

**Sharing Sound: Avian Acoustic Niches in the Brazilian Atlantic Forest**

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Received: \_\_\_\_\_

Revised: \_\_\_\_\_

Accepted: \_\_\_\_\_

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**ABSTRACT**

*In tropical birds, survival is dependent on the ability to effectively communicate with others against a background of high ambient noise. The Acoustic Niche Hypothesis proposes that the deterrent selective force of signal masking has caused animals sharing a habitat to partition their calling behaviour amongst the acoustic bandwidths available, so as to minimise interference between one another. Whether and why species share the so-called 'acoustic space' remains a gap in our understanding of animal ecosystems. The aim of this study was to investigate differences between the acoustic structure of avian communities in two distinct habitats in the montane tropical forests of the Caparaó National Park in south-eastern Brazil, and to test whether the distribution of birdsong at each conformed to the ANH. Birdsong from nine hours of passive acoustic recordings at each study site were analysed using principal component analyses. The results contradicted the ANH, revealing strikingly similar patterns of synchronised vocal behaviour ( $W_{Aleixo} = 0.63$ ,  $p < 0.0001$ ,  $R_A = 0.52$ ;  $W_{Santa\ Marta} = 0.66$ ,  $p < 0.0001$ ,  $R_{SM} = 0.46$ ). No correlation was evident between the acoustic and temporal partitioning behaviour of songbirds ( $p_A \gg 0.05$ ,  $df_A = 55$ ;  $p_{SM} \gg 0.05$ ;  $df_{SM} = 27$ ). This study provides a novel comparative analysis of the acoustic dynamics in two separate and diverse avian communities and support for theories of synchronized vocal behaviour in such groups.*

**Keywords:** *Bioacoustics; partitioning; acoustic niche; birdsong; morning chorus; vocalizations; animal communication; principal component analysis*

**ABSTRACT (BRAZILIAN PORTUGUESE)**

*Em aves tropicais, a sobrevivência depende da capacidade de comunicar-se efetivamente com outras em um ambiente de ruído alto. A hipótese do nicho acústico propõe que a força seletiva de dissuasão pelo mascaramento dos sinais faz com que os animais que compartilham um habitat dividissem seu comportamento de chamada entre as bandas acústicas disponíveis, de modo a minimizar a interferência entre si. Como e por que as espécies compartilham o chamado "espaço acústico" permanece uma lacuna em nossa compreensão das comunidades de animais. O objetivo deste estudo foi investigar as diferenças entre a estrutura acústica dos coros matinais das aves em dois habitats distintos nas florestas tropicais montanas do Parque Nacional do Caparaó, no sudeste do Brasil, e testar se a distribuição do canto dos pássaros em cada hipótese do nicho acústico. Músicas de nove horas de gravações acústicas passivas em cada local do estudo foram analisadas usando análises de componentes principais. Os resultados contradizem a hipótese do nicho acústico, revelando padrões de comportamento vocal sincronizado ( $W_{Aleixo} = 0,63$ ,  $p < 0,0001$ ,  $R_{Aleixo} = 0,52$ ;  $W_{Santa Marta} = 0,66$ ,  $p < 0,0001$ ,  $R_{Santa Marta} = 0,45$ ). Apesar das diferenças na composição de espécies, vegetação e altitude entre os locais de estudo; a ocupação do espaço acústico pelas espécies residentes foi semelhante. Não foi encontrada correlação entre a distância acústica e a distância temporal entre os cantos das espécies de aves ( $R^2 < 0,5$ ; 89% das espécies). Este estudo fornece uma nova análise comparativa da dinâmica acústica em duas comunidades aviárias separadas e ajuda a pavimentar o caminho para estudos futuros de partição acústica e sincronia.*

## 1. INTRODUCTION

Vocalizations are commonly employed as a method for communication to facilitate sexual reproduction, territorial defence, group organization, and other important functions of life (Marler, 2004). The inability to communicate in such a way risks an individual's ability to survive and reproduce (Gil & Brumm, 2014; Sueur & Farina, 2015; Stanley et al., 2016; Medeiros et al., 2017). Misinterpreted signals between conspecifics can result in aggression, while those between different species can cause hybridization and damage to genetic diversity (Sueur, 2002; Luther, 2009; Henry & Wells, 2010; Grether et al., 2017). In habitats dense with sound, interference between signals threatens the capacity for communication (Planque & Slabbekoorn, 2008). Accordingly, conspecifics and similar species will compete harder to be heard in biodiverse forests. Taxa such as felids and ungulates have evolved restrained vocal repertoires of a few types of calls, while others like songbirds and cetaceans employ complex patterns of calls and songs (Kroodsma & Pickert, 1984; Weilgart & Whitehead, 1997; Peters & Tonkin-Leyhausen, 1999; Mooney et al., 2001; Weissengruber et al., 2008; Janik, 2014; Warren et al., 2017). In biodiverse habitats, animals have been found to partition their calling behaviour to minimize interference with ambient sound, maximising their ability to communicate effectively (Duellman & Pyles, 1983; Mossbridge & Thomas, 1999; Chek & Bogart, 2003; Tobias et al., 2014; Ruppé et al., 2015; Lima et al., 2019). The Acoustic Niche Hypothesis (ANH) set in stone by Bernard L. Krause in 1993 implies that animals sharing a habitat will evolve to partition their calling bandwidths to avoid masking and share the so-called 'acoustic space' and has been supported by a growing body of research (Krause, 1993; Villanueva-Rivera, 2014). Evidence of temporal partitioning of calls, that is of individuals using different times of the day to call in order to avoid signal-masking, has also been investigated by a number of studies (Luther, 2009; Luther & Gentry, 2013). Acoustic (or spectral) and temporal partitioning are efficient methods for optimising communication, while preference of one over the other may differ between taxa. The current of body of research, however, has shown weak and fluctuating

evidence for a statistical relationship between acoustic and temporal partitioning in the vocal behaviour animals (Planque & Slabbekoorn, 2008; Shieh et al., 2015).

The accelerating field of bioacoustics is helping to fill knowledge gaps lying between the subtleties of animal communication. Passive acoustic monitoring (PAM) is a proven, cost-effective technique for investigating vocal behaviour in animals (Krause & Farina, 2016; Mulatu et al., 2017; Linke et al., 2018). Through spectrogram analysis, researchers can visualise acoustic communities, detect variations in vocalizations, and explore the behavioural implications associated with them (Celis-Murillo et al., 2009; Obrist et al., 2010; Hedley et al., 2017; Gibb et al., 2019). Bioacoustic analyses in vulnerable conservation areas provides valuable, expansive monitoring and detailed insight into differences amongst isolated fragments of habitat (Mulatu et al., 2017; Gibb et al., 2019; Robert et al., 2019). While habitat fragmentation's negative effect on biodiversity and genetic diversity is well documented, far less is known about its effects on vocal communication in animals. Findings from studies have posed the *cultural erosion hypothesis*, which suggests that animal population declines due to fragmentation could be causing less vocal exchange and learning between individuals, leading to less complex languages in such areas (Schmiegelow & Mönkkönen, 2002; Hart et al., 2018).

