

***Assessing Acoustic Niche Partitioning in Temperate
Forest and Scrub Bird Communities***

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Abstract

According to the acoustic niche hypothesis, animals that communicate vocally are expected to modify the timing or frequency of their vocalizations to avoid overlapping in time and frequency with other vocalizing species. In birds, acoustic niche partitioning (ANP) increases with species richness, community intactness, and levels of background noise. Forest and open habitats are expected to differ in their levels of ANP due to differences in how sound propagates between habitats. I investigated ANP in a forest and a scrub bird community using 24 minutes of audio from four forest sites and four scrub sites in northwestern Pennsylvania. ANP was assessed by determining the number of vocalizations that overlapped in time and frequency and comparing the observed number of overlaps to an expected distribution of overlaps generated by randomizing the start time of each vocalization but holding its duration and frequency range constant. Observed overlaps were not significantly lower than the expected distribution of overlaps in any of the sites, indicating that ANP is not occurring within either of the sampled forest or scrub habitats. Failure to detect ANP could be due to differing conditions in temperate vs. tropical environments as well as an artificially high sensitivity to overlap in my methodology. The study indicates temperate birds tolerate some level of acoustic overlap and suggests future conservation efforts should focus on reducing anthropogenic noise in tropical environments, where such noise is more likely to disrupt avian communication systems than in temperate communities.

Introduction

In many animals, including frogs, birds, mammals, and insects, vocalization is a critical component of communication, territorial defense, and mate selection (Brum & Slabbekoorn 2005). Failure to be heard can reduce mating opportunities, confound territorial responses, and in pigs, disrupt communication between sow and offspring such that piglets in noisy environments gain less milk than those in quiet ones (Gerhardt & Klump 1988; Paez et al. 1993, Algiers & Jensen 1985). To maximize fitness, vocalizations therefore must be capable of propagating sufficiently and distinctly to be picked up by the desired receiver (Ey & Fischer 2009). The problem which arises is that many environments on our planet are inherently noisy or muffling. Vocalizing animals must navigate acoustic disruption from wind, rain, running water, and other vocalizing species (Brum & Slabbekoorn 2005). Dense vegetation can reduce the distance a sound is able to travel (attenuation) more than would occur in open habitats (Yip et al. 2017). Since vocalizations play such a significant role in biological interactions, there should exist strong selection for species to modify their vocalizations to avoid acoustic interference or attenuation (Brum & Slabbekoorn 2005). Such vocal modification has been observed in response to environmental variables. Forest tinamous, for instance, call at a lower average frequency than do tinamous found in more open areas, as lower frequencies can be transmitted with less disruption through obstacles such as dense vegetation (Bertelli & Turbaro 2002).

In addition to natural sound decay and the environmental conditions of a location, biotic factors can contribute to the attenuation and distortion of a sound as it travels through space (Bradbury & Vehrencamp 1998). Vocalizations from different species that overlap in time and frequency will interfere with each other and reduce transmission of

both acoustic signals (Brum & Slabbekoorn 2005). The acoustic niche hypothesis (ANH), states that species will modify the frequency and timing of their vocalizations to reduce acoustic overlap with other species in their community (Krause 1993). Evidence for the ANH — modification of vocalization frequency and timing to reduce interspecific overlap — has been found across a diverse taxonomy of animals. Nine species of cicada in Mexico partition their vocalizations by calling at different times, heights, and frequencies (Sueur 2002). Frogs in the genus *Eleutherodactylus* in Puerto Rico partition their acoustic space by vocalizing at different frequencies but not at different times (Villanueva-Rivera 2014). Several studies have found evidence for acoustic niche partitioning in birds. In Peru, rainforest birds that share frequencies demonstrate less temporal overlap than would be expected by chance (Planqué & Slabbekoorn 2008). Birds have been observed to reduce how frequently they sing when in the presence of other birds or cicadas that use the same frequency (Popp et al. 1985, Hart et al. 2015). In a Brazilian rainforest community, birds chose to sing at different times and locations or utilized different frequencies to avoid acoustic overlap (Luther 2009). A recent study in a deciduous forest in Pennsylvania found that birds avoid singing at the same time as other species that sing at a similar frequency (Chronister et al. 2023).

Acoustic niche partitioning (ANP) in birds varies by latitude, geography, community composition and levels of background noise. Under the ANH, species-rich communities should exhibit higher levels of acoustic niche partitioning than species-poor communities as there is more competition for the available acoustic space (Krause 1993). This prediction has been demonstrated in comparisons between tropical sites and temperate sites, as well as mainland sites and islands. Tropical latitudes are more species-rich than

temperate latitudes, and mainland areas are more species-rich than insular areas, and acoustic niche partitioning follows this exact pattern, with ANP being highest on the tropical mainland and lowest on a temperate island (Robert et al. 2019, Hart et al. 2021). Community composition can also impact levels of acoustic niche partitioning. In theory, acoustic niche partitioning takes place over evolutionary time, with species selected to have less overlap with others in their community. In New Zealand, native bird species exhibited high levels of acoustic niche partitioning, in comparison with introduced bird species, which showed little to none (Azar & Bell 2014). High levels of background noise in a distinct bandwidth may also increase ANP. Tropical forests, in addition to high species richness, have a narrower frequency window for birds to sing and be heard than temperate forests, due to increased levels of insect noise and greater sound attenuation occurring in the higher frequencies in tropical forests (Weir et al. 2012, Roberts et al. 2019). This limitation on the acoustic space in tropical forests may be another factor increasing ANP in such environments, as bird vocalizations concentrate in this narrow frequency window and become more likely to interfere with one another should partitioning not occur (Roberts et al. 2019, Weir et al. 2012, Krause 1993).

