VERUSCRIPT

JOURNAL OF ECOACOUSTICS
www.veruscript.com/jea

Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot

Original paper

Article history:
Received: 29 September 2017
Accepted: 11 March 2018
Published: 9 May 2018

Check for updates

***Correspondence:**
RTB: Rachel.Buxton@colostate.edu

Peer review:
Double blind

Keywords:
diversity; landscape; species richness; Western Ghats; passive acoustic monitoring; shade-grown crop

Citation:
Buxton R. T., Agnihotri S., Robin V. V., Goel A., and Balakrishnan R. (2018). Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot. Journal of Ecoacoustics. 2: #GWPZVD.
https://doi.org/10.22261/JEA.GWPZVD

Rachel T. Buxton[1,*], Samira Agnihotri[2], V. V. Robin[3], Anurag Goel[4], Rohini Balakrishnan[5]

[1] *Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, 80523 Fort Collins, United States*
[2] *School of Natural Sciences and Engineering, National Institute of Advanced Studies, Bengaluru 560012, India*
[3] *Indian Institute of Science Education and Research Tirupati, 517507, Andhra Pradesh, India*
[4] *WAPRED - Worldwide Association for Preservation and Restoration of Ecological Diversity, P.O. Box-101, Madikeri, Kodagu, Karnataka 571201, India*
[5] *Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560012, India*

Abstract

Passive acoustic monitoring is a potentially valuable tool in biodiversity hotspots, where surveying can occur at large scales across land conversion types. However, in order to extract meaningful biological information from resulting enormous acoustic datasets, rapid analytical techniques are required. Here we tested the ability of a suite of acoustic indices to predict avian bioacoustic activity in recordings collected from the Western Ghats, a biodiversity hotspot in southwestern India. Recordings were collected at 28 sites in a range of land-use types, from tea, coffee, and cardamom plantations to remnant forest stands. Using 36 acoustic indices we developed random forest models to predict the richness, diversity, and total number of avian vocalizations observed in recordings. We found limited evidence that acoustic indices predict the richness and total number of avian species vocalizations in recordings ($R^2 < 0.51$). However, acoustic indices predicted the diversity of avian species vocalizations with high accuracy ($R^2 = 0.64$, mean squared error = 0.17). Index models predicted low and high diversity best, with the highest residuals for medium diversity values and when continuous biological sounds were present (*e.g.*, insect sounds >8 sec). The acoustic complexity index and roughness index were the most important for predicting avian vocal diversity. Avian species richness was generally higher among shade-grown crops than in the open tea plantation. Our results suggest that models incorporating acoustic indices can accurately predict low and high avian species diversity from acoustic recordings. Thus, ecoacoustics could be an important contributor to biodiversity monitoring across landscapes like the Western Ghats, which are a complex mosaic of different land-use types and face continued changes in the future.

Introduction

Rapid methods to assess biodiversity and ecosystem health at large spatial and temporal scales are paramount for informing conservation planning (Stem et al., 2005). Because sound-producing species are important indicators of environmental health, acoustic surveys offer an important approach for biodiversity monitoring programs (Gregory and Strien, 2010; Blumstein et al., 2011). Advances in digital recording technology allow standardized acoustic surveying of increasingly large landscapes over longer, coordinated time-periods (Merchant et al., 2015). Passive acoustic monitoring would thus be particularly useful in biodiversity hotspots, where understanding the impact of widespread land conversion on numerous species requires rapid surveying at a large scale.

In order to extract meaningful biological information from the enormous datasets that result from large-scale acoustic monitoring, a number of acoustic indices have been developed (*Buxton et al., in review*). Acoustic indices examine the heterogeneity of the acoustic environment, under the assumption that more species found in a community will produce a greater number of different signals at the same time (Sueur et al., 2008b). By summarizing acoustic energy, this approach foregoes species identification and focuses instead on community level diversity (Towsey et al., 2014). Many types of acoustic indices have been tested and have been found to reflect vocal species diversity and abundance, community composition, vegetation structure, habitat type, human perception of a soundscape, human activity, and ecological condition in terrestrial and aquatic habitats (Sueur et al., 2014). However, the development and standardization of appropriate acoustic indices have occurred predominantly in temperate regions (*Buxton et al., in review*).

The mountain chains of the Western Ghats in southern India are a biodiversity hotspot –with high endemism and extreme rates of habitat loss (Myers et al., 2000). Between 1920 and 1990, the Western Ghats experienced a 40% decline in forest cover due to land conversion for plantations of timber, tea, coffee, and other agriculture (Chandran, 1997; Menon and Bawa, 1997). The Western Ghats are by far the most densely populated and widely altered of global biodiversity hotspots (Cincotta et al., 2000). Human-modified landscapes in the Western Ghats typically retain a matrix of native forest cover and feature high habitat heterogeneity (Anand et al., 2010). Land-use ranges from coffee grown under the shade of native forest trees to open monocultures of tea (Raman, 2006). This juxtaposition of natural areas and different land-use types warrants a biodiversity monitoring approach which accounts for both local and landscape-scale characteristics.

