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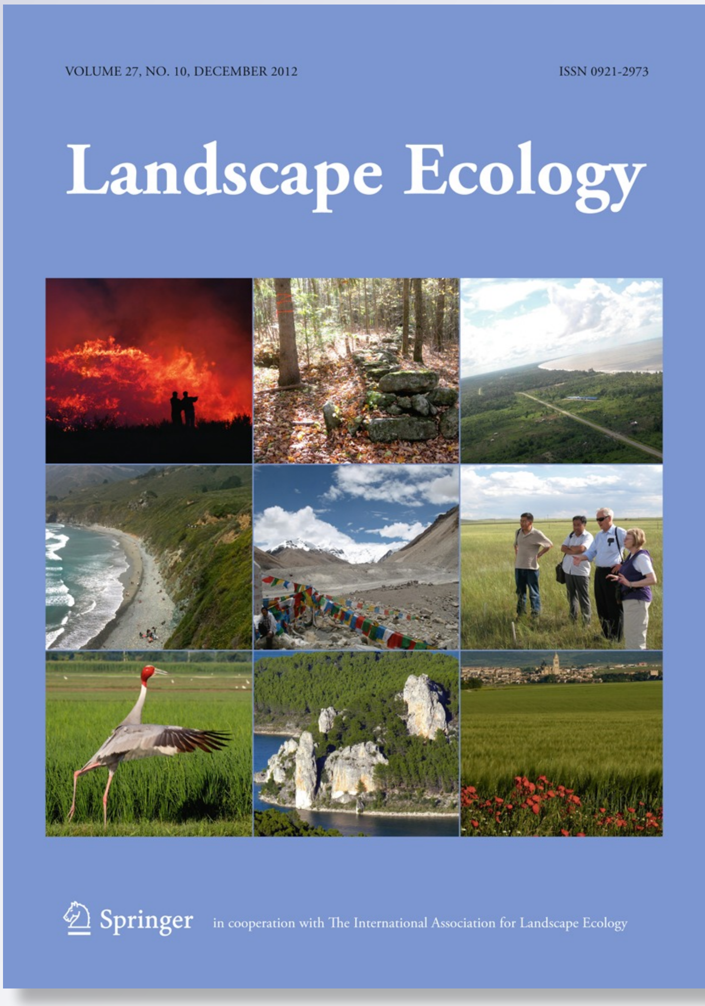

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RESEARCH ARTICLE

Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest

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Abstract We determined the relationship between acoustic diversity and metrics of vertical forest structure derived from light detection and ranging (LIDAR) data in a neotropical rainforest in Costa Rica. We then used the LIDAR-derived metrics to predict acoustic diversity across the forest landscape. Sound recordings were obtained from 14 sites for six consecutive days during dusk chorus (6 pm). Acoustic diversity was calculated for each day as the total intensity across acoustic frequency bands using the Shannon index and then averaged over the 6 days at each site. A 10 m radius around each site was used to obtain several LIDAR-derived metrics describing the vertical structural attributes of the forest canopy. Multiple linear regression (MLR) with Akaike information criterion was used to determine a top-ranked model with acoustic diversity as the dependent variable and the LIDAR metrics as independent variables. Acoustic diversity was modeled for forested areas (where canopy height was >20 m) at 20 m resolution using coefficients obtained from the MLR, and a hotspot analysis was conducted on the resulting layer. Acoustic diversity was strongly correlated ($R^2 = 0.75$) with the LIDAR metrics suggesting that LIDAR-derived metrics can be used to determine canopy structural attributes important to vocal fauna species. The hotspot analysis revealed that the spatial distribution of these canopy structural attributes across the La Selva forest is not random. Our approach can be used to identify forest patches of potentially high acoustic diversity for conservation or management purposes.

Keywords Forest canopy strata · Vertical canopy gaps · Hotspot analysis · La Selva biological station · Anselin Local Moran's I statistic · Multiple linear regression

Introduction

There has recently been a surge of interest in the quantification of sound across landscapes (Sueur et al. 2008;

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Farina et al. 2011; Pijanowski et al. 2011a, b; Villanueva-Rivera et al. 2011). The acoustic composition of a landscape, also called a soundscape (Pijanowski et al. 2011a), is thought to be a function of the physical, biological and anthropogenic features of the local environment (Pijanowski et al. 2011b). Several studies have analyzed the temporal and spatial changes in sound recordings among different broad-scale land use or vegetation cover types (Matsinos et al. 2008; Mazaris et al. 2009; Krause et al. 2011; Depraetere et al. 2012), and with regards to human disturbance (Sueur et al. 2008; Francis et al. 2011; Joo et al. 2011). However, the influence of fine-scale changes in vegetation or forest canopy structure on the acoustic environment has not been previously studied.

