

Article

Species Richness (of Insects) Drives the Use of Acoustic Space in the Tropics

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Received: 26 August 2017; Accepted: 26 October 2017; Published: 27 October 2017

Abstract: Acoustic ecology, or ecoacoustics, is a growing field that uses sound as a tool to evaluate animal communities. In this manuscript, we evaluate recordings from eight tropical forest sites that vary in species richness, from a relatively low diversity Caribbean forest to a megadiverse Amazonian forest, with the goal of understanding the relationship between acoustic space use (ASU) and species diversity across different taxonomic groups. For each site, we determined the acoustic morphospecies richness and composition of the biophony, and we used a global biodiversity dataset to estimate the regional richness of birds. Here, we demonstrate how detailed information on activity patterns of the acoustic community (<22 kHz) can easily be visualized and ASU determined by aggregating recordings collected over relatively short periods (4–13 days). We show a strong positive relationship between ASU and regional and acoustic morphospecies richness. Premontane forest sites had the highest ASU and the highest species richness, while dry forest and montane sites had lower ASU and lower species richness. Furthermore, we show that insect richness was the best predictor of variation in total ASU, and that insect richness was proportionally greater at high-diversity sites. In addition, insects used a broad range of frequencies, including high frequencies (>8000 Hz), which contributed to greater ASU. This novel approach for analyzing the presence and acoustic activity of multiple taxonomic groups contributes to our understanding of ecological community dynamics and provides a useful tool for monitoring species in the context of restoration ecology, climate change and conservation biology.

Keywords: amphibians; ARBIMON; biodiversity monitoring; birds; community ecology; insects; passive acoustic monitoring; rapid assessments; soundscape; species richness

1. Introduction

Acoustic space is a limited resource that is used by all vocal species in a community [1,2] for species recognition [3], mate choice [4] and resource defense [5], but the frequencies used are restricted by body size, phylogeny, habitat structure, and biotic and abiotic sounds in the habitat [6–8]. It is unclear how or if species in a given habitat share or partition the acoustic space. Some studies have suggested that species avoid competition by partitioning acoustic space in time or frequency [9–14], while others have reported temporal synchrony and spectral overlap among species [15,16]. These studies focused on individual taxonomic groups (e.g., fish [14], birds [17], insects [18] and anurans [10,12,15]), so any interactions that may have shaped the observed use of acoustic space would be restricted to within a

group [16]. To our knowledge, no study has assessed patterns of frequency and time use for all species in the acoustic community (0–22 kHz), and few studies have evaluated how the use of acoustic space varies across a gradient of species richness [19,20].

Understanding the relationship between the use of acoustic space and species richness could lead to more effective tools for biodiversity monitoring. Monitoring fauna, particularly in forests, is challenging, yet we rely on these data to understand changes in communities and populations, as well as the implications of anthropogenic activities [21] and climate change [22]. In general, fauna is monitored using intrusive and often intensive methods such as transects, point counts and mark/recapture. Camera trapping is a non-invasive method that has been used extensively, but it mainly detects medium to large mammals, and has a very limited detection range [23]. Acoustic monitoring, another remote-sensing technique, is a complimentary approach that can detect organisms that produce acoustic signals from a broad area, although detection area depends on landscape features and vegetation structure [24,25], as well as the amplitude and frequency of sounds emitted [26]. Furthermore, passive acoustic monitoring is relatively inexpensive, can cover large areas, and can detect a large proportion of the fauna. In addition, each recording is a permanent record of multiple species, which provides invaluable information that can be analyzed by other researchers in the future [27]. To extract useful information from these audio recordings, researchers have identified species by listening to recordings [21,28,29], creating automated species identification algorithms [27,30], or using acoustic indices [31]. The manual approach requires expert knowledge and is time consuming, and this limits the number of recordings, species and sites that can be monitored. The automated approach has only been used for a subset of the fauna at a given site [32], and most acoustic indices are poor predictors of species richness [33]. We propose an alternative approach that describes how acoustic space is being used, specifically, how much of the time/frequency domain is being used and what are the sources of the sounds.