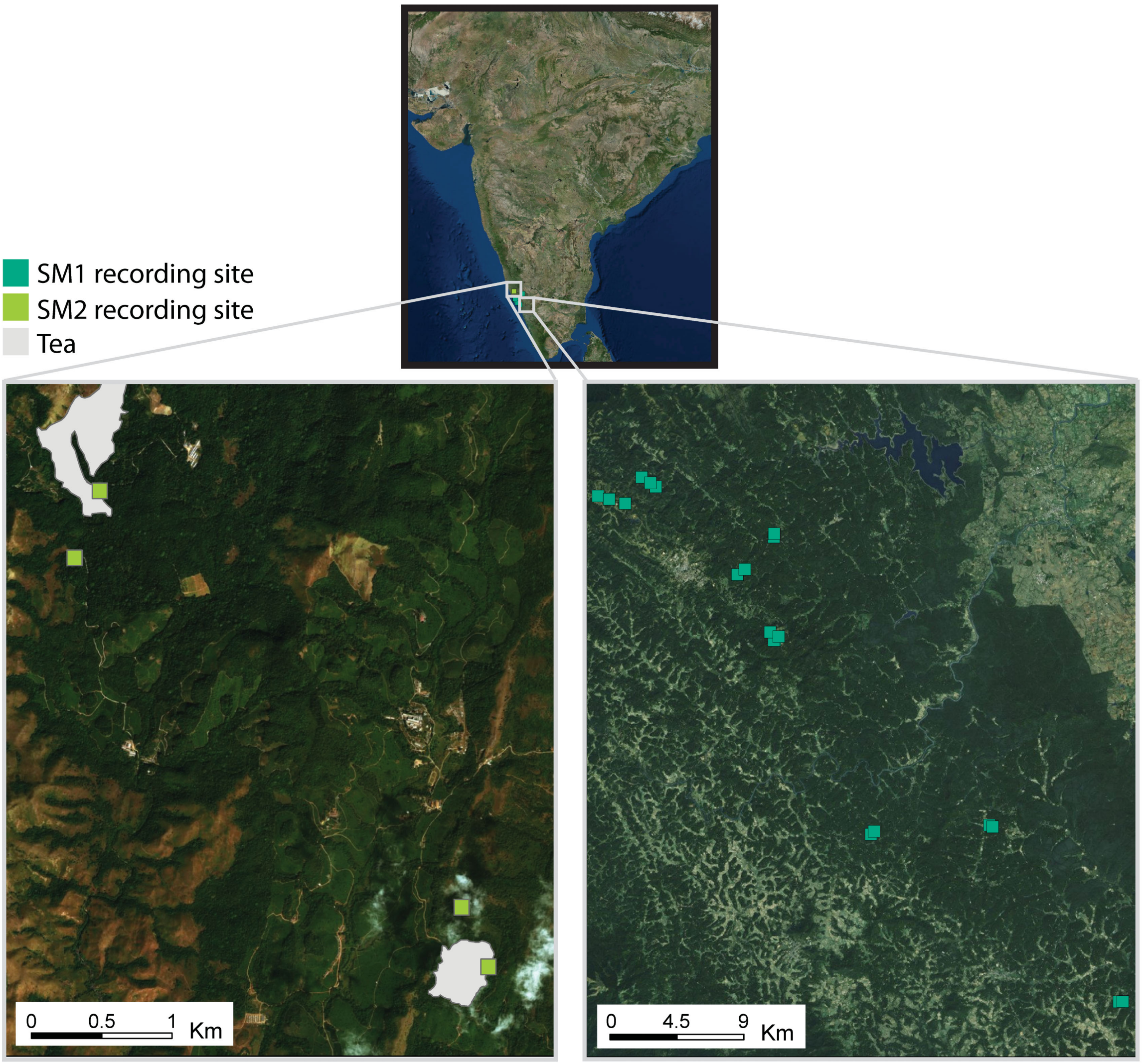
The Western Ghats have an especially high diversity of amphibians, birds, crickets, and cicadas (Mittermeier et al., 2011), many of which produce sounds for territory defense, mate attraction, predator deterrence, navigation, foraging, and maintaining social groups (Brumm, 2013). This high diversity of sound-producing species suggests that acoustic monitoring could be a particularly valuable method. However, properties of the acoustic environment could render the use of acoustic indices for analysis of recordings challenging. For example, there are high densities of insects which produce extended, constant, and broadband vocalizations (Diwakar and Balakrishnan, 2007; Price et al., 2016). This may confound a high diversity of bird song, which is characterized by an intrinsic variability of intensities (Pieretti et al., 2011). Moreover, heterogeneity of the acoustic environment may be expected to increase with avian vocal diversity and reach a threshold due to the redundancies in acoustic characteristics of species (Sueur et al., 2008b). Thus, in a crowded and complex acoustic space, the relationship between acoustic indices and vocal species diversity is unclear.

With a high diversity of species embedded in a complex mosaic of land-use types, the Western Ghats would benefit from a standardized monitoring approach capable of measuring biodiversity at particular places and times, but which is also predictive and scalable across the landscape. Passive acoustic monitoring would be an ideal technique to capture acoustic diversity at large spatio-temporal scales. However, to extract meaningful biological information from large acoustic datasets, an automated approach is required. Here we tested the ability of acoustic indices to predict the richness, diversity, and total number of avian vocalizations in recordings from 28 sites in the tropical wet evergreen region of the Western Ghats. Additionally, using a combination of model predictions and observations from recordings, we compare acoustic diversity and the richness of avian vocalizations between a number of different land-use types, including tea, coffee, and cardamom.

Methods

Recording sites

We obtained acoustic recordings from four sites within Kadumane tea estate in Hassan district and 24 sites at plantations in Kodagu district of Karnataka state in the Western Ghats (Figure 1). The altitude ranged from 900–1,100 m, where rainforest at this elevation is classified as tropical wet evergreen (Champion and Seth, 1968). Kadumane tea estate occupies over 1,000 acres, with extensive areas



Kadumane tea estate Kodagu plantations

Figure 1. Locations of acoustic recorders in the Western Ghats, India.

Four sites were located in the Kadumane tea plantation and 24 sites were located in Mojo plantation. Dark green squares indicate the use of Wildlife Acoustic Song Meter model SM2, light green squares indicate the use of SM1, and light grey shaded areas indicate open tea plantations closest to the recorder. World imagery captured by ArcGIS MapServer.

cleared for tea (*Camellia sinensis*; Figure 2) and small interspersed fragments of remnant forest. The plantations in Kodagu district have a variety of shade-grown crops, including coffee (*Coffea spp.*) and cardamom (*Elettaria cardamomum*), interspersed with black pepper (*Piper nigrum*) vines (Figure 2).

Acoustic recordings

At Kadumane tea estate, recordings were collected for 3–12 days in May 2017 using Song Meters (model SM2; Wildlife Acoustics Inc., Concord, MA; Supplementary material, Appendix 1). Audio data were collected in mono, 16 bit WAV format at a sampling rate of 22,050 Hz with a gain of 48 dB. Song Meters were programmed to record in 5 minutes increments for 2 hours after sunrise and for the first 5 minutes each 30 minutes thereafter. Two Song Meters were placed at the edge of tea fields, two were placed >300 m inside forest fragments, and all recording sites were >300 m to ensure independence of acoustic environments.

At plantations in Kodagu, recordings were collected for 2–4 days from April 2010–January 2011 using Song Meters model SM1 (Supplementary material, Appendix 1). Audio data were collected in stereo, 16 bit WAV format at a sampling rate of 22,050 Hz with a gain of 42 dB for 2 minutes each hour from 0600–0800 IST. Half of the recordings were collected in coffee and half were collected in cardamom plantations. Similar to Kadumane, all recording sites were spaced >250 m apart.

Analysis of recordings

In order to calibrate data acquired from different recording devices we converted all audio data to 1-second 1/3 octave band SPLs measurements from 12.5–8,000 Hz using an end-to-end calibration method (Merchant et al., 2015). We then calculated a total of 36 acoustic indices and acoustic descriptors (Table 1) for each 5 minutes (Kadumane) and 2 minutes (Kodagu) sound file. We used indices calculated at a 1-second 1/3 octave band resolution because we found indices calculated at a finer resolution (0.02 sec, 43 Hz) to be of limited utility (Supplementary material, Appendix 2). Because the lowest frequency of a bird vocalization was found at 230 Hz (Greater coucal, *Centropus sinensis*), we calculated indices intended to capture biological activity using frequency bands from 250–8,000 Hz and those intended to capture background noise (*i.e.*, anthropogenic and weather sounds) using bands from 31.5–200 Hz (Brumm and Slabbekoorn, 2005).

To assess the diversity and richness of bird species vocalizations for comparison with acoustic indices, a trained technician (for Kadumane) and a bird song expert (SA, for Kodagu) identified bird vocalizations in a subset of recordings. The observers used software Raven Pro 1.5 (Cornell University, Ithaca, NY) to visualize spectrograms, listen to audio files, and tag vocalizations. Before analyzing the final dataset, to ensure the technician was able to correctly identify most (>70%) bird sounds, they were asked to identify 65 randomly chosen bird species songs from the Karnataka region of the Western Ghats (bird song accessed from xeno-canto—http://www.xeno-canto.org). Although we were interested in classifying insect vocalizations, they have little frequency modulation; thus, identifying species would require more time-consuming observation of oscillograms or power spectra (Metrani and Balakrishnan, 2005). Instead, we identified all insect sounds as “insect.” Other non-avian sounds were classified as “anthropogenic,” “rain,” “frog,” “squirrel,” or “langur.” Sounds that observers were unable to identify to species (<2%) were labeled as “unknown.”

