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SPECIALTY SECTION

This article was submitted to
Acoustic Remote Sensing,
a section of the journal
Frontiers in Remote Sensing

RECEIVED 22 September 2022

ACCEPTED 27 February 2023

PUBLISHED 09 March 2023

CITATION

Retamosa Izaguirre M and
Barrantes Madrigal J (2023), Soundscape
structure in forests surrounded by
protected and productive areas in central
Costa Rica.

Front. Remote Sens. 4:1051555.

doi: 10.3389/frsen.2023.1051555

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Soundscape structure in forests surrounded by protected and productive areas in central Costa Rica

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Ecosystems are under a multitude of pressures, including land-use change, overexploitation, pollution, and climate change. Most studies, resources, and conservation efforts are allocated to protected areas, while anthropogenic activities in their surroundings may affect them in ways that are poorly understood. We evaluated soundscape structure in forests surrounded by protected or productive areas in central Costa Rica. We sampled soundscapes in 91 recording sites in Grecia Forest Reserve and Poas Volcano National Park, and surrounding areas with productive activities (predominantly agricultural and urban). We classified sampling sites into three clusters according to landscape entropy, forest amount, and fragmentation surrounding recording points: more fragmented, more conserved, and intermediate. The conserved cluster showed higher acoustic diversity or entropy, but lower acoustic complexity, shorter duration of sounds in all frequency ranges, and lower amount of energy in the biological frequency bands than the fragmented cluster. We additionally found a positive significant relationship between the amount of forest and acoustic entropy or diversity indices, but a negative relationship with acoustic activity or energy indices. Indices, such as spectral and temporal entropy, the entropy of spectral variance, and total entropy, seemed to be a better fit than acoustic complexity and bioacoustic indices as indicators of habitat conservation in this study. Acoustic indices revealed that the surrounding matrices of protected areas have an impact on acoustic environments. We encourage researchers and decision-makers to carefully interpret acoustic indices when evaluating habitats showing a higher value in acoustic energy or activity because this might not necessarily reflect either a high level of biodiversity or habitat conservation. Also, we highlight the importance of preserving undisturbed forested matrices around protected areas, as they are important for maintaining acoustic diversity.

KEYWORDS

acoustic indices, soundscape, habitat conservation, biodiversity, landscape metrics

1 Introduction

Ecosystems are under a multitude of pressures, including land use change, overexploitation, pollution, and climate change (Glaser 2015). As conservation measures, a series of protected areas have historically been established, which usually act as islands of protection in a matrix with different degrees of anthropogenic alteration. Most research, resources and conservation efforts are allocated to protected areas, while anthropogenic

activities that take place in their surroundings, impact on them in ways that are poorly understood and managed.

Costa Rica has over 25% of its territory under some category of management within the system of conservation areas (Noches, 2005). These areas play an important role in the conservation of species and global processes (Pimm et al., 2018). But despite these initiatives and efforts to conserve forests, the change in land use and the overexploitation of its products as a result of population growth, still threaten their conservation (Maxwell et al., 2020). Some authors have suggested the need to assess complementary conservation strategies that also contribute to minimizing the problem of isolation of existing protected areas, such as the protection of wooded pastures, forest plantations, living fences, agroforestry systems, and even isolated fragments of natural or managed forest (Naoki et al., 2003).

The central conservation area (ACC), declared as a Biosphere Reserve, shelters 25 protected wild areas and has more than 250,000 ha of forests, which play a fundamental role in protecting biodiversity. In this area there is great biological diversity, the types of vegetation vary from tropical rain forest, low montane rain forest; to the subalpine pluvial or paramo of stunted vegetation in the Irazú Volcano. Currently, threats such as deforestation, hunting, the degradation of hydrographic basins, the expansion of agricultural frontiers and fragmentation due to urban expansion are present in the area. These activities generate significant pollution and exert strong pressure on protected wild areas (SINAC 2014). Other sources of pollution, such as noise, emerge with urbanization. Noise contributes to the degradation of ecosystems and affects wildlife, modifying the behavior and movement patterns of some species (Barber et al., 2011; Pijanowski et al., 2011).

Protected wilderness areas provide values associated with the appreciation of nature, both visual and acoustic, that can be exploited, as in the case of ecotourism, where the acoustic quality of the landscape is an essential element for visitors seeking sites free of noise (Farina et al., 2011). In tropical forests, high biodiversity contributes to a high diversity of natural sounds, so it is important to quantify the impact of the effects of human activity, in relation to sound, on wildlife (Pijanowski et al., 2011; Rodríguez et al., 2014). The loss of habitats and biodiversity causes the disappearance of natural sounds; that is why they must be managed as a natural resource that must be conserved (Pijanowski et al., 2011).

There is a constant need to consider the effect of anthropogenic activities on natural areas and surroundings as a possible source of ecosystem degradation and subsequent threat to biodiversity. It is important to conserve important sectors of land for protection, but at the same time manage the matrix surrounding the protected areas in order to minimize the negative impact of productive activities on them. For this, it is important to have effective monitoring mechanisms that can provide early warning of problems associated with ecosystem degradation in the surroundings of protected areas that could serve as a basis for decision-making and actions aimed at complying with environmental regulations in force in the country by the competent authorities and in agreement with the local stakeholders.

A variety of ecological methods and indicators have been used to assess the impacts of the anthropic activity on biodiversity and habitat conservation. However, one of the greatest challenges in

conservation ecology and biology is the assessment of biodiversity through effective monitoring techniques, which allow covering wide spatial and temporal scales (Depraetere et al., 2012). This knowledge should be the basis for building more robust criteria that lead to better management of the territory, through a centralized monitoring system that allows researchers and decision-makers to have a good general perspective on the results obtained by monitoring programs on a national scale (Marsh and Trenham 2008). For example, cost-efficient techniques have been proposed to automatically collect large amounts of data at larger ecological and spatial scales, such as the recording of sounds to represent and quantify complete acoustic landscapes through a series of acoustic indices. These indices can be used for biodiversity assessments, research on community dynamics and landscape patterns (Sueur et al., 2014) since acoustic landscapes reflect the biophysical properties of the landscape, as well as the communication mechanisms between organisms, and they can function as an indicator of the state of biodiversity and ecosystems (Pijanowski et al., 2011).

Ecosystem sounds create an acoustic landscape composed of acoustic periodicities and frequencies emitted by biophysical entities of the ecosystem (Schafer 1977; Truax et al., 1984; Qi et al., 2008), which can be partitioned into anthropic (anthrophony), biological sources (biophony) and physical (geophony). The proportion between these different components of the acoustic landscape gives us an indication of the impact of the anthropic activity on ecosystems (Napoletano 2004; Qi et al., 2008; Joo et al., 2011; Pijanowski et al., 2011). In addition, there is another series of acoustic indices that estimate the level of complexity in terms of time, frequency, or amplitude of the sound (Sueur et al., 2014), which have been related to traditional biodiversity indices (Sueur et al., 2008; Farina et al., 2011; Depraetere et al., 2012; Gasc et al., 2013; Rodríguez et al., 2014; Pieretti et al., 2015; Trigg 2015; Machado et al., 2017; Mammides et al., 2017; Retamosa Izaguirre et al., 2018; Retamosa Izaguirre et al., 2021a; Retamosa Izaguirre et al. et al., 2021b).

We evaluated soundscape structure in forests surrounded by protected and productive (agricultural and urban) activities as an indicator of habitat conservation in central Costa Rica. In general, we expected that more conserved sites (landscapes with less entropy, larger size of forested patches, and less fragmented forest) would have a higher acoustic diversity and activity, as well as a higher proportion of biophonies than anthrophonies. We discuss the use of acoustic indices as an early indicator of habitat conservation associated with productive activities in the surroundings of protected areas, as a tool to support decision-making and achieve conservation goals.

2 Methods

2.1 Study area

The Central Conservation Area (ACC) is located in the central region of the country, where it incorporates the entirety of the great metropolitan area (Silhouettes, 1987). Due to its location and urban development, it covers approximately 54% of the Costa Rican population in an area of 860 8000 ha, equivalent to 16.84% of the

TABLE 1 Landscape metrics used to describe landscape structure surrounding recording sites in the Central Conservation Area of Costa Rica, 2019–2020.