We predict that as richness of acoustically active species increases, the proportion of the total acoustic space use (ASU) will increase. We expect that increasing ASU will cause species to shift their acoustic activity in time or frequency to avoid signal overlap. Shifting acoustic activity may occur between species within a taxonomic group, but given phylogenetic limitations on sound production and reception, these shifts may be even more evident between taxonomic groups. A shift in frequency use should be more evident in sites with high species richness, where there is greater potential for signal overlap. Furthermore, given that different species groups (e.g., anurans, birds, insects) vary in richness, time of peak activity and frequencies used, their contribution to ASU is likely to be heterogeneous. To address these predictions, we analyzed the use of acoustic space in recordings from eight tropical forest sites that vary in species richness from a relatively low diversity Caribbean forest to a megadiverse Amazonian forest. Specifically, we address the following questions: (1) Is there a positive relationship between species richness and the percent of ASU? (2) How do different taxonomic groups contribute to ASU? And (3) What are the strengths and limitations of using the ASU approach for biodiversity monitoring?

2. Materials and Methods

2.1. Study Sites and Acoustic Data Collection

The recordings used in the analyses were collected in eight tropical forest sites in Peru, Costa Rica and Puerto Rico (Table 1). These sites were selected because they provided existing comparable datasets of recordings and they varied in forest type and regional species richness. One site was classified as montane, one as lower montane, three as premontane, one as lowland wet and two as lowland dry. All sites were sampled during the wet season, and recorders were placed in forested areas away from sources of anthropogenic sound. Sites were sampled for 4.3 to 13.2 days (Table 1).

Table 1. Characteristics of the eight tropical forests sites.

Site	Country	Lat	Long	Elevation (m)	Precipitation (cm)	Forest Type	Date	Recordings	Sampling Days
Amarakaeri	Peru	−12.99E	−71.01S	1000	6000	Premontane	Feb. 2015	1897	13.2
La Selva	Costa Rica	10.43E	−83.98N	37	4000	Lowland wet	Jul. 2015	1043	7.2
Las Cruces	Costa Rica	8.78E	−82.95N	1100	2500	Premontane	Jul. 2015	1251	8.7
Palo Verde	Costa Rica	10.35E	−85.35N	10	1500	Lowland dry	Jun. 2015	616	4.3
Cabo Blanco	Costa Rica	9.57E	−85.10N	30	1500	Lowland dry	Jun. 2015	736	5.1
Las Alturas	Costa Rica	8.93E	−82.83N	1800	2800	Lower Montane	Jun. 2015	1251	8.7
Cuerici	Costa Rica	9.53E	−83.58N	2600	3500	Montane	Jul. 2015	1554	10.8
El Verde	Puerto Rico	18.32E	−65.82N	363	3000	Premontane	Jul. 2015	1696	11.8

At all sites, recordings were collected at an interval of one minute every 10 min for 24 h, for a total of 144 samples per day, and were stored in the Automated Remote Biodiversity Monitoring Network (ARBIMON) platform (<https://arbimon.sieve-analytics.com/>). All recordings were collected using ARBIMON portable recorders (Sieve Analytics Inc., San Juan, Puerto Rico) using the ARBIMON Touch application (<https://goo.gl/CbBavY>). The recording system used a sampling rate of 44.1 kHz/16 bit and recorded sounds between 0–22 kHz, which encompasses the frequency ranges of most birds, amphibians and insects, but excludes most bat species.

2.2. Regional Species Richness

We chose to use bird species richness as a measure of general regional species richness because there is more information regarding species distribution available for birds than for either anurans or insects. Using the global bird diversity dataset available at <http://biodiversitymapping.org>, we determined the number of bird distributions that overlapped with each site [34].

2.3. Acoustic Morphospecies Richness and Composition in Recordings

To determine a measure of species richness and composition of the biophony, we manually reviewed 168 recordings from each site and identified all acoustic morphospecies of anurans, birds, insects and mammals, as well as the presence of geophony (e.g., wind, rain) and anthrophony (e.g., cars). An acoustic morphospecies was defined as a note or series of notes that constitute a unique acoustic signal (Table S1). Each acoustic morphospecies was associated with their specific taxonomic group (i.e., anuran, bird, insect, mammal) for further analyses. There is likely to be a one-to-one relationship between a call and species for most insects and anurans, but bird species can have multiple calls; thus, our methodology could inflate species richness estimates. The presence of mammals, geophony and anthrophony were minimal, and these categories were eliminated from all analyses. In each site, acoustic morphospecies were first identified in 24 1-min recordings (one recording per hour) taken from the first complete day of recordings. These acoustic morphospecies were used as references, and an additional 144 1-min recordings (three per hour during two continuous 24-h periods) were evaluated for new acoustic morphospecies. We noted the frequency range of the reference call of each acoustic morphospecies and linked it to the recording where it was first identified (Table S1). All acoustic morphospecies were independently verified twice to ensure that there were no duplicates and that the source was correctly assigned.