Canopy structure has been known to influence species distributions and diversity for over half a century (MacArthur and MacArthur 1961; Karr and Roth 1971) and is considered a crucial component of biodiversity management and conservation in forests (Lindenmayer et al. 2006). Indices reflecting the structural complexity of the forest canopy have been found to be strongly correlated with elements of biodiversity and species richness (McElhinny et al. 2005), especially in energy-rich landscapes (Verschuyl et al. 2008) such as rainforests. Specific forest structural attributes have also been identified as being important for various assemblages of insects (Halaj et al. 2000; Tanabe et al. 2001; Ishii et al. 2004; Müller and Brandl 2009), birds (Pearman 2002; Diaz et al. 2005; Goetz et al. 2007; Clawges et al. 2008), and anurans (Miyamoto 1982; Duellman and Pyles 1983; Stewart 1985). Thus, vegetation or canopy structure is likely to be strongly associated with the composition and diversity of sounds in forested environments due to its influence on the abundance and richness of vocal fauna such as insects, birds and anurans.

Increased availability of fine resolution active remote sensing data such as light detection and ranging (LIDAR) has prompted interest in the use of remote sensing for the characterization of vertical forest canopy structure (Drake et al. 2002; Lefsky et al. 2002; Parker et al. 2004; Jung and Crawford 2012; Jung et al. 2012) and more recently in the modeling of biodiversity (Vierling et al. 2008). Several studies have already used LIDAR derived metrics of vegetation structure along with field surveys of fauna to model and assess habitat for multiple species at landscape scales (Goetz et al. 2007, 2010; Clawges et al. 2008; Müller and Brandl 2009; Müller et al. 2009). In this study, we use LIDAR-derived metrics of vertical canopy structure and soundscape recordings to model acoustic diversity across a tropical rainforest landscape in Costa Rica.

We took soundscape recordings from multiple sites across our study region during the dusk chorus when acoustic diversity is likely to be particularly high (Sueur et al. 2008; Villanueva-Rivera et al. 2011). The vertical structural attributes of the forest canopy were assessed at each site through several metrics obtained from discrete-return LIDAR. We then determined the relationship between acoustic frequency band composition (and diversity) and the vertical structure of the canopy using multiple regression analyses. The coefficients obtained from the regression analyses were used to predict areas or patches of particularly high acoustic diversity across the whole forest landscape at 20 m resolution. Acoustic diversity, as a natural resource, has inherent value (Dumyahn and Pijanowski 2011) and is also a good proxy for species diversity (Sueur et al. 2008; Depraetere et al. 2012). Consequently, by making high resolution maps illustrating the distribution of acoustic diversity across our study region, we demonstrate a modeling approach for identifying localities within nature reserves, parks, or other areas of interest that are of high importance for conservation and/or further biodiversity monitoring.

Methods

Study area

This study was conducted in a lowland neotropical rainforest between the La Selva biological station and the Braulio Carrillo National Park in Costa Rica (Fig. 1). The mean annual temperature and precipitation at the La Selva biological station are 26 °C and 4,000 mm respectively (Sanford et al. 1994). The elevation ranges from 30 to 140 m above sea level with some areas being waterlogged during the wet season (McDade et al. 1994). The fauna of La Selva is highly diverse even when compared to other rainforests in Costa Rica and Central America (McDade et al. 1994). More than 400 bird species (Levey and Stiles 1994) and 48 amphibian species (Donnelly 1994) have been recorded in the La Selva biological station, an area of only 15 km^2.