In recordings from Kodagu, the number of unique avian species vocalizations was noted for each 2-minute clips (*i.e.*, vocal species richness). In recordings from Kadumane, the technician measured the duration, counted, and classified each vocalization (*i.e.*, vocal species richness and number of each vocalization) in three randomly selected 5-minute clips from each day at each site (58 clips total). Because we were unable to isolate individual animals, the total number of individual sounds from each species was counted. When it was difficult to distinguish individual sounds, the total duration of a series of vocalizations was calculated and divided by the average duration of a single sound.

Because we collected longer recording samples at Kadumane, to standardize vocal species richness among Kadumane and Kodagu we divided the total number of unique avian species heard by the

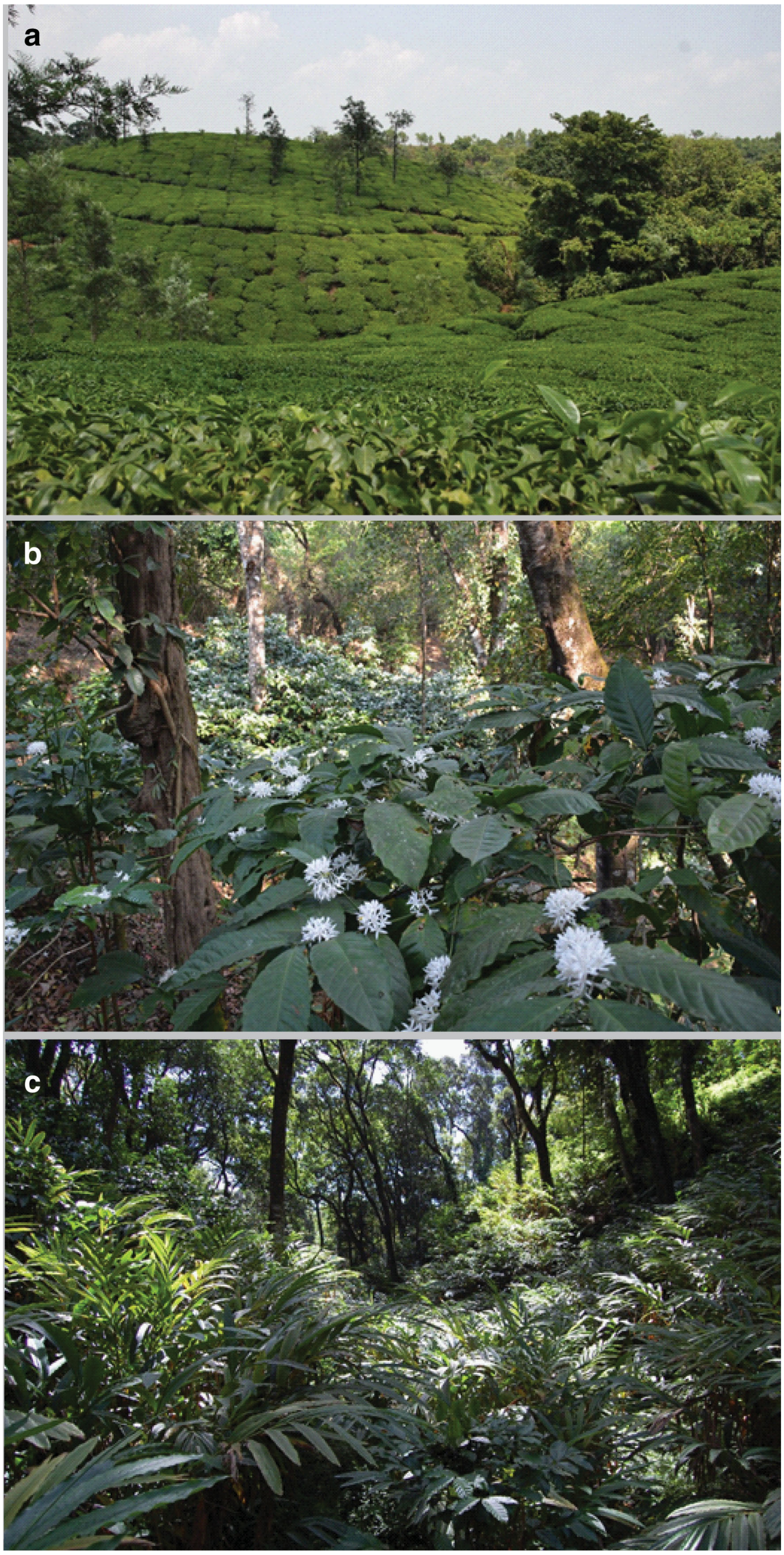


Figure 2. Examples of differences in vegetation structure and composition across different land-use types where recordings were collected in the Western Ghats: a) tea, b) coffee, c) cardamom.

Typically tea plantations have the least canopy cover. Photographs were made by Rachel Buxton and Samira Agnihotri.

Table 1. Full set of acoustic indices calculated on calibrated 1-second 1/3 octave band acoustic data from the Western Ghats, India. The full spectrum of frequency bands spanned from 31.5–8,000 Hz, biological bands spanned from 250–8,000 Hz, and noise bands from 31.5–200 Hz. For full explanation of each index see references and (*Buxton et al., in review*).

Index abbreviation	Index name	Frequency band	References
$L_{10}-L_{90}$	Difference between 10th and 90th exceedence levels	Full spectrum	(Hong and Jeon, 2017)
Mamp	Median sound level	Full spectrum	(Depraetere et al., 2013)
dBA_noise	A-weighted mean sound level	Noise	(Torija et al., 2013)
dBA_bird		Biological	(Torija et al., 2013)
dB_noise	Mean sound level	Noise	(Torija et al., 2013)
dB_bird		Biological	(Torija et al., 2013)
Biophony	Biophony	Biological	(Joo et al., 2011)
Anthrophony	Anthrophony	Noise	(Joo et al., 2011)
avgAMP	Average signal amplitude	Full spectrum	(Desjonquères et al., 2015)
L10AMP	SPL exceeded 10% of the time	Full spectrum	(Torija et al., 2013)
Peakfreq	Peak frequency	Biological	(Sueur et al., 2008a)
AA_noise	Acoustic activity	Noise	(Towsey et al., 2014)
AA		Biological	(Towsey et al., 2014)
AAc_noise	Count of acoustic events	Noise	(Towsey et al., 2014)
Aac		Biological	(Towsey et al., 2014)
AAdur_noise	Duration of acoustic events	Noise	(Towsey et al., 2014)
AAdur		Biological	(Towsey et al., 2014)
Kurtosis	Spectral kurtosis	Biological	(Bormpoudakis et al., 2013)
Skew	Spectral skewness	Biological	(Bormpoudakis et al., 2013)
Hf	Spectral entropy	Biological	(Sueur et al., 2008b)
Ht	Temporal entropy	Biological	(Sueur et al., 2008b)
H	Total entropy	Biological	(Sueur et al., 2008b)
Hm	Entropy of spectral maxima	Biological	(Towsey et al., 2014)
HvPres	Entropy of spectral variance	Biological	(Towsey et al., 2014)
HvSPL	Entropy of spectral variance	Biological	(Towsey et al., 2014)
Roughness	Roughness	Biological	(Rychtáriková and Vermeir, 2013)