To determine the range of frequencies used by the different taxonomic groups, we created histograms based on the frequency range (minimum to maximum) of each acoustic morphospecies for each taxonomic group. For this analysis, we used a bin size of 500 Hz and noted the frequency bins occupied by each morphospecies call.

2.4. Acoustic Space Use (ASU)

To analyze the use of the acoustic space for each site, we used the ARBIMON platform. The soundscape analysis tool allows the user to define the time scale of aggregation (e.g., hour, month, or year), the frequency bin size and the minimum threshold for the amplitude of a sound peak

(i.e., intensity). We aggregated recordings at the time scale of hour of day (24 h), used a frequency bin size of 86.13 Hz and an amplitude filtering threshold of 0.02. This resulted in a three-dimensional ($x = \text{hour}$, $y = \text{acoustic frequency}$, $z = \text{proportion of all recordings in each time/frequency bin with a peak} > 0.02 \text{ amplitude}$) matrix of acoustic activity with a total of 6144 time/frequency bins ($24 \text{ h} \times 256 \text{ frequency bins}$) (Figure 1). For the analyses, we excluded the first five frequency bins (0–429 Hz) because of electronic noise in some recordings, and thus a total of 6024 time/frequency bins were used. A correlation analysis was used to determine if the variation in the number of recordings per site affected the values of ASU.