Metric		Description
Marginal Entropy	Ent	Represents the diversity of spatial categories, it is calculated as the marginal entropy of the distribution (Nowosad and Stepinski, 2019)
Relative Mutual Information	Relmutinf	Spatial autocorrelation causes the value of mutual information to increase with landscape diversity (marginal entropy). This can be corrected by calculating the relative mutual information, which results from the ratio between the mutual information and the marginal entropy. The relative mutual information ranges from 0 to 1 and allows comparison of spatial data with different numbers and distribution of categories (Nowosad and Stepinski, 2019)
Farmland Cover (ha)	Farmland	Area covered by agricultural lands in each cell of the grid
Forest Cover (ha)	Forest	Area covered by forest in each cell of the grid
Urban Cover (ha)	Urban	Area covered by urban areas in each cell of the grid
Number of Patches	NumP	Total number of patches in each cell of the grid (McGarigal and Marks, 1995)
Area Weighted Mean Shape Index	AWMSI	Area Weighted Mean Shape Index in each cell of the grid adjusted for shape size. A measure of shape complexity. It is the same as Mean Shape Index with the addition of individual patch area weighting applied to each patch. MSI is greater than one, MSI = 1 when all patches are circular (polygons) or square (grids). MSI = sum of each patches perimeter divided by the square root of patch area (hectares) for each class (Class Level) or all patches (Landscape Level) and adjusted for circular standard (polygons), or square standard (grids), divided by the number of patches (McGarigal and Marks, 1995)
Mean Patch Size (m ²)	MPS	Average patch size in each cell of the grid (McGarigal and Marks, 1995)
Mean Patch Edge	MPE	Average patch edge in each cell of the grid (McGarigal and Marks, 1995)
Distance to roads	dist.roads	Distance to the nearest road
Distance to rivers	dist.rivers	Distance to the nearest river

country's area (SINAC 2014). Within its delimitation 31 protected areas are included in this conservation area.

The study was carried out in the northwestern region of the ACC, covering the protected areas of the Grecia Forest Reserve and the southern sector of the Poás Volcano National Park and its surroundings. The Grecia Forest Reserve is located approximately 14 km north of the city of Grecia and is bordered to the north by the Poás National Park (Leandro et al., 2016). It has an area of 2,000 ha with an elevation range between 1,600 and 2,500 m above sea level, which includes both areas of native vegetation and cypress and pine plantations (Maglianesi 2010). The average precipitation is 3600 mm per year, and it maintains an average temperature of 16 °C (Leandro et al., 2016). For its part, the Poás Volcano National Park is characterized by high rainfall with an annual rainfall that varies between 3,500 and 8,000 mm and a temperature that oscillates between 10 and 24 °C with an average of 14 °C (Boza 2001). Most of the protected area is covered by forests except places burned by volcanic eruptions, tourist areas and deforested areas. The canopy can generally reach up to 30 m in height, however it usually does not exceed 20 m. The understory is dense and most of the trees are covered with epiphytic plants such as mosses, bromeliads, orchids and ferns (González et al., 2019).

2.2 Landscape structure sampling

To sample the landscape structure around recording points, we overlaid a grid of 250 by 250 m over the study area and calculated 11 landscape metrics (Table 1) for those cells where recording sites were located. These landscape metrics were selected according to the effect reported in the literature on

biodiversity (such as species richness, distribution, the abundance of populations, and genetic diversity, among others; Fahrig 2003), in addition to representing different aspects of interest to describe landscape conservation. We performed this analysis using ArcGIS (ESRI 2016) and landscapemetrics package (Hesselbarth et al., 2019) for R (R Core Team 2020).

2.3 Acoustic sampling

We sampled soundscapes in 91 recording sites in Grecia Forest Reserve and Poas Volcano National Park, and surroundings areas with productive activities (predominantly agricultural and urban). All recording sites were located in forest patches of at least 10 ha, inside or no more than 3 km away from protected areas (Figure 1).

We used Song Meter Digital Field Recorders (SM2 +; Wildlife Acoustics Inc, Supplementary Appendix S1) to sample soundscapes. Two omnidirectional microphones were placed in each recorder, so the recording would be made through two channels, or in stereo. A sampling rate or frequency rate of 44.1 kHz and 16 bits' resolution were used. Audio files were recorded in Microsoft Wave (.wav) format. Audio files were stored on 64 GB capacity SDHC memory cards. At each recording site, the equipment was fixed to the trees at an approximate height of 1.50 m. The recorders were programmed to make continuous recordings during peaks of bird activity (4:00 a.m. - 7:00 a.m. and 15:00 p.m. - 18:00 p.m.), and for periods of 10 min every half an hour during the rest of the day. Acoustic recorders were active for a total of four to six consecutive days during the period July 2019 to June 2020.

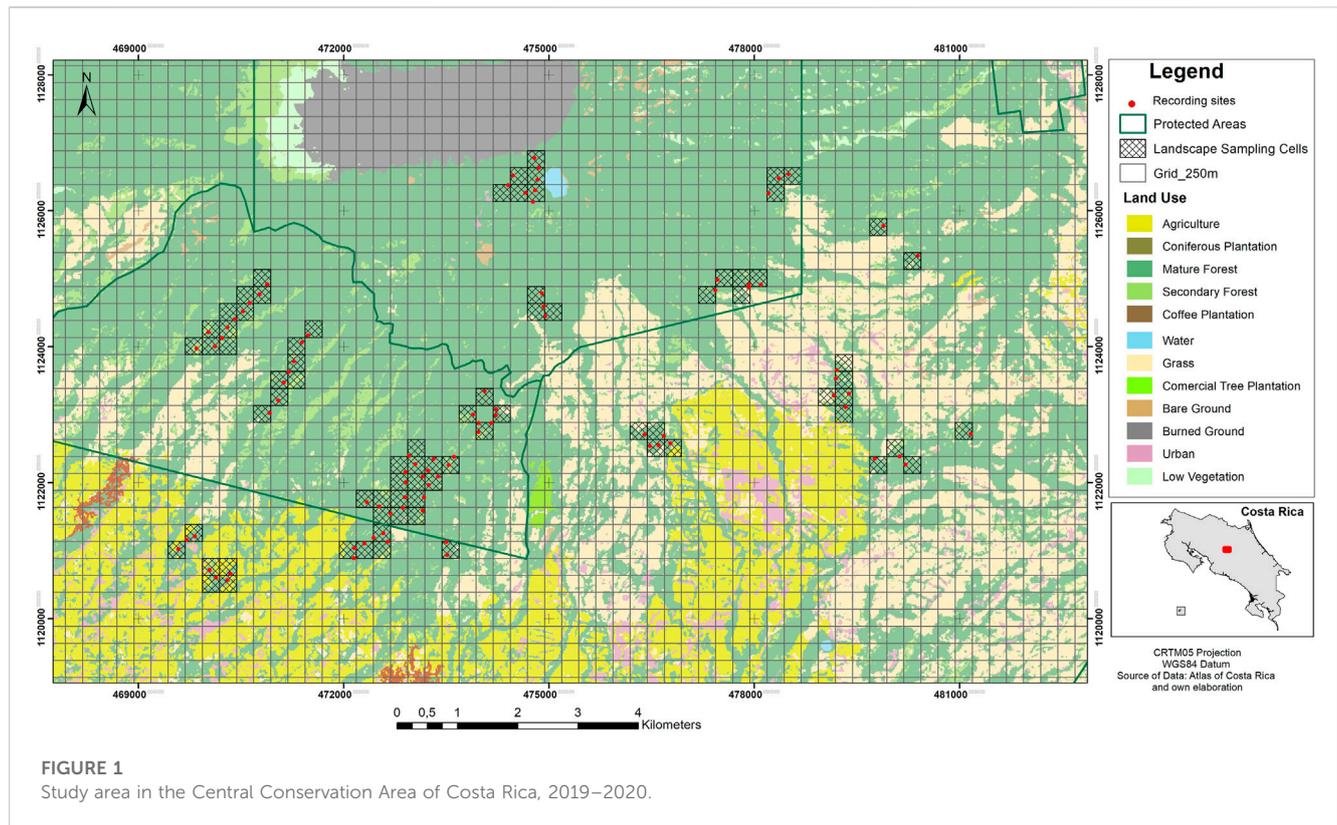


FIGURE 1
Study area in the Central Conservation Area of Costa Rica, 2019–2020.

2.4 Statistical analysis

2.4.1 Cluster analysis with landscape metrics

We ran a K-means cluster analysis (Hartigan & Wong Algorithm, 1979) to classify grid cells into clusters according to the landscape metrics described in Table 1. We selected the K-means method because it is one of the most used in this type of analysis and it has proven good results (Benocci et al., 2022). We specifically used marginal entropy (ent), relative mutual information (relmutinf), Farmland cover (Farmland), Forest cover (Forest), Urban cover (Urban), Mean Patch Edge (MPE), Number of patches (NumP), Area weight mean shape index (AWMSI) and Mean Patch Size (MPS) as classification variables (Table 1). We did not use the variables distance to roads and distance to rivers because this would have incorporated a spatial influence in the analysis and led to grouping the grid cells by their proximity rather than by the characteristics of the surrounding matrix. All variables were scaled to have mean = 0 and sd = 1. The optimal number of clusters was defined using the silhouette index (Rousseeuw, 1987).