Index abbreviation	Index name	Frequency band	References
ACI	Acoustic complexity	Biological	(Pieretti et al., 2011)
ADI	Acoustic diversity	Biological	(Pekin et al., 2012)
Evenness	Acoustic evenness	Biological	(Villanueva-Rivera et al., 2011)
AR	Acoustic richness	Biological	(Depraetere et al., 2013)
NDSI	Normalized difference soundscape index	Full spectrum	(Kasten et al., 2012)
Bio_anth	Ratio of biophony to anthrophony	Full spectrum	(Kasten et al., 2012)
SpecPers	Spectral persistence	Biological	(Towsey et al., 2014)
CLdurDiff	Difference between cluster duration	Biological	(Towsey et al., 2014)
CLpkDiff	Difference between cluster peak frequency	Biological	(Towsey et al., 2014)
CLLeqDiff	Difference between cluster Leq	Biological	(Towsey et al., 2014)
NumCL	Spectral diversity	Biological	(Towsey et al., 2014)

length of the recording sample (in min). For recordings from Kadumane, we calculated the Shannon index of diversity of avian vocalizations (Equations 1, vegan package; (Oksanen et al., 2013), the total number of avian vocalizations, and the total number of the most common avian species vocalizations for each 5 minutes recording sample. The Shannon index was calculated as:

$$H_{\mathrm{Sh}} = -\sum_{i=1}^{S} p_i \log p_i \tag{1}$$

where S was the number of avian species observed in the recording sample and p_i was proportion of unique vocalizations belonging to the ith species (Gotelli and Chao, 2013).

Quantitative analysis

All statistical analyses were performed in R version 3.4.1 (R Core Team, 2017). To predict the richness, diversity, and the total number of avian vocalizations in recordings from acoustic indices, we used a random forest (RF) machine learning procedure (Breiman, 2001; randomForest package; Liaw and Wiener, 2002). First we removed multivariate redundant acoustic indices using QR decomposition (threshold = 0.05; (Golub and Van Loan, 1996). We tested global RF models with all remaining acoustic indices as predictor variables. Using the 58 sub-setted clips from Kadumane and data from Kodagu combined we tested a global RF model with the richness of avian species vocalizations as the response variable. Using the 58 clips from Kadumane only we tested global RF models with one of three response variables: Shannon diversity of avian vocalizations, total number of avian vocalizations, and total number of the most common species vocalizations (Indian scimitar babbler, *Pomatorhinus horsfieldii*, see results). We selected the model with the lowest mean squared error (MSE) and highest R^2 and used a model selection procedure to fit a final model with the fewest number of variables (rfUtilities package; (Evans and Murphy, 2017). We used this final model to predict the diversity of avian vocalizations in all recordings. To examine the importance of each acoustic index we used the mean percent increase in MSE, which is the loss of predictive accuracy due to the permutation of each variable. The more important a parameter, the larger the percent increase in MSE (*i.e.*, the larger the effect on the model; (Breiman, 2001).

Continuous sounds are thought to confound the ability of acoustic indices to detect variation in bioacoustic signals (Pieretti and Farina, 2013; Parks et al., 2014). Thus, we tested whether continuous sounds affected the predictive ability of top acoustic index RF model by examining the relationship between model residuals and the duration and count of different sound types. We used a linear mixed model with absolute values of model residuals as a response variable and the following sound types as predictor variables: the duration (in sec) of anthropogenic (*e.g.*, voices, motorcycles, vehicles) and constant biological sound (sounds >8 sec; *e.g.*, insects, some birds); the presence or absence of rain; and the number insect and frog sounds. We used these sound types as covariates as they are relatively continuous over time and use a wide range of frequencies.

Results

For recordings collected at Kadumane, 290 minutes (5% of total) were manually analyzed to count and categorize all sounds. For recordings from Kodagu, 328 minutes (95% of total) were manually analyzed to count the total number of avian species vocalizations. We found 39 avian species in recordings from Kadumane and 67 in recordings from Kodagu. At both locations, we observed the Large-billed crow (*Corvus macrorhynchos*) in the largest percentage of recording clips (29% and 39% of Kadumane and Kodagu recording clips, respectively). In recordings from Kadumane, the greatest number of total vocalizations was produced by the Indian scimitar babbler (Supplementary material, Appendix 3). Thus, we further analyzed whether acoustic indices could predict the total number of Indian scimitar babbler vocalizations, which were the most common species sounds.

Acoustic indices vs avian vocal activity and diversity

We found that acoustic indices weakly predicted the richness of avian species vocalizations in Kodagu recordings, Kadumane recordings, and recordings from both sites combined ($R^2 < 0.51$, MSE >0.25, Table 2). Similarly, acoustic indices weakly predicted the total number of avian vocalizations and the number of Indian scimitar babbler vocalizations in Kadumane recordings ($R^2 < 0.47$, MSE > 276.35, Table 2). Conversely, acoustic indices were strongly related to Shannon diversity of avian vocalizations in Kadumane recordings ($R^2 = 0.64$, MSE = 0.17, Figure 3, Table 2); thus, we use this model in all further analyses. The top RF model predicting Shannon diversity of vocalizations included the following acoustic indices as predictors: acoustic complexity index (ACI) (Pieretti et al., 2011); spectral and temporal entropy (Sueur et al., 2008b); biophony and mean sound levels in the avian frequency

Table 2. Mean squared error (MSE) and R^2 of global RF models combining acoustic indices to predict Shannon diversity of avian vocalizations, total avian vocalizations, total vocalizations of the Indian scimitar babbler, and avian species richness in acoustic recordings from sites in Kadumane and Kodagu.

Response variable	Recording sites	R^2	MSE
Shannon diversity	Kadumane	0.64	0.17
Total avian sounds	Kadumane	0.47	4,265.40
Total sounds of Indian scimitar babbler	Kadumane	0.33	276.35
Species richness	Kadumane	0.51	0.25
Species richness	Kodagu	0.40	1.35
Species richness	All sites	0.51	1.12

bands (Joo et al., 2011; Tucker et al., 2014); acoustic activity, duration of acoustic events in the avian and noise bands, entropy of spectral maxima, and spectral persistence (Towsey et al., 2014), acoustic evenness index and acoustic diversity index (Villanueva-Rivera et al., 2011); spectral kurtosis (Bormpoudakis et al., 2013); and roughness and the difference between the 10th and 90th exceedance levels (Rychtáriková and Vermeir, 2013; Hong and Jeon, 2017). The most important acoustic indices in this top model were the ACI, roughness, and temporal entropy (Figure 4).

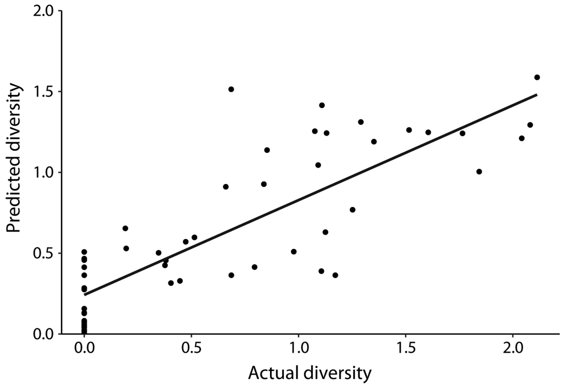


Figure 3. Relationship between the actual and predicted Shannon diversity of species vocalizations within recordings collected from Kadumane tea estate, Western Ghats, India.

Predicted values were calculated using the top random forest model which included a suite of acoustic indices.

Predicting avian vocal diversity among sites

We found that RF models best predicted high and low Shannon diversity of avian vocalizations (Figure 5). Shannon diversity between 0.5–1.5 had the highest model residuals indicating that acoustic indices were less reliable when predicting mid-levels of avian vocalization diversity.