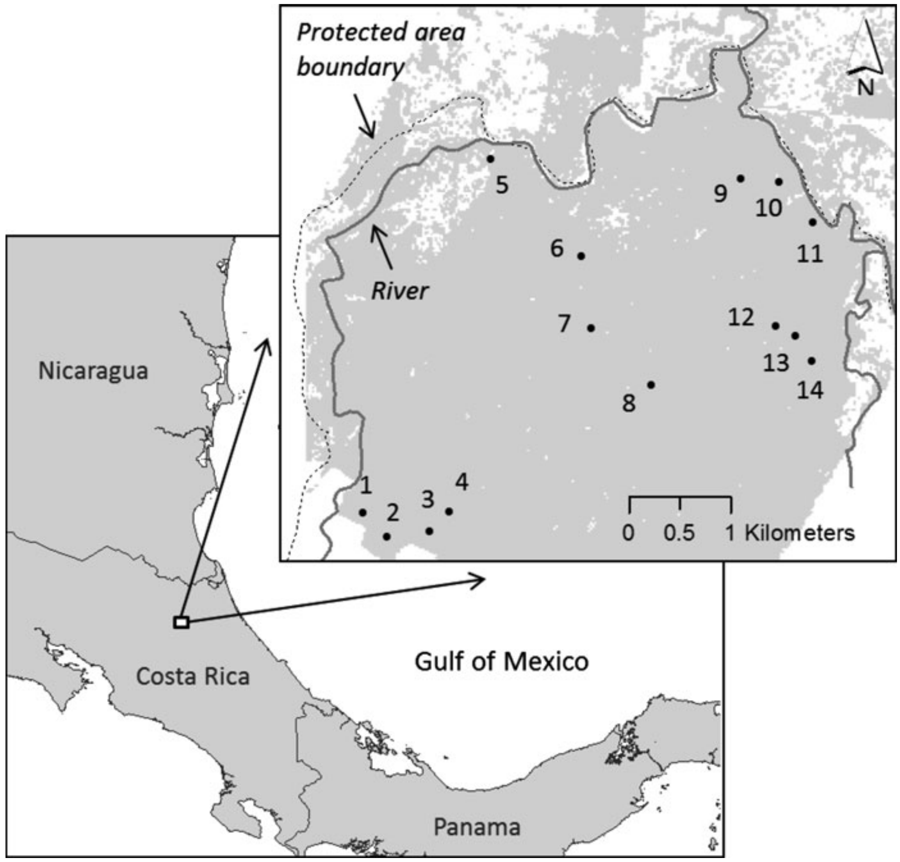

Fig. 1 Location of the study forest near the La Selva biological station in Costa Rica. *Grey areas* inside map *inset* show forested pixels (400 m^2) where canopy height is at least 20 m. Pixels outside of LIDAR coverage or with canopy height of less than 20 m are shown in *white*. Site locations where sound recordings were obtained are shown numbered *1–14*. Sites *9–14* are waterlogged during the wet season (i.e., swamps)

Sound recordings

Sound was recorded for 10 min at every hour from 6:00 pm to 12:00 am over an approximately 3 month period (May–August) during the wet season in 2008 at 14 sites within the study area (Fig. 1). The sites ranged from 25 to 47 m in maximum canopy height and represented much of the variation in elevation across the study area (Fig. 1). Six of the sites (9–14; Fig. 1) were located in lowland areas (<50 m in elevation) that are seasonally waterlogged, and were thus classified as 'swamp' sites. After removing recordings with microphone failures, heavy rain, and abnormal sounds indicating some other recording error, the longest stretch of consecutive error/rain free days remaining was from May 15th to 20th. Because the highest acoustic diversity was observed for the 6:00–6:10 pm recordings, which roughly coincides with the dusk chorus at this time of the season, only the recordings from these times for each of the six consecutive days were included in the study.

Recordings were obtained by placing automated sound recorders at each site (Model SM1, Wildlife Acoustics, Concord, MA) that recorded in wav file format with a sampling rate of 16 kHz using 16-bits. The built-in omnidirectional microphones had a sensitivity of −35 dBV/pa. While a sampling of up to 16 kHz may miss some species whose vocalizations occupy high frequencies, the sampling range in this study is adequate to capture the vocalizations of most insects and anurans (Gerhardt and Huber 2002) and possibly many other animals such as mammal and bird species.

