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REVIEW

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THE STUDY OF BIRD VOCALIZATIONS IN NEOTROPICAL HABITATS: CURRENT KNOWLEDGE AND FUTURE STEPS

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Abstract · Research on avian bioacoustics in the Neotropics has surged over the last several decades due to increased interest in the large diversity of vocal behaviors and vocalization and the broader accessibility of recording equipment and software**.** Here, we present a synthesis of the current and past knowledge of Neotropical bird bioacoustics. This synthesis is the result of the symposium "Bioacoustics in the Neotropics", organized for the XI Neotropical Ornithological Congress in San Jose, Costa Rica, in July 2019. We covered what we consider the main topics in avian bioacoustics that have been studied in this region over the last 30 years. Our review includes repertoire descriptions, geographic variation, diversity in vocal behaviors, seasonality, duetting, genetic association, and playback experiments. Additionally, we present information for what we believe may be the main veins of investigation for the coming future in the Neotropics, considering the large diversity of species that are found in the region and the new investigations developed in other geographic areas. We expect this review to work as a summary of the current literature and a guide to stimulate future research in important areas within the field of avian bioacoustics in the Neotropics.

Resumen · Estudio de las vocalizaciones de aves en hábitats Neotropicales: conocimiento actual y pasos futuros
Las investigaciones sobre bioacústica de aves han aumentado considerablemente en las últimas décadas en la región Neotrópical debido a la gran diversidad de comportamientos vocales y vocalizaciones, así como por la mayor accesibilidad a equipos de grabación y software. Aquí presentamos una revisión del conocimiento pasado y actual sobre la bioacústica de aves neotropicales, producto del simposio "Bioacústica en el Neotrópico", organizado para el XI Congreso de Ornitología Neotropical en San José, Costa Rica, en julio de 2019. Cubrimos lo que consideramos son los principales temas estudiados en esta región en los últimos 30 años, incluyendo descripciones de repertorio, variación geográfica, diversidad en los comportamientos vocales, estacionalidad, duetos, asociación genética y experimentos de playback. Además, presentamos información de lo que creemos pueden ser las principales líneas de investigación para el futuro venidero en el Neotrópico, debido a la gran diversidad de especies que se encuentran en la región y las nuevas investigaciones desarrolladas en otras áreas geográficas. Esperamos que esta revisión pueda funcionar como una guía de lo que tenemos y lo que necesitamos para impulsar la bioacústica de las aves en el Neotrópico.

Key words: *bioacoustics · calls · duets · Neotropics - recordings · songs*

INTRODUCTION

Within Neotropical habitats (from northern Mexico to southern Argentina and Chile, including the Caribbean islands), it is possible to find more than 3300 breeding and migratory bird species that breed and survive (Stotz et al. 1996, Stutchbury & Morton 2001). The avian richness in this area provides a unique opportunity to study diverse vocal behaviors and conduct comparative analyses of behaviors associated with mating, territory defense, and other social interactions. This is especially true because there is greater diversity of unique taxonomic groups compared to northern temperate habitats (Stotz et al. 1996, Stutchbury & Morton 2001). For example, in the Neotropics, it is very common to find families in which many species have female song (e.g., antbirds, curassows, euphonias, flycatchers, icterids, parrots, sparrows, woodcreepers, woodpeckers, and wrens; Odom et al. 2014, Odom & Benedict 2018, Riebel et al. 2019). In some cases, vocal output is even higher for females (Illes & Yunes-Jimenez 2008, Price et al. 2008) such as in Stripe-headed Sparrows *Paucea ruficauda* and Streak -backed Orioles *Icterus pustulatus*. Furthermore, males of some neotropical species sing year-round; in other species, males sing exclusively during the breeding season to establish territories and attract mates (Morton 1996, Kroodsma et al. 1996), and while in others, males form year-round pairs with the same mate over several years, sing to obtain extra-pair copulations during the breeding season (Sandoval et al. 2016). A common vocal behavior in neotropical bird species is duetting, which is produced

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mostly by the coordination of female and male songs (Hall 2009), except for five species of the manakin genus *Chiroxiphia*, where there are two males displaying duets in leks (Snow 1977). It is also common to find bird families (e.g., anis, jays, quails, or wrens) in which closely related (i.e., family groups) or unrelated individuals help defend year-round territories and/or aid in breeding activities (Hale 2006, Bradley & Mennill 2009, Rosa et al. 2016). Many of these behaviors are coordinated using vocalizations such as songs (i.e., choruses: where several individuals coordinate solo songs) or calls (see Sandoval & Graham 2024, for definition of solo songs and calls in this number).

Understanding the origin and maintenance of such great vocal behavioral diversity in the Neotropics is challenging, especially because available recordings are scarce for the majority of species. For instance, the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology) contains one of the largest animal audio recording collections in the world, yet most species classified as occurring in the Neotropics (53.9% of species) have less than 30 recordings (mostly songs), while 144 species have no recordings at all (Figure 1). Addressing this geographical bias in the recordings of different types of vocalizations is essential to begin developing the descriptions of vocal repertoires, analyzing and describing diel patterns, conducting geographic variation studies, and performing functional analyses of vocalization types for Neotropical species. These steps will allow studies of avian vocal behavior to move forward and conduct focused experiments and comparative phylogenetic analyses, to understand the ecological and evolutionary forces shaping the divergence and diversity of vocal characteristics.

This review derives from the symposium "Bioacoustics in the Neotropics", which was organized for the XI Neotropical Ornithological Congress in San Jose, Costa Rica, in July 2019. Our purpose was to discuss the current knowledge of Neotropical avian vocal behavior and assess the importance and potential of several future research programs. Specifically, our objectives were to (1) review avian vocalizations in the Neotropics as a baseline and (2) identify priorities for future investigations of bird species vocalizations.

METHODS

In this review, we conducted a non-systematic review of the ten investigations lines about bird vocalizations in the Neotropics that were detected as the main lines of investigation in the last 20 years: vocal repertoire descriptions, diversity of vocal behaviors, duet functions, diel variation, vocal seasonality, geographic variation, population dynamics in vocal variations, the use of vocalization in taxonomy, sound transmission and playback experiments. These topics were the focus of research presented during the "Bioacoustics in the Neotropics" symposium at the XI Neotropical Ornithological Congress in San Jose, Costa Rica, in July 2019. Finally, we discuss the importance of maintaining these lines of investigation and potential approaches that will increase the impact and knowledge of Neotropical birds' bioacoustics based on the recent lines of investigation developed on this topic in the area or topics that are still undeveloped.

BIOACOUSTIC IN THE NEOTROPICS: WHAT DO WE KNOW?

Quantitative repertoire descriptions. Bird vocal repertoires are a complete library of vocalizations produced by a species (Catchpole & Slater 2008) and may vary between populations of the same species (i.e., dialects or geographic variation), seasonally (i.e., daily and yearly), or socially (e.g., single, mated individuals, or flocks; Catchpole & Slater 2008). To describe vocal repertoires, two complementary approaches may be used: quantitative measurements (i.e., frequency, duration, and entropy) and seasonal variation of each vocalization type (i.e., daily and yearly; Catchpole & Slater 2008). However, for most Neotropical species comprehensive vocal behavior descriptions are missing, although it is possible to find call and song descriptions using words or symbols that try to imitate onomatopoetically the author's perception of bird vocalizations (e.g., Hilty & Brown 1986, Stiles & Skutch 1989, Howell & Webb 1995, Ridgely & Greenfield 2001).

Quantitative vocal repertoire descriptions often use a reduced number of recordings, and sometimes focus on a single population or geographic area. This is due to several limitations in the past, including the cost of equipment, memory storage capabilities, analysis software, and the reduced number of recordists collecting recordings across the geographic areas of species distribution. For example, the description of Banded Wren *Thryophilus pleurostictus*, Sinaloa Wren *T. sinaloa*, Happy Wren *Pheugopedius felix*, and Common Pauraque *Nyctidromus albicollis* song repertoires (Brown & Lemon 1979, Molles & Vehrencamp 1999, Sandoval & Escalante 2011) are all based on analyses from a single population or geographic area. Currently, many of these limitations for describing vocalizations have been greatly reduced, and researchers are using hundreds of recordings to perform quantitative descriptions of vocal repertoires, including several recordings from the same individual within and between years, to ensure that descriptions are based on complete repertoires, especially when songs vary within individuals (Millsap et al. 2011, Sosa-López & Mennill 2014a, Sandoval et al. 2016).