Linear models examining the effect of sounds on residuals from RF models showed that residuals were higher in recordings with longer duration biological sounds (Figure 6). These sounds ranged from 8 to 238 seconds (almost the entire duration of the 300 sec sound clip) and were produced by insects, birds, and frogs (*n* = 12, *n* = 23, and *n* = 5 of 58 respectively). Anthropogenic and rain sounds had little effect on

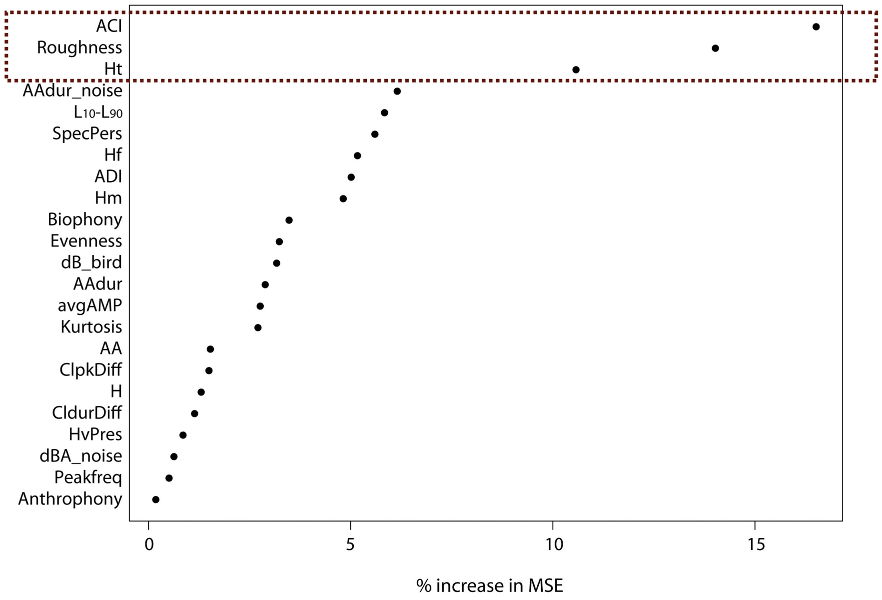


Figure 4. The importance of acoustic indices included in a random forest model predicting Shannon diversity of species vocalizations in recordings collected from Kadumane tea estate, Western Ghats, India (see Table 1 for explanation of abbreviations).

The percent increase in mean standard error (MSE) indicates the loss of predictive accuracy when the predictor variable is permuted. Only indices >0% increase in MSE are shown. The red stippled box indicates the three indices with an increase in MSE >10%.

the predictive ability of models, although they were present in very few of the recording clips analyzed (*n* = 6 and *n* = 2 of 58, respectively).

RF models predicted the highest Shannon diversity of avian vocalizations between sunrise and two hours after sunrise (0600–0800 Indian Standard Time, IST; Figure 7). At some sites, diversity of avian vocalizations also peaked just before sunset (1700–1800 IST). The predicted Shannon diversity of avian vocalizations from acoustic index models were weakly correlated with avian species richness observed in recordings from each site at Kodagu (Table 3). Avian species richness was lowest at the recording sites at Kadumane placed within forest remnants and 1 m from an open tea plantation (Kadumane South remnant forest and Kadumane North tea plantation, Table 3). Generally, we found that avian species richness was higher at sites in coffee and cardamom plantations versus tea plantations or remnant forest stands on tea plantations (Table 3, Figure 8).

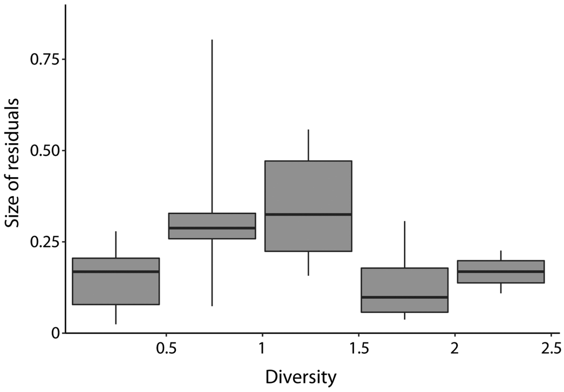


Figure 5. The size of residuals (the difference between the observed Shannon diversity of vocalizations and random forest model predicted Shannon diversity of avian species vocalizations) for each level of Shannon diversity in recordings collected from Kadumane tea estate, Western Ghats, India.

The black bar indicates the median, boxes indicate 75th percentile, and whiskers indicate the 98th percentile.

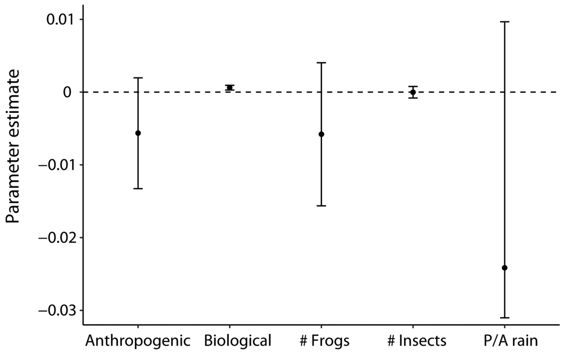


Figure 6. Parameter estimates and 95% confidence intervals (error bars) for covariates in a linear model used to predict the size of residuals of random forest models predicting Shannon diversity of species vocalizations in recordings collected from Kadumane tea estate, Western Ghats, India.

Covariates included the duration (in sec) of constant anthropogenic and biological sounds, the number of frog and insect sounds, and the presence or absence of rain.

Discussion

Acoustic monitoring has long been used to capture the diversity and abundance of vocalizing animals. Rapid technological advances in low-cost digital recorders has increased the potential for relatively cheap and effective passive acoustic monitoring over large extents (Merchant et al., 2015; Sueur and Farina, 2015). This new scope of acoustic monitoring has increased the scale of ecological inference, where large networks of acoustic recorders are poised to be the future of wildlife surveying (Sutherland et al., 2016). Given the urgency of addressing the biodiversity crisis, the rapid, standardized, and large-scale monitoring offered by acoustic recordings is imperative. Critical to acoustic methods is finding a way of quickly extracting meaningful information from enormous datasets. We tested the ability of a suite of acoustic indices to capture the diversity and richness of avian species vocalizations in recordings from the Western Ghats, a biodiversity hotspot.