Birds have served as a popular study subject in bioacoustics due to their importance as ecological indicators and their vocal communication systems being some of the most complex in the animal kingdom (Marler, 2004; Zakaria et al., 2005; Luther, 2008). Their heavy reliance on transmitting and receiving complex vocalisations means avian communities remain vulnerable to changes in ambient noise (Peris & Pescador, 2004; Gil & Brumm, 2014; Farina & James, 2016). It is agreed upon today proximity to anthropogenic activity has a major influence on avian acoustic communities (Reijnen & Foppen, 1995; Patricelli & Blickley, 2006; Habib et al., 2007; Bayne et al., 2008; Halfwerk et al., 2011; Kociolek et al., 2011; Nemeth et al., 2013; Francis, 2015; Deichmann et al., 2017; Marin-Gomez et al., 2020). Fewer researchers, however, have

investigated the effect of differences in habitat and environmental change on bird communication (Brumm, 2004). Transmission of different frequency signals can be significantly affected by habitat type and atmospheric conditions (Dabelsteen et al., 1993; Slabbekoorn et al., 2002; Nemeth et al., 2006). Acoustic conditions differ even between segments of habitat due to unique signatures of background noise (Morton, 1975; Patricelli & Blickley, 2006; Cardoso & Price, 2010). Optimal environmental conditions (less dense forest, for instance, which attenuates sound less quickly than dense forest) may also be accompanied by optimal temporal conditions (such as morning, during which most birds prefer to call) which as selective forces on vocalisations (Henwood & Fabric, 1979; Brown & Handford, 2003; Ruppé et al., 2015). Each segment of habitat thus represents a unique sound signature and more research is now focusing on classifying environments by their soundscapes (Pijanowski et al., 2011; Gasc et al., 2013; Tucker et al., 2014; Fuller et al., 2015; Lomolino et al., 2015; Sueur & Farina, 2015; Gasc et al., 2016; Krause & Farina, 2016; Linke et al., 2018; Ross et al., 2018; Ulloa et al., 2018).

This study aims to visualise the variation of birdsong in the avian community of two distinct areas of the Caparaó National Park in Brazil, test for evidence of the Acoustic Niche Hypothesis, and compare the occupation of acoustic space between two study sites on either side of the park. The hypothesis of this study is three-fold. First, we predict that the distribution of birdsong in acoustic space at each study site will not be random but significantly partitioned, confirming the ANH. Clustering of song in acoustic space represents synchrony, the alternative to this hypothesis. Second, the distributions of birdsong will differ significantly between the study sites, due to environmental differences and their inherently unique soundscapes. Third, analysis of each site will show a significant, negative relationship between the usage of temporal and acoustic partitioning by singing birds, as the use of both is superfluous.

## **2. METHODS**

## 1. Study Site & Sampling Methods

The passive acoustic recordings used in this study were collected from two distinct sites 10.6 km apart in the Caparaó National Park (CNP) of south-eastern Brazil during January 2017. Lying on the border between the Brazilian states of Minas Gerais and Espírito Santo, the CNP is one of the most important remnants of the Atlantic Forest, spanning 31,853 ha and containing a high density of threatened fauna and flora (ICMBIO, 2016). Despite severe fragmentation over centuries, the region still provides sanctuary for more than 20,000 species of flora and 1,400 species of fauna; which makes up roughly 1-8% of the world's species (da Silva & Casteleti, 2003; Santos, 2013). This includes over 600 distinct avian species, which form the target subject group of our study on acoustic niche occupation in Atlantic Forest birds.

The 'Aleixo Valley' (AV) and 'Santa Marta Valley' (SMV) study sites were located on the western and eastern sides of the central Serra do Caparaó range at altitudes of 1687 and 1348 metres, respectively (see Figure 1). The CNP consists of a tropical climate with average annual temperatures ranging between 19-22°C and an average rainfall of 1000-1500 mm/year. 35-50% of the park's annual rainfall occurs during the rainy season between November and January (main reproductive season for animals), while the driest months occur between June and August each year. The park comprises of three main types of vegetation: montane tropical forest, semi-deciduous forest, and alpine meadows. While tropical forest dominates throughout all regions below 1800 metres in the park, the floral species present vary with altitude (IBDF, 1981; ICMBIO, 2016).

Sound recordings used for this study were recorded by MCK in January and March of 2017 using four autonomous recording units (ARU) (SongMeter SM3, Wildlife Acoustics Inc., Concord, MA, USA) deployed across a 'listening post' in Aleixo Valley and another in Santa Marta Valley (20°28'46.49" S, 41°50'25.00" W and 20°29'25.74"S, 41°44'21.55"W). Each listening post comprised of two SongMeters fixed 1.8 m above ground, each attached to two

microphones, facing opposite directions and thus recording in the four cardinal directions (Figure 2). Recordings were sampled at 44.1 kHz and 16 bits per second and recorded in 1-hour segments. A high-pass filter was set at 220 Hz to filter out wind and river noise. Recordings from the two SongMeters at each post were time-synchronized using Garmin GPS's to triangulate the sound source. Three hours of recording from 0800 to 1100 on three consecutive days were used from each site to investigate the singing avian communities. The nine hours of recording taken from each study site combined for a total of 18 hours of recording for this study.

## **2. Vegetation Surveys**

Vegetation plot surveys were conducted at each study site during May 2019. At each site, four 10 m x 10 m plots were randomly positioned within a radius of 100 m from the site of the ARU. Within each plot, the number of short (<10 m), medium (10-15 m), and tall (>15 m) trees were counted and measured for circumference. Only trees with a circumference greater than 10 cm were recorded in this survey. The presence of tall grasses, vines, or saplings was also noted as increased leaf cover and foliage decrease sound transmission through the forest (Dabelsteen et al., 1993). The data from the vegetation plot surveys can be found in Appendix A.

## **3. Data Processing & Analysis**

The 18 hours of recordings were divided into ten-minute time blocks (n = 192 time blocks), with each block analysed in Raven Pro at a fast-Fourier transform (FFT) size of 512 (Tobias et al., 2014). Birdsong from as many different species possible were then identified in Raven Pro and selection boxes were drawn around them to extract key parameters. (Figure 3) Short contact calls did not qualify as songs, which are series of notes, and were not used in this study as their acoustic characteristics vary less from one another. Online databases such as XenoCanto and WikiAves were frequently consulted alongside local ornithologists to maximise species identification accuracy.