The most common techniques used to obtain quantitative acoustic data are focal and autonomous recording methods. The focal recording method consists of following one individual (preferably color-banded) for at least one hour (Sandoval et al. 2016). Recordings generally start before sunrise to record the first vocalization of the day or the dawn songs; for example, songs that for some species, including flycatchers or woodcreepers, are different from the day song (Leger & Mountjoy 2003, Burt & Vehrencamp 2005, Lein 2007, Moseley & Wiley 2013). On the other hand, the autonomous recording method consists of placing Autonomous Recording Units (ARUs) in the center of the territory of the individual or pair of interest and allows for continuous recordings for 24 h periods or more (Blumstein et al. 2011). Additionally, some researchers use these recorders to complement the vocal repertoire obtained with the focal record method or to describe a diel pattern (Sandoval et al. 2016).

Quantitative repertoire descriptions are performed in several ways, depending on the species vocalizations and the researchers' main interest. For example, repertoire descriptions usually focus on a single type of vocalization, such as solo songs. Therefore, researchers report the richness of solo songs or the elements (i.e., the minimum trace of continuous sound) within individuals using accumulation curves to show that the repertoire for each recorded individual was appropriately sampled (Mennill & Vehrencamp 2005, Sosa-López & Mennill 2014a, Harris et al. 2016, Sandoval et al. 2016). This method also allows us to describe the variation within individuals, between sexes, or between populations, and to associate the vocalization function with the type of vocalization (Kroodsma et al. 2002, Benítez Saldívar & Massoni 2018, Price & Yuan 2011, Trejos-Araya & Barrantes 2014). Among the majority of studies that use this method, the most common measurements are the minimum (or lower) frequency, maximum (or higher) frequency, maximum amplitude frequency (or peak frequency), frequency range, and duration (Benítez Saldívar & Massoni 2018, Price & Yuan 2011, Sandoval & Escalante 2011, Trejos-Araya & Barrantes 2014) of elements or groups of elements called syllables or songs. Finally, some authors include diel pattern analysis, which reports the average number of vocalizations produced per hour and all vocalization types produced within the species (Koloff & Mennill 2013a, Sandoval & Mennill 2014, Sosa-López & Mennill 2014b, Maynard et al. 2015, Pérez-Granados et al. 2019). For these latter analyses, it is necessary to collect record-

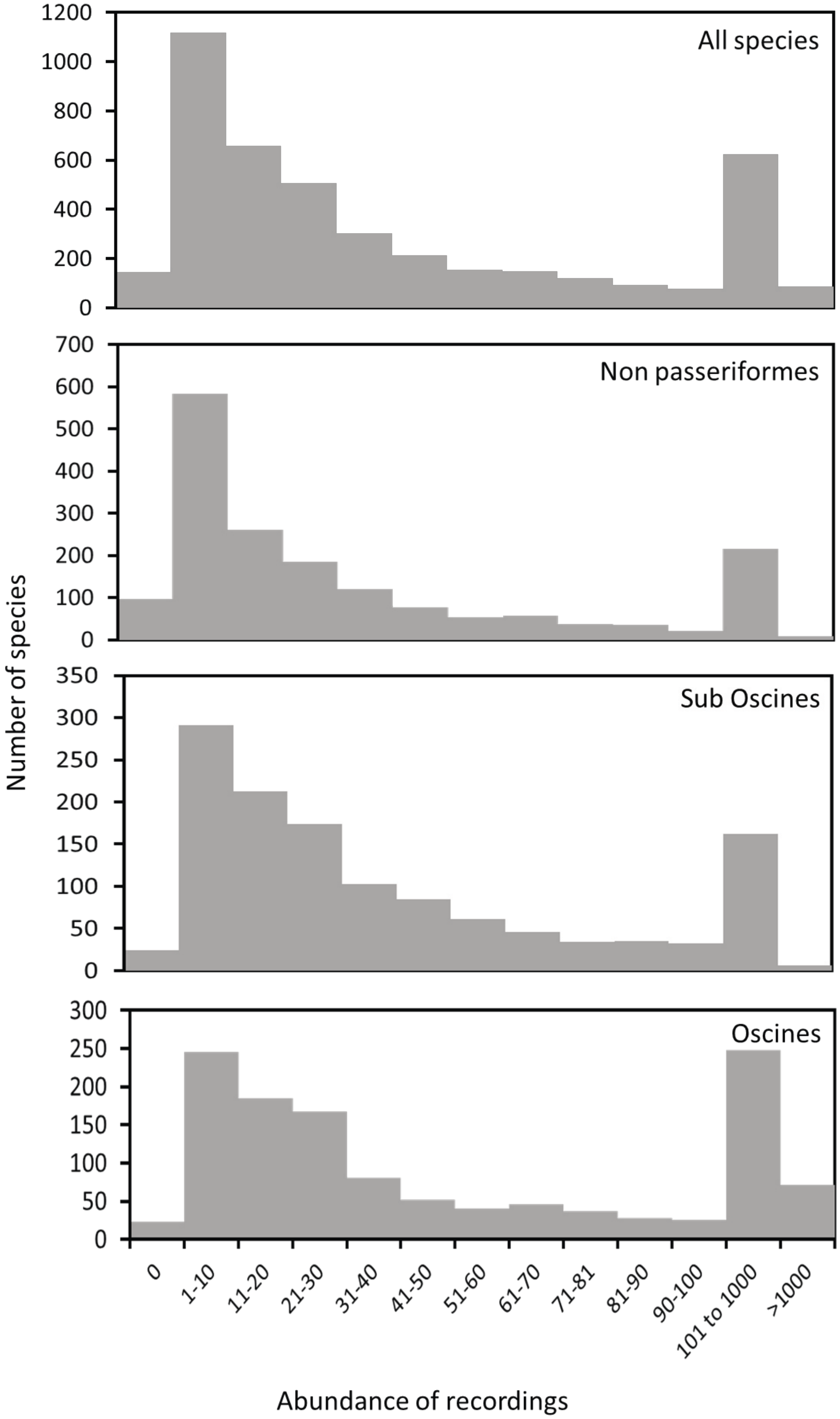

Figure 1. Abundance of Neotropical bird species recordings deposited in the Macaulay Library (Cornell Lab of Ornithology) as of September 2019. Figure shows all species grouped together, as well as abundance for three main species groups found in the Neotropics.

ings every hour throughout the day from multiple individuals (Sandoval et al. 2016).

Diversity of sound production mechanisms. The large diversity of bird species that occur in the Neotropics (Stotz et al. 1996, Stutchbury & Morton 2001) permits the study and comparison of the mechanisms used for sound production that are not present in other geographic areas, including non-vocal sounds using modified wing and tail feathers produced by several taxa, including hummingbirds, snipes, flycatchers, and manakins (Clark & Prum 2015). However, most of the neotropical birds produce sounds using a unique vocal organ called the syrinx. Within the Neotropical area, three different types of syrinx have been described. Tracheal syrinxes are present only in a group of suboscines birds termed tracheophones (i.e., tapaculos, antbirds, antshrikes, and woodcreepers). Bronchial syrinxes are found in a small number of non-passerine groups, notably owls (Strigiformes), cuckoos (Cuculiformes), and some nightjars (Caprimulgiformes). The most common syrinx is the tracheobronchial type, present in most songbirds (Warner 1972).

The vocal diversity of oscines is enormous, thrushes, wrens, and blackbirds are famous for their improvisation and imitation skills, and in some cases, for their vast repertoires. Oscines are considered to have the broadest range of acoustic features in their vocal repertoires and versatility, which may be attributed to refined neuromuscular control of the vibrating membranes rather than anatomical complexity (García et al. 2017). The syrinx of oscines can have between six to seven pairs of muscles, and notably, the morphology of the syrinx in this clade in general is quite similar (Ames 1971, Warner 1972): the basic syringeal anatomy of the oscine passerines is shared by all the families of this speciose clade (Baptista & Trail 1992).