We found that indices were of limited utility to capture the richness of avian species vocalizations, but accurately reflected the Shannon diversity of avian vocalizations in recordings (Table 2). Because indices measure variation in the acoustic environment they depend on both the number of species vocalizing and the abundance of each vocalization. Thus, acoustic indices are more likely to predict the diversity of vocalizations, which takes into account the abundance of each type of vocalization. Other studies found a significant relationship between avian species richness and acoustic indices (Sueur et al., 2008b; Joo et al.,

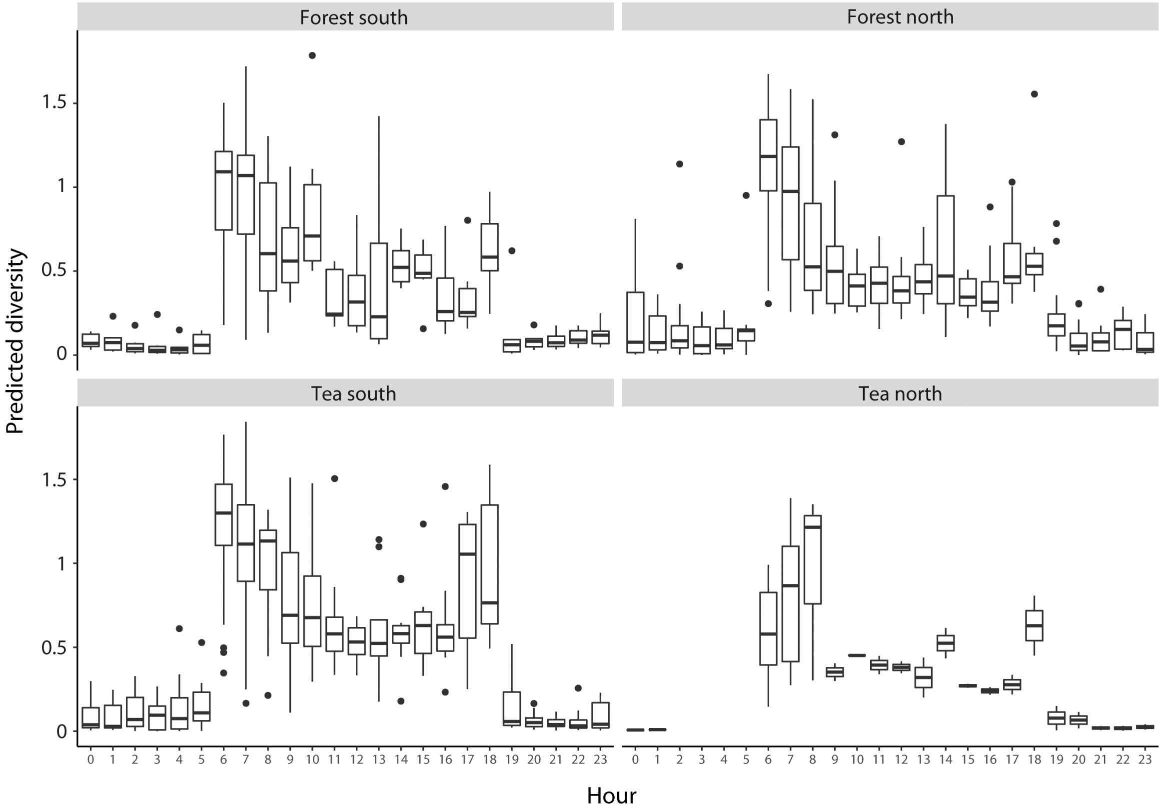


Figure 7. The predicted Shannon diversity of species vocalizations within recordings collected from four sites at Kadumane tea estate, Western Ghats, India.

Predicted values were calculated using the top random forest model which included a suite of acoustic indices. "Forest" sites were 300 m inside remnant forest patches while "tea" sites were within 1 m from an open tea plantation.

2011; Pieretti et al., 2011). However, these recordings were collected in simpler acoustic environments with lower diversity of vocalizing animals (*e.g.*, temperate forests) or indices were compared with simulated avian communities. In an environment with more complex acoustic characteristics, such as the Western Ghats, indices are more likely to reflect a combination of the abundance and different types of vocalizations.

We found that many acoustic indices were included in the top model predicting the diversity of avian vocalizations in recordings. Different indices have different mathematical properties and reflect different components of a soundscape (Gasc et al., 2015). Thus, combining groups of indices in a flexible modelling approach is most effective to predict the variation in the acoustic environment (Towsey et al., 2014). Indices that most affected the predictive ability of models were those that reflected both the temporal and spectral distribution of acoustic energy. For example, the ACI had the highest variable importance (*i.e.*, permutation caused the highest increase in MSE; Figure 4). The ACI is calculated by summing the absolute difference in sound pressure levels (SPL) between adjacent seconds (*i.e.*, temporal variation) divided by the total SPL in the recording sample over all frequency bins (*i.e.*, frequency variation; (Pieretti et al., 2011). Also important was temporal entropy, which measures the evenness of sound over time (Sueur et al., 2008b). We found that acoustic descriptors, or acoustic indices summarizing sound energy (*e.g.*, mean and median sound levels, Table 1), were less important in the model predicting diversity of avian vocalizations, likely because they are less effective at capturing acoustic heterogeneity. Our results suggest that both the variation and evenness in sound over time and frequency bins contribute to predicting the diversity of avian vocalizations in an acoustic sample.

We found some evidence of difference in predictive ability of models between Kadumane and Kodagu plantation recordings (Table 2). The richness of singing bird species per min of observed recordings was

Table 3. The mean observed richness of bird species vocalizations in acoustic recordings per minute of recordings observed and diversity of vocalizations predicted from random forest acoustic index models (± standard error).

Site	Crop	Bird species richness	Predicted diversity
Mojo plantation 3	Cardamom	0.833 ± 0.255	0.761 ± 0.158
Faisal	Coffee	0.556 ± 0.032	0.278 ± 0.009
Subramani	Coffee	0.528 ± 0.052	0.329 ± 0.041
Rainforest R	Cardamom	0.514 ± 0.028	0.602 ± 0.084
Naveen	Coffee	0.5 ± 0.025	0.373 ± 0.054
Faisal	Cardamom	0.5 ± 0.012	0.497 ± 0.043
Shivappa	Cardamom	0.479 ± 0.036	0.206 ± 0.017
Rajeev	Cardamom	0.472 ± 0.064	0.282 ± 0.025
Subaiya	Coffee	0.444 ± 0.059	0.417 ± 0.022
Cloudbowl	Cardamom	0.417 ± 0.05	0.495 ± 0.046
Rajeev	Coffee	0.403 ± 0.056	0.311 ± 0.024
School estate	Coffee	0.403 ± 0.048	0.625 ± 0.043
Mojo plantation 2	Coffee	0.4 ± 0.074	0.494 ± 0.023
School estate	Cardamom	0.375 ± 0.049	0.566 ± 0.028
Uthappa	Cardamom	0.36 ± 0.054	0.383 ± 0.031
Bharat	Coffee	0.35 ± 0.027	0.383 ± 0.036
Golden mist	Coffee	0.347 ± 0.034	0.629 ± 0.04
Kushalappa	Coffee	0.306 ± 0.042	0.267 ± 0.026
Mojo plantation 1	Cardamom	0.278 ± 0.043	0.188 ± 0.013
Uthappa 2	Cardamom	0.253 ± 0.008	0.581 ± 0.036
Vivek	Coffee	0.191 ± 0.011	0.251 ± 0.013
Emmanuel	Cardamom	0.181 ± 0.012	0.346 ± 0.006
Brookview	Coffee	0.139 ± 0.008	0.453 ± 0.027
Brookview	Cardamom	0.095 ± 0.008	0.563 ± 0.023
Kadumane North	Tea	0.089 ± 0.051	0.472 ± 0.007
Kadumane South	Forest (remnant on tea plantation)	0.054 ± 0.005	0.578 ± 0.002
Kadumane South	Tea	0.043 ± 0.002	0.734 ± 0.001
Kadumane North	Forest (remnant on tea plantation)	0.02 ± 0.001	0.62 ± 0.001

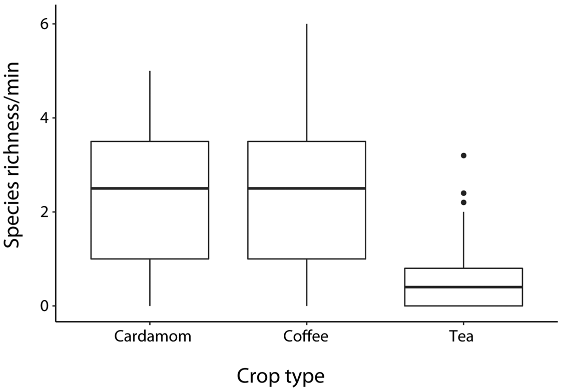


Figure 8. Median avian species richness observed per minute of recordings collected from 28 sites in different crop types in the Western Ghats, India.