One area that has been little explored is how acoustic niche partitioning in bird communities differs between habitat types. The vegetation of a landscape has significant impacts on the distance a given frequency of sound can travel (Boncoraglio & Saino 2007, Morton et al. 1975). Trees and other large, woody vegetation impede the transmission of high-frequency sounds, so forest birds tend to sing at lower frequencies compared with birds in open habitats (Boncoraglio & Saino 2007, Morton et al. 1975). Sounds of all frequencies can travel further in open habitats, so birds of open habitats tend to sing across

a wider range of frequencies than forest birds, a difference most pronounced in tropical environments (Boncoraglio & Saino 2007, Meinzin 2018, Weir et al. 2012). Given that the pressures on the soundscape differ between habitats, it would follow that acoustic niche partitioning also differs between habitats. As discussed above, there is evidence that restriction of suitable frequencies for vocalization may increase levels of acoustic niche partitioning, as seen in tropical forests (Weir et al. 2012, Roberts et al. 2019). This suggests the hypothesis that open habitats would have lower levels of ANP, due to the increased frequency range for vocalizations to be heard in open habitats compared with forest habitats.

Because this hypothesis has never been explicitly tested (to my knowledge), I was interested in investigating how acoustic niche partitioning differs between forest and open habitats. During June of 2022, I recorded the soundscape of both a forest and a scrub community in northwest Pennsylvania and analyzed the sound files for acoustic niche partitioning. Given that the pressures on the soundscape are greater in forested areas, I hypothesized that the forested sites would exhibit greater acoustic partitioning than the scrub sites.

Investigating acoustic niche partitioning bears environmental importance as humans have been dramatically impacting the acoustic environment since the industrial revolution (Ortega 2012). Noise pollution from traffic and industry most severely impacts environments located in urban and suburban areas, but even secluded places suffer from off-road vehicles or from aircraft flying overhead (Ortega 2012). In response to anthropogenic noise, birds have been shown to modify the duration and frequency of their songs (Ortega 2012, Toltino et al. 2018, Courter et al. 2020). Anthropogenic sounds are

composed of low frequencies, so many bird species sing at higher frequencies to avoid acoustic interference in fragmented environments (Bermudez-Cuamatzin 2011, Toltino et al. 2018). In some cases, birds that sing at lower frequencies have been completely displaced from an area due to human noise (Francis et. al. 2011). The modification of vocalizing frequencies and the disappearance of species undoubtedly have a significant impact on the structure of a soundscape. Understanding how acoustic niche partitioning differs across habitat and latitude will give us better insight into how the avian soundscape is structured, and perhaps identify which environments are particularly vulnerable to noise pollution due to their high levels of acoustic partitioning.

Methods

Sampled Region

All data collection occurred in a contiguous forest habitat and a contiguous second-growth scrub habitat within a 6.5 km² area around Hemlock Hill Field Station and the Seneca Division of Erie National Wildlife Refuge in northwestern Pennsylvania (Fig. 1). The forest habitat and the scrub habitat were adjacent to each other, and each sampling location in either the forest or scrub habitat was no more than 1.3 km away from another sampling location. The forest habitat had an open understory with a dense canopy and featured tree species characteristic of northern hardwood forest (Fig. 2). The scrub habitat consisted of grasses and shrubs with a few scattered trees (Fig. 3). The surrounding area was largely agricultural or natural, and both habitats abutted a low-traffic road. Other than the occasional car, levels of anthropogenic noise were minimal.



Figure 1. Site locations in northwestern Pennsylvania. Green dots represent forest sites and orange dots represent scrub sites.



Figure 2: Typical environment of forest sites.



Figure 3: Typical environment of scrub sites.

Data Collection

I collected sound recordings at 8 sites, 4 per habitat, between June 3 and June 13, 2022, during the height of the bird breeding season in Pennsylvania. Sites were located at least 200 m from each other to avoid recording the same individuals at different sites, and at least 50 m from a forested area for scrub sites and 50 m from a clearing for forest sites to avoid picking up vocalizations from the opposite bird community. I collected the GPS coordinates of each site on my phone and then verified the distance from the opposite habitat type and other sites using Google Maps. Sites were located as best as possible away from highly trafficked areas and running water to reduce acoustic interference. At each site, an Audiomoth v1.1.0 recorder with an omnidirectional microphone was set between 1 - 2 meters off the ground and programmed to record the soundscape in 3-minute intervals

every 15 minutes from sunrise to sunset, or 5:15 am to 9:00 pm. Three minutes is the standard sampling period for point counts conducted under the North American Breeding Bird Survey (Smith & Edwards, 2021), and sites were sampled multiple times an hour to reduce random acoustic interference from rain, wind, or human activity. I had access to only one audiomoth, so each site was sampled on a different day. This limitation also resulted in forest sites being slightly more clustered than scrub sites, due to greater challenges in traversing distances in the forest compared with the scrub.