For each song identified, seven key measurements were taken: duration, number of notes, pace (notes per second), minimum frequency, peak frequency, central frequency, and bandwidth (Tobias et al., 2014). Only songs clearly visible on the spectrogram were selected for analysis to minimise visual observer bias. Presence of loud insect noise was occasionally noted in our recordings and birdsong masked by such noise was omitted from selection. Where insect or anthropogenic noise consistently present, omitting masked song could bias the data of species that share frequency bandwidths (from 3 to 6 kHz) with insects or other noise (Hart et al., 2015; Stanley et al., 2016). The recordings in our study, however, did not exhibit any periods with consistently loud insect noise, making any resulting bias on minimum and maximum frequency measurements insignificant. Many bird species have vocal repertoires comprising of multiple songs, so for this data collection only the most common song for each species was used (Stanley et al., 2016). When birds called closer to the microphone, the increased amplitude revealed additional harmonics in their songs. As including these harmonics in the selection boxes could drastically affect average acoustic measurements, only the loudest harmonic (fundamental frequency) was used for consistency (Figure 4) (Stanley et al., 2016). A dataset of the average song measurements (the sum of an acoustic characteristic divided by the number of observed songs) for each identified species throughout the 18 hours of recording was then compiled (Appendix B). Any species with less than two observations was removed from the dataset to reduce the effect from individual song variation, producing a final dataset comprising of 1465 individual songs from 80 distinct species. Though just 29 of species identification were confirmed by local ornithological experts, all species were included in the analysis for a comprehensive investigation of the entire avian acoustic community at each study site. The species observed in this study accounted for at least 75% of the singing community at the time of data collection in each study site.

### Visualising the acoustic structure of the avian community

The acoustic data of species' means (Appendix B) were then used to conduct a principal component analysis (PCA) of birdsong at each study site (Table 1) (Appendix C). Using the '*prcomp*' function from the R '*stats*' package, the data were normalised to unit size prior to analysis to avoid bias (Brumm et al., 2017). Only the first three principal components were determined necessary to retain according an implementation of Horn's parallel analysis using the '*paran*' package in R (Horn, 1965). Correlation matrices of the principal components generated for each site were used to interpret the significance of the axes of variation (Appendix E) Across both sites, the first component (PC1) correlated with song frequency and bandwidth. PC2 correlated with song duration and with the number of notes in the song in both sites. PC3 correlated most with pace (number of notes divided by duration) in the two sites.

To test the first part of our hypothesis, a Shapiro-Wilks test was used to test the 3D distributions of birdsong in PCA space against a random distribution. To discriminate between the main and alternative hypotheses (acoustic partitioning and synchrony, respectively), a further calculation was made of the R-value employed by Clark and Evans, 1954. R-values can be interpreted as an average measure of the spacing between points and are ratios between the mean acoustic distance of the observed distribution and the mean acoustic distance of a random distribution of equal density (Clark & Evans, 1954):

$$R = \frac{\text{Mean AD (observed)}}{\text{Mean AD (random)}}$$

### Temporal Partitioning Analysis

To investigate temporal partitioning in birdsong, a record was kept of which species' songs were observed within each 10-minute time block (Appendix G). Any given species was determined present within a time block when its song was detected on at least three separate

occasions. An exception to this existed for bird species whose songs lasted for longer than 5 seconds. Such ‘long-call’ species were deemed present within a time block if their calls were identified at least once. The mean occupation of birdsong in each time block was calculated as the total number of species observed calling in a given block divided by the total number of species recorded at the site. Though this statistic is influenced by species with scarcely occurring birdsong, its relative magnitudes remains robust: using all species recorded at the site allows for the most comprehensive analysis of sound. This measure was used to represent the temporal component of the mean birdsong at each site and was later used to find the temporal distance of each species’ song to the community average.

### **Temporal Versus Acoustic Partitioning**

The acoustic component of each site’s mean song was represented by the origin  $\{0, 0, 0\}$  of acoustic PCA space, since the data of mean acoustic characteristics were normalised prior to the PCA. The temporal component was represented as a vector of mean occupations of each of the 54 time blocks dividing the temporal activity of each site’s birdsong. Acoustic distance was calculated as the Euclidean distance from each species’ song in PCA space to the origin, while the sum of absolute differences between the binary occupation of a species’ song in a temporal time block and that time block’s mean occupation value was used to represent temporal distance:

$$\textit{Acoustic distance to mean song} = \sqrt{x^2 + y^2 + z^2}$$

$$\textit{Temporal distance to mean song} = \sum_{k=1}^{54} |O_k - \bar{O}_k|$$

Where  $x$ ,  $y$ , and  $z$  are the unitless coordinates for each birdsong in acoustic space, and  $O$  is the occupation value (1 or 0) for the species in each ten-minute time block  $k$ . Values of acoustic and temporal distance from the community’s mean song were calculated for each species recorded at the study sites, stored in Appendix D, and plotted against each other (Figure 7).

Linear regression models were produced to investigate the presence of a relationship between temporal and acoustic partitioning in each avian community (Table 3).

### **3. RESULTS**

#### **1. Structure of the acoustic communities**

Although the principal components for the PCA of each study site's dataset were generated separately and varied slightly between the two sites, the components' correlation matrices at the two study sites were similar enough to justify direct comparison between the distributions of birdsong in three-dimensional PCA space. Together, the first three principal components in Aleixo and Santa Marta accounted for 82.5% and 82.0% of the variation in birdsong, respectively (Table 1) (Appendix C). In both sites, the distributions of song in acoustic space displayed patterns of clustering ( $N_A = 57$ ,  $N_{SM} = 34$ ) (Figures 5 and 6). Both distributions were highly clustered in the centre of the PC2 axis of variation, correlated with song duration and note count.

#### **2. Comparison between study sites**

The distributions of birdsong in acoustic space at each study site were found to be significantly different from a random 3D scatter (Shapiro-Wilk  $W_A = 0.63$ ,  $p \ll 0.001$ ;  $W_{SM} = 0.66$ ,  $p \ll 0.001$ ). R-values calculated as in Clark and Evans (1954) in the two sites confirmed patterns of clustering ( $R_A = 0.52$ ,  $R_{SM} = 0.46$ ) (Table 2) (Appendix F). An R-value of 0.52 for the song distribution in Aleixo Valley can be interpreted as the distribution being roughly twice as clustered as a random distribution with the same density. A uniform distribution, with the same density as the song distributions but with maximum spacing between points, would have yielded an R-value of 2.15 (Clark & Evans, 1954). Thus, the avian community recorded in Santa Marta Valley was slightly more clustered than that in Aleixo Valley, but interestingly appeared more evenly spread along the PC1 axis of variation, correlated with frequency (Figure 6). Though the density of tree cover across three discrete height categories was comparable between the two sites

(Appendix A), Aleixo and Santa Marta comprised of different vegetation classes (semi-deciduous and tropical rainforest, respectively) and are situated at elevations 339 metres apart.

### **3. Acoustic partitioning vs. temporal partitioning**

Linear regression models fitted to the acoustic distances and temporal distances of birdsong to mean birdsong of each site's avian community proved unsuitable ( $F_A = 0.632$ ,  $R^2_A = -0.017$ ,  $p \gg 0.05$ ;  $F_{SM} = 1.131$ ,  $R^2_{SM} = 0.005$ ,  $p \gg 0.05$ ) (Table 3). A plot of acoustic distance versus temporal distance to the community mean for each observed birdsong can be seen in Figure 7. Though these results fail to produce evidence for a relationship between temporal and partitioning behaviour, they do not confirm the absence of any such link.

