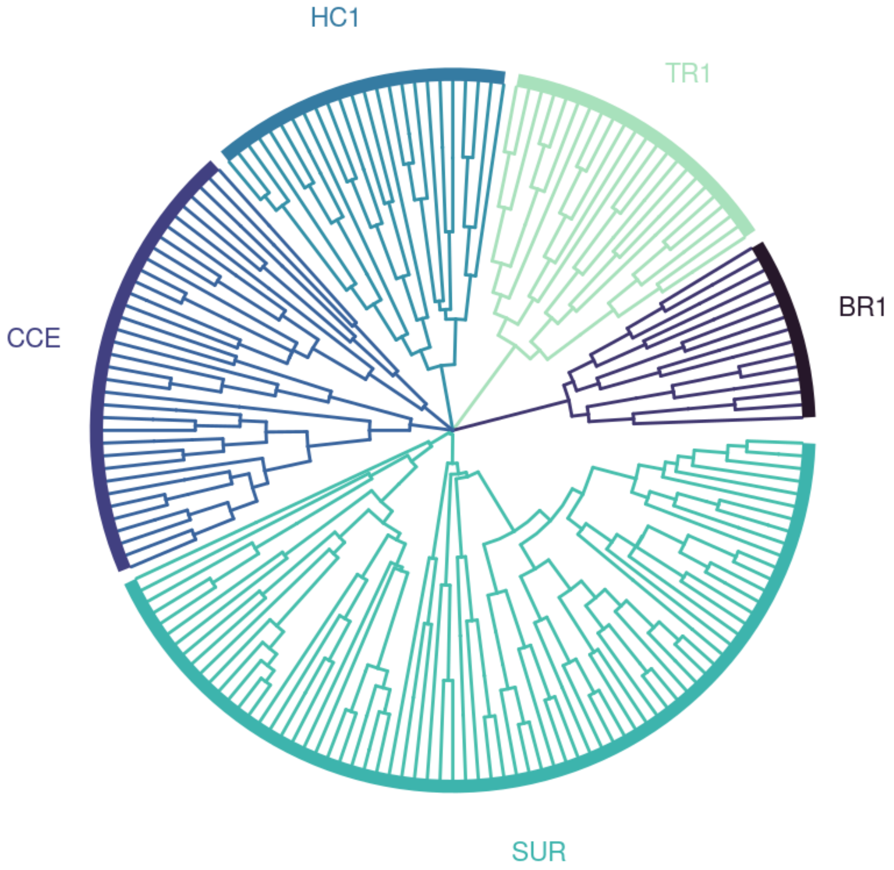

Figure 5. The super cultural tree is composed of five different cultural reconstructions belonging to unique social units (leks), each color represents one of these leks and every tip a song type.

Results

The song type classification resulted in 95 unique categories from 7460 songs, with a mean of 78.52 songs recorded per song type (± 117.42 S.D.), each song type was re-recorded across an average of 1.93 years (± 1.36 S.D.). Among the five leks studied, each lek had 4.27 song types co-occurring per year (± 1.96 S.D.).

Repeatability was moderate to high for most acoustic features (mean = 0.75 ± 0.2 SD), except for kurtosis and peak time, which were excluded from further analyses (table S1). Phylogenetic signal was moderately high for both single features (mean = 0.67 ± 0.2 S.D.) and as a combined multidimensional trait (multivariate phylogenetic signal = 0.79 CI) (Figure 6; table S2). The only feature that had a lower phylogenetic signal was minimum frequency (Figure. 6).

