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An allometric prior enhances acoustic niche partitioning signal

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The acoustic niche hypothesis suggests that vocal signals of sympatric animal species are structured so as to minimize acoustic interference and facilitate communication. Accordingly, each species attempts to establish its own acoustic bandwidth so that intra-species signals are not masked. Detecting a non-random partitioning of the frequency spectrum among sympatric species could constitute evidence for the existence of acoustic avoidance behaviour. However, results from previous studies have been mixed or inconclusive, possibly as a consequence of overlooking the importance of physiological and ecological constraints. Here we introduce an improved test that incorporates prior information on body mass to account for the allometric correlation between mass (size) and vocalization frequency. By correcting for the bias induced by this correlation, the new test uncovers evidence of acoustic niche partitioning as a function of frequency in several tropical bird communities that would not be detected under a more standard test. Separately, we introduce a spatial version of the acoustic partitioning test which, in theory, could prove effective when data are collected from multiple sites located in close spatial proximity.

1. Introduction

Segregation of niche space by sympatric species in order to reduce competition is a fundamental concept in ecology [1]. An ecological niche can generally be thought of as a hypervolume in the space of factors required for the existence of a given species [2]. Typical factors considered include material and energetic considerations such as food, habitat and environmental conditions. However, information transmission and signalling efficiency could also have fitness consequences [3] for instance through territorial defence and mate attraction [4]. Since acoustic signals with similar temporal patterns and frequencies tend to mask each other [5], signals of related species may diverge in temporal or spectral characteristics to minimize competitive interference [4].

In this sense, 'acoustic space'—just like more traditional ecological factors—represents a scarce resource that organisms compete for [6–9], especially in crowded, dark habitats with dense vegetation, where optical cues become less reliable. If the acoustic partitioning hypothesis were true, we would expect to see a non-random segregation of signal frequency (and/or other signal properties such as trill rate) among co-occurring species. Such segregation could manifest itself as an effective repulsive force between signal frequencies of neighbouring species, resulting in a distribution of signal spacings that is more even than would be expected under the null hypothesis.

Results of published studies have been mixed, [3,10–14], perhaps in part due to the existence of alternative strategies for alleviating acoustic interference, such as temporal avoidance (on short or long scales), spatial avoidance (horizontally or vertically) or tuning recognition space [15]. Attempts to detect acoustic partitioning can also be undermined by study design choices [10], such as relatively small sample sizes (less than 30 species), using microphones with a low signal-to-noise ratio [16,17], or sampling on an excessively large spatial scale. Additionally, we argue that physiological and ecological

constraints play an important role and must be accounted for when investigating the acoustic niche hypothesis. In particular, vocalization frequency scales with body mass [7,8,18], which induces a bias in the distribution of vocalization frequencies, an effect largely ignored in the literature. For instance, a meta-analysis study on frog communities failed to account for this bias, generating data under the null hypothesis by sampling uniformly between the minimum and maximum frequencies of each dataset [12].

2. Constraints

While a uniform prior might be appropriate for a black-box type system, it is generally not appropriate for systems that are well understood. Accordingly, in this paper we investigate whether using a prior that takes into account the known correlation between body mass and vocalization frequency ('allometrically informed prior') can yield an improved statistical model. To gauge whether the allometrically informed prior improves upon the uniform prior, we will run both statistical tests on our five study site locations. Since our study sites encompass tropical locations with very high diversity of bird species, we expect that an improved statistical model will generally yield higher probabilities that acoustic partioning is present in at least some of these sites.

Applying our new statistical test on bird vocalization data collected from five tropical locations, we find evidence of acoustic niche partitioning in at least three locations. Such evidence would not have been detected using a uniform prior, which suggests that incorporating prior information enhances the signal from the data. In addition, we propose a novel statistical test that might be appropriate for detecting acoustic partitioning in the context of measurements taken at several sites located in close spatial proximity.

2.1. Mass distribution

In most animal species, the distribution of log-mass is unimodal and skewed. While the underlying cause of this constraint is not well understood, it may be attributed, for example, to the multi-scale nature of an environment (resulting in more space available for smaller species) or to size-dependent speciation and extinction [19]. Interestingly, the mass distribution tends to be conserved for a given taxonomic level, spatial scale and latitude [19–21]. Figure 1a illustrates the latitude dependence using bird body-mass distribution data from four locations of equal area. While locations at comparable latitudes have very similar distributions, indicating that the mass constraint is fairly strong, the shape of the distribution clearly changes with latitude. Notably, the distribution weight shifts towards smaller masses (higher frequencies) with decreasing latitude, which is the direction that allows for more even partitioning in frequency space.

2.2. Frequency–mass scaling

Vocalization frequency v is inversely correlated with size and thus with body mass m across many orders of magnitude: $v \sim m^{-\alpha}$ with $\alpha \in [0.3 - 0.4]$ [18,22]. Figure 1b shows that the correlation is maintained, in particular, across bird species.