## **4. DISCUSSION**

### **1. Drivers of song clustering in acoustic space**

Surveying two separate avian communities of 57 and 34 distinct species in Aleixo Valley and Santa Marta Valley, respectively, we found the usage of acoustic space by each to be clustered, in contradiction to the acoustic niche hypothesis. The results reject the null hypothesis of randomly distributed bird song and support the alternative hypothesis that singing avian communities tend toward synchrony, perhaps around the optimal acoustic properties of their habitat. Other biotic noise and environmental factors are additional driving factors potentially influencing clustering in the acoustic community. The presence of cicada choruses, for example, has been found to alter the temporal calling behavior of birds to avoid the insects' calling times, in doing so causes increased synchrony in the avian acoustic space (Luther & Gentry, 2013; Stanley et al., 2016; Aide et al., 2017). In this study's data, cicada noise was observed in 59% of the recorded Santa Marta data but not in any of the Aleixo data. Birdsong overwhelmed by noise was omitted to avoid bias from masking of minimum and maximum frequency measurements by noise, although employing the more robust method of taking these measurements using power spectra thresholds

would have allowed for the inclusion of these songs in the data (Francis et al., 2011; Goodwin & Shriver, 2011). Visual observer bias is inherent in this study as it is in most bioacoustic research (Zollinger et al., 2012; Brumm et al., 2017). We believe that the high replicability of the selection rules used for making song selections, the consultations with local ornithological experts in Minas Gerais, and the large volume of observations recorded maintain robustness in the results of the study.

Optimal acoustic properties of the habitats may have also supported the clustering of avian birdsong (Prum, 2014). Without partitioning evident in either community, the incentive to compete for optimal calling bandwidths may have outweighed the benefits of avoiding signal masking. This could be due to signal interference having a less detrimental effect on bird communication than previously expected. Though many studies continue to focus on partitioning in birdsong, far less research has investigated the evolutionary selectivity of the receiver's ability to discern vocal signals amidst background noise (Patricelli & Blickley, 2006; Luther, 2008; Luther & Gentry, 2013). Increased accuracy in signal detection amongst birds would allow them to compete in clustered acoustic space with less risk of misinterpreting signals.

Spectral or temporal overlapping of vocalisations is often associated with negative consequences, yet another possible explanation for synchrony in avian communities is represented by the potential collective benefit by an avian community in synchronizing its birdsong (Halfwerk & Slabbekoorn, 2013; Gil & Brumm, 2014). Theories of *interactive communication networks* predict the prevalence of cross-species vocal interaction for mutual benefit over acoustic partitioning. In dense, biodiverse environments, communication between species in a shared bandwidth may be evolutionary advantageous in helping to mediate territorial defense and aggression and even provide warnings against mutual predators (Cardoso & Price, 2010; Tobias et al., 2014; Kirschel et al., 2019; Keen et al., 2020). Despite expected negative

implications for calling in a busy region of acoustic space, the results of this study appear to support these alternative motivations to do so. Coordinated signalling systems may also span vast habitats. While such speculation requires further investigation, clustering and synchronization of avian acoustic space may well serve as an initial clue toward understanding other coordinated behaviour in animals.

Avian communities in the Aleixo and Santa Marta valleys are separated from each other by approximately seven miles, which encompasses the central Serra do Caparaó mountain range (Figure 1). The similarity between the distributions of song in 3D PCA space between them was nonetheless striking, as there was minimal overlap in species makeup (only five species were present at both sites). Such parallels in spite of the geographical separation between communities suggests possible convergent evolution of the acoustic community, invoking interesting questions for future studies regarding the relationship between birds and their acoustic environment. The two valley sites of our study exhibited two different terrains but shared a similar vegetation profile dominated by small trees and grasses, both on similar inclines (Appendix A). Previous research has investigated the role of the acoustic environment in habitat selection by animals (Morton, 1975; Pijanowski et al., 2011; Pekin et al., 2012; Mullet et al., 2017). Given closer examination, convergent acoustic behaviour by separate avian communities could support such hypotheses.

Synchronization in the use of the acoustic space of avian communities found in the results of this study supports a growing body of research theorising that convergence of vocal signals help to mediate behavioural interference between species. The evolutionary consequences of cross-species interaction are well-documented and with rapid environmental change causing shifts in migrations, it is particularly important to understand how interactions between different species are governed by vocalisations (Grether et al., 2017). Two distinct groups of bird species

can be separated from results of the principal component analysis (Figures 5 and 6): those singing in the central cluster and busiest region of acoustic space and those singing toward the periphery. Species vocalising in heavily-occupied regions of acoustic space exhibit the ability to co-exist with other species there, while the outlying species of the periphery may prefer to avoid signal masking and may not participate in cross-species communicative networks (Luther, 2009). Suggestions from the data such as these are particularly important to consider for future ecological planning purposes, as species in tropical regions like the Atlantic Forest will continue to migrate in more unpredictable patterns due to quickening environmental change.

This study focused on the avian use acoustic space in the Caparaó National Park. Analysing only birdsong does not, however, constitute a complete view of avian acoustic space and fails to account for other biotic and non-biotic sound in the forests that likely influence birdsong (Galindo-Leal & de Gusmão Câmara, 2003). Future studies should include analysis of as many different sounds in a single habitat as possible for a more comprehensive understanding of the science. This may shed more light on theories such as interactive communication networks between different taxa.

## **2. Temporal versus acoustic partitioning**

Our results are consistent with previous studies that similarly found no relationship between acoustic and temporal partitioning in birdsong. These results do not, however, confirm the absence of a link between birds' avoidance of one another's vocalizations temporally and spectrally. Vocal behaviours in many animal species vary across different populations and throughout the seasons (Van Parijs et al., 1999; Rehm & Baldassarre, 2007; Tremain et al., 2008). With the data for this study collected over six days, it would be incomplete to presume apply to the results study to all times of the year and/or different habitats. Further research on causalities between acoustic and temporal partitioning in birdsong is necessary, particularly when

accounting for the entire acoustic soundscape and not just avian birdsong. Planque & Slabbekoorn (2008) suggested using temporal distancing in frequency bands (regardless of which species are using them) as a potentially superior analysis. Vocal behaviour is paramount to the survival of individuals in bird species and better understanding when spectral or temporal partitioning is preferred is crucial to mitigating impacts on them by changing environments.

#### **STATEMENTS OF DISCLOSURE AND DATA AVAILABILITY**

In accordance with Biotropica policy and my ethical obligation as a researcher, I am reporting that I have no financial interests in any company or party that may be affected by the research reported in the enclosed paper. The data that support the findings of this study are openly available in [repository name] at [http://doi.org/\[doi\]](http://doi.org/[doi]), reference number [reference number].