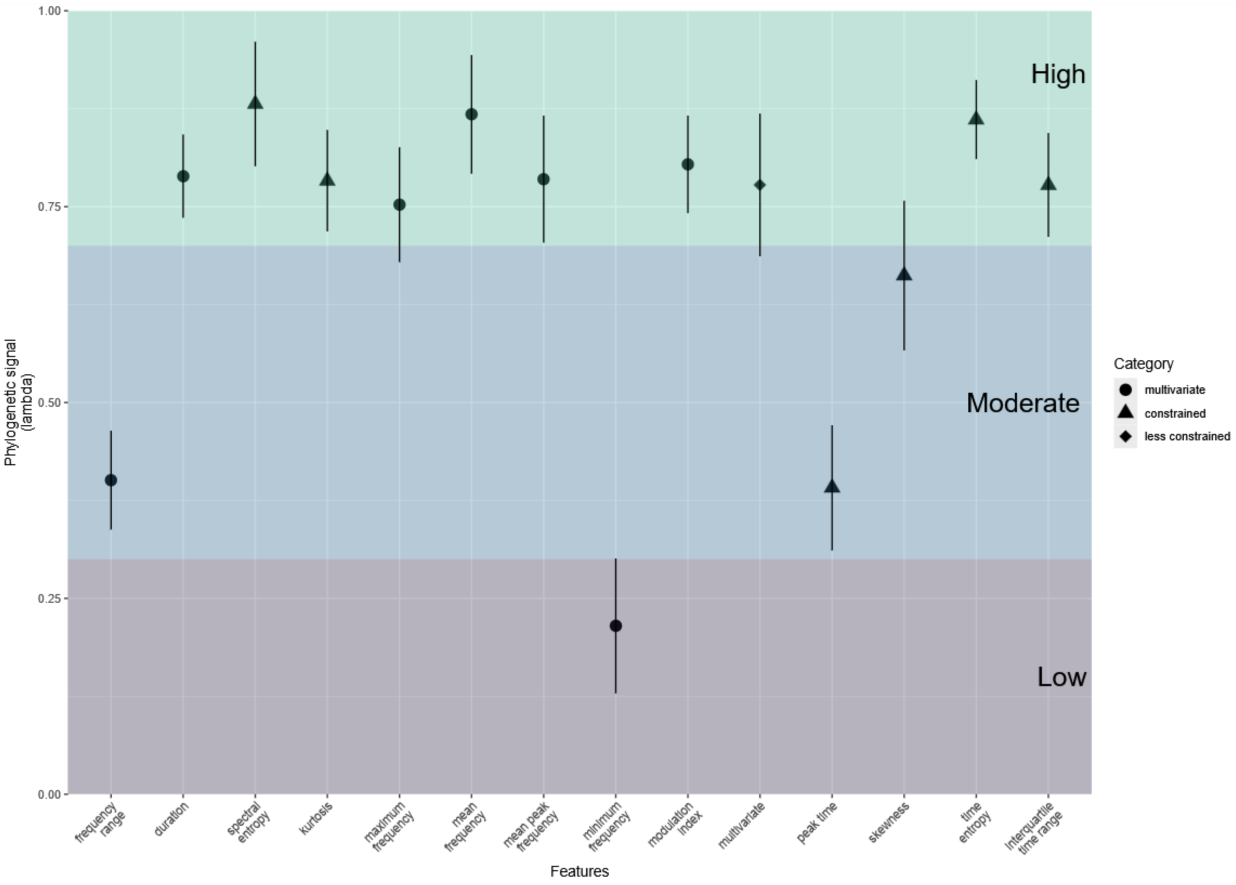

Figure 6. Phylogenetic signal of acoustic features (and 95% confidence intervals), and the respective category of strength of the signal.

The combined evolutionary rate of highly constrained acoustic features was significantly lower than that from features experiencing lower constraints (P = 0.002, effect size = 2.44). The non-restricted features had a higher evolutionary rate.