The vocal diversity of non-passerines and suboscines (those taxa that do not need an external input to develop their songs) also appears to be very diverse, but it is difficult to find species with diverse repertoires. Most vocal variations can be found between species. In Tyrannidae and Pipridae, the spectrum of vocalizations runs from notes as simple as those of the broadbills to songs as complex as those of oscines; however, in all cases, individual repertoires are limited (Baptista & Trail 1992). There is great diversity in syringeal anatomy among the families of suboscine passerines (García et al. 2017). Although large repertoires are not the rule, between species variation might be very high. In this case, the diversity of sounds is attributable to the complex syrinx morphology. Non-passerines and suboscines have restricted musculature; they possess between two to four pairs of muscles but show remarkable morphological diversity (Ames 1971) which in suboscines, at least, has been associated with the diversity of their vocalizations (García et al. 2017).

Few studies about the syrinx of Neotropical birds are found in the literature (Ames 1971, Amador et al. 2008, García et al. 2017), yet these studies have focused on morphological features to propose systematic relationships between clades (Prum 1990, Mauricio et al. 2012). Recently, however, there has been some interest in the physiology of sound production in Neotropical birds, especially in tracheophones and broncheophones, the two clades of suboscines (Amador et al. 2008, García et al. 2017). For instance, sound generation in tracheophones relies on a more complex morphology than previously assumed. The presence of three vibratory sources (one pair of membranes in the trachea and two in the bronchi) gives rise to diverse sound features and may have played a determinant role in the diversification of this clade (García et al. 2017). In addition, sound production and control of sound frequency in the Great Kiskadee *Pitangus sulfuratus* were investigated by recording air sac pressure and vocalizations during spontaneously generated songs. In all songs and calls recorded, the modulations of the fundamental frequency were highly correlated with air sac pressure, but not with the effect of muscles (Amador et al. 2008). These results suggest that the control of the sound frequency of a song is not determined by neural instructions through syringeal muscles, but is directly transduced from pressure through biomechanical properties of the membrane folds (Amador et al. 2008). Whereas suboscines evolved morphological mechanisms in the absence of vocal learning, oscines show much less morphological diversification of the syrinx but produce similar acoustic effects through diverse neuromuscular control (García et al. 2017). We think that the study of the morphology of the syrinxes in suboscines and the study of the physiology of sound production in most Neotropical species will allow us to better understand the diversification of bird vocalizations in the Neotropics.

Duetting. Avian vocal duets exhibit a broad taxonomic distribution; duets have been described for over 400 species and are present in 40% of all bird families (Hall 2009). Furthermore, avian vocal duets exhibit considerable variation with respect to complexity, coordination, and spectrotemporal structure (Dahlin & Benedict 2014). Given that duetting involves vocal interactions between two individuals, hypotheses focusing on the function of duetting have been divided into two main categories: cooperative and conflict between partners (Hall 2004, 2009). To date, most studies have been conducted on oscines, resulting in the duets of many suboscine and non-passeriform birds being overlooked (but see Wright & Dorin 2001, Koloff & Mennill 2013b).

Territory defense is the best-supported hypothesis for the function of vocal avian duets (Hall 2004, 2009). Duetting appears to be particularly common in sedentary species because mated pairs exhibit longer pair bonds in the absence of migration, and the cooperative nature of duetting may aid in the year-round defense of resources and territories (Logue & Hall 2014, Mikula et al. 2020). Multiple studies using song playback experiments have demonstrated the cooperative nature of duets and supported this improved territory defense hypothesis by demonstrating that pairs respond more intensely to duets than to solo songs, both physically and vocally (Mennill 2006, Sandoval et al. 2018). Additionally, vocal duets may serve other cooperative functions, including maintaining contact (Cobb 1897) and ensuring reproductive synchrony (Dilger 1953). This first hypothesis may be important for species that live in habitats with dense vegetation (Mennill & Vehrencamp 2005); although, as Hall (2004) noted, this hypothesis does not appear to be a widespread function of duetting.

Some playback studies have revealed that each sex appears to target aggression towards same-sex conspecifics, suggesting that mate-guarding may serve as an important function for duetting (Mennill 2006, Dahlin & Wright 2012, Koloff & Mennill 2011, Odom & Omland 2017, Sandoval et al. 2018). These observations highlight the potential conflicts between partners that may arise as a result of duetting. Specifically, mated pairs may duet as a means of guarding their mates (Stokes & Williams 1968) or, in the case of males, to protect paternity (Sonnenschein & Reyer 1983). Playback studies have found that tropical birds use duets, often in conjunction with physical responses, to guard their mates (Hall 2000); in particular, males, may use duets to guard their mates from rival males (Levin 1996, Seddon & Tobias 2006, Tobias & Seddon 2009a, Diniz et al. 2018). The low rates of extra pair paternity found for duetting tropical birds in comparison to non-duetting tropical birds support the idea that tropical birds may use duets to protect their paternity (Haydock et al. 1996, Cramer et al. 2011, Douglas et al. 2012). By comparison, other studies found no evidence that birds use duets or physical behaviors to guard mates (Gill et al. 2005, Hall et al. 2015). Therefore, these contradictions in duet functions require further investigation in Neotropical species.

Daily singing activity. Animal vocalization patterns are ubiquitous behaviors that are well known for their variation throughout the day (Staicer et al. 1996). Most animals that vocalize or produce sound to communicate vary their communication daily, and the optimal pattern depends on the ecological characteristics of the species. The labile nature of acoustic behavior allows individuals to adjust their behavior to match socio-ecological conditions and optimize their fitness benefits. This plastic response to daily environmental variation results in what we refer to as a singing routine. Such singing routines of organisms are shaped by how the costs and benefits of performing a behavior change across the day, and daily changes in the cost—benefit relationship may vary due to fluctuations in temperature, light levels, and interactions with other conspecifics and heterospecifics (McNamara et al. 1987, 1994, Hutchinson 2002).

For most birds, this plastic response to daily variation consists of high song output in the early morning (dawn chorus), with output decreasing towards midday (Catchpole & Slater 2008). Our empirical understanding of daily singing routines is largely based on studies focusing on the dawn chorus (e.g., the start of the singing routine) of temperate birds, especially oscine birds (Mace 1987, Thomas et al. 2002). Less is known about dawn chorus in the tropics (Staicer et al. 1996, Berg et al. 2006, Chen et al. 2015), and almost nothing is known about the singing routine throughout the rest of the day (e.g., Sosa-López & Mennill 2014b). For example, some flycatchers, greenlets, and vireos can sing throughout the day, a behavior that may be used to avoid acoustic competition. This implies that there is a bias in our understanding of daily singing routines because studies have focused on only one part of the dawn chorus and because there are a substantial number of suboscine and non-passerine taxa residing in the tropics that have a high diversity of morphology, foraging modes, and behavioral adaptations that have resulted in daily singing routines that have not been studied.

The phylogenetic diversity of life history strategies in Neotropical communities provides a unique opportunity to study the factors affecting bird singing routines using comparative analyses. Studies in tropical communities can be used to test different hypotheses regarding the factors shaping the time singing routines of birds. The most comprehensive analyses of the dawn chorus of Neotropical species to date comes from data from a tropical forest in Ecuador, involving 57 species from 27 families of birds (Berg et al. 2006). This study showed that most of the studied species sang during the dawn chorus and that foraging height was the best predictor of the time of first song for passerine birds. Their results showed that canopy birds sang earlier than birds foraging closer to the forest floor. For passerine birds, eye size also predicted time of first song, with larger eyed birds singing earlier, although this was only the case after controlling for body mass, taxonomic group, and foraging height. However, the general trend partly supports the results of Thomas et al. (2002), in which birds with larger eyes sang earlier than birds with small eyes. It is often thought that ambient noise may affect dawn chorus patterns (Hart et al. 2015), comparisons of the dawn chorus across an urbanization gradient found that noise levels did not impact the timing of the peak of the singing activity or the first song in the morning (Marín-Gómez & MacGregor-Fors 2019).