"Tea" sites were 1–300 m inside remnant forest patches on Kadumane tea plantation, while "cardamom" and "coffee" sites were in the Kodagu region. The black bar indicates the median, boxes indicate 75th percentile, and whiskers indicate the 98th percentile.

higher in the Kodagu plantation recordings (Table 3). Moreover, the composition of vocalizing bird species was slightly different between the two locations. Although acoustic indices should be insensitive to the identity of species vocalizations, there is some evidence from previous research that indices may change with the presence of particular species (Gasc et al., 2015). Thus, to ensure acoustic indices reflect vocal diversity among locations, future research should investigate the effect of different sets of species and the density of species richness in the acoustic environment.

Acoustic index models predicted high and low vocal species diversity with higher accuracy. Acoustic characteristics are expected to be more readily distinguishable between recordings with low and high diversity relative to sites where acoustic characteristics are only slightly different. Thus, some error can be expected for vocalizing communities with intermediate numbers of species. Moreover, we found that relatively continuous sounds (>8 sec, generally insects) affected the ability of index models to predict vocal diversity. In this sense, the acoustic environment of the Western Ghats makes the use of acoustic indices challenging—particularly, the high density of animals that produce extended sounds covering a broad spectrum of frequencies (*e.g.*, cicadas, (Diwakar and Balakrishnan, 2007; Price et al., 2016). However, the relationship between model residuals and continuous biological sounds was weak (confidence intervals near zero—Figure 6). This suggests that the indices we included in predictive models captured at least some of the variability relating to the presence of continuous sources. The development of new indices may help identify and remove or control for the presence of unwanted continuous sources of broadband sound in long-term recordings. Further research may also consider the presence and effect of anthropogenic sounds, which were rare at our recording sites.

Although we were unable to quantify the richness of insect species, their stridulation sounds are not only an important feature of the acoustic environment, but also reflect a significant component of local biodiversity. Similarly, we did not focus on identifying anuran vocalizations to species. Previous studies have established that richness of insect and anuran species differs across different land-use types (Daniels, 2003; Mone et al., 2014). Thus, future research could focus on developing new indices or examining the predictive ability of a subset of existing acoustic indices for non-avian species diversity.

We found lower avian species richness at recording sites near open tea fields and in remnant forest stands on tea plantations versus sites in coffee and cardamom plantations (Figure 2). These findings are similar to earlier studies, where shade-grown crops are known to maintain higher levels of biodiversity (Sidhu et al., 2010). Because coffee and cardamom are generally grown under the shade of native rainforest trees (Figure 2), habitats are more complex, and some plantations are known to resemble neighboring remnant forest structure (Bhagwat et al., 2008). Conversely, tea plantations are intensively managed, dense monocultures of tea bushes with a sparse canopy of alien tree species, representing the most extreme habitat alteration relative to native rainforest (Raman, 2006). Tea plantations are a major form of land-use in the Western Ghats, having increased by 6,200 Ha (5.5%) between 2000 and 2006 (Mudappa and Raman, 2007). Moreover, recent observation suggests that coffee and cardamom plantations are shifting towards lower canopy cover. Thus, rapid assessments of biodiversity in these altered Western Ghat landscapes could be especially important given the potential for further land-use change.

We caution that recordings were collected at different times of year and in different years between sites at Kadumane and Kodagu. Recordings were collected in May at Kadumane, towards the end of peak breeding season of birds in this part of Western Ghats (Betts, 1952). Recordings were collected between October and March at sites in Kodagu (Table S1.1), which spans the post-monsoon to pre-breeding season, when several migrant species are present in southern India. Many avian species are less vocal outside of the breeding season, likely resulting in less vocal activity during the winter period. Although we would expect species richness of vocalizations to be inflated in Kadumane recordings, we observed the opposite, reinforcing our conclusion that avian species richness is lower in tea plantations. However, we recommend standardizing the season when recordings are collected to examine patterns between land-use types. Moreover, future research could focus on annual patterns in avian vocal diversity, examining the changes in patterns when winter migrants arrive and when resident birds breed. Finally, standardizing recording specifications, such as microphone gain and temporal sampling schemes are important when planning acoustic monitoring strategies (Pieretti et al., 2015).

Conclusions

We found that combining a suite of acoustic indices using a flexible modeling approach accurately predicted high and low avian species vocal diversity in recordings from sites in the Western Ghats, India. We also found that avian species richness was lower in tea versus shade-grown coffee and cardamom plantations.

The Western Ghats are a biodiversity hotspot, with high levels of diversity, endemism, and a complex mosaic of different land-use types. This fragmented landscape faces further changes, with the synergistic impact of continued development, habitat loss, and climate change threatening the persistence of biodiversity (Ponce-Reyes et al., 2013). In this context, acoustic recordings analyzed using acoustic indices represent a promising method of measuring avian diversity at large spatio-temporal scales.

Supporting material

S1. Supplementary material. (DOCX)

Acknowledgements

We thank B. Seymoure, C. K. Vishnudas, and K. Maranthe, S. Mone, and Kushalappa for helping place acoustic recorders in the field and K. Kunte for assistance with field logistics. We thank K. M. Cariappa, Senior Manager, Kadamane Estates Company, whose personal interest was central to our successful data collection from Kadumane and the Kadamane Estate for providing us with logging and field assistance. Permission to work at Kadumane tea estate was generously granted by M. M. Venkatachalam and field work was facilitated by the NCBS Museum and Field Stations Facility. Sound recording equipment was provided by the Natural Sounds and Night Skies Division of the National Park Service with assistance from C. Garsha and M. McKenna. We thank V. Joshi for identifying bird sounds in recordings.

Funding sources

VVR was supported by the Science and Engineering Research Board, Department of Science and Technology, from the Government of India (SERB, DST Grant No. SB/S3/EECE/296/2016). RTB's trip to India was funded by the Indo-U.S. 21st Century Knowledge Initiative (Grant title: Partnering to sustain India's biological diversity in the context of rapid environmental change: research, education and community outreach, Grant recipient: Dr. Barry Noon).

Competing interests

All authors declare that they have no conflict of interest.

References

Anand M. O., Krishnaswamy J., Kumar A., and Bali A. (2010). Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter. Biological Conservation. 143 (10): 2363–2374. https://doi.org/10.1016/j.biocon.2010.01.013.

Betts F. N. (1952). The breeding seasons of birds in the hills of south India. Ibis. 94 (4): 621–628. https://doi.org/10.1111/j.1474-919X.1952.tb01875.x.

Bhagwat S. A., Willis K. J., Birks H. J. B., and Whittaker R. J. (2008). Agroforestry: A refuge for tropical biodiversity? Trends in Ecology & Evolution. 23 (5): 261–267. https://doi.org/10.1016/j.tree.2008.01.005.