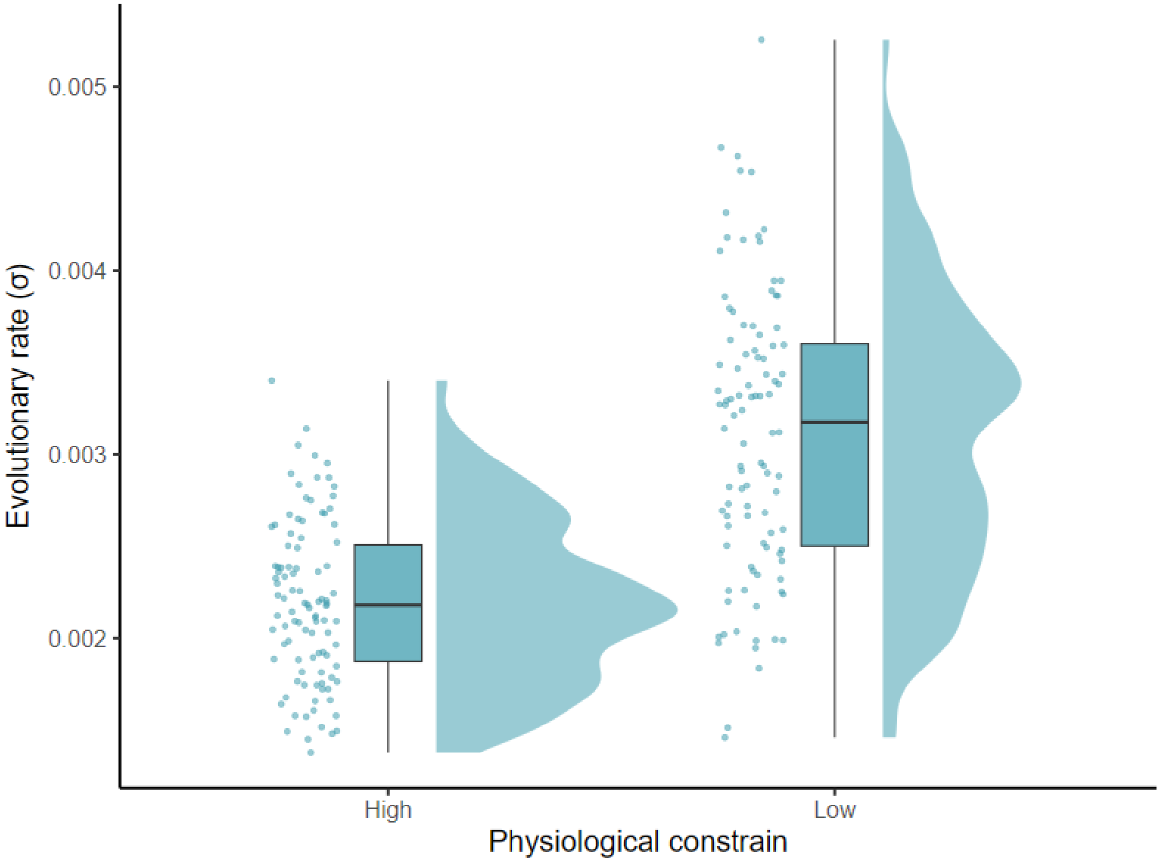

Figure 7. Comparison of evolutionary rates (σ) between high and low physiological constraints. Points represent raw values from individual iterations from a bootstrap resampling removing 10% of the song types on each iteration. Box plots show the median and interquartile range, and the error bars show the 95% data. The envelope depicts the kernel density distribution.

Discussion

In this study, we investigated the role of the physiological constraints in shaping the cultural evolution of songs in the Long-billed Hermit (*Phaethornis longirostris*) and tested if physiology limits the lability of acoustic features during the cultural evolution of songs. We found that song type relatedness strongly predicts the features measured, and a clear link between the evolutionary rates of the song types' features and the degree of physiological constraint, supporting a role.

The strong phylogenetic signal observed in most song features suggests that cultural evolution in this species follows a structured, non-random pattern, with song types being inherited and modified in a manner analogous to genetic evolution (Mesoudi, 2017; Williams & Lachlan, 2022). This finding supports the idea that learned vocalizations are subject to selective pressures that shape their transmission and persistence over time (Podos *et al.,* 2004a; Garland *et al.,* 2022). Notably, the lower phylogenetic signal in some features suggest that their changes during the cultural evolution are more independent to the structure shape used to build the tree (Hay *et al.,* 2024). These features might have stronger stabilizing selections. This might be the case with minimum frequency, due to higher biomechanical constraints, limits its diversification compared to other song traits (Podos *et al.,* 2004b; Mason *et al.,* 2017).

Consistent with previous studies in birds (Podos *et al.,* 2009; Derryberry *et al.,* 2018; Podos & Sung, 2020), we found that features such as frequency range, duration, and modulation index, which are tightly linked to vocal tract morphology and respiratory control, evolved more slowly than time-domain features (*e.g.,* spectral entropy, skewness) (Figure 7). This pattern suggests that while cultural evolution can introduce rapid changes in certain aspects of vocalizations, biomechanical limitations impose boundaries on the extent of variation possible in others (Podos *et al.,* 2004a; Schmidt & Goller, 2016).

The faster evolutionary rates observed in less constrained features (*e.g.,* time entropy, skewness) may reflect greater flexibility in motor control and learning biases, allowing for more rapid diversification. This aligns with the idea that traits less tied to fixed anatomical structures are more susceptible to drift, innovation, and social learning biases (Williams *et al.,* 2013; Mesoudi & Thornton, 2018). Such dynamics could facilitate the emergence of local song dialects or individual signatures, as seen in other vocal-learning species (Medina-García *et al.,* 2015; Vernes *et al.,* 2021).