2.3. Sound perception

It is unclear whether absolute frequency, relative frequency or spectral shape dominate song pattern recognition in birds

[23]. It has been argued that a logarithmic scale should be used in quantitative studies of vocal communication [24]. Accordingly, we test for acoustic partitioning in both normal frequency space (v) and log-transformed frequency space ($\tilde{v} \equiv \log v$), as in figure 4b.

2.4. Habitat

The primary environment-dependent factors that interfere with avian communication are background noise and frequency-dependent attenuation (e.g. due to trees and vegetation). Tropical forests, for example, exhibit higher levels of background noise, primarily due to higher abundance and diversity of insect species.

Electronic supplementary material, figure S1 shows non-avian noise levels (black) as well as excess attenuation (red) in tropical and temperate forests. Tropical forests have relatively high attenuation and background noise, except in a range of approximately 1–4 KHz (electronic supplementary material, figure S1), within which most birds probably communicate.

2.5. Sampling scale

Since acoustic niche partitioning is a local effect (requiring co-location or spatial proximity), it would be ideal to collect acoustic signals from a single point in space, as is the norm [17]. However, sampling scales comparable to typical species' ranges, communication distances (of the order of 100 m [5]) or recording devices' detection distances [17] may also be adequate. Conversely, recording sounds and aggregating them from multiple locations spaced more than approximately 100 m away is likely to weaken any potential spectral partitioning signal, intermixing data from spatially distant sites.

3. Null model for acoustic niche hypothesis

If we sort the vocalization frequencies of species in a given community (assuming, for simplicity, that every species can be characterized by a well-defined frequency rather than a frequency range), we can visualize the result as a set of points distributed along a line segment (figure 1d). Since acoustic interference is strongest between species with similar communication frequencies, a simplification is to only look at the distances between neighbouring points on the line; for example, if these distances are very small in some places (many species communicating within a narrow frequency band) but very large in other places, this could indicate the absence of acoustic partitioning. To formalize this intuition and quantitatively test the acoustic niche hypothesis, we require a function that takes in a set of intervals and outputs a score (typically normalized in the [0, 1] range) that quantifies how even the size of these intervals is (figure 1d).