#### **ACKNOWLEDGEMENTS**

We would first like to thank Marianne Kaizer, who allowed me to use her passive acoustic recordings collected back in January and February of 2017 and helped to organise my excursion to the Caparaó National Park in May, 2019. A special thanks is extended to Claudio Novaes and Prof. Daniel Ferraz, who assisted me with the collection of vegetation data in Caparaó National Park and with the identification of caller species. Ornithologist Luiz Gabriel Mazzoni also assisted with species identifications in the recordings. We would also like to thank Prof. Robert Young for review of the manuscript. Acknowledgments extend to the LJMU Go Global fund, which allowed me to visit the Caparaó National Park study sites and collect environmental data. Finally, I would like to thank Dr. Luiza Figueiredo Passos for all her support with the project.

#### **Author Contribution Statement**

According to the CRediT Author Role Taxonomy endorsed by Biotropica, the author contribution for this study was as follows:

KLEYN AND PASSOS

Tristan Kleyn –

Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Validation, Visualization, Writing – original draft, Writing – review & editing

Dr. Mariane Kaizer –

Investigation, Methodology, Supervision

Dr. Luiza Figueiredo Passos –

Funding Acquisition, Methodology, Project Administration, Resources, Software, Supervision, Writing – review & editing

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## TABLES

Table 1

<b>Aleixo</b>	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>Santa Marta</b>	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>
<i>Eigenvalue</i>	1.724	1.246	1.118	<i>Eigenvalue</i>	1.783	1.221	1.034
<i>Proportion of variance</i>	0.424	0.222	0.179	<i>Proportion of variance</i>	0.454	0.213	0.153
<i>Min. Freq.</i>	<b>-0.4089</b>	0.0348	<b>-0.4994</b>	<i>Min. Freq.</i>	<b>0.4733</b>	-0.0376	0.1950
<i>Max. Freq.</i>	<b>-0.5482</b>	-0.1778	0.1938	<i>Max. Freq.</i>	<b>0.5340</b>	0.2191	-0.0355
<i>Central Freq.</i>	<b>-0.5563</b>	-0.0955	-0.0975	<i>Central Freq.</i>	<b>0.5340</b>	0.0781	0.1221
<i>Duration 90%</i>	0.2183	<b>-0.6506</b>	-0.0379	<i>Duration 90%</i>	-0.1538	<b>0.7210</b>	0.1198
<i>Bandwidth 90%</i>	<b>-0.3713</b>	-0.2267	<b>0.5679</b>	<i>Bandwidth 90%</i>	<b>0.3244</b>	<b>0.3654</b>	-0.2585
<i>No. of notes</i>	0.1110	<b>-0.6952</b>	-0.2178	<i>No. of notes</i>	-0.2417	<b>0.4978</b>	<b>-0.3356</b>
<i>Pace (notes/sec)</i>	-0.1581	0.0083	<b>-0.5763</b>	<i>Pace (notes/sec)</i>	0.1354	-0.2084	<b>-0.8672</b>

Table 2

<b>Study Site</b>	<b>N</b>	<b>Mean AD</b>	<b>St. Dev</b>	<b><math>\rho</math></b>	<b>R</b>	<b>W</b>	<b>p</b>
<i>Aleixo</i>	57	3.157	1.819	0.007	0.518	0.632	<b>1.091e-10</b>
<i>Santa Marta</i>	29	3.303	1.571	0.005	0.455	0.657	<b>5.392e-07</b>

Table 3

<b>Site</b>	<b>F-statistic</b>	<b>SE</b>	<b>Adj. R<sup>2</sup></b>	<b>p</b>	<b>df</b>
<i>Aleixo</i>	0.6324	0.0781	-0.017	0.800	55
<i>Santa Marta</i>	1.1310	0.1275	0.0047	0.297	27

## FIGURE LEGENDS

**Figure 1** – The Caparaó National Park lies on the border between the Brazilian states of Espírito Santo and Minas Gerais. The study sites chosen are situated on either side of the park's central mountain range and at altitudes 339 m apart.

**Figure 2** – The 'listening post' deployed at each study site consisted of two ARU's attached to microphones recording in opposite cardinal directions. Recordings were time-synchronized using Garmin GPS units.

**Figure 3** – Examples of birdsong selections made in Raven Pro 1.5 from the passive acoustic recordings in Aleixo Valley on January 26, 2017. (a) *H. poicilotis*; (b) *L. albicollis*; (c) *C. gujanensis*; (d) *H. poicilotis*; (e) *T. ruficapillus*.

**Figure 4** – Three characteristic songs of *L. squamatus*, showing the variability in the amplitude of the upper harmonic of its song. The upper harmonic is the most visible in (b), while the song in (c) is less detectable with the harmonic too faint to detect at all.

**Figure 5** – Distribution of birdsong at Aleixo Valley in three-dimensional PCA space (top) shows patterns of clustering in the mean acoustic characteristics of species' song ( $N = 57$ ,  $R = 0.52$ ,  $p = 1.1 \text{ e-}10$ ). The axes of variation are shown with the proportion of total variance they account for. A two-dimensional PCA plot (bottom) reveals heavier clustering along the PC1 axis of variation in the Aleixo birdsong data. Song is visibly more clustered along the PC2 axis, correlating with song duration, than along the PC1 axis, correlating with song frequency.

**Figure 6** – Distribution of birdsong at Santa Marta Valley in three-dimensional PCA space (top) shows similarly significant clustering in the mean acoustic characteristics of species' song to that in Aleixo Valley ( $N = 29$ ,  $R = 0.46$ ,  $p = 5.4 \text{ e-}7$ ). The two-dimensional PCA plot (bottom) reveals heavier clustering along the PC1 axis of variation, as was also seen in the Aleixo analysis (Figure 4). Song is visibly more clustered along the PC2 axis, correlating with song duration, than along the PC1 axis, correlating with song frequency.

**Figure 7** – No significant correlation was found between the acoustic and temporal distances of species' song to the mean birdsong in either of Aleixo valley (top;  $R^2 = -0.017$ ,  $p \gg 0.05$ ,  $df = 55$ ) and Santa Marta valley (bottom;  $R^2 = 0.0047$ ,  $p \gg 0.05$ ,  $df = 27$ ).

**Table 1** – Correlation matrix between the principal components and the seven key acoustic parameters used for the study. Significant values are highlighted with bold. Three components from each PCA were retained following a parallel analysis of factors. The interpretations of the first three principal components were comparable between the two study sites.

**Table 2** – Four-dimensional song distribution statistics for each study site, where significant p-values are shown in bold.

Mean AD = mean acoustic distance (nearest-neighbour distance);  $\rho$  = Distribution density; R = Clustering value (Clark & Evans, 1954); W = Multivariate Shapiro-Wilk statistic; p = Shapiro-Wilk p-value

**Table 3** – Linear regression models did not fit the acoustic and temporal distance data for avian community, producing insignificant results which contradicted the third part of the study's hypothesis. Regressions were produced and analysed in R Studio.