Previous studies have shown that individuals tend to change/learn the song depending on the lek they aim to join, suggesting two levels of song template selection: first, aligning with the target lek and then with the specific neighborhood within that lek (Gonzáles & Ornelas, 2009; Gonzáles & Ornelas, 2019; Araya-Salas *et al.,* 2019). Furthermore, documented cases of lek switching are rare. When it does occur, individuals learn and exclusively vocalize the novel song type of their new lek. This pattern suggests that horizontal transmission of song types between leks is minimal, as cultural units remain highly discrete, even though males may encounter multiple leks while foraging (Araya-Salas *et al.,* 2019; Rueda-Uribe *et al.,* 2025). Therefore, our reconstruction of the cultural evolution of songs at the lek level likely provides a fair representation of the historical process generating variation in these signals.

Our findings contribute to a growing body of literature demonstrated that cultural evolution is not solely driven by social learning but is also shaped by the interplay between innovation and production constraints (Podos & Sung, 2020; Williams & Lachlan, 2022). The fact that some song features are more evolutionarily labile than others suggests that vocal learning may prioritize certain acoustic dimensions over others, depending on their functional relevance and feasibility with which they can be modified.

By combining phylogenetic tools with bioacoustic analysis, we demonstrate that the cultural evolution of learned vocalizations is shaped by both social transmission and physiological constraints. Features under stronger biomechanical limitations exhibit slower evolutionary rates, whereas those linked to motor flexibility diversify more rapidly. These findings highlight the multidimensional nature of cultural evolution and underscore the importance of considering production mechanisms when studying the dynamics of learned behaviors.

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Supplementary material

Table S1. Repeatability values of each feature, the confidence intervals of the regression and the categories determined by dividing the data into three categories.

Feature	Rep	Low confidence interval	High confidence interval	Category
Mean frequency	0.97	0.96	0.97	high
Minimum frequency	0.83	0.80	0.85	high
Maximum frequency	0.90	0.88	0.91	high
Frequency range	0.89	0.87	0.90	high
Spectral entropy	0.79	0.76	0.81	moderate
Modulation index	0.94	0.93	0.95	high
Duration	0.84	0.82	0.86	high
Mean peak frequency	0.52	0.48	0.56	moderate
Skewness	0.55	0.50	0.59	moderate
Kurtosis	0.44	0.40	0.48	low
Time entropy	0.86	0.84	0.88	high
Interquartile time range	0.81	0.791	0.84	high
Peak time	0.341	0.29	0.38	low

Table S2. The Phylogenetic signal of features expressed in lambda, the Log-Likelihood comparison values, and their significance.

Feature	Lambda	LogL	LogL0	P
Mean frequency	0.87	-145.1	-201	3.96E-26
Minimum frequency	0.21	-216.16	-217.83	0.067
Maximum frequency	0.75	-183.1	-208.76	7.88E-13
Frequency range	0.4	-193.6	-206.41	4.17E-07
Spectral entropy	0.88	-177.96	-207.01	2.50E-14
Modulation index	0.8	-189.98	-215.98	5.56E-13
Duration	0.79	-170.12	-209.88	4.78E-19
Mean peak frequency	0.79	-199.15	-226.76	1.08E-13
Skewness	0.66	-209.73	-215.8	0
Kurtosis	0.78	-217.72	-223.69	0.001
Time entropy	0.86	-145.45	-199.59	2.33E-25
Interquartile time range	0.78	-181.02	-212.38	2.38E-15
Peak time	0.39	-202.52	-207.35	0.002