Such functions have already been studied in the ecology literature, where they are called diversity indices and used, for example, to quantify the evenness of species abundances in ecological communities [25]. These same evenness indices can be repurposed to quantify the evenness of frequency intervals between 'neighbouring' species (neighbouring when arranged by vocalization frequency). Since many versions of diversity indices exist and some may have greater statistical power than others, here we have taken the approach of testing several indices on simulated data (see electronic supplementary material) to identify the best performing indices to use on the actual data.
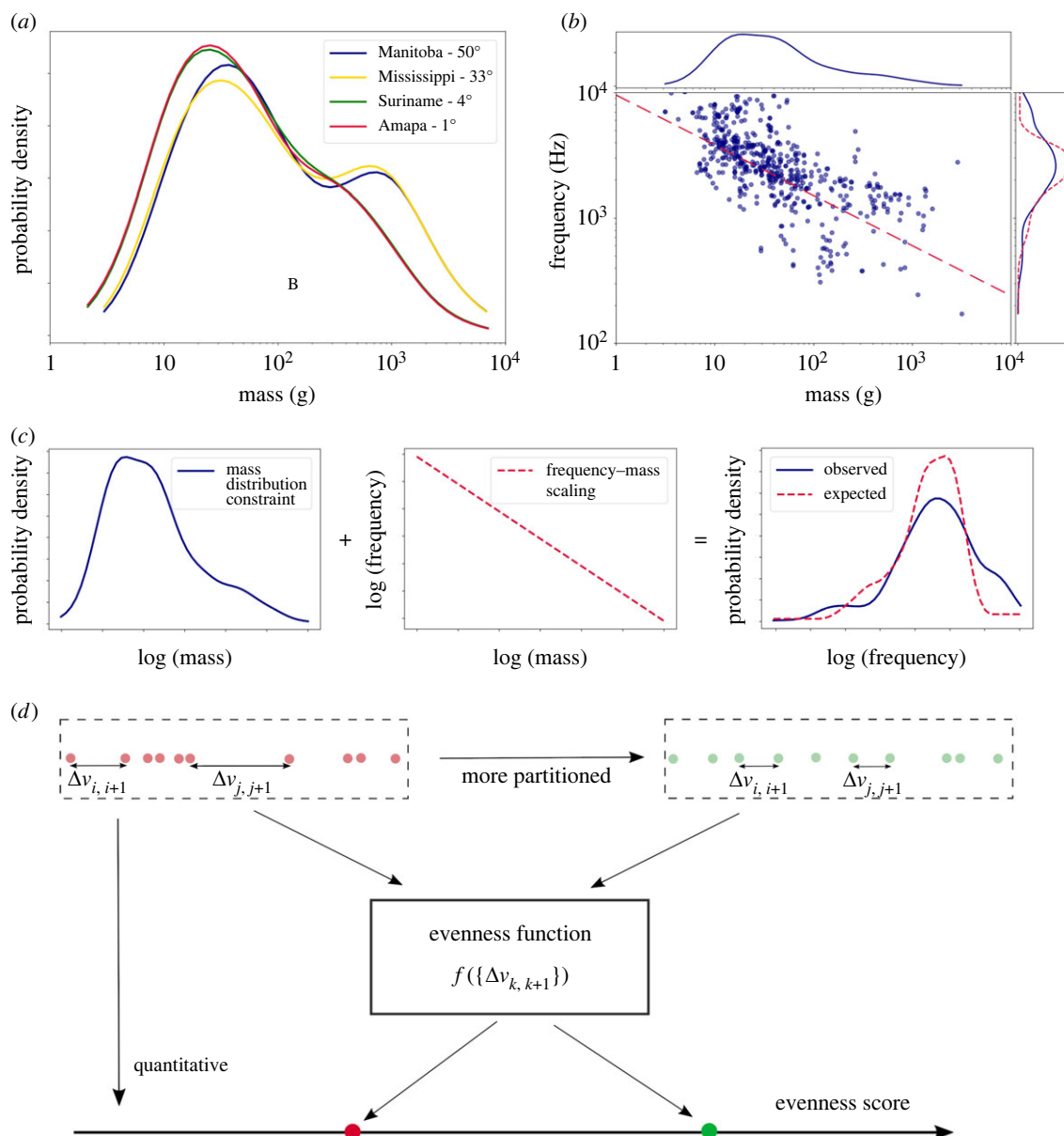
Figure 1. (a) Mass distribution constraint: log body-mass distribution of bird species in four regions of approximately equal area from different latitudes. The regions, labelled by the larger geographical unit they are part of, are: Amapa (red), Suriname (green), Manitoba (blue) and Mississippi (yellow). (b) Frequency–mass correlation constraint: correlation between body mass m and vocalization frequency v across the tropical bird species used in this study. The Pearson correlation coefficient is $r = -0.66$. The red-dashed line represents the best-fit line, with a slope of -0.36. Top inset: kernel density estimate for the distribution of body masses. Side inset: kernel density estimate for the distribution of vocalization frequency (blue) and for the predicted distribution of vocalization frequency (red, dashed) if the mass distribution were transformed into a frequency distribution according to the best-fit line. (c) The mass constraint (relative abundance as a function of log-mass, left) and the frequency–mass scaling (idealized here for simplicity, centre) bias the expected frequency distribution (red-dashed line, right) away from uniform. Consequently, the observed frequency distribution (blue line, right) should be compared with the expected distribution rather than with a uniform distribution. (d) Quantifying acoustic partitioning: going from a qualitative (top) to a quantitative (bottom) assessment of the evenness in nearest neighbour spacing intervals along the frequency line requires a function that takes in a set of frequency intervals and outputs an evenness score.