FIGURES

Figure 1

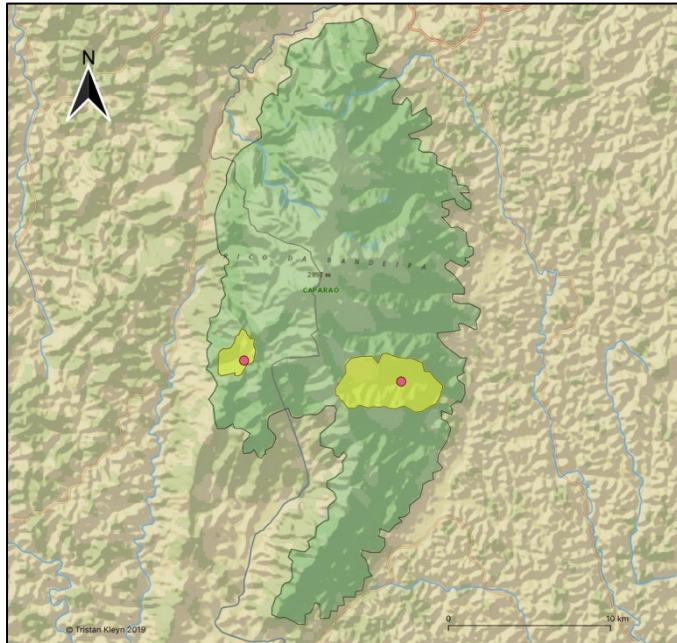


Figure 2

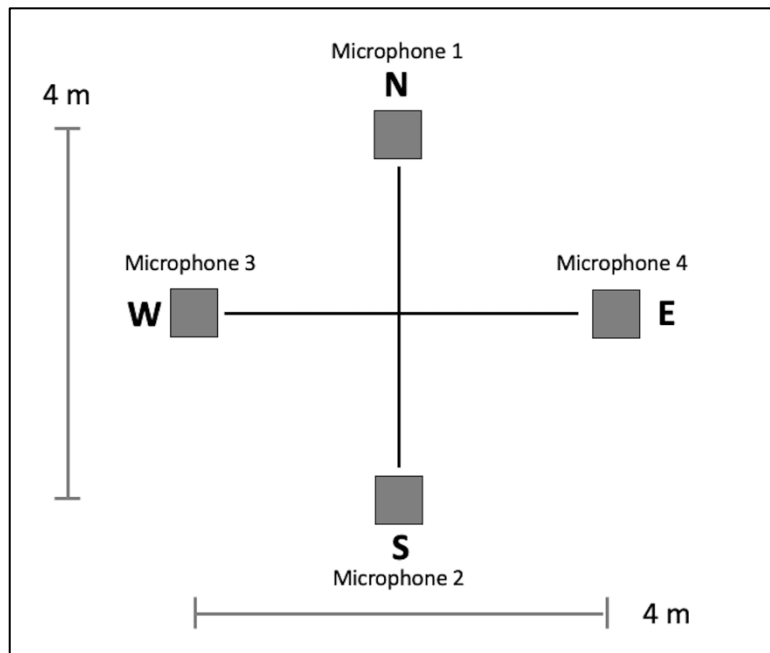


Figure 3

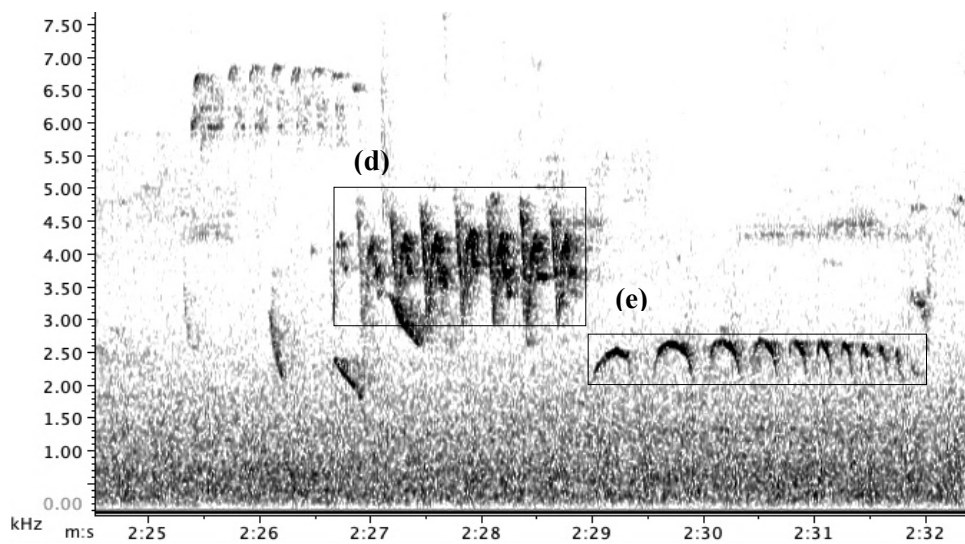
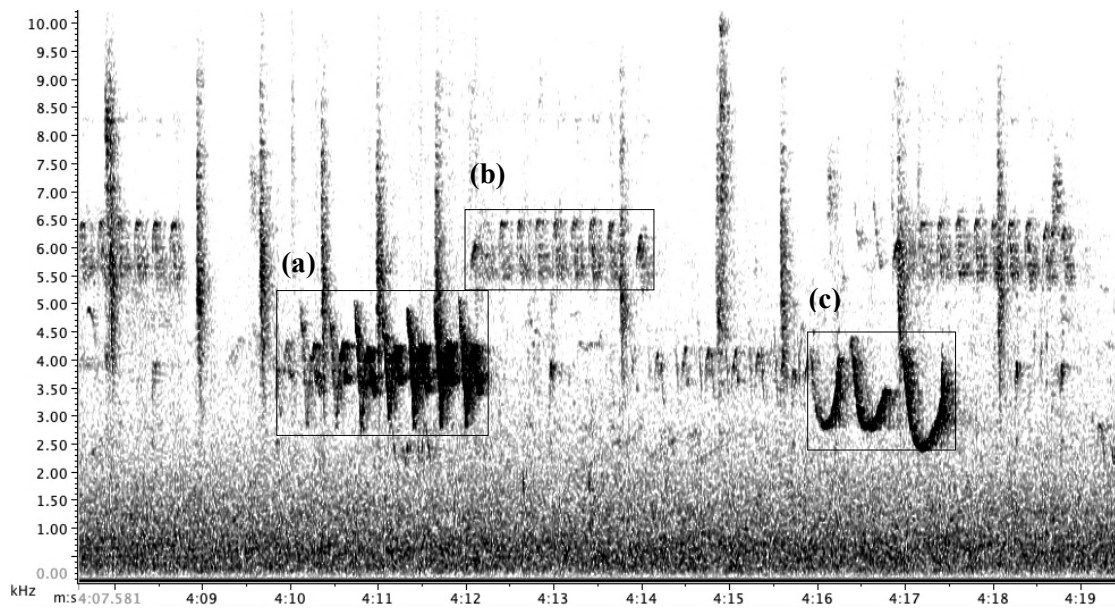