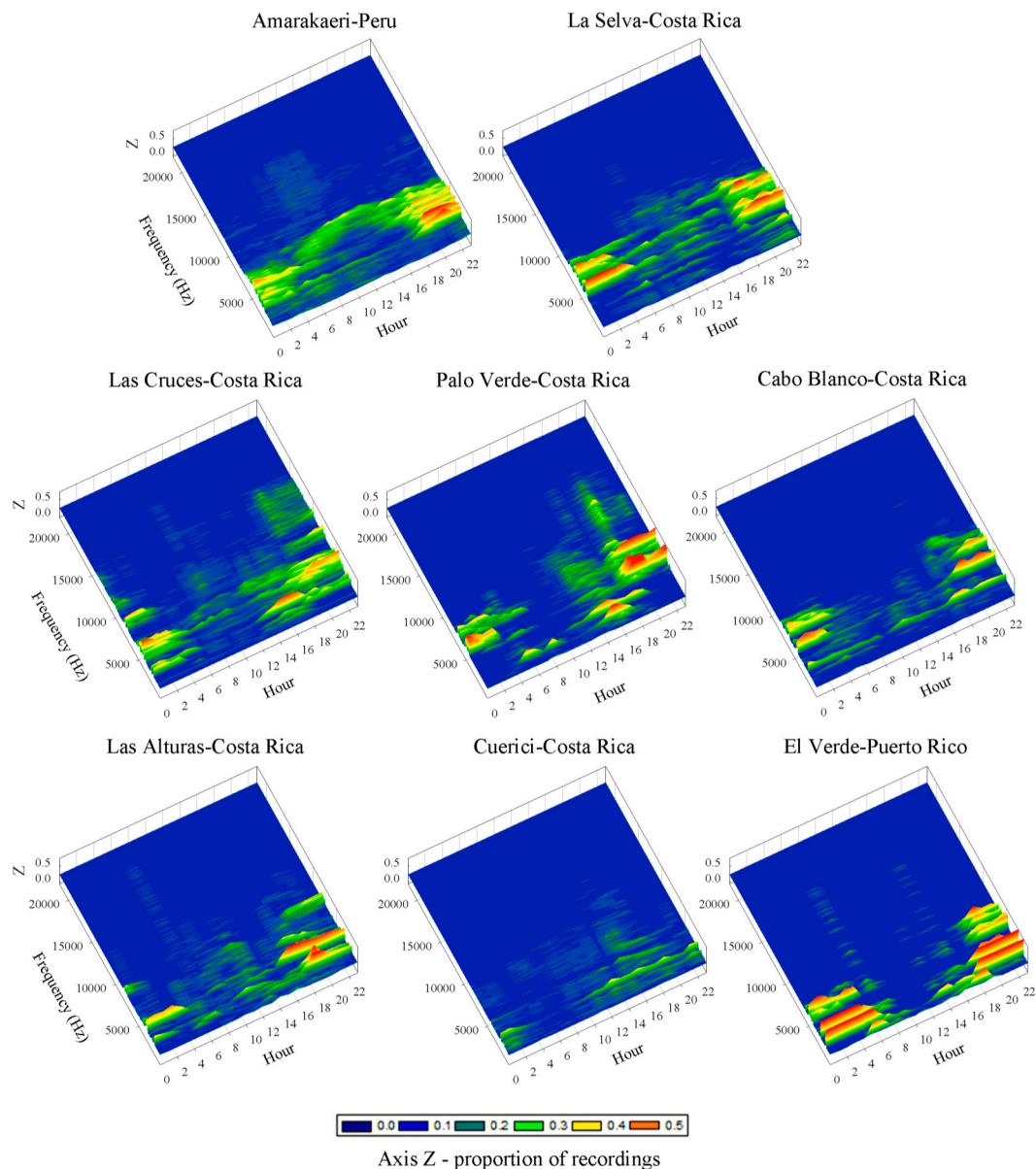


Figure 1. Visual representations of acoustic space use (ASU) from the eight forest sites. The axes represent hour (x), frequency (y) and the proportion of observations (z). The figure includes 6024 time/frequency bins ($24 \text{ h} \times 251 \text{ frequency bins}$). ASU was calculated by summing the number of time/frequency bins that were occupied.

To calculate the amplitude, we used the `meanspec` and `fpeaks` functions from the `seewave` package in R [35]. The value of each peak was normalized using the maximum amplitude value within all recordings in the soundscape (i.e., site), and thus values ranged from 0 to 1. The number of frequency peaks was determined by counting the number of recordings with a peak within each of the 251 frequency bins that were equal to or greater than the amplitude threshold. To control for the different number of recordings in each site and each time interval (i.e., hour), we divided the number of recordings with a peak in each time/frequency class by the total number of recordings collected during each hourly interval.

Acoustic space use (ASU) was calculated as the percent of time/frequency bins used in each site ($24 \text{ h} \times 251 \text{ frequency bins} = 6024 \text{ time/frequency bins}$). A time/frequency bin was considered “used” if a recording had a sound with an amplitude >0.02 detected in that bin. The relationship between ASU and regional and acoustic morphospecies richness (anurans, birds and insects) was determined using a Spearman rank correlation. In addition, regression models were compared using Akaike information criterion (AICc) [36] to determine the relative importance of anurans, birds and insects in explaining the variation in ASU.

3. Results

3.1. Species Richness and Acoustic Space Use (ASU)

Acoustic morphospecies richness (i.e., anuran, bird and insect acoustically unique morphospecies identified in the recordings) had a strong positive correlation with the percent ASU in the eight sites (Table 2, Figure 2a, Spearman rank correlation coefficient = 0.85, $p = 0.01$). Cuerici and El Verde had the fewest number of acoustic morphospecies (<40) and only 10–15% of the acoustic space was occupied. In contrast, we identified >85 acoustic morphospecies in Amarakaeri and Las Cruces, and these sites had values of ASU $>25\%$. Although sites were sampled for different lengths of time, there was no significant correlation between the number of recordings collected and ASU ($R^2 = 0.17$, $p > 0.3$).

Similarly, bird regional richness (i.e., number of bird species distributions that overlap with each site) had a strong positive correlation with the percent ASU in the eight sites (Table 2, Figure 2b, Spearman rank correlation coefficient = 0.85, $p = 0.01$). Cuerici and El Verde had the lowest regional richness (<200 spp.) and only 10–15% of acoustic space was occupied. In contrast, Amarakaeri with the highest regional richness (>500 spp.) had an ASU value of 34%. Although the regional richness of Las Cruces (352 spp.) was the third highest, its ASU (28%) was higher than the La Selva site, which had a regional richness value >400 species.