The recordings were separated into eight frequency bands each representing a 1,000 Hz range such that band 1 = 0–1,000 Hz, band 2 = 1,000–2,000 Hz, band 3 = 2,000–3,000 Hz, band 4 = 3,000–4,000 Hz, band 5 = 4,000–5,000 Hz, band 6 = 5,000–6,000 Hz, band 7 = 6,000–7,000 Hz, and band 8 = 7,000–8,000 Hz. Several diversity indices common to community ecology have been previously applied to sound recordings (Sueur et al. 2008;

Pijanowski et al. 2011a; Villanueva-Rivera et al. 2011; Depraetere et al. 2012). We calculated the diversity across frequency bands at each site for each day using an acoustic diversity index (ADI) based on the Shannon index following Pijanowski et al. (2011b) and Villanueva-Rivera et al. (2011) with Eq. 1:

$$ADI = \sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

where p_i is the fraction of sound in each ith frequency band in S number of frequency bands. ADI thus measures how full each of the 1,000 Hz bands are overall, which indicates the extent different acoustic niches are occupied in the recording. Only sounds above −50 dBFS were used in order to get rid of background noise. The cutoff of −50 dBFS was determined after listening to the sound recordings to ensure local fauna vocalizations were not being inadvertently excluded. The acoustic diversity of each site was then obtained by averaging the ADI values at each site over the six-day period. All sound recordings are publicly available at http://purdue.edu/soundscapes/.

LIDAR metrics

Discrete-return airborne LIDAR data was acquired by flying an Optech ALTM 3100EA sensor over the study region on 26 September 2009. The ALTM 3100EA system operates at 1,064 nm and has a maximum pulse rate of 100 kHz, and a maximum scan angle of 50°. The LIDAR system was flown at altitude of 1,500 m with a scan angle of 20° (±10°) and a 70 kHz pulse repetition frequency (PRF), which resulted in an average point density of 3.3 points/m^2.

Information regarding the vertical structural attributes of the canopy at each site was obtained by processing the LIDAR point cloud data within a 10 m radius buffer plot around the location of the recorder. Points were classified into ground and non-ground classes using LAStools (Isenburg, http://lastools.org), and the ground points were used to generate digital terrain model (DTM) using natural neighbor interpolation. The DTM was then used to convert the reference of elevation of points from the elevation above sea level to elevation above ground. See Jung et al. (2012) for details on LIDAR data processing for the study region. The LIDAR point cloud data was also processed at 20 m resolution across the whole study region for use in modeling of acoustic diversity.

Several metrics were calculated from the LIDAR data following Müller and Brandl (2009) and Müller et al. (2009) including: (1) maximum canopy or tree height (H; the height of highest LIDAR return point within the plot), (2) canopy openness (O; sum intensity of the ground points) which reflects the amount of light penetration to forest floor, (3) cover of lower canopy (sum intensity of the non-ground points between 0 and 10 m above ground) divided by canopy openness (C_L:O), (4) cover of upper canopy (sum intensity of the non-ground points between above 10 m) divided by canopy openness (C_U:O), (5) cover of lower canopy divided by cover of upper canopy (sum intensity of the non-ground points 10 m and above), i.e., C_L:C_U, which reflects the level of complexity and development of mid-story trees, (6) the number of layers/strata in entire canopy (S; defined by clusters of LIDAR return values of at least 1 % of total intensity), (7) size of vertical gaps in entire canopy (G; total distance between individual canopy strata), and (8) size of vertical gaps in lower canopy (G_L; total distance between individual canopy strata between 0 and 10 m above ground). Equations used to calculate each metric are shown in Table 1, and the canopy attributes used in the equations are illustrated in Fig. 2.

Statistical analyses and modeling

cca function in the R (R Development Core Team 2009) package 'vegan'. A canonical (constrained) correspondence analysis (CCA) (Ter Braak 1986; Müller et al. 2010) with the *cca* function in the R package 'vegan' (Oksanen et al. 2012) was used to assess the correlation between the LIDAR metrics and acoustic frequency band composition (i.e., relative intensity across frequency bands). The *lm* function in the base stats package in R was used to conduct a multiple linear regression (MLR) (Wilkinson and Rogers 1973) with acoustic diversity as the dependent variable and the LIDAR metrics and habitat (swamp or not) as the independent variables. The independent variables were normalized by subtracting each value by the mean and dividing by the standard deviation prior to MLR analyses. Because our objective was to determine a set of environmental variables best explaining acoustic diversity rather than to test individual hypotheses, all combinations of independent variables were initially considered. The models with the combination of variables providing the lowest