Figure 4

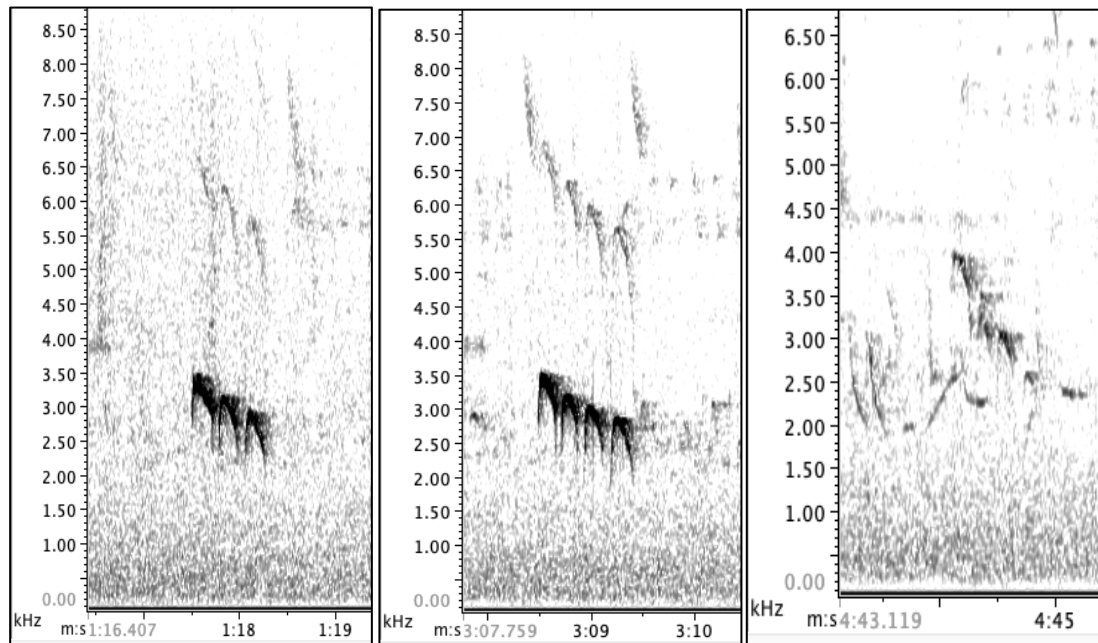


Figure 5

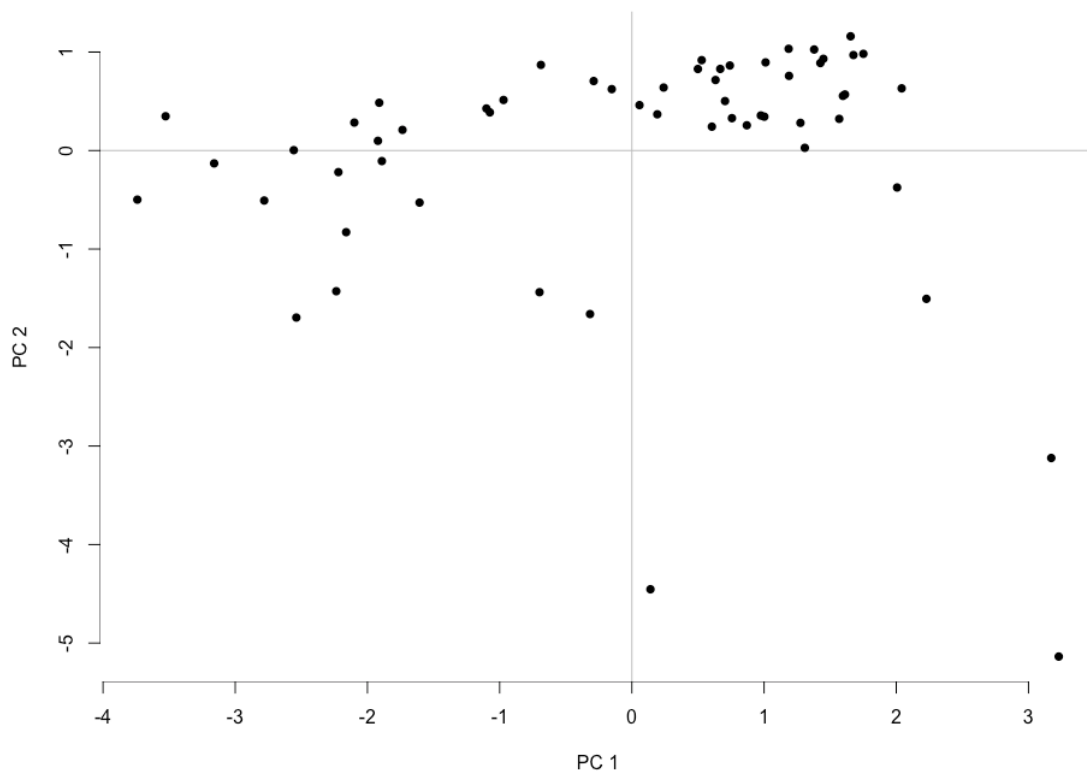
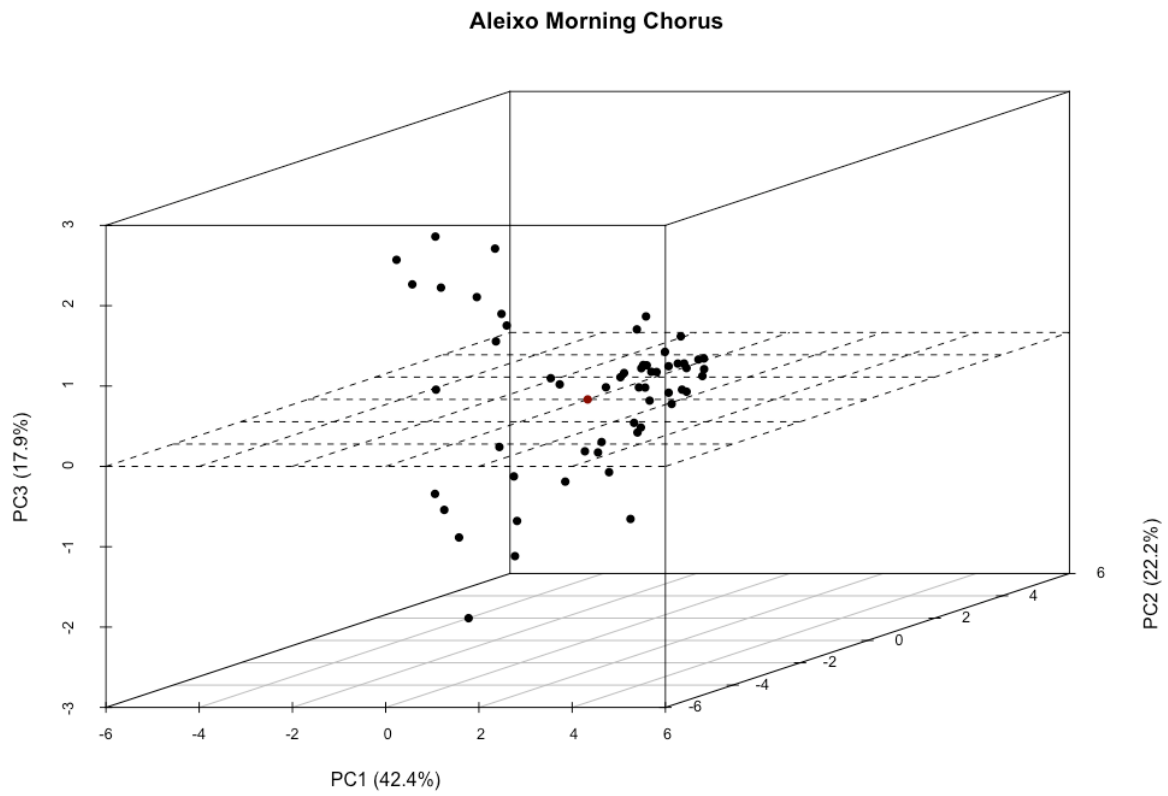