2.4.2 Preselection of acoustic indices

Recordings were processed to obtain a series of 38 acoustic indices (Table 2) for every one-minute audio segment using packages Soundecology, version (1.3.3) (Villanueva-Rivera & Pijanowski, 2018) and Seewave, (version 2.0.5) (Sueur et al., 2008) for R (R Core Team 2020), and additional code developed by the Buxton et al. (2018). To reduce the number of indices for analysis, we evaluated the acoustic indices according to their performance to discriminate between clusters of grid cells classified using landscape variables. We ran a random forest classification model (Breiman 2001) using the median per hour and per cell of the grid of acoustic indices as

explanatory variables to classify each grid cell into clusters. The percentage of importance of each index in the classification process was taken as a criterion to select acoustic indices for further analysis. We also eliminated the acoustic indices that were redundant or highly correlated and kept the indices that had demonstrated good performance as ecological indicators in other studies (Buxton et al., 2018; Eldridge et al., 2018; Ross et al., 2021). We finally reduced the set to 19 acoustic indices (Table 3), which represent a different characteristics of the sound, including entropy and acoustic diversity (ADI, AEI, Hf, Ht, TE, HvSPL, Hm), acoustic activity (ACI, AAdur, AAduranth, roughness), acoustic energy (BIO, NP, dif_L10L90, msldbA_low, MAE, mdbGL, NDSI) and dominant frequencies (dfreq).

We used the median per hour and per cell of the grid of every acoustic index for all analyses to avoid extreme values that may have occurred during a one-minute segment and to improve analysis performance. We manually listened and reviewed two recorders per site, for a total of 69331 min, labeling periods of heavy rain. We used this information to train a Random Forest model to predict the occurrence of heavy rain every minute according to the selected acoustic indices (Breiman 2001). Minute files containing heavy rain were not considered for further analyses.

2.4.3 Analysis of acoustic indices according to cluster created by the landscape metrics analysis

For evaluating the behavior and contrasting acoustic indices by clusters, we fitted generalized linear mixed-effects models using Template Model Builder (Brooks et al., 2017) using the median per hour and per cell of the grid of every acoustic index as the response variable while cluster, time (hour of the day), and the interaction between both, as fixed effects. The recorder ID was used as a random effect.

TABLE 2 Acoustic indices run initially for each sampling point in the Central Conservation Area of Costa Rica, 2019–2020.

Acoustic indices	Name	Reference
AA	Acoustic activity (2000–11000 Hz)	Townsey et al. (2014)
AAanth	Acoustic activity (0–2000 Hz)	Townsey et al. (2014)
AAc	Count of acoustic events (2000–11000 Hz)	Townsey et al. (2014)
AAcanth	Count of acoustic events (0–2000 Hz)	Townsey et al. (2014)
AAdur	Duration of acoustic events (2000–11000 Hz)	Townsey et al. (2014)
AAduranth	Duration of acoustic events (0–2000 Hz)	Townsey et al. (2014)
ACI	Acoustic Complexity Index	Pieretti et al. (2011)
ADI	Acoustic Diversity Index	Villanueva-Rivera et al. (2011)
AEI	Acoustic Evenness Index	Villanueva-Rivera et al. (2011)
AthPh	Anthrophony	Joo et al. (2011)
avgAMP	Average signal amplitude	Townsey et al. (2014)
BIO	Bioacoustic Index	Boelman et al. (2007)
Bio_anth	Ratio of biophony to anthrophony	Buxton et al. (2018)
BioPh	Biophony	Joo et al. (2011)
dfreq	Average Dominant Frequency	-
dif_L10L90	Difference in exceedance levels	Buxton et al. (2018)
Hf	Spectral Entropy	Townsey et al. (2014)
Hm	Entropy of spectral maxima	Townsey et al. (2014)
Ht	Temporal Entropy	Townsey et al. (2014)
HvPress	Entropy of spectral variance	Townsey et al. (2014)
HvSPL	Entropy of spectral variance (dB)	Townsey et al. (2014)
L10AMP	L10 exceedance level	Buxton et al. (2018)
MAE	Median Amplitude Envelope	Depraetere et al. (2012)
Mamp	Median sound level	Buxton et al. (2018)
mdBGL	Median background level	Buxton et al. (2018)
mldb_bio	Mean sound level with dB (2000–11000 Hz)	Buxton et al. (2018)
mldb_low	Mean sound level with dB (0–2000)	Buxton et al. (2018)
mldbA_bio	Mean sound level with dBA 2000–11000 Hz)	Buxton et al. (2018)
mldbA_low	Mean sound level with dBA (0–2000)	Buxton et al. (2018)
NDSI	Normalized Difference Soundscape Index	Kasten et al. (2012)
NP	Number of Peaks	Gasc et al. (2013)
NumCL	Spectral diversity	Towsey et al. (2014)
Pk	Peak frequency	Buxton et al. (2018)
pkd	Spectral kurtosis	Bormpoudakis et al. (2013)
pks	Spectral skewness	Bormpoudakis et al. (2013)
Roughness	Roughness	Rychtáriková and Vermeir (2013)
SP2	Spectral persistence	Towsey et al. (2014)
TE	Total Entropy	Towsey et al. (2014)

TABLE 3 Description of acoustic indices calculated for each sampling point in the Central Conservation Area of Costa Rica, 2019–2020.

Acoustic indices	Code	Description
Acoustic Complexity Index	ACI	Measures the variability of sound intensity over time and frequency [9]. Higher values indicate more complex soundscapes. Range = [0, +]
Acoustic Diversity Index	ADI	Summarizes sound intensity distribution applying the Shannon index over the proportion of signals above an intensity threshold across the spectrum [10]. Higher values indicate that acoustic energy is spread evenly across frequency bands. Range = [0, +]
Acoustic Evenness Index	AEI	Same as the ADI, but the Gini index is applied across all frequency bins, instead of the Shannon index [10]. High values indicate acoustic energy is restricted to a narrow frequency range. Range = [0, 1]
Bioacoustic Index	BIO	It is a function of both amplitude and number of occupied frequency bands between 2–11 kHz. It is calculated as the area under each curve included all frequency bands between 2–11 kHz associated with the dB value that was greater than the minimum dB value for each curve. Higher values indicate greater disparity between bands [15]. Range = [0, +]
Median Amplitude Envelope	MAE	The median of the amplitude envelope normalized by the maximum value to give results between 0–1. Higher values reflect noisier soundscapes [18]. Range = [0, 1]
Normalized Difference Soundscape Index	NDSI	The ratio (biophony – anthrophony)/(biophony + anthrophony). Where biophony is the energy on the frequency range 2–8 kHz and anthrophony between 1 and 2 kHz [11]. Higher values indicate a higher proportion of acoustic energy in the biophony band. Range = [-1, 1]
Number of Peaks	NP	Counts the number of major frequency peaks obtained on a mean spectrum. Higher values indicate a greater frequency spectral complexity [14]. Range = [0, +]
Spectral Entropy	Hf	Divides intensity values by the sum of intensity in a frequency band. Calculates the entropy for these values using the negative sum of each value multiplied by the log of the value and divided by the log of the number of intensity values [3]. Higher values indicate evenly distributed sound across frequency bands. Range = [0, 1]
Temporal Entropy	Ht	Divide the intensity values by the sum of intensities in a time interval. Calculates entropy for these values using the negative sum of each value multiplied by the log of the value and divided by the log of the number of intensity values [3]. Higher values indicate evenly distributed sound over time. Range = [0, 1]
Total Entropy	TE	It is the product of Hf * Ht. Quantifies the entropy across time and frequency [3]. Higher values indicate evenly distributed sounds across frequency and time. Range = [0, 1]
Entropy of spectral variance (dB)	HvSPL	It measures the entropy in the variance of the sound pressure values of each frequency band. High values indicate evenness in the distribution of acoustic activity (modulations) across the frequency spectrum. Low values indicate that the acoustic activity is concentrated in few frequency bands. Theoretically, high values indicate greater activity and acoustic diversity distributed throughout the spectrum or a very flat or quiet signal
Entropy of spectral maxima	Hm	It quantifies the entropy in the distribution of dominant frequencies through time. High values indicate little dominance; energy distributed throughout the spectrum. Low values indicate dominance of a frequency band (usually insects)
Duration of acoustic events (2000–11000 kHz)	AAdur	Estimates the average duration of sounds above the background noise threshold in each frequency band. High values indicate domain of signals of longer duration, low values indicate short pulses
Duration of acoustic events (0–2000 kHz)	AAduranth	Estimates the average duration of sounds above the background noise threshold in each frequency band. High values indicate domain of signals of longer duration, low values indicate short pulses
Difference in exceedance levels	dif_L10L90	Calculates the difference between the sound pressure level that bound the 10% of the largest values and the 10% of the smallest values. The resulting value is representative of the variation in the sound pressure level in the analyzed time interval. High values indicate the presence of strong signals
Roughness	roughness	Indicates the median change in acoustic energy from one time frame to the next in an audio segment. High values correspond to audios with greater acoustic activity, generally related to greater biological activity
Average Dominant Frequency	dfreq	Indicates the average dominant frequency
Mean sound level with dBA (0–2000)	msldBA_low	Converts values of sound pressure level (dB) to pressure values (linear scale), takes the average pressure of the values of all frequency bands in a time interval (1 min), and converts it back to sound pressure levels (dB)
Median background level	mdBGL	Provides a measure of the median background noise level. Noisier sites have a higher value