Data Analysis

For this project, I analyzed 3 minutes from each site for acoustic niche partitioning. From those 8 sites, I selected one 3-minute period with the least acoustic interference between 5:15 am and 5:45 am during the peak of bird vocal activity, recording the species, start time and end time, and minimum and maximum frequency in Hz of every vocalization within the sample. Vocalizations from the same individual separated by more than a second were counted as distinct vocalizations. When I could tell multiple individuals of the same species were in the recording (due to differing volumes or overlapping signals), I marked them as separate individuals. If I could not identify a vocalization from the recording, I gave it a unique name (e.g. “chip 5 -7 kHz” or “warble 2 -3 kHz”) so it could still be included in the analysis. I used Raven Pro 1.6 software to visualize the recordings as spectrograms and extract temporal and frequency data. Only selected vocalizations > 5 dB FS/Hz of the background noise of each recording were included in the analysis. All signals were measured using a Hann window type and a window size of 10.7 ms, window overlap of 50%, and DFT (discrete Fourier transform) size of 1024 samples. A total sample of 848

vocalizations in forest and 907 vocalizations in scrub met the inclusion criterion and were included in the analysis of ANP.

Assessment of Acoustic Niche Partitioning

To calculate the level of acoustic niche partitioning in each community, I manually counted with a clicker the number of times two vocalizations of any species overlapped in time and frequency in each three-minute sample. I then randomized the start time of each vocalization while maintaining its frequency range and duration and repeated 500 times in R to get an expected distribution of vocalization overlap, as modeled in Hart et al. (2021). If the observed number of overlaps fell significantly below the simulated distribution of number of overlaps ($p = 0.025$), acoustic niche partitioning would be occurring in the community.

Results

None of the eight sample sites had an observed number of overlaps significantly below the expected distribution of overlaps, indicating acoustic niche partitioning is not occurring in either habitat (Fig. 4). In fact, half the sites ($n = 4$) had a significant number of observed overlaps higher than the expected number of overlaps, and every site, significant or not, had an observed number of overlaps higher than the mean of the expected distribution (Fig. 4). The number of overlaps per site increased linearly with the number of vocalizations at each site, the opposite trend we'd expect to see if acoustic niche partitioning were occurring (Fig. 5). Scrub sites had significantly higher numbers of species and unique vocalizations per site than did forest sites (Fig. 6), with 19 species being identified in scrub sites compared with 11 species in forest sites (Appendix A). There was a

significant difference in average call duration between the two habitats, with vocalizations given in scrub sites being slightly longer than in forest sites (Fig. 7A). In terms of the average number of vocalizations per site, average number of overlaps per site, and average frequency of all vocalizations per site, there was no statistical difference between forest sites and scrub sites (Fig. 7B, Fig. 8, Fig. 9).