3.1. Frequency bias

The constraint on the mass distribution in a given environment translates, through frequency–mass scaling, into a constraint on frequencies: frequencies corresponding to more abundant masses also tend to be more abundant (figure 1d). Such a frequency bias acts to disrupt the spectral partitioning we are interested in detecting, i.e. while species might still actively 'repel' each other in spectral space, the average spacing between neighbouring signals may vary non-uniformly, in accordance with the frequency bias induced by constraints.

Consequently, to detect spectral partitioning, we must either deconvolve the effect of the frequency bias or force

the same constraints onto the null model. In the first case, we might apply the spectral unfolding technique developed in random matrix theory [26–28], while in the second approach we could design a null model that corrects for the bias. In this paper, we focus on the latter approach, as the data are too noisy to use spectral unfolding.

3.2. Statistical testing

Given a real-world dataset of bird songs, we can quantify how evenly the species are segregated along the frequency line using an evenness index as explained above. Even though the resulting score is normalized in the [0, 1] range,
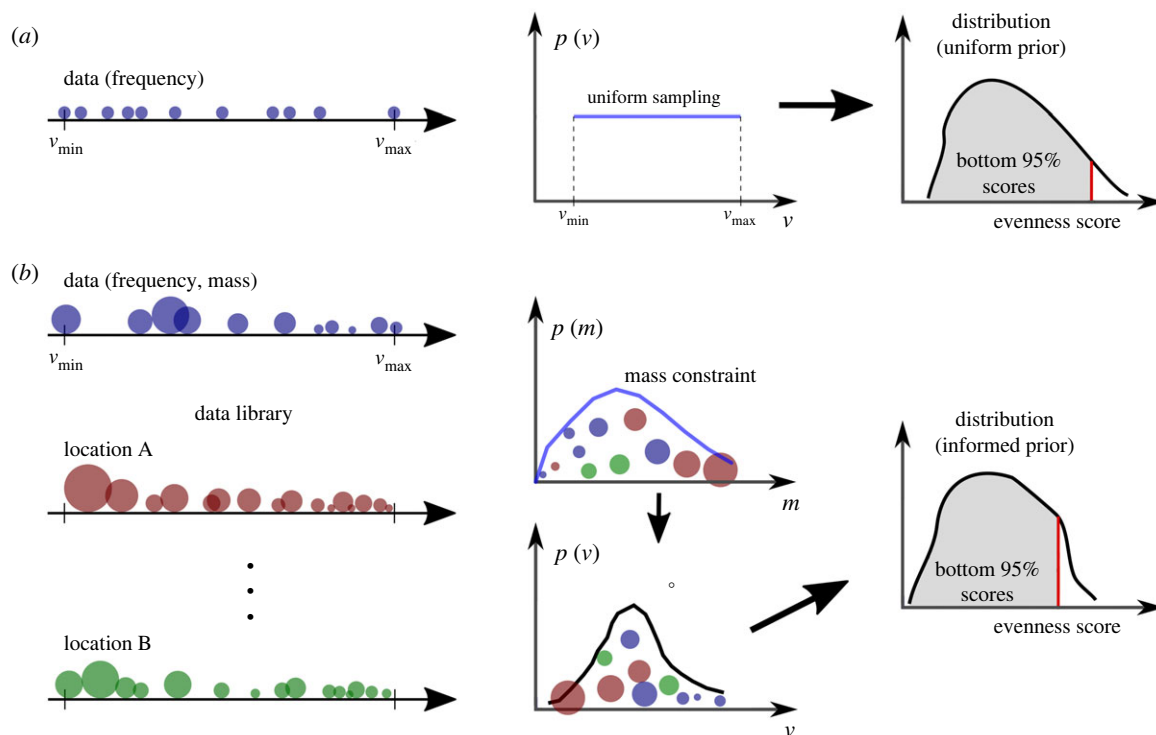
Figure 2. (a) Testing for acoustic partitioning under a uniform random prior assumption. Given some real data comprising N species' signals (left), we generate a large number of synthetic datasets such that in each of them we sample N signals uniformly at random between the minimum and maximum frequencies of the original data (centre). We can then compute the distribution of evenness scores of the synthetic data (right) as well as the score of the real dataset. The percentile of the score of the real data can be taken as an indicator of the statistical significance of the null hypothesis being false, with the 95th percentile corresponding to a p-value of 0.05. (b) Testing for acoustic partitioning under an allometrically informed prior assumption. Given a dataset comprising species' signals as well as their body masses (left, with masses indicated through dot size), we first create a data library (data pool) by aggregating several other datasets. We then sample from the pooled distribution generating a large number of hypothetical bird communities under the constraint of maintaining the same mass distribution p (m) as the real dataset undergoing the test (centre). The synthetic datasets generate a distribution of evenness scores under the null hypothesis and the percentile of the score of the real dataset can be taken as an indicator of the statistical significance of the null hypothesis being false.

it is not very informative on its own, i.e. it lacks a baseline to be compared against. In our case, the baseline is the distribution of evenness scores for hypothetical communities in which the vocalization frequencies of species are randomly distributed, i.e. not subject to any kind of effective repulsion or avoidance behaviour. These randomly distributed hypothetical datasets act as our null model, but the precise meaning of 'randomly distributed' depends on the prior we use. For our analysis, we conduct partitioning tests both under a uniform prior and our proposed 'allometrically informed prior' in order to compare the results.

Under a uniform prior assumption, we compare the evenness score of a given real-world dataset containing N species with the evenness scores of 100 theoretical/hypothetical bird communities of the same size N, generated such that each simulated frequency v_s is sampled uniformly from the frequency range $[v_{min}, v_{max}]$: $v_s^* \sim \mathcal{U}(v_{min}, v_{max})$, where $\mathcal{U}$ denotes a function for drawing samples from a uniform distribution (figure 2a). We then compute the evenness score $E_{1/D}$ of the real bird community data as well as the scores of the theoretical communities. $E_{1/D}$ is a diversity index obtained by taking the inverse of Simpson's dominance index $D = \sum_{s=1}^{s=S} p_s^2$, typically used to assess community composition, where p_s is the relative abundance of species s and S is the total number of species. However, for quantifying acoustic niche partitioning, p_s should be taken as the normalized difference between the vocalization frequencies of species $s+1$ and s (arranged by vocalization frequency). Thus, D represents the sum of squared nearest neighbour spacing in scaled frequency space and $E_{1/D}$

is the scaled inverse of D: $E_{1/D} = (1/D)/(S-1)$. Note that $E_{1/D}$ takes values between 0 and 1, with larger values corresponding to higher evenness.

Intuitively, if the real data has a higher evenness score than, say, 98 out of 100 simulated datasets (98th percentile in terms of evenness), then we may be fairly confident that it is significantly more even than expected at random, under the current null model. The percentile can be used to estimate a p-value, i.e. a 98th percentile score can be interpreted as a p-value of 0.02. Here, we will use the 95th percentile as a significance threshold, since it corresponds to a p-value of 0.05.