2.4.4 Analysis of dominant frequencies by cluster

We analyzed the dominance of each 1 kHz frequency band from 0–11 kHz according to clusters. Frequencies below 500 Hz were discarded to avoid bias in the dominant frequencies due to the self-noise of the recorder. Therefore, the first frequency band consisted of frequencies between 0.5–1 kHz. We performed generalized linear

mixed-effects models (Maglianesi, 2016) for each frequency band using the hourly median of the number of times each frequency band was dominant as the response variable. The explanatory variables cluster, the hour of the day, and the interaction between the two were considered fixed effects. Recorder ID was taken as a random effect. The model also incorporated a zero-inflated formula,

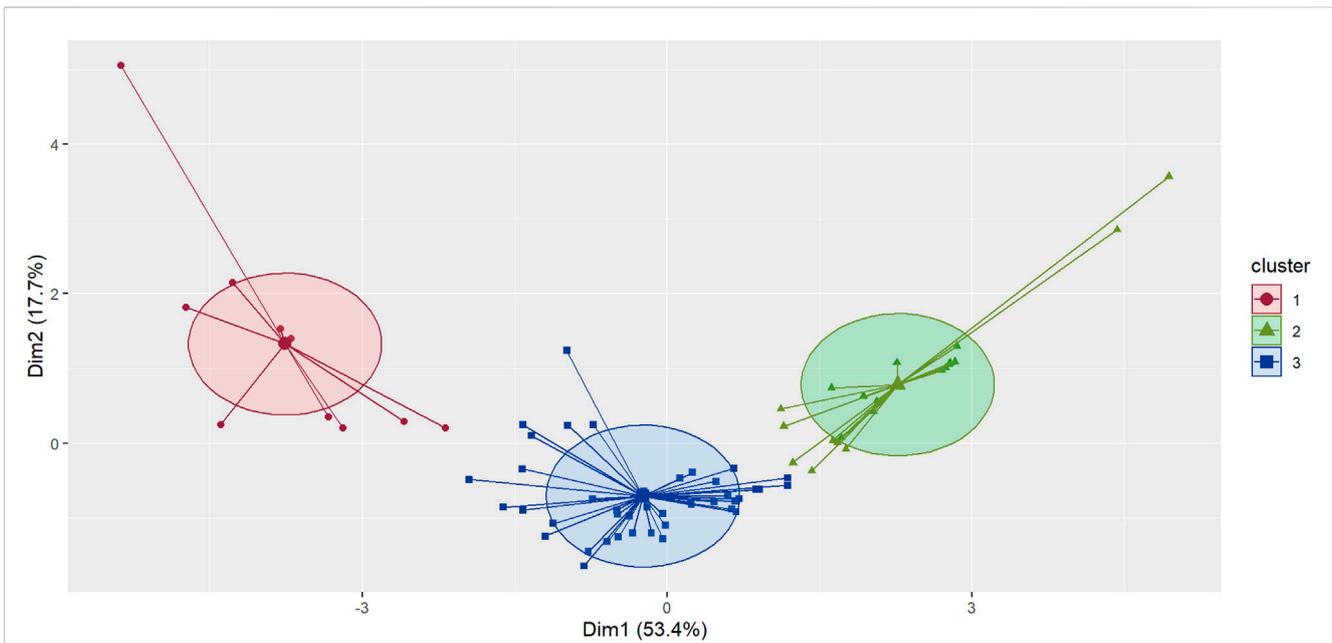


FIGURE 2
K-means cluster classification of sampling cells in the Central Conservation Area of Costa Rica, 2019–2020.

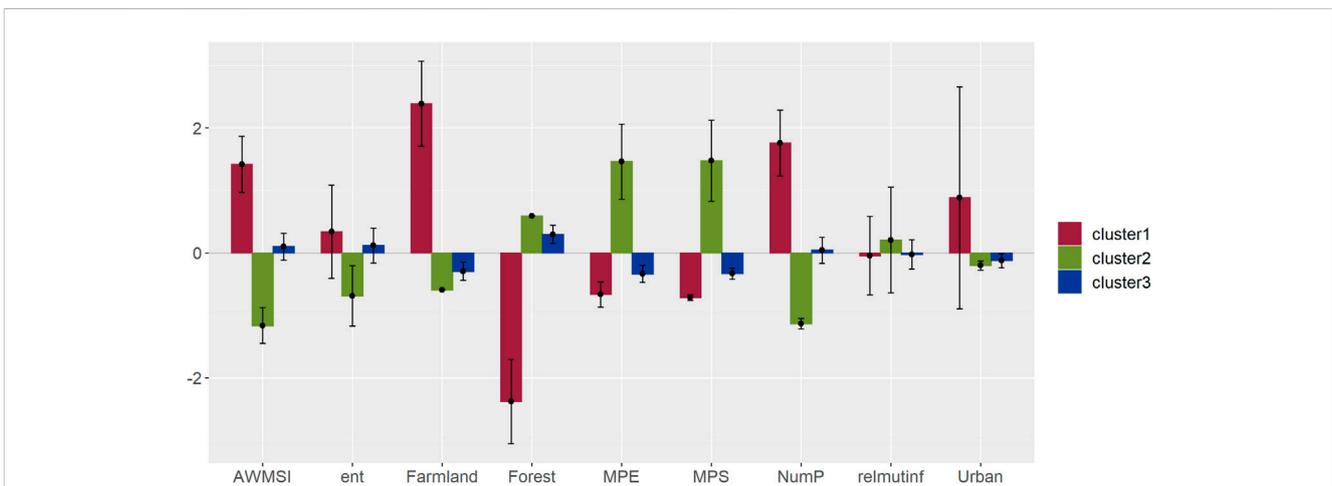


FIGURE 3
Geographic distribution of recording sites according to cluster classification created by the landscape metrics analysis.

since the dominant frequency values had many zeros (for example, in all the minutes where a frequency band was not dominant). We first fitted models using Poisson distribution because the values of the dependent variable are integers (they represent counts of times in which the frequency band was dominant for every one-minute audio segment). However, this distribution generated an overdispersion, so a negative binomial distribution was finally used.

2.4.5 Modeling the relationship of acoustic indices with landscape metrics

We analyzed the relationship between acoustic indices and landscape metrics (ent, Forest, dist.rivers, dist.roads, NumP and

MPE; Table 1). We did not used in this analysis other landscape metrics because they were highly correlated.

We performed generalized linear mixed-effects models to analyze the relationship between each acoustic indices and landscape variables. Models were fitted using the median per hour and per cell of the grid of every acoustic index as the response variable, the landscape metrics as independent fixed effects, and the recorder as a random effect. We included an autoregressive covariance structure (AR1) for hour of the day to account for potential temporal autocorrelation. Acoustic indices outliers were removed before analysis. Landscape metrics were standardized to improve model convergence.

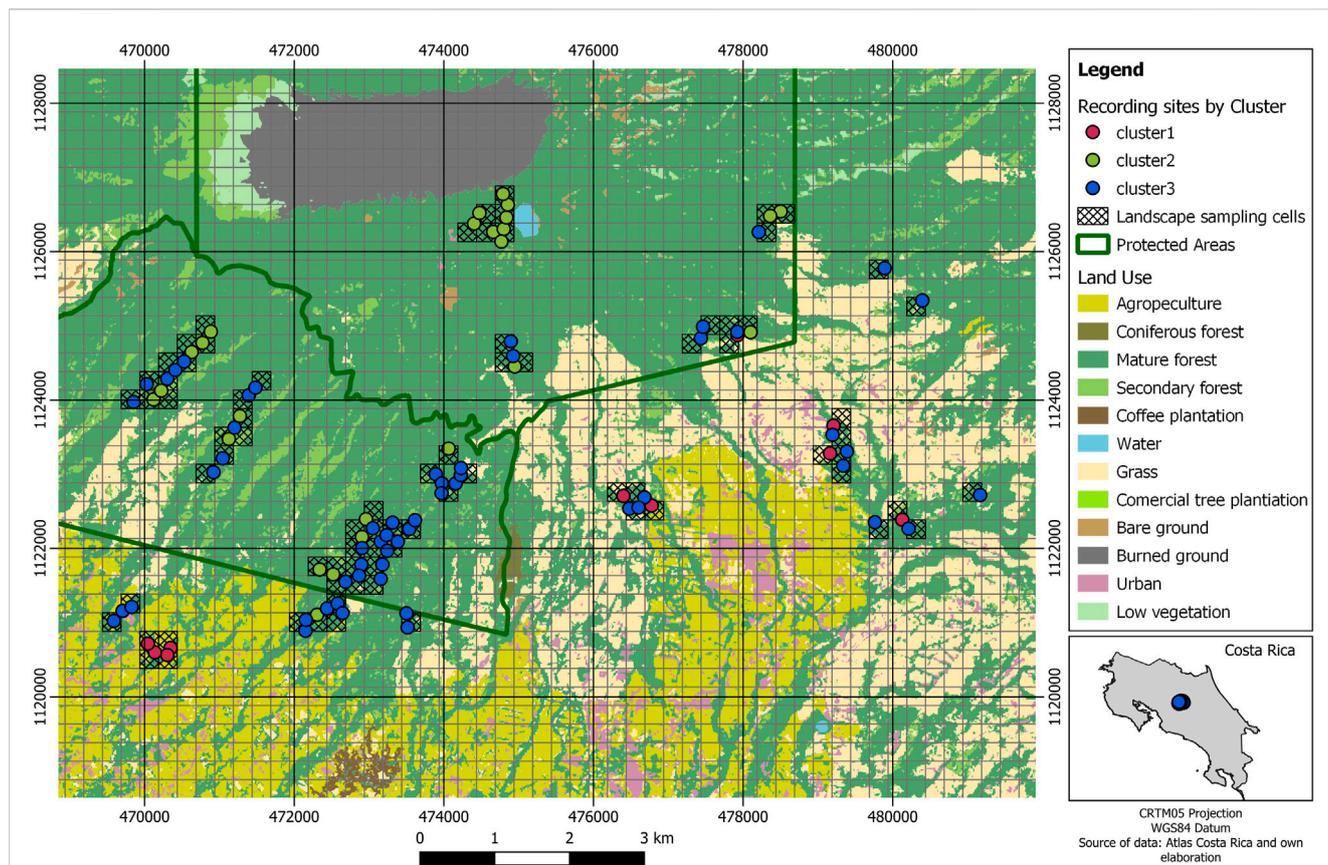


FIGURE 4

Mean values of the landscape variables for every cluster in the Central Conservation Area of Costa Rica, 2019–2020. Black lines represent the 95% confidence interval for the mean calculation. Y-axes represent the value of the scaled variable, where 0 represents the global mean for all values.