Figure 6

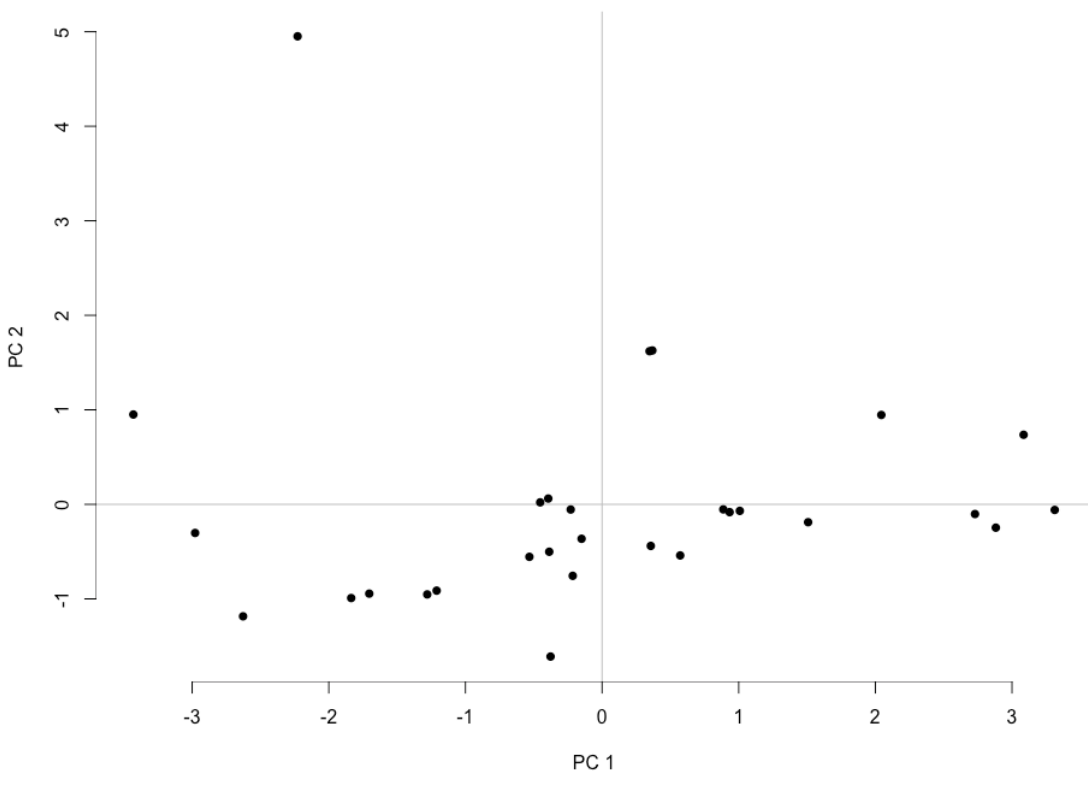
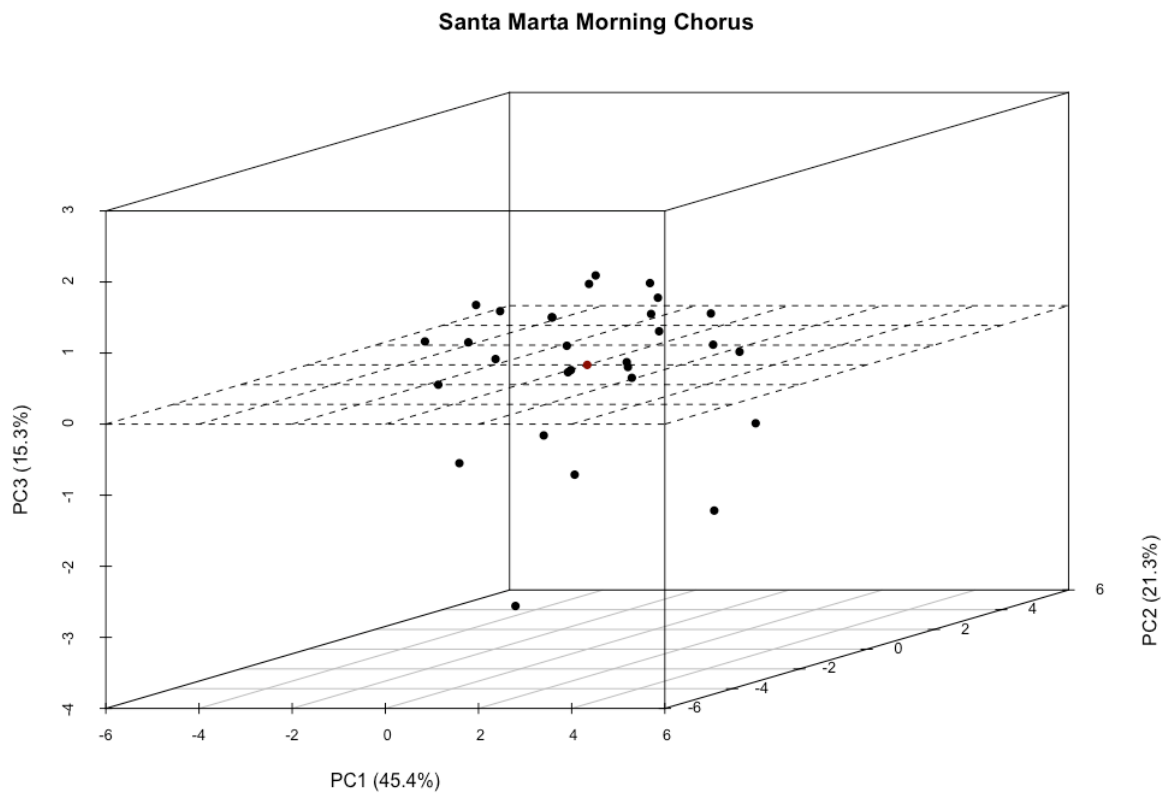


Figure 7