For the informed prior tests (figure 2b), we generate the hypothetical communities by sampling without replacement from a data pool in such a way that the random datasets have the same mass distribution as the original data $p^*(m) \approx p(m)$ (see electronic supplementary material). The data pool or data library can be constructed by aggregating together several real tropical bird communities; for instance, we construct the data pool by aggregating data from all five study site locations. We compute the percentile of the evenness scores $E_{1/D}$ and $\bar{S}_3$ of the data among the respective scores of the theoretical communities, where $\bar{S}_3$ is derived from a similarity index (see electronic supplementary material), which is designed to measure the similarity between two probability distributions (with the most well-known example being perhaps the Jensen–Shannon divergence). By setting the second probability distribution to be uniform, we can repurpose similarity indices to measure evenness (i.e. how similar a distribution is to a uniform distribution can indicate how even it is).

Table 1. Summary of tropical data locations used in this paper and their abbreviations. Two locations include both data compiled by us from online/commercial as well as data collected from the literature. Literature datasets are always abbreviated in lower case, while the rest are abbreviated in upper case.

name	notation	location	elevation (m)	species analysed	description	source
La Selva	[LS]	Ecuador	200	140	Located within the Amazon region inside Ecuador's Yasuní Biosphere Reserve, in the province of Napo, Ecuador. The dominant ecosystem is the Humid Tropical Rainforest which forms part of the upper Amazon basin.	[29]
Los Amigos Biological Station	[LA], [la]	Peru	250	70, 180	Located in lowland Amazonian forest at the base of Peru's southern Andes, in Department of Madre de Dios, the research station sits on a high terrace at the confluence of the Madre de Dios River and Los Amigos River.	[10,30,31]
Rio Cristalino Reserve	[RC], [rc]	Brazil	200	100, 80	Located 40 km northeast of the town of Alta Floresta, Mato Grosso. Consists of uncut lowland tropical moist forest.	[32,33]
Cabanas San Isidro	[SI]	Ecuador	2000	80	A large reserve with some of the best access to primary mid elevation cloud forest in Ecuador, located in Cosanga on the eastern Andean slope, surrounded by a cloud forest nature reserve.	[29]
Mirador de Quetzales	[M]	Costa Rica	2800	70	Located in Cerro de la Muerte, 6 km away from the entrance to San Gerardo de Dota and Los Quetzales' National Park. The park predominantly protects cloud forest.	[34]

4. Results

We consider five study sites, described in table 1 and mapped in figure 3*a*. We test the acoustic niche hypothesis for each site, using on-site bird song recordings that were either made publicly available via open-source bird song libraries or via commercially available bird song CDs (see table 1). In two cases, we were able to retrieve datasets from published research articles consisting of data collected from one of our study sites (Los Amigos Station and Rio Cristalino Reserve); we also included these datasets in our analysis, as a check of consistency. For these two study sites, we distinguish between data sourced by us and data collected from previously published studies by the case used in the abbreviated name (e.g. [RC] versus [rc]). Upper-case abbreviations such as [LA] refer to data sourced by us, while lower-case abbreviations such as [la] refer to previously published datasets (table 1).

4.1. Clustering in frequency and mass

For each species recorded in a given location we source its mass by scraping data from an online reference book [35] and estimate the dominant frequency of its vocalizations by averaging peak frequency across all recordings of the species in that location (see electronic supplementary material). Figure 3*b* shows normalized frequency histograms for the seven datasets, revealing their apparent clustering into two groups: the first one in which most of the bird song frequencies are contained within the 1000–4000 Hz band (blue), and a second one in which signals are spread out within the 1000–8000 Hz band (green). We believe this apparent clustering is connected to environmental conditions (e.g. tropical rainforests versus cloud forests), as figure 3*a* shows that locations in the first group are all low-altitude (less than 300 m) while locations in the second group are high-altitude (greater than 2000 m). The smaller available frequency range for bird species in tropical rainforests (compared with the range in tropical cloud forests) may be attributed to lower elevations having a higher abundance of insects with high frequency calls and/or large food items such as fruits (which would favour larger bird species that tend to vocalize at lower frequencies). Interestingly, the mass distributions also cluster, although the groups are slightly different now, as [RC] clusters with the higher altitude sites despite being a low-altitude site (figure 3*c*).

4.2. Results with uniform prior

Figure 4*b* shows the $E_{1/D}$ evenness score for the seven tropical and three non-tropical datasets, computed in both frequency (red) and log-frequency (yellow) spaces. We find that evenness scores are consistently higher in normal frequency rather than in log-frequency space (figure 4*b*, red and yellow bars, respectively) such that from now on we examine partitioning only in normal frequency space.