TABLE 4 Center values for every cluster and 95% confidence intervals in the Central Conservation Area of Costa Rica, 2019–2020.

Variable	Cluster 1	Cluster 2	Cluster 3
Ent	0.745 ± 0.32	0.299 ± 0.21	0.64 ± 0.12
Relmutinf	0.414 ± 0.13	0.465 ± 0.17	0.418 ± 0.05
Farmland cover (%)	0.474 ± 0.11	0.001 ± 0.001	0.476 ± 0.023
Forest cover (%)	0.517 ± 0.11	0.998 ± 0.001	0.951 ± 0.023
Urban cover (%)	0.009 ± 0.014	0.0002 ± 6 × 10 ⁻⁴	0.0009 ± 0.001
MPE (m)	225.49 ± 33.19	572.42 ± 97.90	279.16 ± 22.06
NumP	20.50 ± 3.25	2.64 ± 0.50	9.89 ± 1.29
AWMSI	2.332 ± 0.18	1.30 ± 0.11	1.81 ± 0.086
MPS (m)	3186.99 ± 509.9	28186.26 ± 7398	7587.52 ± 984.16

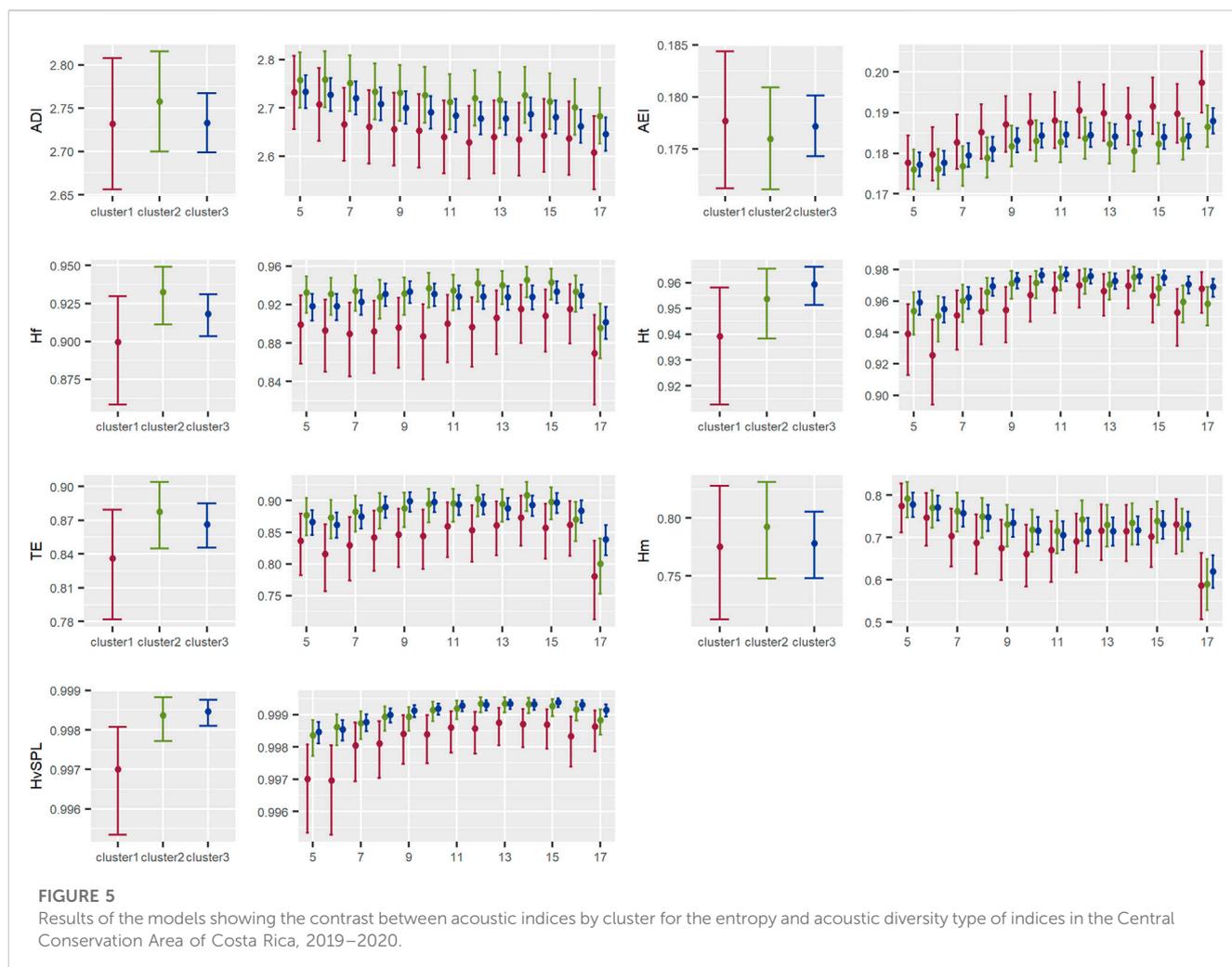
We fitted NDSI, Hf, Ht, TE, MAE, Hm and HvSPL indices with beta error structure; NDSI was transformed before the analysis to convert its values between 0–1 using the formula $(NDSI + 1)/2$ (Fairbrass et al., 2017). ACI, BIO, AAdur, AAduranth, dif_L10L90, roughness and dfreq were fitted using a gamma structure and log link function; ADI, msldBA_low and

mdBGL with a Gaussian structure; and NP with a negative binomial structure as it is a count variable. Models were built using the R package glmmTMB (Brooks et al., 2017) and assumptions were checked using DHARMA package (Hartig, 2022).

2.4.6 Aural detection of biophonies and anthrophonies

A thorough review of the audio from 13 recorders was carried out aurally. We reviewed 10 min every half hour from 5:00 a.m. to 6:00 p.m. for three consecutive days in each recorder. The audios were searched for acoustic events, such as biophonies and anthrophonies, using the Adobe Audition program for listening and visualization. Biophonies were classified into taxonomic groups of birds, insects, amphibians, and mammals. We registered the duration in time (seconds) of each category of acoustic events for each hour of the day. We then summarized all categories into their mean and standard error per hour for comparison among clusters.

The distribution of the selected recorder was three from cluster 1, two from cluster 2, and eight from cluster 3. We used only birds and insects in the biophony category because mammals and amphibians were underrepresented in audio recordings.



3 Results

3.1 Cluster analysis with landscape metrics

The cluster analysis classified the sites into three clusters (Figures 2, 3). Cluster 1 was characterized by more farmland and less forest cover, higher patch shape complexity, a higher number of patches, and the total edge. Cluster 2 and cluster 3 did not differ markedly regarding the amount of forest, however, cluster 2 presented more forest and less farmland cover than cluster 3. In addition, cluster 2 presented a lower number of patches, total edge, and patch shape complexity than the other clusters. Marginal entropy and relative mutual information did not differ between clusters (Figure 4; Table 4).