Table 2. Summary of the percent ASU, regional richness and acoustic morphospecies of the eight tropical forests sites.

Site	% ASU	Regional Richness	Acoustic Morphospecies			
			Total	Anuran	Bird	Insect
Amarakaeri	34.3	583	84	4	27	53
La Selva	20.3	423	56	3	20	33
Las Cruces	28.2	352	91	5	31	55
Palo Verde	14.9	330	38	0	21	17
Cabo Blanco	11.8	311	46	1	23	22
Las Alturas	18.5	262	50	3	26	21
Cuerici	13.3	190	17	0	14	3
El Verde	11.6	184	37	6	12	19

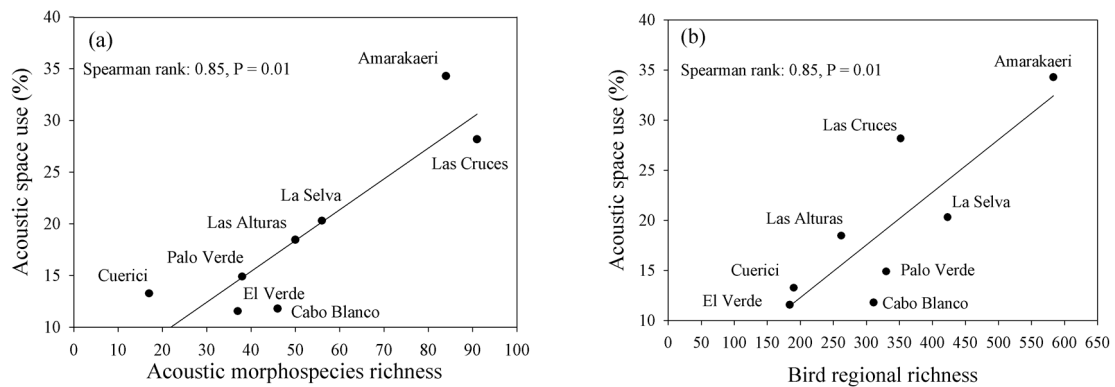


Figure 2. The relationship between percent acoustic space use (ASU) and (a) acoustic morphospecies richness in 168 1-min recordings from each site and (b) bird regional richness. The lines represent the least-squares linear regression.

3.2. Acoustic Morphospecies Composition and Acoustic Space Use (ASU)

In addition to acoustic morphospecies richness, acoustic morphospecies composition may also influence ASU. Insects dominated the high ASU sites (e.g., Las Cruces, Amaraeri and La Selva) with 40 or more insect acoustic morphospecies (Figure 3). Birds were the dominant taxonomic group in the low ASU sites, with the exception of El Verde that was dominated by insects. The number of bird acoustic morphospecies was between 20 and 35 in most sites, but was lower in the Cuerici and El Verde sites. Anurans were the least-abundant taxonomic group with less than 10 acoustic morphospecies in all sites.

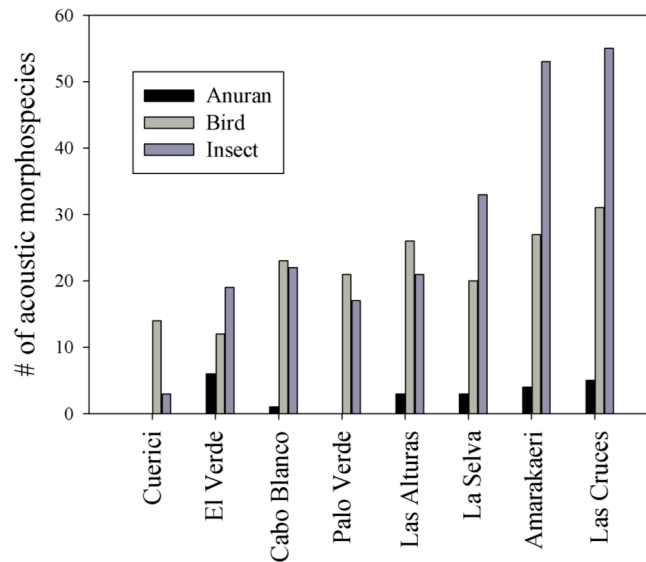


Figure 3. The number of anuran, bird and insect acoustic morphospecies in 168 1-min recordings in each site.