The dashed line at $E_{1/D} \approx 0.51$ indicates the mean $E_{1/D}$ evenness score of a uniform random dataset of size 100 while the shaded region encompasses the 5–95 percentiles of random dataset scores. If we take as our significance criterion an $E_{1/D}$
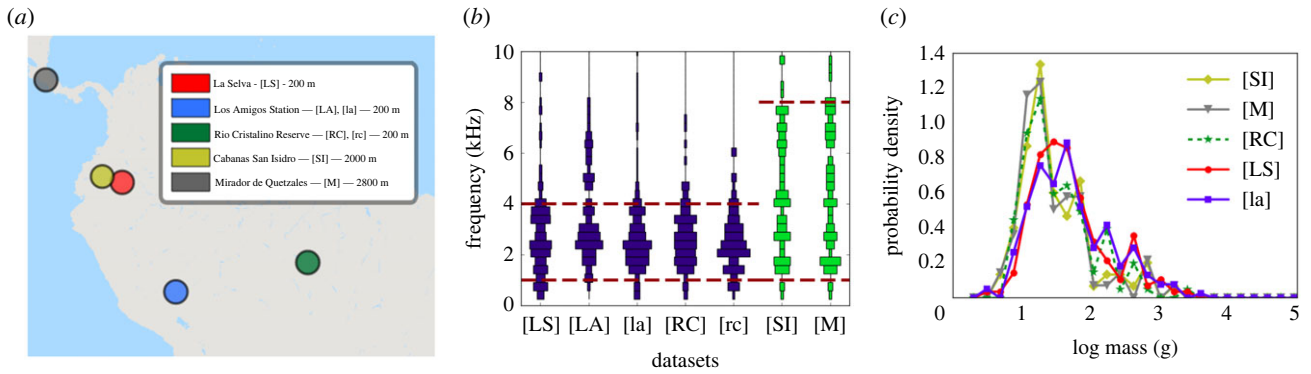
Figure 3. (a) Tropical dataset locations and the abbreviations of their corresponding datasets. Data are collected either from online bird sound databases (upper-case abbreviations) or from published papers (lower-case abbreviations). (b) Side-by-side frequency histograms for tropical datasets. The size of a bar indicates the number of bird species within the respective frequency bin. Colours indicate perceived clustering of datasets into two groups: [LS], [LA]/[la] and [RC]/[rc] (blue); [SI] and [M] (green). Red-dashed lines indicate the frequency cut-offs used for each dataset (see electronic supplementary material). (c) Normalized log-mass distributions for five tropical datasets. Clustering into two groups is apparent: [SI] (yellow), [M] (green) and [RC] (black, dashed); [LS] (blue) and [la] (purple).
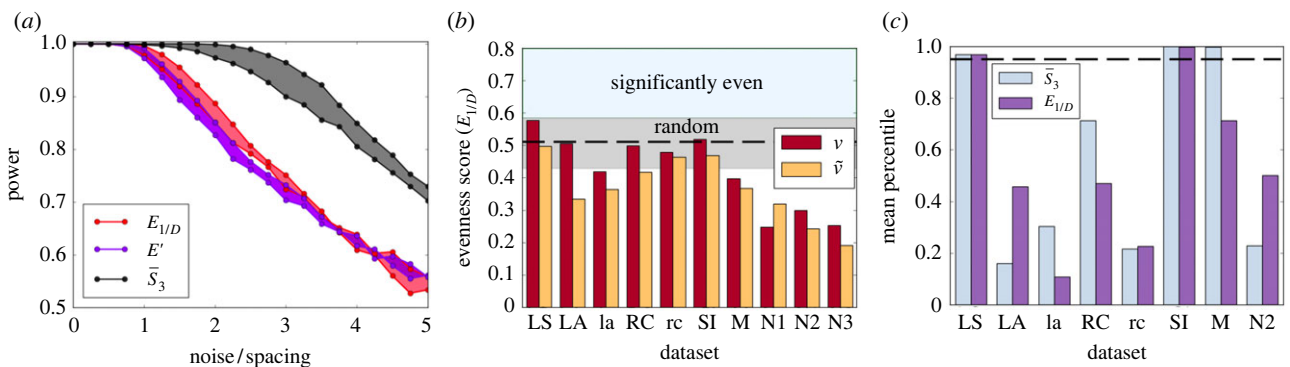

Figure 4. (a) Statistical power (the probability of correctly rejecting the null hypothesis, i.e. identifying when partitioning is present) for the top three evenness metrics as identified in our simulations (see electronic supplementary material), $\bar{S}_3$, (black) $E_{1/D}$, (red) and E' (blue). Simulations involve starting with a uniformly spaced set of points, sampling a fraction f of those points, adding Gaussian noise on top and computing the percentile of the evenness score of the resulting data against the evenness score of hypothetical datasets generated under a uniform prior. The horizontal axis represents the standard deviation of the added Gaussian noise scaled by the mean spacing between points. Upper curves for each index correspond to a sampling fraction $f = 1$, while lower curves correspond to $f = 0.75$. (b) Uniform prior test: evenness scores of all datasets using the $E_{1/D}$ index in frequency (red) and log-frequency (yellow) space. The black dashed line at 0.51 marks the mean $E_{1/D}$ score of a completely random dataset of size 100 while the shaded black region encompasses the 5–95 percentile of random scores. None of the datasets rise above the 95 percentile threshold (light blue), neither in frequency nor in log-frequency space. Three datasets denoted [N1], [N2] and [N3] that aggregate non-tropical birds from various locations were also tested as a control; these displayed the lowest evenness scores. (c) Allometrically informed prior test: percentile of evenness score for each dataset compared against evenness scores of hypothetical datasets generated by randomly sampling from a data library subject to maintaining the same distribution of body masses as the dataset being tested. Two sets of evenness scores are computed, using $\bar{S}_3$ (lighter blue) and $E_{1/D}$ (darker blue).

score higher than 95% of random dataset scores, none of the datasets can be said to be significantly partitioned (figure 4b). As a control, we collected datasets [N1], [N2] and [N3] from the literature, each of which assembles bird species from various locations around the world. As would be expected if the acoustic niche hypothesis were true, these non-tropical, allopatric datasets register the lowest evenness scores.