3.2 Analysis of acoustic indices by cluster

To facilitate the interpretation, we present the results of the models showing the contrast between acoustic indices by cluster according to three categories of acoustic indices: 1) acoustic entropy and diversity indices (ADI, AEI, Hf, Ht, Hm, HvSPL, and TE) 2) acoustic activity or events indices (ACI, roughness, AADur,

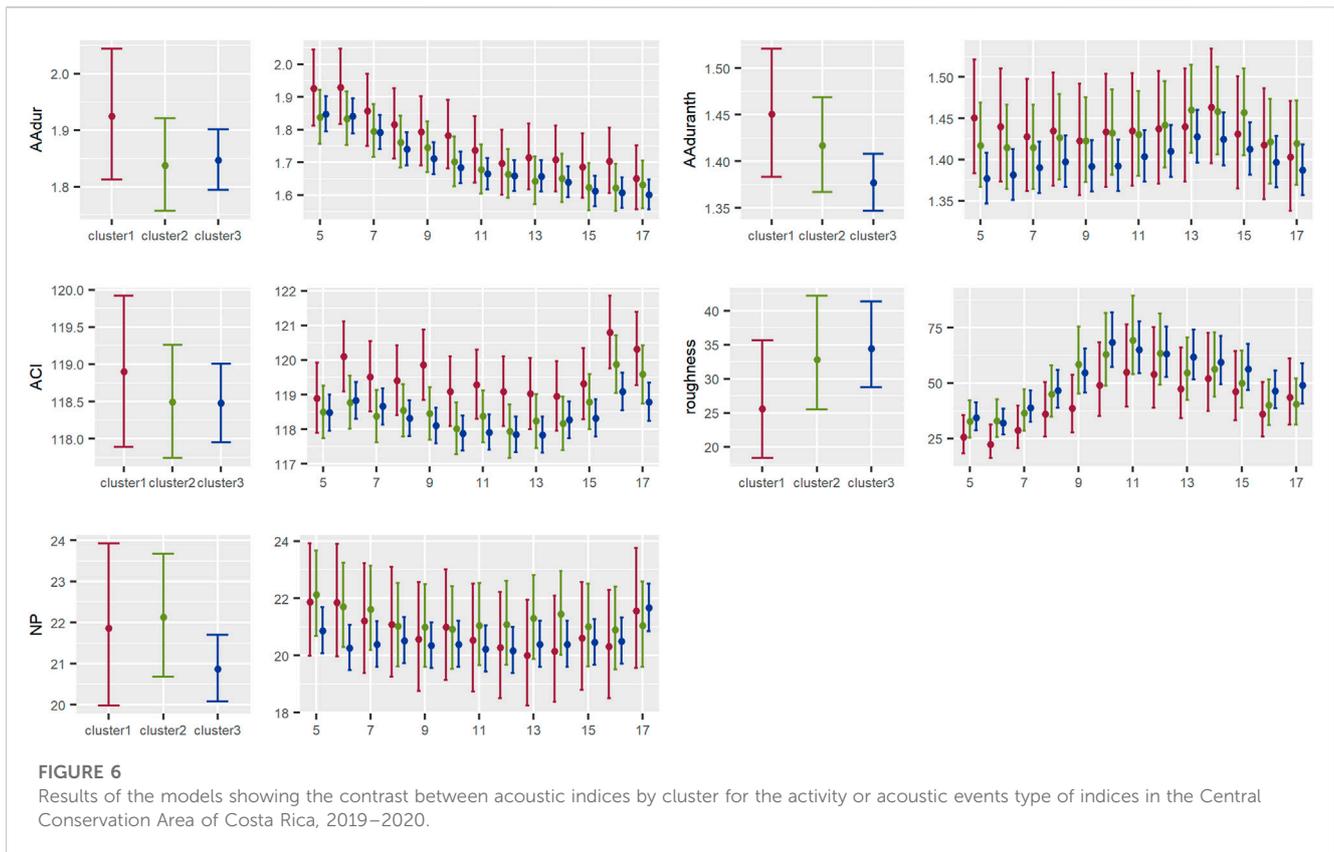
AADur, and NP), and 3) summary of acoustic energy indices (BIO, dif_L10L90, mslBA_low, MAE, mdBGL, NDSI and dfreq). In general, we observed a higher variability in all acoustic indices in cluster 1 than in clusters 2 and 3 (Figures 5–7).

3.2.1 Acoustic entropy and diversity indices

There was a general tendency, although statistically non-significant, of higher entropy or diversity in clusters 2 and 3 than in cluster 1, being more noticeable between clusters 2 and 1 in the afternoon hours. Following the opposite pattern, a lower AEI value (meaning a higher acoustic evenness) was detected in clusters 2 and 3 than in cluster 1. Besides, cluster 1 presented less variation in the variance of the energy among frequency bands than in clusters 2 and 3 (Figure 5).

3.2.2 Acoustic activity or events indices

There was a general tendency, although statistically non-significant, for a longer duration of sounds above the background noise threshold in each frequency band in cluster 1 than in clusters 2 and 3, both for the range of frequencies events between 0–2000 kHz and 2000–11000 kHz. On the other hand, acoustic complexity seemed to be higher in cluster 1 than in clusters 2 and 3; a contrasting result with roughness, given that both



indices depict similar information about the acoustic activity. But, in general, none of the indices showed strong differences among clusters (Figure 6).

3.2.3 Summary of acoustic energy indices

As shown by BIO values, biological frequency bands in cluster 1 contained a higher amount of energy than cluster 2 during the day, although statistically non-significant for most hours, except at 6 a.m. The difference was not so notorious between clusters 1 and 3. This was reflected also in NDSI values, showing a higher proportion of acoustic energy in the biophony band in cluster 1 than in clusters 3 and 2, although less noticeable between clusters 2 and 3. Moreover, NDSI values were statistically significantly higher in cluster 1 than in cluster 3 at 6 a.m., 9 a.m., and from 2 p.m. to 5 p.m. There was a notorious increase in NDSI values in all clusters at 5 p.m. (Figure 7).

There also was a statistically non-significant tendency of higher dif_L10L90 values in cluster 1 than in clusters 3 and 2, which indicated the presence of stronger signals in cluster 1 than in the other clusters. A similar tendency was seen in the average dominant frequency, being higher (although statistically non-significant) in cluster 1 than 3 and 2 (Figure 7).

3.3 Analysis of dominant frequencies by cluster

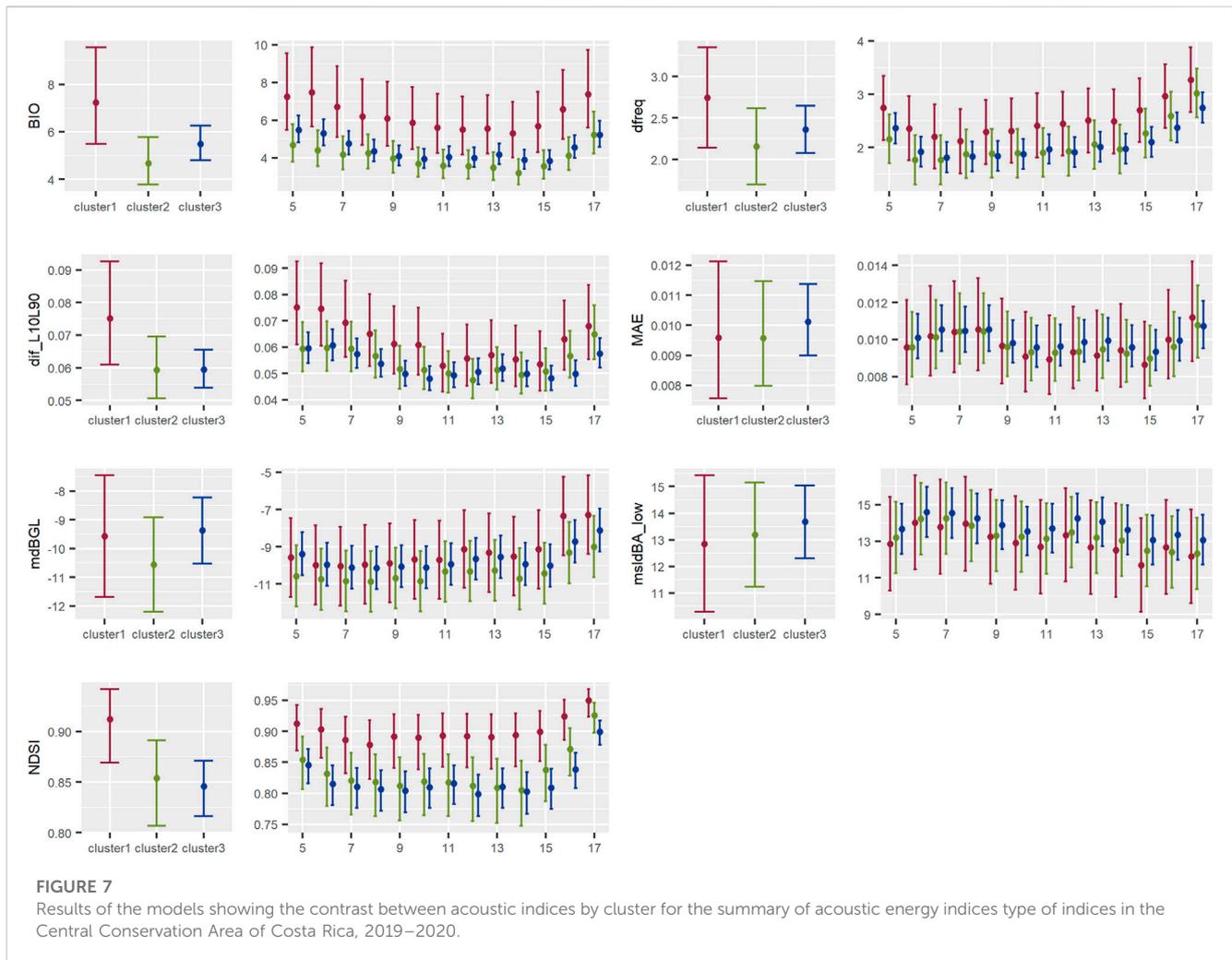
The distribution of dominant frequencies between clusters was variable during the day (Figure 8). Low frequencies, from 0–1 kHz, were more dominant in cluster 2 than cluster 1 during all day, but only

statistically significant at 17:00 p.m. The dominance of frequency bands between 1–4 kHz was similar in all clusters, except frequency band from 2–3 kHz, what was more dominant in cluster 1 than the other clusters, especially during the morning. Frequencies at intermediate level, from 4–7 kHz, were more dominant in cluster 1 than clusters 2 and 3. Mid-high frequency bands, from 7–9 kHz, presented a similar dominance across the three clusters. Higher frequencies, from 9–11 kHz, showed higher dominances in cluster 2 than the other clusters, what was most noticeable during the afternoon (Figure 8).