Most studies in the Neotropics and elsewhere, conducted on the factors affecting singing routines, have focused only on the time species start singing, probably because the start time and the peak of singing can be easily measured. However, the dawn chorus is just part of the singing routine, and ignoring the interesting plastic adjustment of singing routines throughout the day provides an incomplete picture of birds' plastic adjustments to daily fluctuations of socio-ecological conditions. We can gain a better understanding of dawn chorus in general if we apply new statistical tools to the study of daily patterns of singing in the Neotropics. If we study singing behavior in tropical communities within a reaction norm framework, we can have accurate statistical descriptions of the signing routines of interacting species, estimate its phylogenetic signal, and test the ecological factors affecting the different components of the singing routine. A nonlinear reaction norm will allow capturing the peak of the singing output and the preceding increase or subsequent decline in the singing output. This approach will improve our understanding of the ecological factors and phylogenetic constraints that shape the diversity of singing strategies found in the Neotropics.

Seasonality vs. non-seasonality. The study of bird songs initially focused on variables related to the temporal and spectral structure of the song, the syntax, repertoires, dialects, and the effect of habitat on the structure of the song (Morton 1975, Marler 2004). However, few studies have concentrated on aspects related to the production of songs at broad time scales (e.g., annual and supra-annual) and their relationship with climatic cycles, especially the seasonality of rainfall (Chiver et al. 2015). When and how often birds sing in the Neotropics are questions that still have no answer for most Neotropical birds, and present interesting topics to further explore; the production cycles of songs and their relationship with climatic seasonality remain relatively unknown within the Neotropics (Stutchbury & Morton 2001). In temperate regions, seasonality is higher and determines a great part of the annual cycle of birds that breed at high latitudes. The tropics are characterized by lower seasonality, and thus a large proportion of species are residents year-round (Stutchbury & Morton 2001, Chiver et al. 2015). The study of the annual cycles of birds has focused on understanding the periods of molt and reproduction, and on assessing the temporal interaction between them (Payne 1969, Johnson et al. 2012). Vocal activity plays an important role in territory establishment, territory defense, and mate attraction, and seasonal changes in vocal activity can therefore be related to the breeding phenology of birds (Pérez-Granados et al. 2019); however, little attention has been given to this crucial part of the annual cycle in tropical birds (Chiver et al. 2015). We do not know if the energy expenditure of singing is comparable to that invested in moving, molting, or reproducing, but singing is time-consuming and may entail other costs, such as an increase in the risk of being predated. Studies on acoustic communication, social, and sexual selection would benefit from understanding the costs that birds accrue when singing over longer time frames (Krams 2001, Gil & Gahr 2002). Further, energy expenditure may be affected by gradients in the degree of seasonality within tropical forests and combined these factors can determine seasonal patterns in vocal activity, which has not been not previously studied. It has been shown that within the tropics there is variation in the level of seasonality depending on the type of habitat, forest stratum, or foraging guild (Levey & Stiles 1992). Secondary forest, border, or canopy species are subject to much more seasonal climatic conditions than birds that live in the undergrowth of mature forests (Levey 1988).

Among tropical birds, some species sing seasonally: tinamous (Negret et al. 2015, Pérez-Granados et al. 2019), curassows (Cuervo et al. 1999, Baldo & Mennill 2011), robins (Stutchbury et al. 1998), ant-tanagers (Chiver et al. 2015), brush-finches, and tyrannulets (OL unpubl. data; Figure 2) only sing at certain times of the year, especially during the dry season just before the reproductive season begins. Other more territorial species such as antbirds (Wikelski et al. 2000) and wrens (Topp & Mennill 2008) sing throughout the year, although it has been shown that they have some seasonality in vocal activity (Odom et al. 2016). Vocal activity appears to be related to changes in precipitation and photoperiod (Wikelski et al. 2000, Topp & Mennill 2008). Based on these observations, two types of annual vocal activity strategies could be defined: seasonal and non-seasonal (Figure 2).

With the development of ARUs, new opportunities to record and a new research front known as sound landscape ecology have arisen (Farina & Pieretti 2012). Furthermore, the use of ARUs allows large datasets to be recorded with less effort (Kirschel et al. 2011, Buxton et al. 2013). Analyzing these datasets can be problematic because of the large volume of data collected. For this reason, some research groups have partnered with computer programmers and engineers to develop automatic recognition algorithms to process the greatest amount of information in shorter amounts of time (Aide et al. 2013, Ducrettet et al. 2020).

Geographic variation*.* The analysis of geographic variation focuses on describing vocal variations within a species across its natural geographic range (Gould & Johnston 1972). Based on current inferences, bird diversity is underestimated in the Neotropics (Milá et al. 2012), and the implementation of vocal geographic variation studies is of special relevance. Furthermore, the use of vocalizations helps identify new bird species (e.g., Lara et al. 2012, Seeholzer et al. 2012, Hosner et al. 2013), and to evaluate the taxonomic status of many others. This indicates that vocalizations are key to understanding of Neotropical avian diversity (e.g., Chesser et al. 2012, 2013, 2019, Remsem et al. 2019, Krabbe et al. 2020).

The study of geographic vocal variation also offers useful opportunities to elucidate the origins of acoustic signal divergence and its relationship with reproductive isolation and speciation (e.g., Demko et al. 2019). Variation in vocal attributes may arise from multiple evolutionary processes: (1) through random genetic or cultural mutations between isolated populations of learning taxa (cultural and genetic drift; Podos et al. 2004) as it is thought to occur in Nightingale-Thrush *Catharus frantzii* where genetic and vocal divergence are highly correlated (Ortiz-Ramírez et al. 2016); (2) through diverse mechanisms of sexual selection driven by female choice or male-male competition (reviewed by Podos et al. 2004), such as in Rufous-collared Sparrows' females *Zonotrichia capensis* that respond with higher intensity to their natal dialect in comparison to a dialect from an allopatric population (Danner et al. 2011); and (3) through environmental factors (such as habitat structure) influencing variation of vocalizations by constraining sound transmission (sensory-drive hypothesis; Tobias et al. 2010a, Slabbekoorn & Smith 2002), as has been found in the vocalizations of Yungas Manakins *Chiroxiphia boliviana* with acoustic traits adapted to the changing habitat structure along an elevational gradient, enhancing sound transmission (Villegas et al. 2018). Thus, geographic variation in vocalizations may arise due to neutral processes and/or as a response to different selection