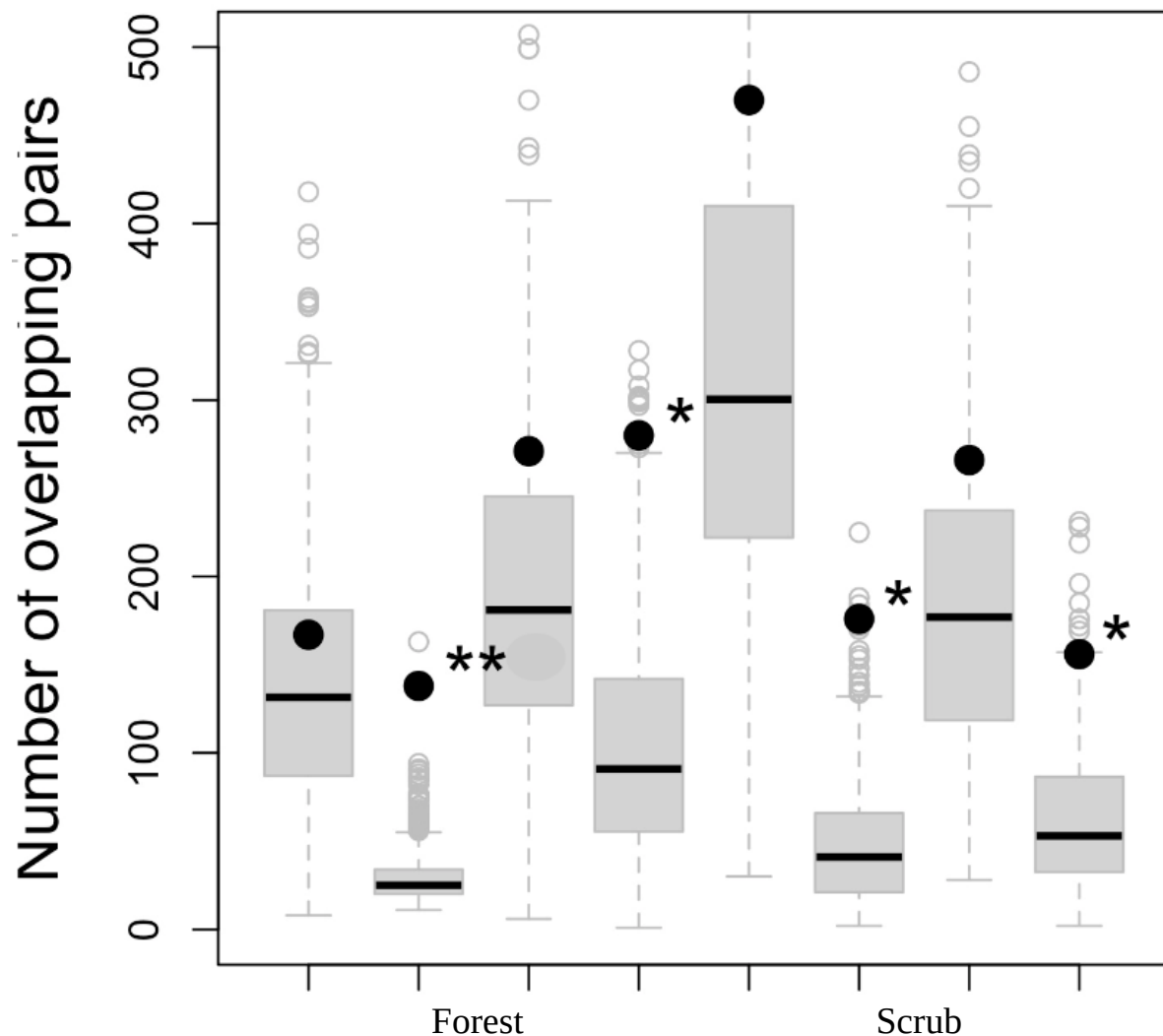


Figure 4: Box plot comparison of observed (filled black circles) and expected number of heterospecific pairs overlapping in both time and frequency between the four forest sites and the four scrub sites (significance: * = < 0.05, ** = < 0.01). Null distributions were generated by randomizing the start time of a vocalization 500 times while keeping the duration and frequency range constant.

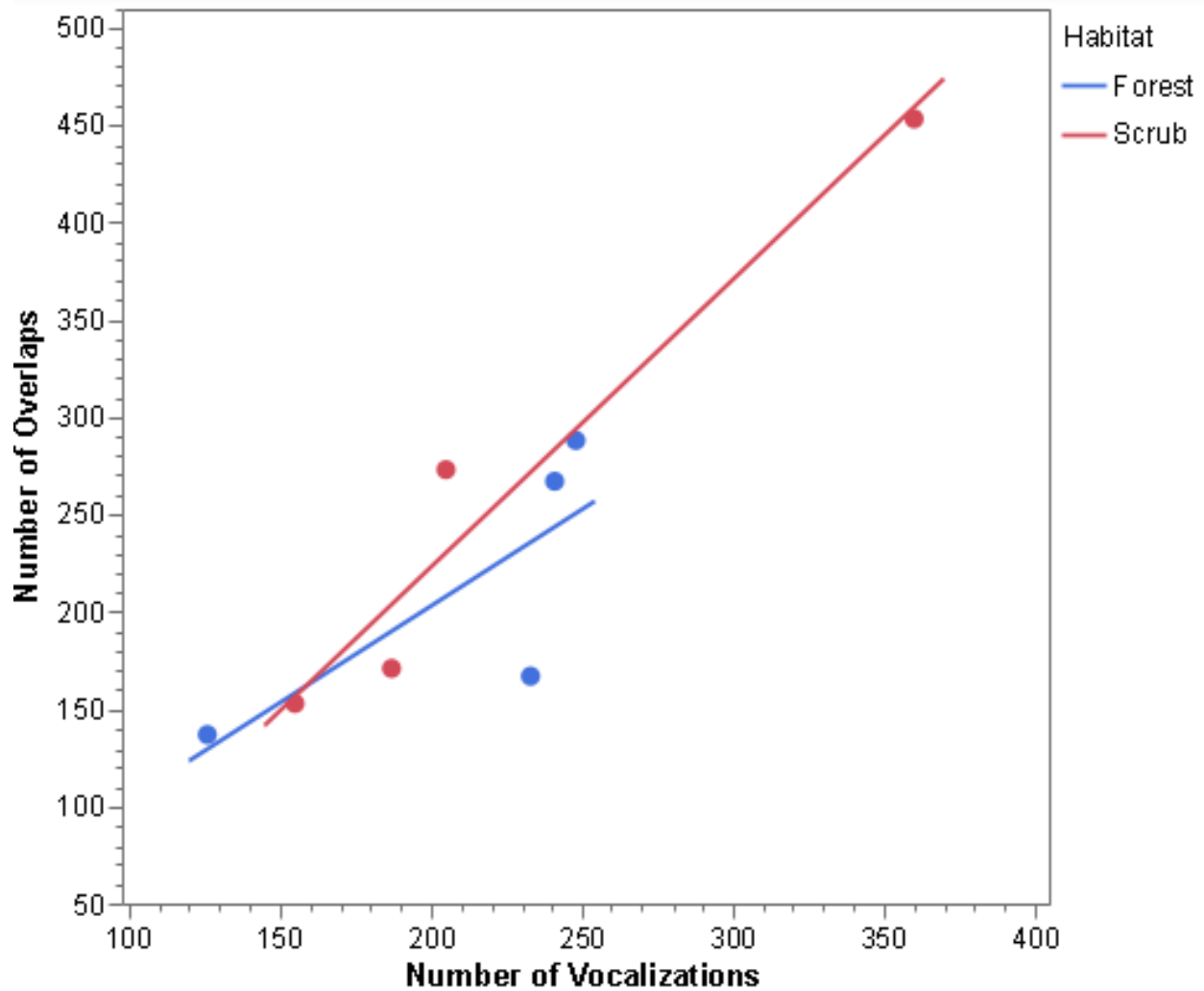


Figure 5: Linear regression of the number of overlaps in time and frequency by the number of vocalizations observed in three-minute recordings taken between 5:15 and 5:45 am in forest and scrub habitats. $R^2 = 0.59$ for forest sites and 0.95 for scrub sites.