3.4 Modeling the relationship of acoustic indices with landscape metrics

Landscape metrics had different effects on acoustic indices. Forest cover and distance to rivers were the variables that had a significant effect over more acoustic indices, followed by entropy (ent) and the number of patches (NumP). Distance to roads (dist.roads) and Mean patch edge (MPE) did not have a significant effect on any of the acoustic indices evaluated (Table 5; Supplementary Appendix S2).

There was a positive significant relationship between the amount of forest and acoustic entropy and diversity indices. However, sites with a higher amount of forest seemed to present a negative relationship with acoustic activity/events or acoustic energy summary type of indices. Accordingly, the higher the entropy at the landscape level, the lower the acoustic entropy, but the higher the acoustic activity/events (Table 5; Supplementary Appendix S2).



However, there was a negative relationship between the number of patches at the landscape level and acoustic energy summary indices. Distance to rivers also behaves in a counterintuitive way regarding acoustic indices, because the longer the distance from rivers, the higher acoustic diversity or entropy, as well as the duration and strength of signals (Table 5; Supplementary Appendix S2).

3.5 Aural detection of biophonies and anthrophonies

The mean duration (seconds) of biophonies per hour was higher in cluster 1 all day, followed by cluster 3 and cluster 2. This pattern was consistent when we analyzed only the sound produced by birds. The results for insects were similar between clusters in the morning, but cluster 2 and cluster 3 showed higher mean duration (seconds) of biophonies from insects in the afternoon. On the other hand, the mean duration (seconds) of anthrophonies was higher in the morning (5:00 a.m.–10:00 a.m.) and at 4:00 p.m. and 5:00 p.m. in cluster 1 than in the other clusters (Figure 9).

4 Discussion

Our study sites were classified according to a series of landscape metrics reflecting forest amount and fragmentation around the recording points, resulting in a more fragmented cluster (cluster 1), a more conserved cluster (cluster 2), and an intermediate cluster (cluster 3). We expected that more conserved sites would have, in general, greater acoustic diversity and activity, as well as a higher proportion of biophonies than anthrophonies. The results were partially under these predictions. For example, we did find that there was a general tendency for higher acoustic entropy or diversity type of indices (for example Hf, Ht, Hm, HvSPL, and TE) in conserved (clusters 2 and 3) than in fragmented sites (cluster 1). Consequently, more conserved sites showed higher acoustic diversity, i.e. acoustic energy was more evenly distributed throughout the entire frequency spectrum. Moreover, more conserved sites presented more variation in the variance of the energy among frequency bands. These findings may reflect a higher diversity of species producing sounds in more conserved sites. Other authors have suggested that acoustic production might increase in diversity with different individuals and species vocalizing, resulting in more diverse acoustic communities in highly diverse

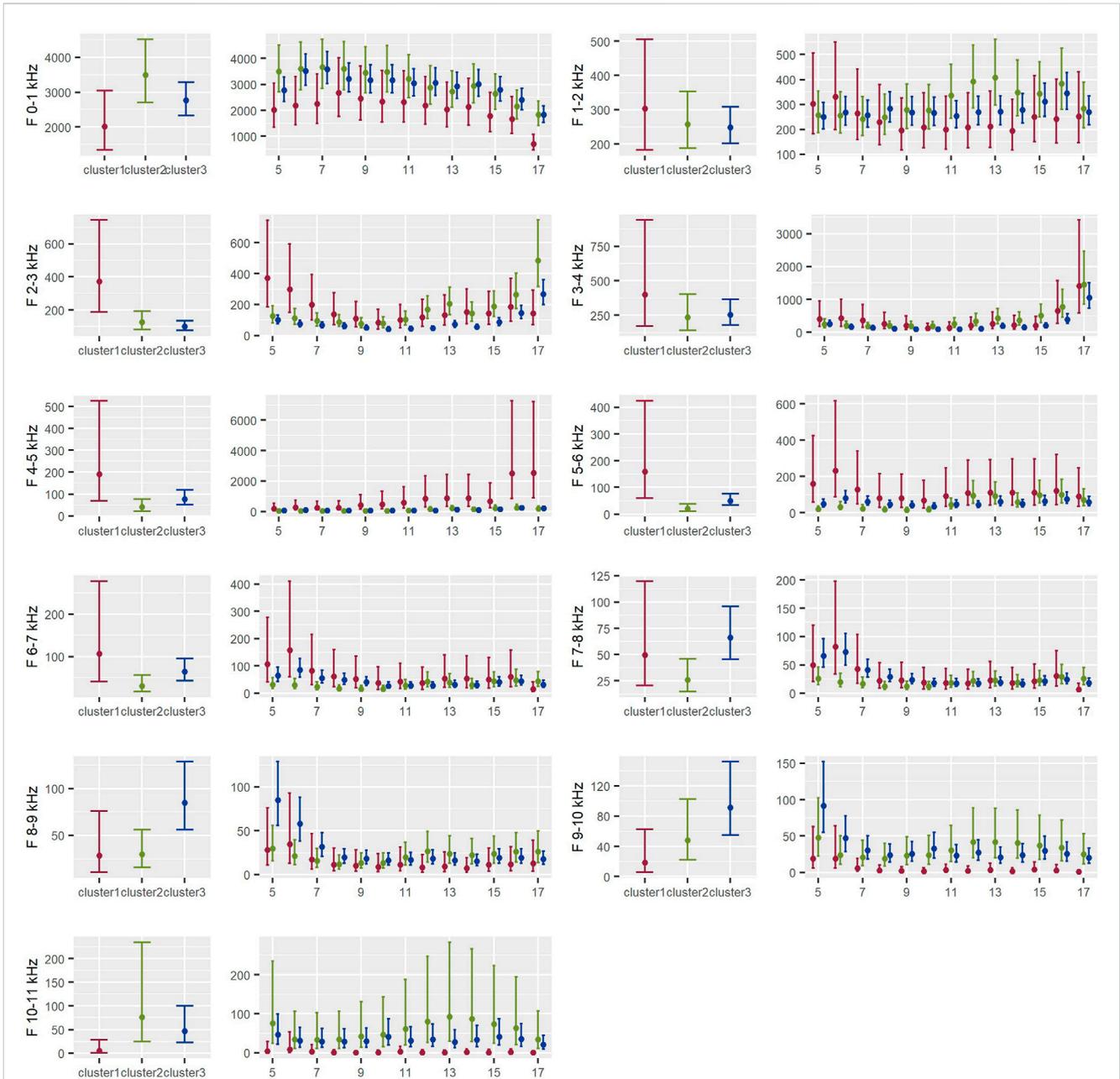
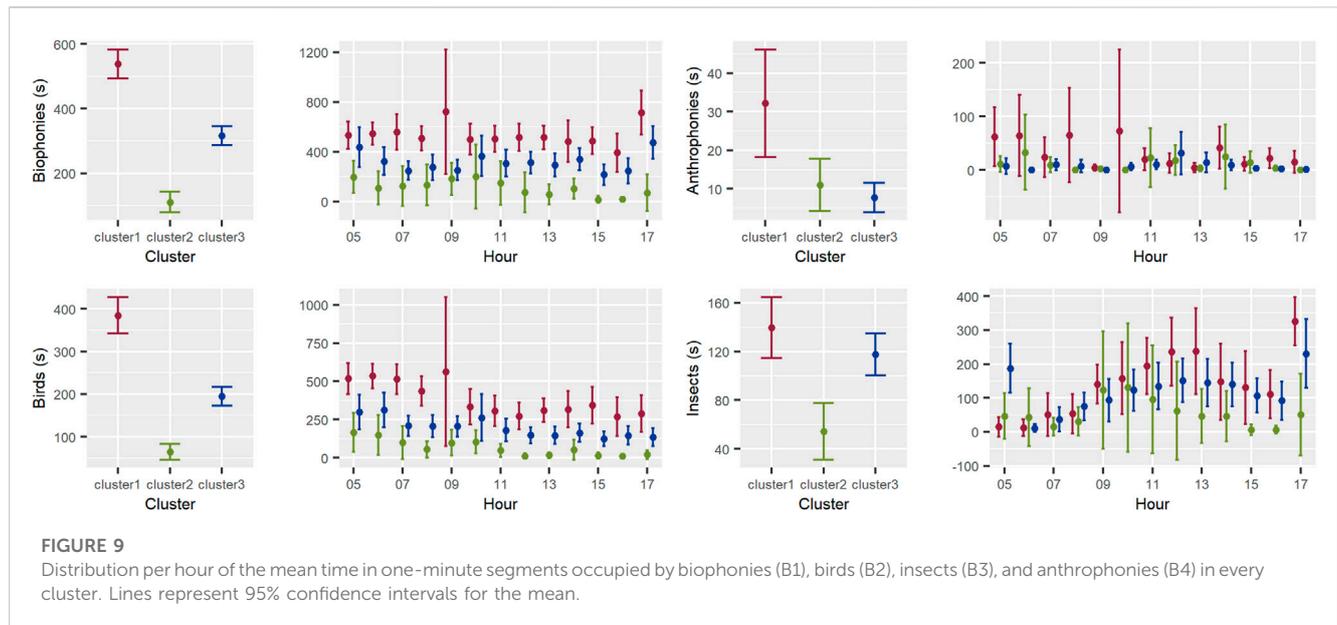


FIGURE 8 Distribution of dominant frequencies between clusters during the day in the Central Conservation Area of Costa Rica, 2019–2020.