Table 1 LIDAR metrics used to characterize vertical profile of the forest canopy, and the equations used to calculate them

Metrics	Canopy attributes	Description
H	Max	Maximum canopy height
O	S_1	Canopy openness
C_L:O	S_2/S_1	Cover of lower canopy relative to canopy openness
C_U:O	S_3/S_1	Cover of upper canopy relative to canopy openness
C_L:C_U	$S_2/(S_2 + S_3)$	Cover of lower canopy relative to upper canopy
G	$G_1 + G_2$	Total size of vertical gaps in entire canopy
G_L	G_1	Total size of vertical gaps in lower canopy
S	n_S	The number of strata in entire canopy

An illustration of the canopy attributes is provided in Fig. 2

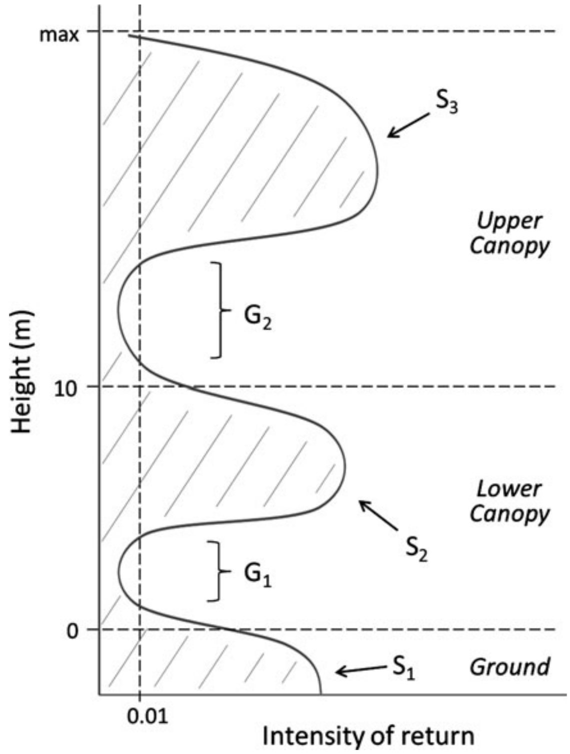

Fig. 2 Attributes describing the vertical profile of the forest canopy obtained from discrete-return LIDAR data. Strata (*S*) were defined as the total intensity of LIDAR return (shown on *x*-axis) within portions of the vertical profile where the return intensity was greater than 0.01 out of maximum possible intensity of one. Gaps (*G*) were defined as the area between strata, and their size was calculated as the distance between nearest strata. The attributes were used to calculate the metrics shown in Table 1

Akaike information criterion values were determined. Because our sample size was small ($n = 14$), an Akaike information criterion adjusted for sample size (AICc) was used to avoid overfitting (Burnham and Anderson 2004) and determine the top-ranked model.

Raster layers (with 20 m resolution pixels) were made for each of the independent variables using the processed LIDAR point cloud data. Only pixels of continuous developed forest (i.e., where the maximum canopy height within a 20 × 20 m pixel was at least 20 m) within the continuous protected area boundary were used since they represent forest habitat with no current human impacts such as livestock grazing. The pixel values on each of the layers were then normalized and acoustic diversity was predicted for the study region using an equation containing the coefficients of variables included in the top-ranked MLR model. A hotspot analysis was conducted on the predicted acoustic diversity values using Anselin Local Moran's I statistic (Anselin 1995) with the *Cluster and Outlier Analysis* tool in ArcMap 10.0 (ESRI 2010). Anselin Local Moran's I statistic identifies clusters of pixels on a map with significantly higher (hotspots) and significantly lower (coldspots) values than would be expected from a random distribution. Individual pixels (outliers) with very high values surrounded by pixels with low values, and individual pixels with very low values surrounded by pixels with high values are also identified. These outliers represent locations where the value is more than two standard deviations from the mean value (Anselin 1995). Thus, they can be used to single out individual pixels with exceptionally high or low values in areas that don't display spatial autocorrelation, i.e., where there are no hotspots or coldspots.

Results

Acoustic diversity of the sites

Mean ADI value ranged from 0.155 to 0.242 and the maximum ADI value on any given day ranged from 0.224 to 0.320 across the sites. The site with the highest mean ADI (0.242; site 6; Fig. 1) and the site with the highest maximum ADI (0.320; site 7; Fig. 1) were both located in the interior of the study region.