4.3. Results with allometrically informed prior

While figure 4b is indicative of partitioning tests that neglect the frequency bias constraint, figure 4c shows the results of partitioning tests under an informed prior which corrects for the bias. The vertical axis is the mean percentile of the target dataset's evenness score relative to the scores of synthetic datasets sampled from the data pool in a way that satisfies the mass constraint (see electronic supplementary material). Results

computed with the top two indices identified in our simulations that assesed a large number of potential evenness indices (see electronic supplementary material), $\bar{S}_3$ and $E_{1/D}$, are shown in light and dark blue, respectively. The dashed black line in figure 4c corresponds to a mean percentile of 95%, which we take as a significance threshold.

Using the best performing index, $\bar{S}_3$ (figure 4a), to quantify evenness deems three datasets significantly partitioned—[LA], [SI] and [M] (if instead we use $E_{1/D}$, the latter dataset drops below significance). The datasets from the other two tropical locations, [RC], [rc] and [LA], [la], respectively, are well below the 95% threshold (as is the control, non-tropical dataset [N2] sampled from all over Europe and North America).

Thus, while a constraint-agnostic analysis would find no significant signs of acoustic partitioning along the frequency line, a more careful analysis uncovers evidence of partitioning

in three of five tropical locations surveyed. For the other two locations, it is possible that the signal is obscured by excessively large sampling scales which can introduce redundancy. For instance, the [rc] data were sampled at three sites separated by 500 m to 1 km [33], while the [la] data were sampled at 91 sites spaced at least 100 m apart [10].

4.4. Effect of considering species abundances

Since not all bird species present in a given region are equally abundant, they should not necessarily be weighed equally when quantifying evenness. While there are ways to factor species' abundances into evenness metrics [36], they are not rigorously investigated here. Instead, we simply note that the $E_{1/D}$ evenness scores increase when we remove the rare species (which may contribute relatively little to the acoustic competition landscape because of their low numbers). The $E_{1/D}$ evenness score for [RC] increases from 0.5 to 0.67 if we only keep the 20 species marked as the most common [37]. However, with the reduction in sample size, the threshold for statistical significance also increases, from 0.58 to 0.69. In conclusion, restricting the [RC] dataset to the most abundant species pushes the evenness score very close to the significance threshold (but still below it).

4.5. Spatial correlation partitioning test

As noted previously, when the sampling scale is excessively large, we expect the spectral partitioning signal to deteriorate as a result of combining data from locations that are too distant. However, a special case is when we possess data from multiple sites that are relatively close, but not close enough to be lumped together without deteriorating the signal. Here, rather than testing for acoustic partitioning on each site independently, a more sensitive test might be to look at correlations between these sites.

Suppose we have a set of sites located in close proximity to each other, with a common set of 'core' species present in all of them. As a concrete example, in the [LS] data, 48 core species were observed at all four main sites (labelled G, M, T, Y) but each site also had 24, 34, 20 and 48 other (non-core) species, respectively [38]. Intuitively, if the percentage of core species is sufficiently large, there will only be a few gaps in the frequency spectrum where non-core species can insert themselves so as to avoid interference with core species; these gaps, then, are the same across all sites (assuming the core species 'use up' the same frequency bands at all sites). Thus, if acoustic niche paritioning were happening, we would expect to see more similarity than expected at random between the vocalization frequencies of non-core species at different sites.

To quantify similarity, we use $\bar{S}_4$, a metric equivalent to Jensen–Shannon divergence (see electronic supplementary material, appendix and equation S12). For each pair of sites we determine the percentile of their similarity scores relative to the scores of datasets generated randomly through a shuffling procedure (see electronic supplementary material). The result is shown in figure 5a, where colour indicates mean percentile. The same procedure was repeated for the [LA] data (figure 5b), though the finer scale data in this case was in the form of habitat associations rather than actual spatial sites (see electronic supplementary material). Habitats are labelled B (bamboo), F (floodplain), R (riverine succession and clearings), S (secondary—shrubs, low-stature secondary forest and other regrowth), T (tall evergreen forest on raised
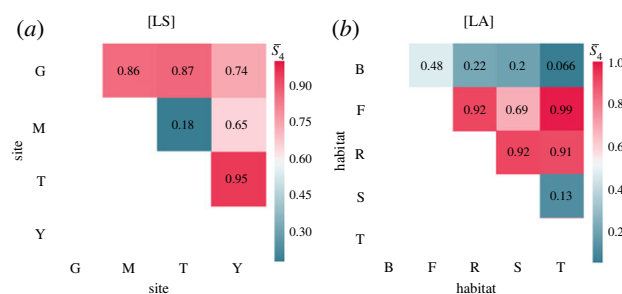