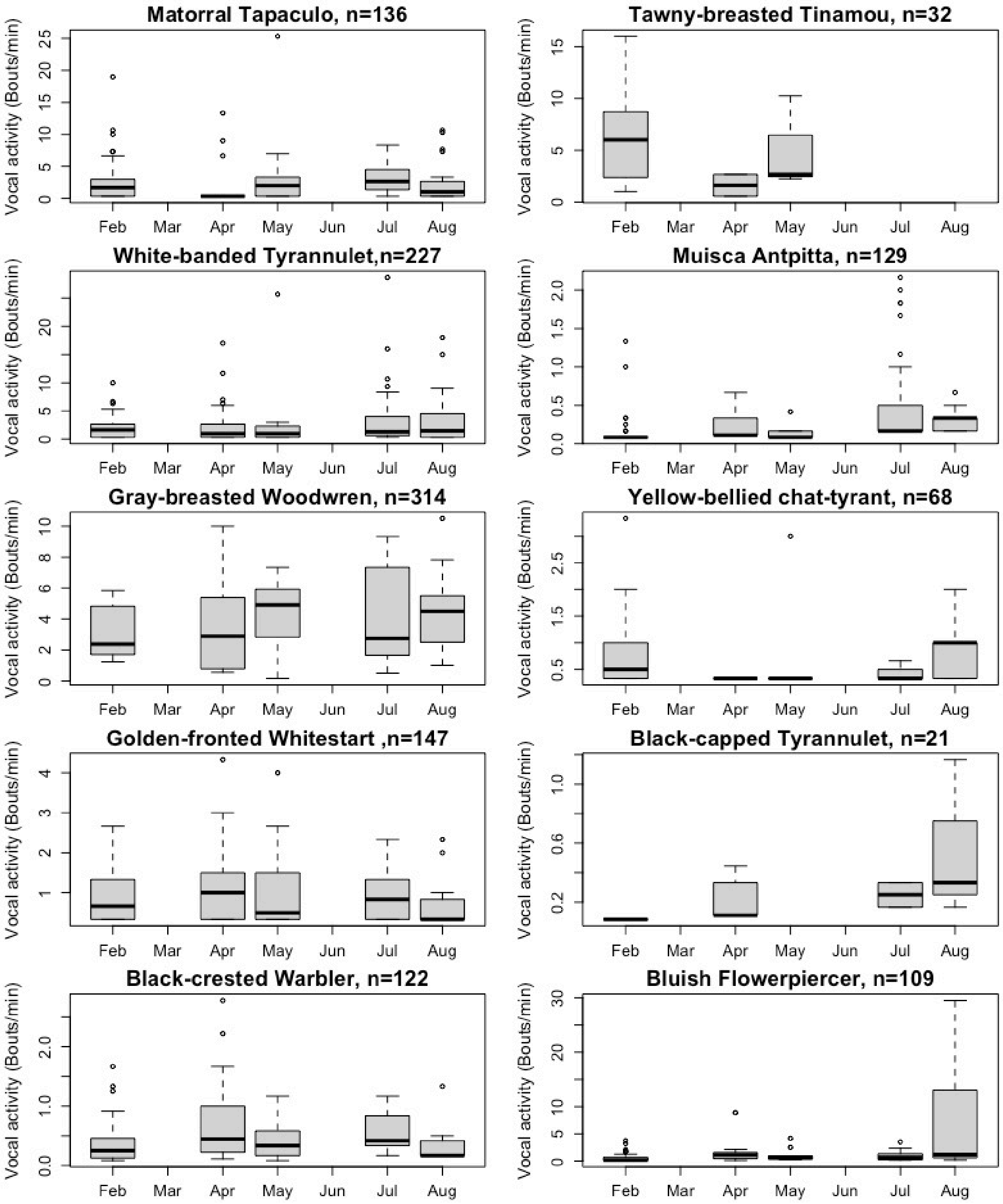

Figure 2. Patterns of song production measured as number of bouts per minute (mean, first and third quartile, and 95% of confidence intervals) in ten species of montane tropical birds, from January to August. On the left panel, non-seasonal birds that sing year-round; on the right panel, seasonal birds.

pressures (Wilkins et al. 2013), and its assessment is useful for understanding the factors driving the evolution of vocalizations in the Neotropics (Shy 1983).

Patterns of acoustic and genetic divergence. Patterns of vocal divergence among populations have been used to delimit species boundaries (Isler et al. 1998, Halley et al. 2017). For example, the Gray-faced Petrel *Pterodroma gouldi*, Choco Screech-Owl *Megascops centralis*, Socorro Parakeet *Psittacara brevipes*, Blue-black Grosbeak *Cyanoloxia cyanoides*, Yucatan Gnatcatcher *Polioptila albi*ventris, and Cabanis' Ground-Sparrow *Melozone cabanisi* are currently treated as different species based on their vocalizations, morphology, and genetic traits (Davis 1972, Howell & Webb 1995, Sandoval et al. 2014, García et al. 2016, Krabbe 2017, Wood et al. 2017). Given the strong role that song plays in mate acquisition and reproductive success (Catchpole & Slater 2008), many studies have looked the parallel between the evolution of culture and genetic divergence (Ortiz-Ramírez et al. 2016). Specifically, it has been proposed that birds use songs for assortative mating, and that song dialects in conjunction with mate preferences for songs may reduce gene flow and promote genetic divergence among populations (MacDougall-Shackleton & MacDougall-Shackleton 2001). Although acoustic and genetic patterns appear to be linked for tropical species that do not learn their songs (Isler et al. 2006), there is limited support for the idea that culture affects genetic divergence for species that learn their songs, because song learning is influenced by many factors, including environmental or selection pressures (Handford & Lougheed 1991, Ortiz-Ramírez et al. 2016). In contrast, Danner et al. (2017) found a link between dialect and genetic divergence for populations of Rufous-collared Sparrows, while Price & Lanyon (2004) found that acoustic data accurately estimated the molecular phylogenetic relationship for the Green Oropendola *Psarocolius viridis*, suggesting that song carries a phylogenetic signal for this species.

Although acoustic and genetic patterns often exhibit similar patterns of divergence, the relationship between these two variables is complex. Despite that acoustic and genetic patterns might evolve independently for song-learning species, gene flow appears to play a role in the geographic patterns of acoustic variation, as demonstrated in a long-term study of parrots. Wright et al. (2005) found that post-dispersal song-learning of local calls by immigrants explained the patterns of geographic variation despite ongoing patterns of gene flow across dialect boundaries. Further, Graham et al. (2017) also found a relationship between dispersal and acoustic variation. They analyzed acoustic and genetic data to show that dispersal is sex-biased for Rufous-and-white Wrens and that song-sharing differences between males and females likely arise as a result of contrasting patterns of dispersal. Studies of Gray-breasted Wood-Wren subspecies that are genetically distinct yet capable of hybridizing found that ecological niche segregation appears to explain acoustic differences between Gray-breasted Wood-Wren populations, and the resulting acoustic divergence may have facilitated reproductive isolation between these subspecies (Dingle et al. 2008).

Combining these examples demonstrate the importance of studying songs and genetic patterns together. Analyzing acoustic and genetic data together can provide greater insight into the diversity, ecology, and evolution of tropical birds as well as test long-standing hypothesis at broader scales. For example, Tobias et al. (2010a) used song and genetic data to examine signal divergence of avian communities across an ecological gradient. Their analysis of 17 species pairs from bamboo and terra-firme forests, revealed that acoustic adaptation, and not genetic divergence, plays an important role in the evolution of song. This study emphasizes how ecological differences drive acoustic divergence, which may lead to reproductive isolation over time, thus playing an important role in the diversification of many tropical birds.

Species definition. Inside the tropics, most species' taxonomy remains unclear due to the limited number of samples for each species throughout their geographic range (Isler et al. 1998, Hayes & Sewlal 2004). In recent years, however, avian taxonomy has been analyzed with a broader approach that includes genetic data, morphological analysis, niche modeling, and behavioral data (Tobias et al. 2010b). Avian vocalizations are one of the most widely used behavioral traits, especially the analysis of solo song characteristics, because vocalizations are used for mating, and differences between populations may be indicative of reproductive isolation (Emlen 1972, Catchpole & Slater 2008). Quantitative and qualitative analyses of vocalizations can provide evidence for relationships between taxa. The qualitative method visually compares the structural aspects of vocalizations and decides whether the observed differences are enough to suggest biological divergences among populations, such as in the solo song of Common Pauraque or duet structure of wrens (Thurber 2003, Mann et al. 2009). The quantitative method uses measurements of frequency (i.e. lowest, highest, and maximum amplitude), duration, rate, pace, or inflections, and compares vocalizations with statistical approaches (e.g., discriminant function analysis, linear models, similarity indices, potential for individual coding scores, or pairwise diagnosability index) to objectively quantify the observed differences (Sandoval et al. 2018, Benedict & Najar 2019). In most cases, these analyses are conducted by combining different recording resources such as recordings from internet databases (i.e., xeno-canto) with sound libraries (e.g., Maculay Library, Borror Laboratory of Bioacoustics, Colección de Sonidos Ambientales-Instituto Humboldt, Laboratorio de Bioacústica Universidad de Costa Rica), and the researchers' own recordings (Millsap et al. 2011, Areta & Pearman 2013, Sandoval et al. 2014, Sosa-López & Mennill 2014a). The recording sources are combined to broadly cover the distribution range of the taxa and to increase the sample size for comparisons. The use of different recording sources may be problematic when MP3 and WAV files are combined in the analysis; this approach needs to be avoided because it is known that both files produce different measurements for frequency parameters (Araya-Salas et al. 2019).