Subset regression models showed that insect acoustic morphospecies richness was by far the best predictor of the variation in percent of ASU (Table 3). Each of the top three models (Delta AICc) included a single variable: insect acoustic morphospecies (Akaike weight = 0.92), bird acoustic morphospecies (0.026) and anuran acoustic morphospecies (0.003).

Table 3. Subset regression model results for the top three models explaining variation in the percent of acoustic space use (ASU). Residual SS is the sum of squared errors of the prediction and AICc is the difference between a given model and the best model. See Table S2 for all candidate models.

Model Variables	Residual SS	Akaike Weight	Delta AICc	Adjusted R ²
Insects	92.0	0.925	0	0.77
Birds	223.7	0.026	7.1	0.45
Anurans	389.6	0.003	11.5	0.04

The frequencies used by anuran, bird and insect acoustic morphospecies varied greatly and were significantly different (Kruskal–Wallis = 390, $p < 0.001$; Figure 4). The median frequency used by anurans was the lowest at 3750 Hz (range 1250–8250 Hz), while the median frequencies used by birds and insects were 5250 Hz (250–18,750 Hz) and 8750 Hz (250–20,750 Hz), respectively. In this study, there were few anuran acoustic morphospecies, and the range of frequencies used by anurans overlapped completely with the distribution of frequency used by birds and insects. The major area of overlap for all acoustic morphospecies was between approximately 4000 and 7000 Hz.

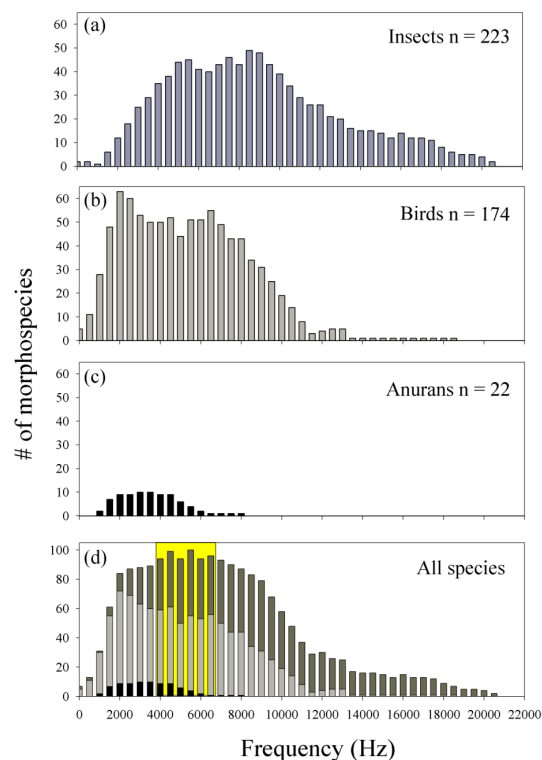


Figure 4. Distribution of frequencies used by (a) insects, (b) birds and (c) anurans for all 419 acoustic morphospecies across all eight sites. The stack bar figure (d) includes all acoustic morphospecies across all sites, and highlights the frequencies with the greatest number of acoustic morphospecies, i.e., region of greatest overlap. This region was assigned to the six bins with the greatest number of acoustic morphospecies.

4. Discussion

As predicted, sites with higher bird regional species richness and acoustic morphospecies richness exhibited a greater proportion of acoustic space use (ASU). Given this definition of acoustic morphospecies, it is important to note some caveats regarding the relationship between acoustic morphospecies richness and true species richness. For example, many species of birds have a repertoire

of calls and some mimic the calls of other species. Therefore, there may not be an exact one-to-one relationship between the acoustic morphospecies richness and the actual species richness. However, the same methodology of acoustic morphospecies identification was applied to all sites by the same pair of researchers, and the same relationship is shown between acoustic morphospecies richness and ASU, and an actual measure of species richness (bird regional richness) and ASU. For this reason, we are confident in the positive and significant relationship between species richness and ASU demonstrated in the results and recommend that biodiversity monitoring studies use ASU as a measure to compare richness of acoustic species across spatial and temporal scales.