Site 2, located in the southwest corner of the region (Fig. 1) displayed both the lowest mean (0.155) and lowest maximum (0.224) ADI values. Sites with the second lowest mean ADI (0.177) and the second lowest maximum ADI (0.234) were 11 and five respectively. Nonetheless, there was a strong positive correlation ($R = 0.62$) between mean ADI and maximum ADI across the sites based on the Pearson's correlation coefficient. The effect of the canopy metrics on acoustic diversity was tested using the mean ADI value since this index is likely to better represent long-term acoustic diversity at the sites.

Variation in acoustic composition with canopy structure

The separation in frequency band intensity between sites was largely driven by the LIDAR-derived metrics of forest canopy structure as illustrated by the CCA (Fig. 3). Canopy structure and habitat (the presence of swamps) explained a large proportion (60 %) of the variation in acoustic frequency band composition across the study sites. Low frequency bands (0–4,000 Hz) were separated from high frequency bands (4,000–8,000 Hz) along CCA axis 1 which was mostly driven by the canopy structural variables H and C_U:O, C_L:O and S (Fig. 3). The separation of frequency bands along CCA axis 2 was mostly driven by G, G_L, C_L:C_U, O and habitat (Fig. 3).

Multiple linear regression results

The five MLR models with the lowest AICc values all included the independent variables C_L:O, C_L:C_U and G_L (Table 2). Four of the models, including the MLR with the lowest AICc, included the independent variable H (Table 2). The independent variables S and swamp were also included in two of the models (Table 2). O, C_U:O and G were not included in any of the MLR models (Table 2). While, the MLR model with the lowest AICc value explained a large amount ($R^2 = 0.75$) of the variation in acoustic diversity across the sites, the most variability in acoustic diversity was explained by the MLR with the fifth lowest AICc, which included six variables (Table 2). The MLR with the four independent variables H, C_L:O, C_L:C_U and G_L was selected as the top-ranked model because its AICc value was over five lower than the next best model (Table 2).

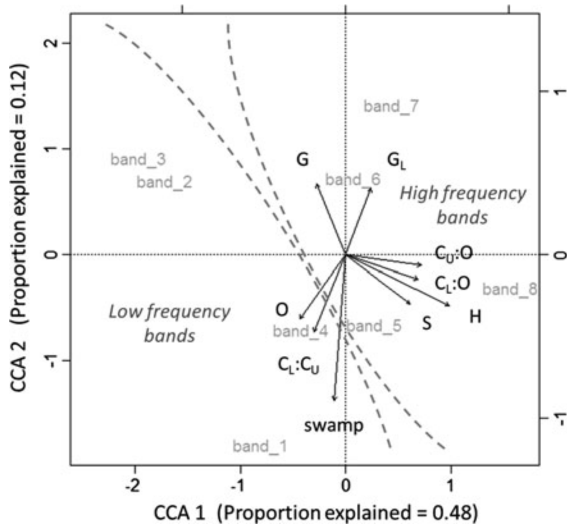

Fig. 3 Canonical correspondence analysis (CCA) showing the influence of LIDAR-derived metrics of forest canopy structure (described in Table 1) and the presence of nearby swamps on the intensity of sound within eight acoustic frequency bands (each representing a 1,000 Hz range) recorded across 14 sites near the La Selva biological station

According to the top-ranked model, acoustic diversity increased most strongly with G_L and C_L:C_U as indicated by their coefficients (estimates) (Table 3). A moderate increase in acoustic diversity with C_L:O, and a moderate to weak increase in acoustic diversity with decreasing H was also observed (Table 3).