Another way that vocalizations help us understand taxonomical relationships and the speciation process is using playbacks, to test whether acoustic differences (both qualitative and quantitative observations) in allopatric populations of the same species may act as a mating barrier (Freeman et al. 2017). These experiments compare the response of individuals (males or females) to songs from their same population to the response of individuals to songs from other populations (Freeman et al. 2017). A greater response to songs from the same population supports the hypothesis that birds discriminate divergent song characteristics between populations, and that these response differences are indicative of ongoing species divergence. Conversely, a response of similar intensity to songs from the same and different populations has been used to reject the hypothesis that birds discriminate divergent song characteristics, or that these behavioral response differences are indicative of ongoing species divergence (Caro et al. 2013). This interpretation is somewhat problematic because several "good" species respond with the same aggressiveness to other species' songs (e.g., Brenowitz 1982, Tobias & Seddon 2009b). Consequently, the results of these experiments need to be interpreted carefully and combined with other evidence to support species recognition. For example, several studies have found that while a population discriminates between both vocal stimuli, another does not (e.g., *Henicorhina* or *Catharus* species) making the process of speciation less apparent (Dingle et al. 2010, Jones et al. 2019).

Finally, all studies on this topic include different amounts and types of measurements to compare vocalizations within the taxa of interest, and currently there is no framework in place to determine how many differences are necessary (both minimum and maximum), and which differences in vocalizations are most important to suggest that the analyzed taxa are different. This is important because increasing the number of measurements usually increases the probability of detecting differences between taxa even when they are not biologically significant. Therefore, a reduced number of measurements may be more optimal for identifying divergent taxa.

Acoustic transmission. Although many hypotheses have been developed in temperate systems and environments, the Acoustic Adaptation Hypothesis was first developed and tested in a tropical system (Morton 1975). Morton (1975) proposed that an animal's acoustic signal should be optimized for transmission through the environment it lives and communicates in, especially signals used for long-range communication, which experience greater attenuation and degradation the further they transmit through the environment. Habitat specialization and adaptation has likely played a role in the evolution of the acoustic signals of tropical birds and may explain patterns of geographic variation (Handford & Lougheed 1991, Tobias et al. 2010a, Slabbekoorn & Smith 2002). Given the large number of species found in the tropics, it is hypothesized that acoustic space may be limited and that there is a greater potential for signal overlap (Hart et al. 2015, Tobias et al. 2014, Robert et al. 2019), this has been called the acoustic niche hypothesis (Krause 1993). Further anthropogenic changes to habitat and increased urbanization in the tropics alter acoustic environments (Slabbekoorn & Peet 2003). Finally, the function of the acoustic signal may dictate the transmission properties and characteristics of avian acoustic signals. Given the important effects that environmental factors including temperature, humidity, ambient noise, and habitat have on the acoustic properties of avian vocalizations, it is important to test the transmission properties of these vocalizations. In particular, transmission studies allow for the possibility to test the physical properties of songs and calls and to test hypotheses about how habitat and environment act on avian vocalizations.

With the diversity of habitats present in the tropics it is no surprise that songs often vary across habitats. Handford & Lougheed (1991) found that the spectro-temporal characteristics of Rufous-collared Sparrow songs from birds living in open habitats (i.e., grassland, desert, and puna habitats) were different from birds living in closed habitats (i.e., chaco, alder woodland, and forest habitats); birds living in open habitats produced shorter, faster-trilled songs with a narrower bandwidth, whereas birds from closed habitats produced songs with a slower trill. Slower-trilled, low frequency, tonal songs are characteristic of birds that live in closed habitats, as Morton (1975) and Ryan & Brenowitz (1985) found in their comparisons of avian communities living in forests to those living in open habitats. Experimental studies using song playback show that these spectro-temporal characteristics reduce the effects of degradation and attenuation on long-range communication within the natural habitats of birds (Barker et al. 2009).

To avoid acoustic overlap, birds may alter the frequency, and timing of their songs. Within the tropics, cicadas are present across many forest habitats and produce loud broadband vocalizations that may overlap with the acoustic signals of other species within forest communities. Hart et al. (2015) found that many birds alter the timing and frequency of their songs to avoid being overlapped by cicada vocalizations; birds either stopped singing or produced vocalizations at frequencies that did not overlap with cicada vocalizations. Similarly, birds that live in urban areas may have their songs masked by anthropogenic noise sources (Kunc & Schmidt 2019). Villarreal et al. 2024 found that Southern House Wrens living in urban areas avoided song overlap from anthropogenic noise sources by increasing the minimum and dominant frequency of their songs to avoid overlap. Subtle differences in the spectro-temporal characteristics of bird song among populations may reflect ambient noise differences among populations and contribute to patterns of geographic song variation (Graham et al. 2018).

Although many birds produce acoustic signals designed for long-range transmission, others may use quiet acoustic signals for close-range communication. Sandoval et al. (2015) found that the duets and solo songs of White-eared Ground-sparrows showed similar patterns of song attenuation and degradation, and thereby facilitate communication at similar distances. Further analysis of the calls of this species (Piza & Sandoval 2016) revealed that the *chip* calls, used for close-range communication, experience greater attenuation and degradation than the *tseet* calls, which are used for long-range communication when birds are outside of visual contact. Other studies (e.g., effect of perch height in antbird songs and soft songs of thrushes) have revealed similar patterns about the relationship between function and sound propagation (Nemeth et al. 2001, Vargas-Castro et al. 2017).

Playback experiments. The most common technique used to understand the function of communication are playback experiments. These experiments simulate several events of communication between individuals of the same species or between individuals of different species, and allow to control variables that can confound *in situ* communication interactions (Smith 1996, Catchpole & Slater 2008). These types of experiments also provide the opportunity to create and simulate individual interactions that would be difficult to record in the wild within short time periods (Smith 1996, Catchpole & Slater 2008). For example, playback experiments in the Neotropics have been used to measure territorial intrusion effects and the effect of seasonality on territory defense (Morton et al. 2000, Sandoval 2011, Sosa-López et al. 2017, Demko & Mennill 2018); to understand the response by individuals to the vocalizations of opposite sex individuals inside territories (Fedy & Stutchbury 2005, Illes & Yunes-Jimenez 2008, Sandoval et al. 2018); to measure the effect of coordination in territory defense (Logue & Gammon 2004, Marshall-Ball et al. 2006, Kovach et al. 2014); or to simulate the presence of predators (Motta-Junior & Santos-Filho 2012, Sandoval & Wilson 2012). In these cases, the experiments provided information about the ultimate and proximate causes of the acoustic variation between signals and their functions.

Playback experiments can be split according to the number of speakers used —single or multiple speaker experiments— or by the number of stimuli used in non-interactive and interactive experiments (Dabelsteen & McGregor 1996, Smith 1996, Douglas & Mennill 2010). The single-speaker playback experiments have been used to test differences in response to call rates, analyze territorial defense using solo songs and duets that are produced in close proximity, or the effect of predator vocalizations (Fedy & Stutchbury 2005, Illes & Yunes-Jimenez 2008, Motta-Junior & Santos-Filho 2012, Sandoval & Wilson 2012, Koloff & Mennill 2013b, Sandoval et al. 2018). The multiple-speaker experiments have been used mostly with two-speaker design when researchers are interested in testing the response of territorial species to simulated intrusions of other pairs, when both individuals are separated more than 1 m apart, such as with the Chestnut-backed Antbirds *Myrmeciza exsul* and the Rufous-and-white Wren *Thryophilus rufalbus* (Mennill 2006, Fishbein et al. 2018). This experiment reproduces more natural stimuli than a single-speaker playback, because it accounts for the separation of the pair members during duet production and allows the receivers to respond differently to each sex during territory defense (Douglas & Mennill 2010).