TABLE 5 Acoustic indices with a positive or negative statistically significant effect on each landscape variable in the Central Conservation Area of Costa Rica, 2019–2020.

Variable	Significant negative effect	Significant positive effect
Forest	AAdur, AAdurant, ACI, BIO, dfreq, dif_L10L90, NDSI	Ht, HvSPL, roughness, TE
ent	Ht, roughness, HvSPL	AAdur, ACI
NumP	ACI, dfreq, dif_L10L90, NDSI	-
MPE	-	-
dist.roads	-	-
dist.rivers	AEI, BIO, mdBGL	AAdur, AAdurant, ADI, dif_L10L90, Hf, Hm



communities in terms of the number of species and individuals (Sueur et al., 2014).

However, the opposite and unexpected pattern was found for acoustic activity (for instance ACI, AAdur, and Aaduranth) or summary of acoustic energy type of indices (BIO, NDSI, and dif_L10L90). For example, more conserved sites tended to present lower acoustic complexity, shorter duration of sounds above the background noise threshold for the range of frequencies events between 0–2 kHz and 2–11 kHz, and lower amount of energy in the biological frequency bands during the day. NDSI also followed the same pattern, given the relationship with the previous indices (BIO).

We additionally found a positive significant relationship between the amount of forest and acoustic entropy or diversity type of indices. However, sites with a higher amount of forest seemed to present a negative relationship with acoustic activity or energy type of indices. Moreover, the higher the entropy at the landscape level, the lower the acoustic entropy, but the higher the acoustic activity or energy. These results are consistent with other studies conducted by our group in the tropics (Retamosa Izaguirre et al., 2018; Retamosa Izaguirre et al., 2021a; Retamosa Izaguirre et al., 2021b), providing support to our notion that, in the tropics, acoustic indices such as ACI and BIO seem to be indicating acoustic activity or energy rather than acoustic diversity, behaving as a weak or incomplete indicator of biodiversity or habitat conservation. In this sense, one or a few species with persistent vocal activity can result in high values of ACI or BIO, although the site might not be highly diverse or well conserved. However, acoustic entropy or diversity indices, such as Hf, Ht, HvSPL, and TE, might be more suitable to represent biodiversity and habitat conservation. In accordance, Do Nascimento et al. (2020) found that different habitat types had unique and predictable soundscapes; specifically, Ng et al. (2018) found a significant correlation between AEL, ADI, and H with a BioCondition Score that discriminated among woodland condition types, and Fuller et al. (2015) reported that AEI, H, and NDSI best reflected the soundscape with landscape characteristics, ecological condition, and bird species.

Consistently, the aural detection of biophonies showed that the mean duration in seconds of biophonies per hour was higher in cluster 1 (more fragmented) throughout the day, followed by cluster 3 (intermediate) and lastly cluster 2 (more conserved). These results were driven by birds, which replicated the same general pattern as biophonies. As indicated by other authors (Temple and Wiens, 1989; Niemi et al., 1997; Campos-Cerqueira et al., 2020), birds might not be the best indicator of habitat conservation, given the great plasticity and variety of life histories found in this group. There usually are some bird species that can take advantage of, or even benefit from, a certain degree of habitat alteration (Carrara et al., 2015). For instance, younger forests usually present a high environmental heterogeneity at horizontal and vertical levels (MacArthur and MacArthur, 1961), providing a variety of niches for some opportunistic species, or a mixture of species with different habitat requirements. Other authors have even indicated that forests at earlier stages of succession maintain a greater dynamic of food production than mature forests (Flores and Dezzio, 2005), which may help increase the variety of species guilds inhabiting them (Almazán-Núñez et al., 2009). We highlight the importance of including other groups, for example, amphibians or insects as indicators of habitat conservation, or even using other parameters that measure behavior, activity, and overall condition or reproductive success for some selected wildlife species.

Regarding the mean duration (seconds) of anthrophonies, it was higher in the morning (5:00 a.m.–10:00 a.m.) and at 4:00 p.m. and 5:00 p.m. in cluster 1 (more fragmented) than in the other clusters. This is congruent with regular commercial activity, including the transit of service vehicles transporting goods and services, which tends to be more intense in the morning hours (Halfwerk et al., 2018). Besides, the peak in anthrophonies at 4:00 p.m. and 5:00 p.m. in cluster 1 might be associated with the transit of people returning home from regular-hour jobs. However, and how it was observed before, these changes in anthrophonies were not reflected in the NDSI index, given the higher energy in the biophony range detected in cluster 1, which

also increased NDSI values. Nevertheless, both measures depict different information.

NDSI values reflect the ratio of the amount of energy between anthropony and biophony bands, while with the aural detection we measured the mean time where only anthroponies were found on each one-minute segment of audio, regardless of the amount of energy. Therefore, if the anthroponies had low energy, even if they were reflected in the aural analysis, they would not affect the NDSI index.

On the other hand, we found higher dominant frequencies in the more conserved and forested cluster (cluster 2), while intermediate frequencies dominated in the fragmented cluster (cluster 1). This might be due to the presence of species with persistent or loud vocalizations, resulting in dominant mid-frequencies in cluster 1 at specific periods, such as dawn and dusk, where the contrast in dominant frequencies between clusters was more noticeable. This idea is supported by the fact that we did not find evidence of higher acoustic diversity in cluster 1. Conversely, acoustic diversity seemed to be higher in cluster 2. Moreover, we suggest that conserved sites might be more acoustically diverse but quieter or with species less vocally active than fragmented sites.

Acoustic indices, as well as traditional indices in ecology, have the advantage of summarizing ecological information, but at the expense of not taking into account the composition of ecological communities (Izsák & Papp 2000). For this reason, we recommend combining information from acoustic indices with more specific acoustic or ecological information from selected species, that may serve as indicators of the pattern and process under investigation. However, acoustic entropy or diversity indices did behave well as indicators of habitat conservation or condition in this, as well as other studies (Fuller et al., 2015; Ng et al., 2018; Bradfer-Lawrence et al., 2020; Do Nascimento et al., 2020).

On a final note, the lack of statistical power to detect differences in acoustic indices among clusters might be due partially to the fine-scale landscape variability surrounding sampling sites. However, on a broad scale, sites were located mostly inside, near, or connected to big forest fragments included in protected areas (Volcan Poas National Park and Grecia Forest Reserve). Moreover, Costa Rica has conducted strong efforts to implement environmental services payment initiatives (Brownson et al., 2020), that in association with a strong ecotourism culture in the country, might have helped to maintain forest patches in the matrices around protected areas (Hunt & Harborpro 2019; Beita et al., 2021).

In conclusion, acoustic indices revealed that the surrounding matrices of protected areas have an impact on acoustic environments. Although disturbed environments with less-forested and more fragmented matrices registered higher values of acoustic energy and activity in certain biological frequency bands, sites with a higher percentage and more continuous forest cover showed higher values of acoustic entropy and diversity, reflecting a more diverse acoustic community. Given this pattern, we emphasize to researchers and decision-makers to carefully interpret acoustic indices when evaluating disturbed ecosystems showing a high value in acoustic energy or activity, because this might not accurately

reflect a more biodiverse or conserved habitat. Finally, we highlight the importance of preserving undisturbed habitats with forested matrices, as they are important for maintaining acoustic diversity.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

Conceptualization, MR and JB; fieldwork, JB and MR; data analysis, JB and MR; writing of the manuscript, MR and JB. All authors have read and agreed to the published version of the manuscript.

Acknowledgments

We thank the staff of Grecia Forest Reserve and Poas Volcano National Park for their collaboration during fieldwork and the owners of the farms who allowed us access to data collection. We also thank the students of the National University who helped us in data collection and management (Marilyn Ureña Chaves, Gerardo Servellón Velado, Natalia Segura Vargas, Yanory Monge Fernández). We thank Manuel Spínola for the statistical analysis recommendations.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frsen.2023.1051555/full#supplementary-material>

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