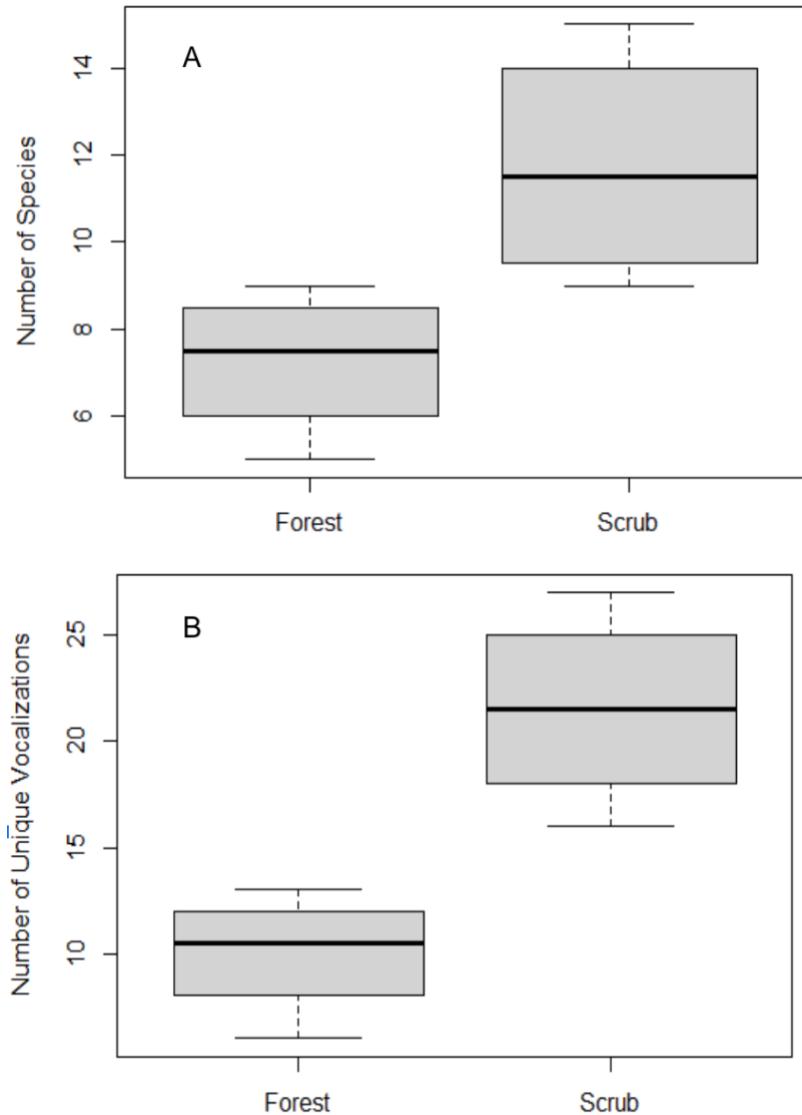


Figure 6: Box plots showing the number of species (**A**) and the number of unique vocalizations (**B**) detected in a three-minute time-period between 5:15 and 5:45 a.m. for forest and scrub habitats. Unique vocalization number includes bird vocalizations unidentified to species, while species number does not. Both differences were statistically significant (two-tailed t test, $p = 0.032$, $p = 0.011$, respectively).