Most of the playback experiments inside the Neotropics have been non-interactive, meaning that the stimuli do not vary according to the behavior of focal individual or pair (Douglas & Mennill 2010). This is because it is easier to perform a playback experiment and allow for a more controlled replication given that rate, type, and amplitude are presented in the same way to all the receivers. However, some effort has been conducted to perform interactive playbacks, especially in the last decade. With the emergence of new software and more portable equipment, which allow for the recording and visualization of the responses of the receivers' *in-situ*, it is possible to reproduce the corresponding vocalizations required by the experiment goal (Douglas & Mennill 2010). This technique has been used mostly for duetting species such as Black-bellied Wrens (Logue & Gammon 2004). Contrary to the non-interactive experiment, this approach has the advantage of more accurately replicating the interactions of species in the wild and allows for simulated escalation and de-escalation of interactions (Dabelsteen & McGregor 1996, Smith 1996, Douglas & Mennill 2010).

PRIORITIES FOR FUTURE RESEARCH

Based on the discussion at the symposium, we have summarized some priorities for future research (Table 1). Our prioritization includes several specific topics, goals, and actions for future research on bioacoustics of Neotropical birds.

Record more birds. To achieve the goal of improving our knowledge about vocal behavior for Neotropical birds (i.e., quantitative description of vocalizations and repertoire, analysis of geographic and individual variation, or changes through time), it is necessary to increase the number of available recordings. This is because less than 45% of all Neotropical species are well represented in sound archives, although this percentage is based on the number of recordings that have been made public. It is likely that this percentage would increase if other archives also made their recordings public. In the future, this discipline would benefit from researchers depositing the recordings used in publications inside sound archives, and the catalogue number for these recordings should be included in all publications. These small steps will increase our knowledge in this field and provide recordings for future investigations

Understand song variation at different levels of organization. Vocalizations could mediate the acceleration of the evolutionary process, but they can also be a source of phenotypic stasis (Huey et al. 2003; Duckworth 2008). To understand why and when vocalizations will increase or decrease the rate of phenotypic evolution, it is necessary to understand their variation. In the Neotropics, the rich species diversity is matched by similarly rich diversity in song characteristics and vocalization types. Phenotypic variation is hierarchically structured in different levels of biological organization and so is the variation in vocalization features. Variation in vocalization features may occur among-species, within-species among-populations, and within-populations among-individuals. In the case of characters that are repeatedly expressed throughout the life of an individual (labile characters), such as vocalizations, variation can also exist within-individuals among-expressions (Westneat et al. 2015).

Over the last couple of decades, there have been repeated

Table 1. Summary of priorities for future research in the Neotropics. Included are the goal of each area of research and different suggestions on how to contribute to these topics.

Topic	Goal	Research Approach
Record more birds	To describe quantitatively the vocal diversity, geographic and individuals variation, and changes of vocalization structures and repertoires throughout time	To record a minimum of 5 to 10 min recording per species including description of the behavior displayed. To indicate when the same individual or pair are recorded in the same area in different days and distance between recordings. To report when different individuals are recorded in the same location during the same day.
Understanding song variation at different level of organization	To analyze the role of vocalizations in the evolutionary process and understand the adaptive nature of differences within and among species in their behavior	Multivariate mixed effect models have been the statistical tool of choice to study the different levels of phenotypic variation.
Acoustic and genetic divergent pattern	To analyze the relationship between genetic and acoustic patterns.	To study species that inherits their vocalizations. To study species that produce duets and choruses.
Call studies	To describe the diversity of calls within species, its function, and how the information is encoded	To record species calls (e.g., mobbing, distress, food, begging, or alarm) and annotated the context under display. To conduct playback experiments to evaluate the function of different calls and call rates. To conduct transmission experiments to evaluate the range where the call transmit the information.
Audition and neurobiology	To evaluate the pattern described for species audition and compare between species.	To study species of taxa not analyzed until today. To study how species in noisy enviroments perceive the signals under those new obstacles.
Decoy experiments	To evaluate simultaneously visual and acoustic signals for species interaction.	To conduct playback experiments switching vocalizations between decoys. To manipulate decoy characteristics but keeping vocalization characteristics stable.
Urban bioacoustics	To compare the species response to urban noise, light pollution, and heavy metal contamination.	To record species from taxa not common study in urban areas as non-passerines or sub-oscines. To compare changes in vocal characteristics and repertoires through time in urban adapter and survivor species.
Sound-scape analysis	To describe the complexity of sounds in one of the most diverse habitats in the world	To record sound-scape in different forest at different time of day and at different seasons between years. To compare the structure of sound scape correcting by the richness of the species that occur in each site

calls for integrating both the among- and within-individual levels of variation in behavior in an evolutionary context (Nussey et al. 2007, Dingemanse & Wolf 2010). The need to integrate different levels of phenotypic variation to understand evolutionary processes has been clear since Darwin and Wallace, who connected among-species and among-individual variation through the process of natural selection (Darwin 1859). Recently, interactions between other levels have received more interest, such as individual variation in the consistency of behavioral expression and in its plasticity (Araya-Ajoy et al. 2015). In the context of song production, signal consistency is key to accurate information transmission and thus can be a trait under selection (Bradbury & Vehrencamp 2011). To study the evolutionary ecology of such process it is necessary to quantify the variation among individuals in how much within-individual variation they express. The Neotropics provide unique opportunities for comparative studies about how the different levels of variation can vary between species, as there are many coexisting species within habitats. There are some key outstanding questions in behavioral evolution that can only be studied in tropical ecosystems. For instance, what factors determine the amount of among-individual variation in the vocalizations of interacting species? Are there more plastic species than others and why? How do species' interactions affect the variation in acoustic space that individuals can use? Are species with variation in song expression more phylogenetically related?

Investigate patterns of acoustic and genetic divergence. As with many of the topics covered in this review, studies incorporating genetic and acoustic data need to encompass more species and families. In particular, more studies are required for those species that inherit their vocalizations. Species that inherit their vocalizations offer natural systems to test whether birds use song for assortative mating. Further studies of contact zones, where two or more species come into contact and hybridize, would be also valuable. For species that learn their songs, do they learn elements from both parental species and produce a hybrid song(s), or do they only learn the song(s) of one of the species? This would be especially informative in species that inherit their songs, as it would help to determine song's heritability. Advances in genomic technology may help to determine the genes that are associated with song development; combining genomic methods with the focal recording methods explained above will allow for further insights into the relationship between acoustic and genetic divergence.

The study of calls. Given the broad diversity of bird species in the Neotropics, the study of calls —including their quantitative description and association with function— could help us understand the evolution of calls, and test which forces act on their evolution, including habitat characteristics, call function, morphology, or phylogeny. Additionally, it is important to encourage studies that analyze the perception of calls by receivers, because this will help to elucidate the dynamics of interspecific learning and which variants of the same call are necessary to produce different responses. Furthermore, it is necessary to quantitatively study all calls, especially distress calls or calls used during mobbing; how similar these calls are between species remains unknown. Importantly, we do not know which vocal characteristics are used by the species to recognize their own species from others. Finally, studying calls will give us the opportunity to study more species outside of oscines (the group focused on most frequently for bioacoustic studies) because both non-passerines and suboscine species have a large repertoire for these types of vocalizations (Cortopassi & JW Bradbury 2006, Baldo & Mennill 2011, Isler & Maldonado-Coelho 2017).

Audition and neurobiology. Hearing abilities have only been measured in approximately 50 of the 10,000 species of extant birds (Dooling et al. 2000). On average, for the few bird species studied, they hear best between about 1 and 5 kHz (Dooling 2004). However, some species like fruiteaters and bushfinches vocalize at around 8 kHz, and must hear best outside of the average range described. Of the 50 species where hearing abilities have been described, only two Neotropical species are found: the oilbird and the barn owl (Konishi & Knudsen 1979, Knudsen 1981). On many of the basic measures of hearing, the different bird species that have been tested are remarkably similar (Dooling 1982). Nevertheless, with such diversity present in the Neotropics we would expect to find differences in hearing abilities across different taxa. Hearing can be studied using techniques such as behavioral test, auditory brainstem response (ABR) and distortion products of autoacoustic emissions (DPOEs). Behavioral studies require months of animal training, and work best with animals in captivity (Crowell et al. 2015). The non-invasive auditory brainstem response (ABR) represents a good approach, and researchers are increasingly turning to ABR to obtain estimates of hearing sensitivity, and of auditory system function and development (Crowell et al. 2015). Recently, DPOEs have been used to study moths and bats and produced very good results (Mora et al. 2013, Wetekam et al. 2019), but very few bird studies have used this novel technique (Xia et al. 2016). Why should we study the hearing of tropical birds? Predators, for example, use their ears to search for prey, and studying audition in predators will give us a better understanding of how this selective force has shaped the song structure of many songbirds in tropical habitats.