Table S3. Code snippet of the adapted function from “compare.multi.evol.rates” in geomorph (Revell, 2024).

```
# Compare evolutionary rates between features
CompareRates.multTrait <-  function(phy,x,TraitCov=T,ms.err=NULL,ms.cov=NULL){
  #Compares LLik of R-matrix vs. LLik of R-matrix with constrained diagonal
  #TraitCov = TRUE assumes covariation among traits (default)
  #ms.err allows the incorporation of within-species measurement error. Input is a matrix of species (rows) by within-species
  #variation for each trait (columns).
  #ms.cov allows the incorporation of within-species covariation between traits. Input is a matrix of species (rows) by within-species
  #covariation for each pair of traits (columns). These must be provided in a specific order, beginning with covariation between trait 1
  #and the rest, then trait 2 and the rest, etc. For instance, for 4 traits, the columns are: cov_12, cov_13, cov_14, cov_23, cov_24 cov_34.
  #Some calculations adapted from 'evol.vcv' in phytools (Revell, 2012)
```

```
  x<-as.matrix(x)
  N<-nrow(x)
  p<-ncol(x)
  C<-vcv.phylo(phy)
  C<-C[rownames(x),rownames(x)]
  if (is.matrix(ms.err)){
    ms.err<-as.matrix(ms.err[rownames(x),])}
  if (is.matrix(ms.cov)){
    ms.cov<-as.matrix(ms.cov[rownames(x),])}

  #Cholesky decomposition function for diagonal-constrained VCV
  build.chol<-function(b){
    c.mat<-matrix(0,nrow=p,ncol=p)
    c.mat[lower.tri(c.mat)] <- b[-1]
    c.mat[p,p]<-exp(b[1])
    c.mat[1,1]<-sqrt(sum((c.mat[p,])^2))
    if(p>2){
      for (i in 2:(p-1)){
        c.mat[i,i]<-ifelse( (c.mat[1,1]^2-sum((c.mat[i,])^2) )>0,
                            sqrt(c.mat[1,1]^2-sum((c.mat[i,])^2)), 0)
      }}
    return(c.mat)
  }

  #Fit Rate matrix for all traits: follows code of L. Revell (evol.vcv)
  a.obs<-colSums(solve(C))%*%x/sum(solve(C))
  D<-matrix(0,N*p,p)
  for(i in 1:(N*p)) for(j in 1:p) if((j-1)*N<i&&i<=j*N) D[i,j]=1.0
  y<-as.matrix(as.vector(x))
  one<-matrix(1,N,1)
  R.obs<-t(x-one%*%a.obs)%*%solve(C)%*%(x-one%*%a.obs)/N
  if (TraitCov==F)    #for TraitCov = F
  { R.obs<-diag(diag(R.obs),p)  }
  #Calculate observed likelihood with or without measurement error
  LLik.obs<-ifelse(is.matrix(ms.err)==TRUE,
                  -t(y-D%*%t(a.obs))%*%ginv((kronecker(R.obs,C)+
diag(as.vector(ms.err))))%*%(y-D%*%t(a.obs))/2-N*p*log(2*pi)/2-
                   determinant((kronecker(R.obs,C)+ diag(as.vector(ms.err))))$modulus[1]/2 ,
                  -t(y-D%*%t(a.obs))%*%ginv(kronecker(R.obs,C))%*%(y-D%*%t(a.obs))/2-
N*p*log(2*pi)/2-
                   determinant(kronecker(R.obs,C))$modulus[1]/2
  )

  #Fit common rate for all traits; search over parameter space
  sigma.mn<-mean(diag(R.obs))   #reasonable start value for diagonal

  #Within-species measurement error matrix
  if(is.matrix(ms.err)){m.e<-diag(as.vector(ms.err))}

  #Within-species measurement error and trait covariation matrix
  if (is.matrix(ms.err) && is.matrix(ms.cov)){
```

```
    within.spp<-cbind(ms.err,ms.cov)
    rc.label<-NULL
    for (i in 1:p){ rc.label<-rbind(rc.label,c(i,i)) }
    for (i in 1:p){
      for (j in 2:p){ if (i!=j && i<j){rc.label<-rbind(rc.label,c(i,j))} }}
    m.e<-NULL
    for (i in 1:p){
      tmp<-NULL
      for (j in 1: :p){
        for (k in 1:nrow(rc.label)){
          if(setequal(c(i,j),rc.label[k,])==T) {tmp<-cbind(tmp,diag(within.spp[,k]))}
        }
      }
      m.e<-rbind(m.e,tmp)
    }
  }

  #likelihood optimizer for no trait covariation
  lik.covF<-function(sigma){
    R<-matrix(0,nrow=p,ncol=p)
    diag(R)<-sigma
    LLik<-ifelse(is.matrix(ms.err)==TRUE,
                -t(y-D%*%t(a.obs))%*%ginv((kronecker(R,C)+ m.e))%*%(y-D%*%t(a.obs))/2-
N*p*log(2*pi)/2-
                  determinant((kronecker(R,C)+ m.e))$modulus[1]/2 ,
                -t(y-D%*%t(a.obs))%*%ginv(kronecker(R,C))%*%(y-D%*%t(a.obs))/2-
N*p*log(2*pi)/2-
                  determinant(kronecker(R,C))$modulus[1]/2
    )
    if (LLik == -Inf) { LLikk <- -1e+10  }
    return(-LLik)
  }

  #likelihood optimizer with trait covariation
  lik.covT<-function(sigma){
    low.chol<-build.chol(sigma)
    R<-low.chol%*%t(low.chol)

    LLik<-ifelse(is.matrix(ms.err)==TRUE,
                -t(y-D%*%t(a.obs))%*%ginv((kronecker(R,C)+ m.e))%*%(y-D%*%t(a.obs))/2-
N*p*log(2*pi)/2-
                  determinant((kronecker(R,C)+ m.e))$modulus[1]/2 ,
                -t(y-D%*%t(a.obs))%*%ginv(kronecker(R,C))%*%(y-D%*%t(a.obs))/2-
N*p*log(2*pi)/2-
                  determinant(kronecker(R,C))$modulus[1]/2
    )
    if (LLik == -Inf)  {LLikk <- -1e+10  }
    return(-LLik)
  }

  ##Optimize for no trait covariation (methods: "Nelder-Mead"  or "SANN")
```

```
  if (TraitCov==F)
  { model1<-optim(sigma.mn,fn=lik.covF,method="L-BFGS-B",lower=c(0.0))}
  ##Optimize with trait covariation
  R.offd<-rep(0,(p*(p-1)/2))
  if (TraitCov==T)
  {model1<-optim(par=c(sigma.mn,R.offd),fn=lik.covT,method="L-BFGS-B")}

  #### Assemble R.constrained
  if (TraitCov==F){R.constr<-diag(model1$par,p)}
  if (TraitCov==T){
    chol.mat<-build.chol(model1$par)
    R.constr<-chol.mat%*%t(chol.mat)}

  if(model1$convergence==0)
    message<-"Optimization has converged."
  else
    message<-"Optim may not have converged.  Consider changing start value or
lower/upper limits."
  LRT<- (-2*((-model1$value-LLik.obs)))
  LRT.prob<-pchisq(LRT, (p-1),lower.tail=FALSE) #df = Nvar-1
  AIC.obs<- -2*LLik.obs+2*p+2*p #(2p twice: 1x for rates, 1x for anc. states)
  AIC.common<- -2*(-model1$value)+2+2*p #(2*1: for 1 rate 2p for anc. states)
  return(list(Robs=R.obs, Rconstrained=R.constr,Lobs=LLik.obs,Lconstrained=(-
model1$value),LRTest=LRT,Prob=LRT.prob,
              AICc.obs=AIC.obs,AICc.constrained=AIC.common,optimmessage=message))
}
```