Figure 5. Mean percentile of similarity score between frequency distributions at pairs of (a) sites within [LS] or (b) habitats within [LA]. For each pair, similarity scores are computed via the index $\bar{S}_4$ (equivalent to the Jensen–Shannon divergence) and compared against scores of the same pair after performing a large number of random shuffles in the presence–absence matrix. Colour indicates percentile according to the colourbar. Higher percentiles (more red) indicate that a pair of sites or habitats is more similar than expected at random under the null model.

terraces). Running the spatial partitioning test across habitats rather than physical sites is not ideal, as—for example—there could be substantial variation in the level of background noise and frequency-dependent attenuation across the various habitat types.

In both cases, pairwise similarities are high (around the 90th percentile) about half of the time, which can be interpreted as a signal of spatial segregation by competitive exclusion in acoustic space [10], i.e. acoustic competition/ partitioning, albeit not a conclusive signal. The fact that for the [LA] dataset such a signal was not detected using the allometrically informed prior partitioning test (figure 4c) might then suggest that the spatial correlation test can be more powerful when the sampling scale is too large. Intuitively, using the finer scale data, rather than lumping everything together, may improve the signal-to-noise ratio by discounting the group of species that occurs at all sites and thus increasing the typical spacing between signals.

5. Discussion

We have shown that the frequency–mass scaling and the mass distribution constraints can lead to a bias in the distribution of signal frequencies, which needs to be taken into account through the use of an adequate null model for acoustic niche partitioning. For the data analysed here, if this bias is ignored (using a uniform prior), none of the datasets would be deemed as significantly partitioned. By contrast, using a null model that corrects for the bias seems to reveal significant evidence of partitioning along the frequency line in three locations. In the other two locations there is evidence suggesting that the acoustic partitioning signal may be reduced due to excessive geographical separation between the multiple sampling sites. At one of these locations, a spatial correlation test finds high similarity between frequency distributions at different samplings sites, which we interpret as a signal of acoustic partitioning.

Whether such competitive exclusion is acoustically or ecologically driven is debatable, as in addition to selection for reduced acoustic interference/reduced signal confusion, another force that can shape the evolution of acoustic signals is selection for optimal morphology [12,39]. Indeed, a broader question is whether acoustic frequency divergence in bird

communities is a result of adaptive processes to minimize masking interference, or merely a consequence—through the frequency–mass scaling—of sympatric species evolving divergent morphological traits to reduce ecological niche overlap [4]. The latter is the conclusion reached by Krishnan & Tamma [4], who find that sympatric species of Asian Barbets are divergent in both morphological traits and vocal frequencies, but that closely related species are more divergent in terms of morphology but not in terms of peak frequency than expected under a Brownian model of evolution. Other authors, however, find evidence for both ecological and acoustic mechanisms operating in tandem [39] or find evidence of frequency partitioning, but no corresponding pattern in body size [12].

A similar question can be posed as to whether the body-mass distribution constraint, whose origin is not well understood [19], may be acoustically or ecologically driven. The fact that we found an apparent clustering of the body-mass distributions into two groups such that the cloud forest datasets have distributions that peak at smaller masses (which would allow for a more even partitioning at the higher frequencies observed in these locations) might suggest the constraint is acoustically driven. However, the fact that the mass distribution seems remarkably conserved within the two groups might suggest a mechanism that depends on mass (or body size) directly, rather than indirectly through signal frequency. In any case, while the data do not rule out acoustics playing a role in determining the mass distribution constraint in birds, more careful study is needed to understand the relative roles of ecological and acoustic factors.

Interestingly, in running simulations for determining the indices best suited to detect acoustic partitioning, we found that a non-traditional index which—to our knowledge—has never been used before in the context of detecting acoustic partitioning, was the best performer. We denoted this index $\bar{S}_3$ and derived it—together with a few other indices—from a family of similarity indices used to measure how similar two probability distributions are. $\bar{S}_3$ outperformed all the evenness indices we tested, which are normally used to quantify community composition but have also been used frequently to quantify acoustic partitioning. A possible explanation for $\bar{S}_3$ performing better is that similarity indices may be more resilient to high levels of noise. Whereas diversity indices used to quantify community composition take as input the frequency intervals between neighbouring species (when sorted by vocalization frequency), which are very noisy since the intervals are typically small, the similarity indices instead aggregate species into several bins, which possibly averages out some of the noise.

In conclusion, our results suggest that competition for acoustic space is an important force in shaping tropical bird communities. Here, we have not factored species abundances into our calculations, except at a basic level by restricting the dataset to the species marked as being the most common. A more detailed analysis that factors species abundances into evenness indices could achieve greater statistical power. We also neglect phylogenetic relationships. Future studies could perhaps include such factors, or examine temperate bird assemblages, where competition for acoustic space should be lower.

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