Spatial modeling of acoustic diversity at landscape level

Acoustic diversity (AD) was predicted using coefficients from the top-ranked MLR with equation 2.

$$AD = -0.0118\,(H) + 0.0243\,(C_L{:}O) + 0.0733\,(C_L{:}C_U) + 0.0894\,(G_L) \quad (2)$$

Hotspots, i.e., clusters of pixels with high values, were generally concentrated in the north and northwest corner, along the eastern edge, and in several large patches scattered throughout the interior of the study region (Fig. 4). Hotspots were generally surrounded by pixels with average (non-significant) values and few pixels with low outlier values (i.e., individual pixels with low values surrounded by high values) (Fig. 4). Forest gaps, i.e., pixels where maximum canopy height was less than 20 m, were also found within close proximity of hotspots, particularly

Table 2 Combinations of variables providing the five multiple linear regression (MLR) models with the lowest Akaike information criterion adjusted for sample size (AICc) ordered from left to right

	AICc = −69 $\Delta_i = 0$ $R^2 = 0.75$	AICc = −64 $\Delta_i = 5$ $R^2 = 0.80$	AICc = −63 $\Delta_i = 6$ $R^2 = 0.48$	AICc = −62 $\Delta_i = 7$ $R^2 = 0.75$	AICc = −59 $\Delta_i = 10$ $R^2 = 0.85$
H	x	x		x	x
O					
C_L:O	x	x	x	x	x
C_U:O					
C_L:C_U	x	x	x	x	x
G					
G_L	x	x	x	x	x
S		x			x
Swamp				x	x

The adjusted R-squared (R^2) is also shown along with the AICc and Delta AICc (Δ_i) for each MLR model

Table 3 Coefficients of the top-ranked multiple linear regression (MLR) model

	Est.	*SE*	*P*
H	−0.0118	0.0034	0.0070
C_L:O	0.0243	0.0051	0.0011
C_L:C_U	0.0733	0.0150	0.0009
G_L	0.0894	0.0158	0.0003

The estimate (*Est.*), standard error (*SE*) and *P* value (*P*) are shown for all variables in the model

in the northwest corner and along the eastern edge. Coldspots (i.e., clusters of pixels with low values) and high value outliers (i.e., individual pixels with high values surrounded by low values) were common throughout the study region (Fig. 4). In fact, high value outliers were almost exclusively located between coldspots (Fig. 4).

Discussion

Our results suggest that the acoustic diversity observed at any given point in the La Selva forest environment is strongly linked to the vertical structure of the local canopy. Seventy-five percent of the variation in acoustic diversity was explained by only four LIDAR metrics and up to 85 % was explained when habitat (the presence of swamps) was taken into account. However, the higher R-squared obtained by including the swamp variable may be due to overfitting since the model that included habitat had a relatively high AICc value compared to the top ranked model. Several other studies have demonstrated the high utility of LIDAR data in modeling biodiversity in temperate forests (Goetz et al. 2007, 2010; Clawges et al. 2008; Müller and Brandl 2009; Müller et al. 2009). Canopy structural attributes are a stronger predictor of animal species diversity than even plant species composition (MacArthur and MacArthur 1961) as demonstrated by a recent study in central European forests (Müller et al. 2010). In this study, we show that LIDAR-derived metrics of vertical canopy structure are useful for modeling acoustic "as well as species diversity" in structurally complex forest environments.

While the variation in acoustic frequency band composition across our study sites was driven by several metrics of canopy structure, structural attributes related to the size of gaps and the proportion of cover in the lower canopy (0–10 m from the forest floor) were the strongest predictors of acoustic diversity. Our results further suggest that a forest patch that has large gaps while at the same time containing dense foliage in the lower canopy, and a relatively open upper canopy, will harbor the greatest diversity. Clawges et al. (2008) also observed the highest bird species diversity where the canopy contained relatively more foliage near the forest floor in North American pine/aspen stands. In energy rich environments such as rainforests, animal species richness is predicted to decrease as the overstory shades out and reduces the structural complexity in the lower parts of the canopy (Verschuyl et al. 2008). Thus, vocal fauna, particularly birds, may benefit from a more developed and structurally complex mid and understory