We propose three explanations for the positive relationship between species richness and ASU. Firstly, as the number of species increases, we expect an increase in the diversity of when and how species communicate. In other words, more species means more diversity of acoustic signals at different times of day, resulting in greater use of acoustic space. This is clearly demonstrated by the increase in the proportion of insects in the high-richness sites (Figure 3), and the diverse range in frequencies used by insects (Figure 4), which together results in high values of ASU.

Secondly, if there is an optimal frequency range for effective transmission in a given habitat, this could lead to greater call overlap. Furthermore, acoustic communication is important for individual fitness, but there is a tradeoff between energetic cost and effective transmission [37,38]. While there may be an optimal transmission range defined by the physical structure of the habitat and local environmental conditions, species are limited by their hearing and sound-production abilities. In general, anurans can hear between ~50–4000 Hz, birds between ~50–12,000 Hz and insects can hear from the infra- to ultrasound [39–41]. These differences in frequency use are reflected in the distributions used by the acoustic morphospecies in this study (Figure 4), which included large frequency overlap between anurans and birds, and birds and insects. This suggests that individuals do not only compete with other individuals of the same species, but with other species within other taxonomic groups in the acoustic community. Competition for acoustic space in these areas of overlap can be reduced or avoided by shifting acoustic activity to different times of day or frequencies outside of the optimal range, which will result in greater ASU; nevertheless, the ability of species to use frequencies outside the optimal range will still be physiologically and phylogenetically constrained [8].

Thirdly, sites with high species richness had a greater proportion of insects, and insects use a large range of frequencies including high frequencies (Figures 3 and 4; Table 2). The combination of many insect acoustic morphospecies using many frequencies throughout the day and night resulted in insects driving ASU in these tropical forest sites (Table 3). The importance of insects in the use of acoustic space cannot be overstated. Insects are the most species-rich group of sound-producing animals [42,43], yet most acoustic studies in the tropics have focused on birds, followed by anurans. While the potential role of insects in shaping the evolution of avian and anuran vocalizations has been recognized (e.g., [7,44,45]), few studies have pursued the function of sound-producing insects in driving the structure of ASU in tropical forests. Nonetheless, insects have repeatedly been recommended for use in acoustic monitoring to evaluate changes in biodiversity [46,47]. We reiterate the recommendation that insects be incorporated into all acoustic monitoring studies, given that they are the largest component of the acoustic community, they drive total ASU in tropical forests, and they can influence when and what frequencies are used by other acoustically active species [45].

Although the percent and composition of ASU have been useful in describing variation in acoustic communities across these tropical sites, there are some limitations to this study and approach. For example, all sites were sampled during a relatively short period, which provided a snapshot in time. A longer sampling period would undoubtedly detect more species, but we do not expect this to change the relationship between species richness and proportion of ASU. In addition, the recording range (20–22,000 Hz) excluded many species of bats and some insects (e.g., some katydids) that use ultrasonic frequencies (>22,000 Hz). Most importantly, ASU does not weigh all species equally because bandwidth and call/activity duration are specific to each species (taxonomic group). For example, the signal of a species with a large bandwidth (i.e., the range of frequencies used by an individual species) will occupy

more frequency space (Table 4). In general, in this study birds had larger bandwidths than insects and anurans (Appendix A). In contrast, call/activity duration is often longer in insects. An individual insect stridulation (i.e., call) can last for more than one minute, and its population (e.g., cicadas) can call for hours, affecting the time domain. In general, the calls of anurans occur more frequently and they often call for longer periods compared to birds that typically call at irregular intervals with the majority of their acoustic activity occurring during the dawn chorus. These factors result in the average insect having a slightly greater weight in comparison to birds and anurans in ASU.

Table 4. A qualitative evaluation of the impact of different species groups on the use of acoustic space. +, ++, and +++ represent the relative impact of each acoustic parameter of each taxonomic group on ASU.