Decoy experiments. It is known that multi-component signals elicit better responses than single-component signals (Candolin 2003), and available research suggest that receivers' perception might play an important role in the ecology and the evolution of signals (reviewed in Rowe 1999; Candolin 2003). Studies on signal recognition, mating, or male-male interactions indicate that perception plays an important role in evolutionary mechanisms such as premating barriers (reviewed in Rowe 1999; Candolin 2003). However, most studies on Neotropical bird species focus on only a single divergent signal (usually vocalizations or plumage), and few studies have tested multimodal signals in other parts of the world (e.g., Baker & Baker 1990, Patten et al. 2004, Uy et al. 2009, Greig et al. 2015). Specifically, experiments using a combination of both taxidermic mounts and playbacks, are strong tools to evaluate the importance of behavioral isolation in the early stages of avian speciation. The use of decoys in experiments has also been useful to understand the use of signals under aggressive and social contexts (e.g., Baker et al. 2012, Linhart et al. 2013, Barnett et al. 2014), but very few of these studies were carried out in the Neotropics. For instance, Gill et al. (2008) used a combination of song playbacks and decoys to test hypotheses using single females, single males, and paired individuals' decoys in Buff-breasted Wrens *Thryothorus leucotis*. Further, the use of decoys in combination with acoustic playbacks could be informative to understand mechanisms of use of multimodal signaling in natural noise conditions, and to test whether birds use similar mechanisms to deal with noise in urban settings (i.e., use of songs and plumage under urban noise conditions).

Urban bioacoustics. Urban area cover will increase in the future due to the movement of people from rural areas to cities (McDonald et al. 2008). This will reduce and fragment the natural habitats inside and around cities, imposing new or increasing the current challenges for acoustic communications; these challenges include more anthropogenic noise, light pollution, changes in habitat structure, and arrival or departure of species (McDonald et al. 2008, Biamonte et al. 2011, Seto et al. 2012, Lepczyk et al. 2017). Therefore, studying how urban development is affecting acoustic communication in our region is critical as many cities exhibit large species richness (i.e., non-passerines, sub-oscines, and oscines). Further, many vocalizations outside of solo songs (e.g., calls, duets, choruses, and dawn songs), are produced year-round (MacGregor-Fors & Escobar-Ibáñez 2017). Urban bioacoustics has been developed over the last few years inside the Neotropics. Similar to studies in the rest of the world, the focus is mostly on the effect of anthropogenic noise in male solo songs characteristics, such as frequency and duration, and mainly in passerine species (Redondo et al. 2013, Mendes et al. 2017, de Magalhães Tolentino et al. 2018). For that reason, we need to begin studying the effect in other groups that inherit their songs, including furnariids, flycatchers, and pigeons, and in groups that learn their songs, including hummingbirds and parrots, which are common inside cities (Leveau & Zuria 2017). We also need to study the effect of noise on other vocalizations, such as the duets and calls produced by urban species for territorial and social communication (Méndez et al. 2021). Specifically, analyses of repertoire length and the proportion of low- and high-frequency vocalizations are necessary. Given that not all populations of the same species appear to respond in the same way to changes anthropogenic noise (Juárez et al. 2021), we encourage comparative studies that include several populations of the same species under different levels of anthropogenic noise to understand this urban factor in a broad sense.

Sound-scape analysis. New audio technology allows for the deployment of ARUs that can collect tons of data over long periods of time, in remote areas and in many places at the same time (Deichmann et al. 2018). ARUs have already proved to be efficient and can complement other methods (e.g., point counts, transects, focal recordings), notably in locations with reduced visibility (Aide et al. 2013). The amount of information collected by ARUs over a short time, however, can be very hard to process manually (Aide et al. 2013, Sueur et al. 2014, Ulloa et al. 2016, Gasc et al. 2017). Although bioacoustics is a discipline that focuses on recording focal individuals in relation to specific behaviors, rarely does this field connect with other levels of ecological complexity like community, landscape, or ecosystem (Sueur et al. 2014). However, with the recent development of ARUs, new disciplines have arisen. Two examples are s*oundscape ecology* (Pijanowski et al. 2011), defined as “the collection of biological, geophysical, and anthropogenic sounds that emanate from a landscape and which vary over space and time”, and *ecoacoustics,* defined as “a discipline that studies sound along a broad range of spatial and temporal scales in order to tackle biodiversity and other ecological questions” (Sueur et al. 2014). Given that bird vocalizations have been widely studied in different contexts and are well known, the contributions provided by Neotropical habitats can help in the improvement of soundscape databases, interpretation of soundscape metrics (Aide et al. 2017), and validation of soundscape theories (Gasc et al. 2017).

Two approaches can be implemented when analyzing the large datasets collected using ARUs. On one hand, automatic recognition and classification methods can be applied to large acoustic datasets to detect, recognize, and classify bird sounds (Ulloa et al. 2016). This approach may allow researchers to monitor spatial (e.g. elevational shifts in avian distributions, Campos-Cerqueira et al. 2017) and temporal changes in vocal activity of birds, in relation to different aspects of their behavior at broader scales (Ulloa et al. 2016, Campos-Cerqueira & Aide 2016); it allows for the deep study of the phenological patterns of songs of birds (Buxton et al. 2016; Pérez-Granados et al. 2019) and may help to understand its relationship with other vital aspects in the life of birds such as reproduction and molting (Wikelski et al. 2000). It also may be useful to assess species presence, abundance, and evaluate the consequences of current species management for conservation practices (Campos-Cerqueira & Aide 2016, Shonfield & Bayne 2017). On the other hand, characterizing the acoustic bird community using acoustic indices might be an alternative to species identification (Sueur et al., 2014), although its use needs to be careful (Sandoval et al. 2019). Instead of focusing on individual species or sets of species, acoustic indices aim to describe the general structure of the soundscape; being a mathematical summary of the distribution of acoustic energy across time and frequency, they can be used to estimate and describe the diversity of sounds in a recording (Sueur et al. 2014, Sandoval et al. 2019), or in aggregations of recordings (Aide et al. 2017, Herrera-Montes 2018). Many types of acoustic indices have been developed and tested in different habitats, and have been found to reflect the diversity, abundance, composition and vocal activity of avian communities (Pieretti et al. 2011, Gasc et al. 2017, Sandoval et al. 2019). These indices revealed, for example, that the soundscape of a tropical forest has changes through time and is very heterogeneous in space (Aide et al. 2017). These temporal changes are probably linked to endogenous factors that rule out the acoustic time activity of animal species (i.e., diel patterns of activity), to the vertical stratification of singing communities or guilds, to horizontal variations in the distributions of species, and to vegetation spatial heterogeneity (Rodriguez et al. 2014). However, these studies have also revealed that tropical soundscapes are sensitive to background noise, to variation in the distance of the animals to the sensor, and the relative sound amplitude or calling rate of the signaling animal (Gasc et al. 2015).

CONCLUSIONS

This review indicated that most bird species in the Neotropics lack quantitative descriptions of vocalizations, including comparisons between populations and across their distributions. These are basic steps to begin asking more experimental and functional questions, or even to help understand the taxonomy of several species and groups in the region. This review also showed that most studies have been conducted on oscine species, although the great diversity of species that occurs within this area provides us with raw material (a large richness of sub-oscines and nonpasserines species) to study, and broaden our understanding of avian vocal communication. Thus, researchers should aim not only to continue recording male solo songs, but to also include in their studies descriptions of female vocal traits and other types of vocalizations. Future steps will be guided by the development of new technologies that are cheaper and thus more accessible for researchers and students in this region, but also by collaborations between researchers throughout the region. Although there is less information published about bioacoustics in the Neotropics, we have the potential to provide more robust and new information on bird communication, given that most species in the Neotropics behave in different ways compared to the species used as model organisms in temperate regions.

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