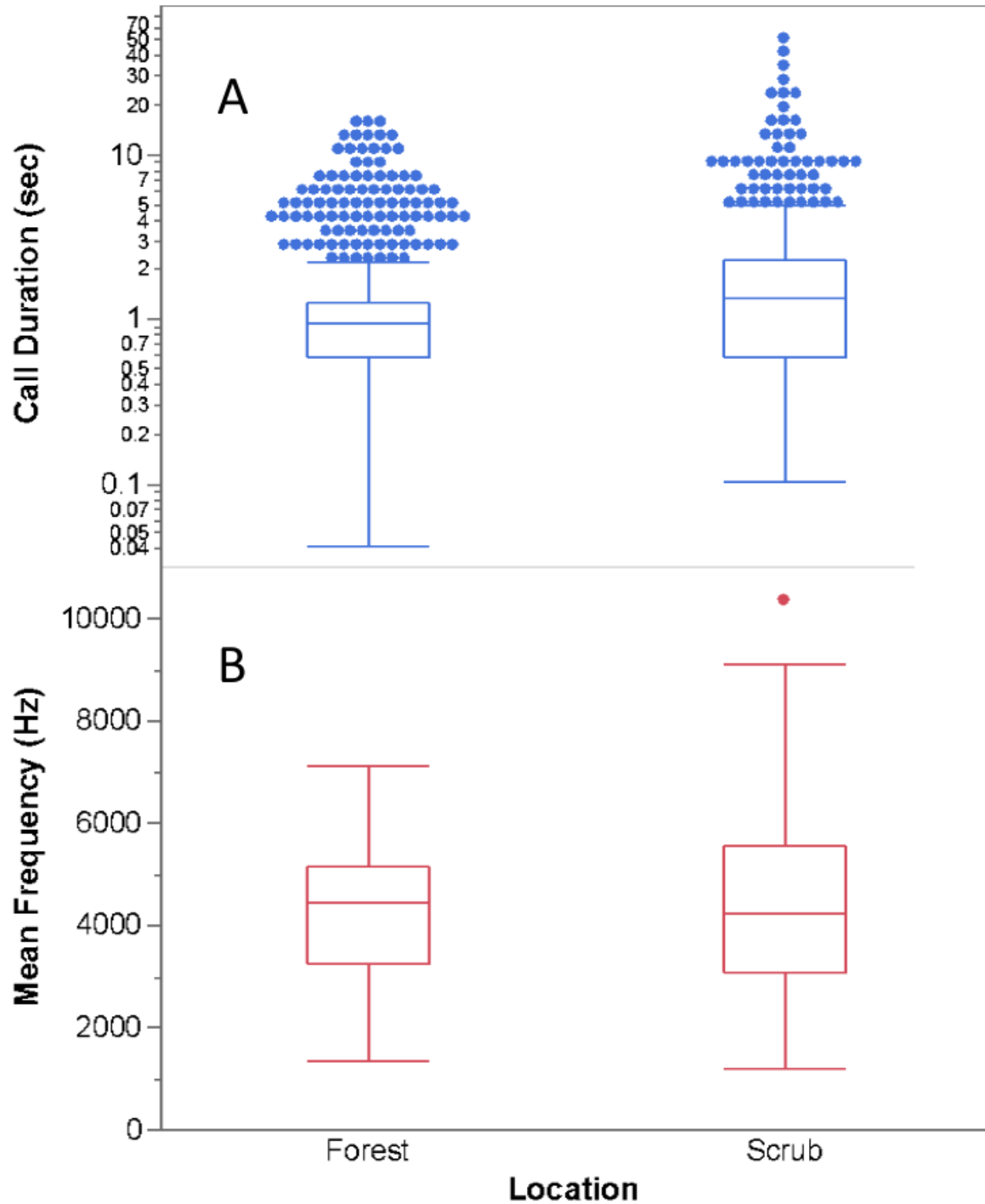


Figure 7: Box plots of call duration (**A**) and average frequency (**B**) in a three-minute time-period between 5:15 and 5:45 a.m. for forest and scrub habitats. A log transform on a general linear mixed model for call duration with habitat as a fixed effect and recorder as a random effect was statistically significant ($p = 0.03$). A general linear mixed model for average frequency with habitat as a fixed effect and recorder as a random effect was not statistically significant ($p = 0.74$).

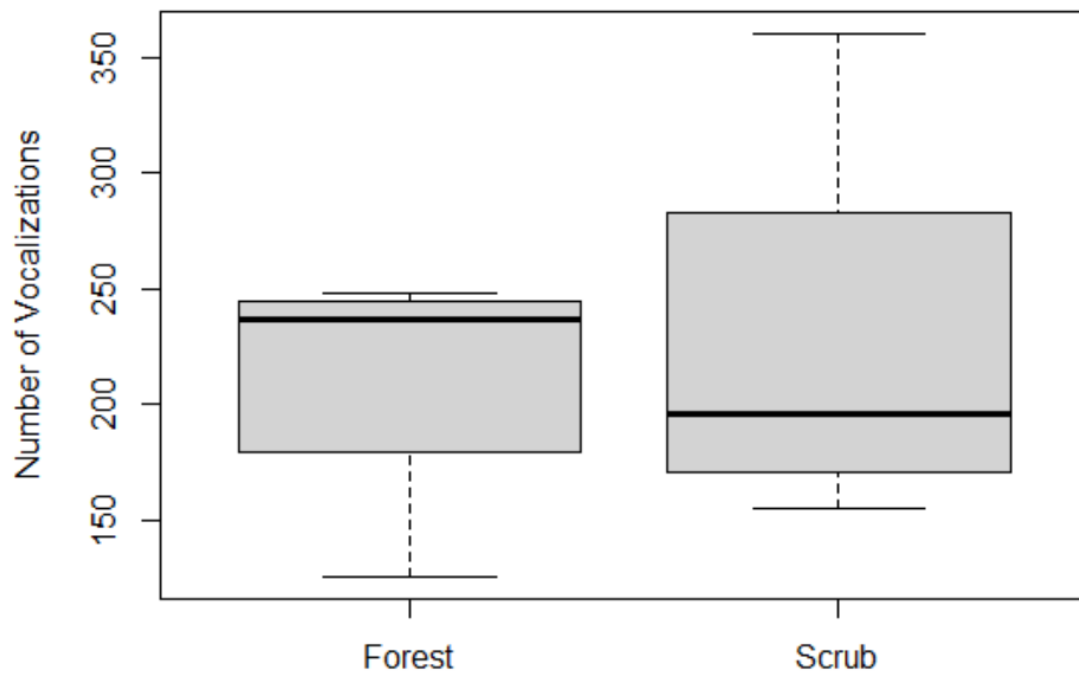


Figure 8: Box plots of the number of individual vocalizations given in a three-minute time-period between 5:15 and 5:45 a.m. for forest and scrub habitats. Differences between habitats were not statistically significant (two-tailed t test, $p = 0.794$).