	Anurans	Birds	Insects
Bandwidth (max–min)	+	+++	++
Call/activity duration	++	+	+++
Impact on ASU	Low	Medium	High

An additional concern of the ASU approach for estimating species richness is that it does not specifically address the problem of imperfect detection of species. We attempt to standardize data collection by controlling for habitat structure (all sites were forested) and seasonality (all sites were sampled during the wet season), but by not taking into account imperfect detection (i.e., false negatives), we may be underestimating species richness. Nevertheless, the strong positive correlation between ASU and regional bird richness reinforces the utility of the ASU approach for monitoring fauna and for estimating species richness.

5. Conclusions

Acoustic space use (ASU) is a practical proxy for estimating and making cross-site comparisons of species richness in tropical forests. In addition, we show that insect richness drives ASU because insect species are more common and occupy a larger portion of the time and frequency domains than species from other taxonomic groups. Our findings have important implications for biodiversity monitoring, especially in high-diversity sites such as the tropics. ASU can be used both in rapid assessments and long-term monitoring programs to identify changes in species richness and composition due to natural and human-induced impacts, such as hurricanes and climate change. Changes in the use of acoustic space could also provide information about success of habitat restoration, although it will be necessary to manually review a subset of the recordings or to use automated species-recognition models to identify the individual species responsible for newly occupied frequencies. Moreover, ASU information can be combined with information provided by other spatial and environmental remote-sensing methods to better describe and predict changes in biodiversity. Because ASU can contain valuable information about species richness and composition of many taxonomic groups, ASU should be measured as part of worldwide biodiversity monitoring projects to improve our understanding of biological and ecological processes at large spatial and temporal scales.

Supplementary Materials: The following are available online at www.mdpi.com/2072-4292/9/11/1096/s1, Table S1: Characteristics and link to the recording with each of the 419 acoustic morphospecies and Table S2: The list of all candidate models for the subset regression analysis between ASU and the number of acoustic morphospecies for the three taxonomic groups.

Acknowledgments: We thank Miguel Acevedo, Carlos Corrada-Bravo, Ricardo Betancur and three anonymous reviewers for their comments on an earlier version of the manuscript. MCC was supported by the fellowship “Science Without Borders” from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) at Brazil (8933/13-8). We thank Hunt Oil Exploration and Production Company of Peru for financial and logistical support and the Ejecutor del Contrato de Administración de la Reserva Comunal Amarakaeri (ECA-RCA) for allowing access to the site to collect the Amarakaeri recordings.

Author Contributions: T. Mitchell Aide and Andrés Hernández-Serna conceived and designed the study; Andrés Hernández-Serna, Marconi Campos-Cerqueira, and Jessica L. Deichmann collected most of the recordings; T. Mitchell Aide, Andrés Hernández-Serna, Marconi Campos-Cerqueira, and Orlando Acevedo-Charry analyzed the data; all authors contributed to the writing of the paper.

Conflicts of Interest: T. Mitchell Aide, Marconi Campos-Cerqueira, and Orlando Acevedo-Charry are employees of Sieve Analytics Inc., the company that hosts the ARBIMON platform that was used for data analyses. The authors had no other conflicts of interest.

Appendix A

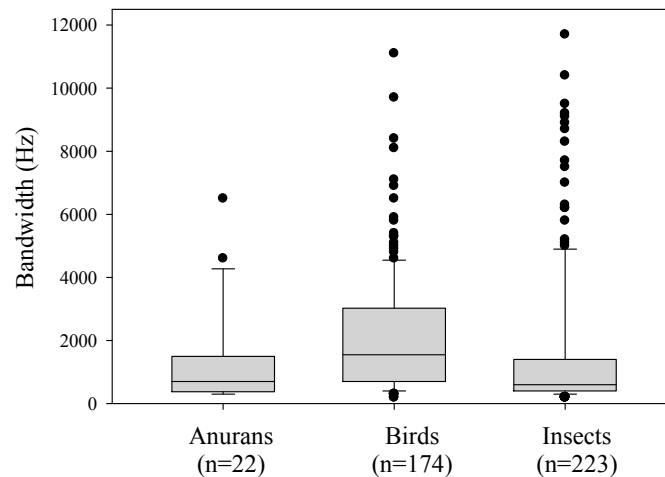


Figure A1. Box plots of the distribution of bandwidths of the acoustic morphospecies of anurans, birds and insects. Kruskal–Wallis = 47.5., $p < 0.001$.

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