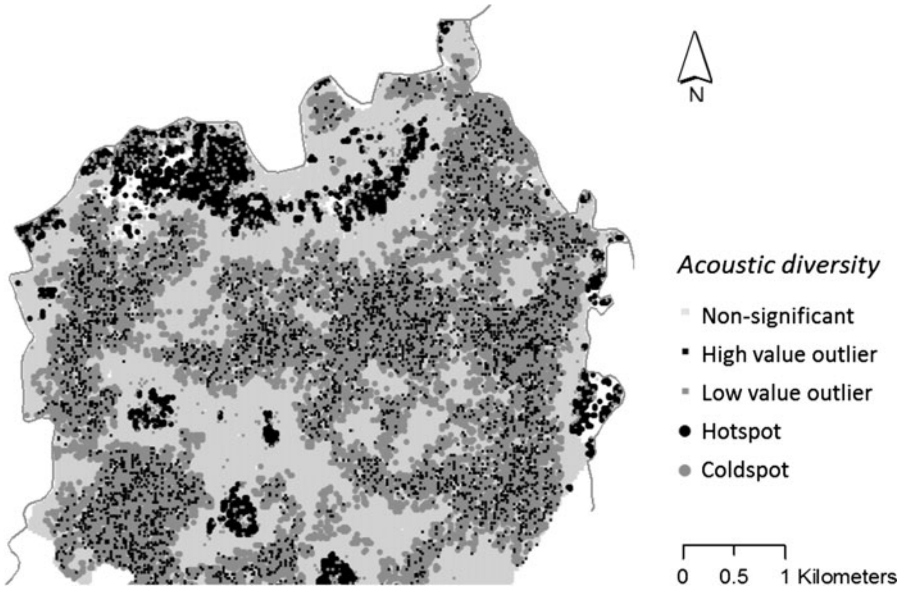

Fig. 4 Forested areas in La Selva (shown in *grey* and *black*) predicted to support high and low acoustic diversity. Forest areas are where maximum canopy height (within 400 m^2 pixels) is >20 m. Hotspots (clusters of pixels with high values), coldspots (clusters of pixels with low values), and outliers (individual pixels with especially high or low values) are significantly higher or lower (P value < 0.05) than surrounding pixel values based on Anselin Local Moran's I statistic

resulting from increased light penetration through the upper canopy.

Acoustic diversity is a good proxy for overall faunal richness, at least of vocal fauna (Depraetere et al. 2012), because the vocalizations of different species of animals are known to generally occupy different acoustic frequencies (Sueur 2002; Sueur et al. 2008; Pijanowski et al. 2011a, b). However, we do not seek to model species diversity in this study. It has recently been argued that soundscapes are a natural resource in themselves, and landscapes should be managed in a way as to conserve their acoustic diversity (Dumyahn and Pijanowski 2011). Accordingly, our objective is to develop an approach to mapping hotspots of acoustic diversity for the purpose of guiding soundscape conservation efforts in structurally complex forests. Our hotspot analyses show that the spatial distribution of canopy structural attributes important for acoustic diversity across the La Selva forest is not random. While individual pixels with structural attributes likely to support high acoustic diversity (i.e., high value outliers) are distributed throughout the region, several large patches of forest supporting high diversity (hotspots) also exist. The extensive distribution of high outlier values among patches of forest with low acoustic diversity (coldspots) illustrates the heterogeneity in habitat supporting vocal fauna throughout this neotropical forest which is likely to be a reflection of the highly dynamic nature of the La Selva forest canopy (Kellner et al. 2009).

Both the identification of large patches and individual pixels with high habitat value can be useful for focusing conservation efforts or management practices within nature reserves, parks, cities, or other areas of interest. While hotspots are commonly used to identify areas important to the biodiversity of a larger region or the globe (Olson and Dinerstein 1998; Myers et al. 2000; Werner and Buszko 2005), the ability to identify outlier pixels at smaller spatial scales also holds potential for use in wildlife conservation or management based research. For example, the location of such outliers can be used to pinpoint where the establishment of biodiversity monitoring or surveying plots will be most effective in parts of the landscape where hotspots are not present or the spatial distribution of values is random.

Conclusion

We demonstrated the use of LIDAR-derived metrics and sound recordings for identifying canopy structural attributes supporting high acoustic diversity in a neotropical forest environment. What is unique about this study is that it integrates two high density data sources (i.e., LIDAR and soundscape recordings) for high resolution modeling over large areas. The study is also the first to show that the composition of acoustic frequency bands and acoustic diversity are strongly linked with the vertical structure of the local canopy in forested environments. By coupling LIDAR with acoustic data we were also able to develop a framework for identifying individual pixels as well as clusters of pixels (hotspots) within forests with canopy structural attributes that are likely to be important for vocal fauna. Given the recent interest in soundscape conservation and the relative ease with which LIDAR and sound data can be obtained at large scales, our approach holds high potential for landscape level assessment of acoustic conservation value within forested environments.

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