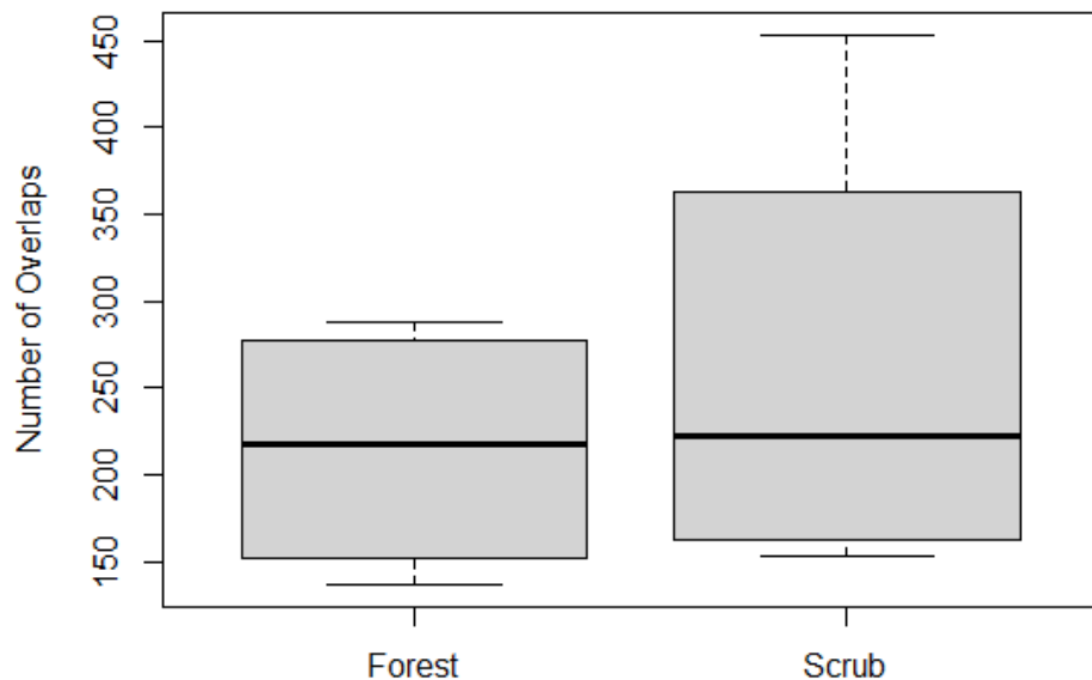


Figure 9: Box plots of the number of overlaps in time and frequency observed in a three-minute time-period between 5:15 and 5:45 a.m. for forest and scrub habitats. Differences between habitats were not statistically significant (two-tailed t test, $p = 0.563$).

Discussion

Contrary to my hypothesis, I found no evidence of acoustic niche partitioning (ANP) occurring in the bird communities of either forest or scrub habitats. Indeed, at several sites, birds were found to be overlapping their vocalizations even more than what was expected from the null model.

The difference between these results and the studies that have found positive results for ANP in birds could be due to different levels of ANP between tropical and temperate communities. Most of the research that has detected ANP in birds has been conducted on tropical forest communities (Planqué & Slabbekoorn, 2008, Luther 2009, Chronister et al. 2023). Hart et al. (2021), the primary paper I used for my methods, found evidence for temporal partitioning of bird vocalizations using the same model I used, but studied tropical bird communities in Hawaii and Costa Rica. In a direct comparison between a tropical and temperate forest community, birds in the temperate environment exhibited significantly less acoustic avoidance, overlapping more in time and frequency, than the tropical environment (Robert et al. 2019). Some of this difference can be attributed to the inverse relationship between species richness and latitude (Hillebrand 2004). Species richness is higher in the tropics and acoustic niche partitioning increases with species richness, as demonstrated by Robert et al. (2019) where ANP was highest in tropical, mainland sites and lowest in temperate, insular sites. Higher acoustic niche partitioning likely occurs in the tropics as a direct consequence of the increased number of interspecific interactions (Hillebrand 2004, Roberts et al. 2019, Brumm and Slabbekoorn 2004).

Weir et al. (2012) noted that tropical forests, unique among tropical grasslands and temperate forested and open habitat, have a very narrow frequency window where birds can vocalize and be heard, due to higher levels of background noise, primarily from insects, and greater sound degradation in tropical forests. Temperate forests lack these acoustic restrictions, due to a reduction in the amount of background insect noise and perhaps a difference in plant growth forms (Robert et al. 2019, Spicer et al. 2020). As a result, birds in temperate forests sing at higher frequencies and across wider bandwidths than their tropical counterparts (Weir et al. 2012). Higher interspecific interaction and a narrower frequency window perhaps force tropical birds to partition their vocalizations to a degree not necessary in temperate environments. Reduced ANP between tropical and temperate environments could thus explain why the null model that detected ANP in Costa Rica and Hawaii did not find it in my study in Pennsylvania.