Conclusiones

En el primer capítulo observamos que la evolución cultural genera suficiente variación en la propagación y degradación de los tipos de cantos. Sin embargo, esta no tiene un vínculo claro con la prevalencia de los cantos en la población. Adicionalmente, los experimentos de propagación indicaron que los cantos se transmiten mejor a la altura de vuelo de los individuos que no forman parte del lek, favoreciendo la comunicación con las hembras y machos buscando integrarse a un lek. La ausencia de un efecto significativo de la selección ecológica sobre la propagación de los tipos de cantos va en contra de la suposición central de la hipótesis de adaptación acústica. Sin embargo, más que descartar su influencia, estos resultados sugieren que dicha presión selectiva carece de la fuerza y direccionalidad necesarias en esta especie para moldear de manera significativa la estructura del canto.

En el segundo capítulo encontramos que el usar reconstrucciones filogenéticas para generar árboles culturales fue vital para comprender el proceso de evolución cultural de la estructura de los cantos del Ermitaño Piquilargo. El análisis de este proceso evolutivo nos permitió identificar características estructurales con menor labilidad evolutiva, en concordancia con las restricciones teóricas impuestas por el sistema de producción vocal. También, estas características de los tipos de canto mostraron una fuerte asociación con la estructura de su contorno.

En conjunto, ambos capítulos demuestran la fuerza de los mecanismos en el proceso evolutivo cultural en señales de comunicación complejas. Siendo en ambos casos el primer aporte al entendimiento de estos mecanismos reguladores de la diversidad de estas señales, contribuyendo al debate sobre su papel en la evolución de las señales acústicas.