A few studies, however, have documented ANP in temperate bird communities. A study conducted in Wisconsin found that Ovenbirds, Wood Thrush, Great-crested Flycatchers and Eastern Wood-Pewees avoid singing at the same time as the other three species when two or more are vocalizing in the same place (Popp et al. 1985). Another study published earlier this year found significant negative correlation between frequency overlap and temporal overlap of bird vocalizations in a Pennsylvania forest community, indicating that birds that sing at similar frequencies are more likely to avoid singing at the same time (Chronister et al. 2023). The latter of these two studies took place in a similar bird community only 120 miles south of my study region. One explanation for the difference between our two studies is that my methods for determining overlap were binary; that is, either a vocalization overlaps with another, or it does not, while Chronister

et al. (2023) used a weighted method. In my methods, any vocalization that overlapped another vocalization in frequency at all was considered an overlap, while Chronister et al. (2023) quantified frequency overlaps on a scale by how much they overlapped with another vocalization and how disruptive they would be to another vocalization based on their central power density. Chronister et al. (2023) noted in their paper that only 16% of temporally overlapping vocalizations in their dataset completely avoided any overlap in frequency. This suggests that birds in temperate forests may not unilaterally be avoiding all overlap in frequency, but instead may be selectively avoiding the songs that most interfere with their own vocalizations (Chronister et al. 2023). My study characterized overlaps using a binary methodology when actual ANP in these habitats may be occurring on a more nuanced scale.

Another factor in my methodology was that I counted as an overlap any vocalization that fell during the duration and between the minimum and maximum frequency of another vocalization, which may have artificially increased the number of observed overlaps. In many bird vocalizations, the frequency changes throughout the song's duration, allowing for instances where two concurrent vocalizations could avoid spectral overlap but still fall within the minimum / maximum frequency of the other vocalization. In a forest community in Italy, certain bird species sing concurrently with other bird species that share the same frequency range, but the vocalizations are timed exactly to avoid actual spectral overlap (Malavasi and Farina 2013). Birds may still be avoiding frequency overlap in my sampled habitats, but my methods were not sensitive enough to detect it.

One final issue in detecting ANP could be that I did not collect a large enough sample of vocalizations. Hart et al. detected ANP using 150 minutes of annotated recordings with a

total of 7370 vocalizations, while I was only able to analyze 24 minutes of recording for a total of 1756 vocalizations. Many of the habitats had a relatively low number of vocalizations, meaning just a few overlaps could cause the observed number of overlaps to score significantly higher than the expected number of overlaps. This low vocalization rate probably explains why four of the sites had observed values significantly higher than expected, as those sites were also the ones with the fewest vocalizations. A larger sample size with a greater number of vocalizations could possibly bring those sites below significance.

Regarding both ANP and other characteristics, scrub and forested habitats were fairly similar to one another. This may be because there are fewer differences between temperate forest and field habitats than between tropical forest and field habitats (Weir et al. 2012). Oscine birds in both temperate forest and temperate field habitats sing at an average frequency of 4.3 kHz, which is very close to the average frequency value I found in the two habitats (Weir et al. 2012). Scrub sites had a significantly higher number of species vocalizing than did forest sites. This could represent a true difference in species richness between scrub and forest habitats, or it could reflect the acoustic features of each habitat. Sound travels farther in open habitats and it's possible this increase in recording range also increased the number of detected species (Boncoraglio & Saino 2007, Yip et al. 2017, Meinzin 2018). As an example, two of the scrub recorders picked up a singing Wood Thrush, a distinctly forest species, while none of the forest recorders picked up any scrub species.

My study reveals the complexity of testing for acoustic niche partitioning and indicates birds in temperate field and forest habitats are not avoiding one another's songs

in terms of time and absolute frequency. Failure to detect ANP could be due to the small sample size, a more sensitive criteria for overlaps than similar studies, and a true reduction in ANP between tropical and temperate communities. From a conservation perspective, the study reveals that temperate birds tolerate considerable acoustic overlap, suggesting they may be resilient to a certain level of anthropogenic noise. In contrast, tropical forest communities are highly partitioned acoustically within a very narrow frequency range, and future conservation efforts should focus on reducing anthropogenic noise in those environments.

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Appendix A

Species Identified at Forest Sites

American Crow, *Corvus brachyrhynchos*
 Eastern Wood-Pewee, *Contopus virens*
 Acadian Flycatcher, *Empidonax virescens*
 Wood Thrush, *Hylocichla mustelina*
 American Robin, *Turdus migratorius*
 Hooded Warbler, *Setophaga citrina*
 American Redstart, *Setophaga ruticilla*
 Black-throated Blue Warbler, *Setophaga caerulescens*
 American Goldfinch, *Spinus tristis*
 Scarlet Tanager, *Piranga olivacea*
 Northern Cardinal, *Cardinalis cardinalis*

Species Identified at Scrub Sites

American Crow, *Corvus brachyrhynchos*
 Eastern Wood-Pewee, *Contopus virens*
 Alder Flycatcher, *Empidonax alnorum*
 Eastern Kingbird, *Tyrannus tyrannus*
 Gray Catbird, *Dumetella carolinensis*
 Wood Thrush, *Hylocichla mustelina*
 American Robin, *Turdus migratorius*
 Cedar Waxwing, *Bombycilla cedrorum*
 Blue-winged Warbler, *Vermivora cyanoptera*
 Common Yellowthroat, *Geothlypis trichas*
 Yellow Warbler, *Setophaga petechia*
 Chestnut-sided Warbler, *Setophaga pensylvanica*
 Chipping Sparrow, *Spizella passerina*
 Field Sparrow, *Spizella pusilla*
 Song Sparrow, *Melospiza melodia*
 Eastern Towhee, *Pipilo erythrophthalmus*
 American Goldfinch, *Spinus tristis*
 Northern Cardinal, *Cardinalis cardinalis*
 Indigo Bunting, *Passerina cyanea*