Blumstein D. T., Mennill D. J., Clemins P., Girod L., Yao K., et al. (2011). Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. Journal of Applied Ecology. 48 (3): 758–767. https://doi.org/10.1111/j.1365-2664.2011.01993.x.

Bormpoudakis D., Sueur J., and Pantis J. (2013). Spatial heterogeneity of ambient sound at the habitat type level: Ecological implications and applications. Landscape Ecology. 28 (3): 495–506. https://doi.org/10.1007/s10980-013-9849-1.

Breiman L. (2001). Random Forests. Machine Learning. 45 (1): 5–32. https://doi.org/10.1023/A:1010933404324.

Brumm H. (2013). Animal Communication and Noise. Berlin, Germany: Springer-Verlag.

Brumm H. and Slabbekoorn H. (2005). Acoustic communication in noise. Advances in the Study of Behaviour. 35: 151–209. https://doi.org/10.1016/S0065-3454(05)35004-2.

Buxton R. T., McKenna M. F., Clapp M., Meyer E., Angeloni L., et al. (Accepted). Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Conservation Biology.

Champion H. G. and Seth P. K. (1968). A Revised Survey of the Forest Types of India. Delhi, India: Manager of Publications.

Chandran M. D. S. (1997). On the ecological history of the Western Ghats. Current Science. 73 (2): 146–155.

Cincotta R. P., Wisnewski J., and Engelman R. (2000). Human population in the biodiversity hotspots. Nature. 404: 990–992. https://doi.org/10.1038/35010105.

Daniels R. J. R. (2003). Impact of tea cultivation on anurans in the Western Ghats. Current Science. 85 (10): 1415–1422.

Depraetere M., Pavoine S., Jiguet F., Gasc A., Duvail S., et al. (2013). Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. Ecological Indicators. 13 (1): 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006.

Desjonquères C., Rybak F., Depraetere M., Gasc A., Le Viol I., et al. (2015). First description of underwater acoustic diversity in three temperate ponds. PeerJ. 3: e1393. https://doi.org/10.7717/peerj.1393.

Diwakar S. and Balakrishnan R. (2007). The assemblage of acoustically communicating crickets of a tropical evergreen forest in southern India: Call diversity and diel calling patterns. Bioacoustics. 16 (2): 113–135. https://doi.org/10.1080/09524622.2007.9753571.

Evans J. and Murphy M. (2017). rfUtilities. R package version 2.1-0. Available at: https://cran.r-project.org/package=rfUtilities. August 2017.

Gasc A., Pavoine S., Lellouch L., Grandcolas P., and Sueur J. (2015). Acoustic indices for biodiversity assessments: Analyses of bias based on simulated bird assemblages and recommendations for field surveys. Biological Conservation. 191: 306–312. https://doi.org/10.1016/j.biocon.2015.06.018.

Golub G. H. and Van Loan C. F. (1996). Matrix Coputations, 3rd edition. Baltmore, USA: Johns Hopkins University Press.

Gotelli N. J. and Chao A. (2013). Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Encyclopedia of Biodiversity, Volume 5, edited by Levin S. A.: Waltham, USA: Academic Press. 195–211.

Gregory R. D. and Strien A. v. (2010). Wild bird indicators: Using composite population trends of birds as measures of environmental health. Ornithological Science. 9 (1): 3–22. https://doi.org/10.2326/osj.9.3.

Hong J. Y. and Jeon J. Y. (2017). Exploring spatial relationships among soundscape variables in urban areas: A spatial statistical modelling approach. Landscape and Urban Planning. 157: 352–364. https://doi.org/10.1016/j.landurbplan.2016.08.006.

Joo W., Gage S. H., and Kasten E. P. (2011). Analysis and interpretation of variability in soundscapes along an urban-rural gradient. Landscape and Urban Planning. 103 (3–4): 259–276. https://doi.org/10.1016/j.landurbplan.2011.08.001.

Kasten E. P., Gage S. H., Fox J., and Joo W. (2012). The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology. Ecological Informatics. 12: 50–67. https://doi.org/10.1016/j.ecoinf.2012.08.001.

Liaw A. and Wiener M. (2002). Classification and regression by randomForest. R News. 2: 18–22.

Menon S. and Bawa K. S. (1997). Applications of geographic information systems, remote-sensing, and a landscape ecology approach to biodiversity conservation in the Western Ghats. Current Science. 73: 134–145.

Merchant N. D., Fristrup K. M., Johnson M. P., Tyack P. L., Witt M. J., et al. (2015). Measuring acoustic habitats. Methods in Ecology and Evolution. 6 (3): 257–265. https://doi.org/10.1111/2041-210X.12330.

Metrani S. and Balakrishnan R. (2005). The utility of song and morphological characters in delineating species boundaries among sympatric tree crickets of the genus Oecanthus (Orthoptera: Gryllidae: Oecanthinae): A numerical taxonomic approach. Journal of Orthoptera Research. 14 (1): 1–16. https://doi.org/10.1665/1082-6467(2005)14[1:TUOSAM]2.0.CO;2.

Mittermeier R. A., Turner W. R., Larsen F. W., Brooks T. M., and Gascon C. (2011). Global biodiversity conservation: The critical role of hotspots. In: Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas, edited by Zachos F. E. and Habel J. C. Berlin, Heidelberg: Springer Berlin Heidelberg.

Mone S., Kusha K. M., Jathanna D., Ali M., and Goel A. (2014). Comparison of insect biodiversity between organic and conventional plantations in Kodagu, Karnataka, India. Journal of Threatened Taxa. 6 (9): 6186–6194. https://doi.org/10.11609/JoTT.o3778.6186-94.

Mudappa D. and Raman T. R. S. (2007). Rainforest restoration and wildlife conservation on private lands in the Western Ghats. In: Making Conservation Work, edited by Shahabuddin G. and Rangarajan M. Ranikhet, India: Permanent Black. 201–240.

Myers N., Mittermeier R. A., Mittermeier C. G., Fonseca G. A. B., and Kent J. (2000). Biodiversity hotspots for conservation priorities. Nature. 403: 853–858. https://doi.org/10.1038/35002501.

Oksanen J., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., et al. (2013). Vegan: Community Ecology Package. R package version 2.0–7. Available at: http://CRAN.R-project.org/package=vegan. September 2016.

Parks S. E., Miksis-Olds J. L., and Denes S. L. (2014). Assessing marine ecosystem acoustic diversity across ocean basins. Ecological Informatics. 21: 81–88. https://doi.org/10.1016/j.ecoinf.2013.11.003.

Pekin B., Jung J., Villanueva-Rivera L., Pijanowski B., and Ahumada J. (2012). Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. Landscape Ecology. 27 (10): 1513–1522. https://doi.org/10.1007/s10980-012-9806-4.

Pieretti N., Duarte M. H. L., Sousa-Lima R. S., Rodrigues M., Young R. J., et al. (2015). Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. Tropical Conservation Science. 8: 215–234. https://doi.org/10.1177/194008291500800117.

Pieretti N. and Farina A. (2013). Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. The Journal of the Acoustical Society of America. 134: 891–900. https://doi.org/10.1121/1.4807812.

Pieretti N., Farina A., and Morri D. (2011). A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). Ecological Indicators. 11 (3): 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005.

Ponce-Reyes R., Nicholson E., Baxter P. W. J., Fuller R. A., and Possingham H. (2013). Extinction risk in cloud forest fragments under climate change and habitat loss. Diversity and Distributions. 19 (5–6): 518–529. https://doi.org/10.1111/ddi.12064.

Price B., Allan E., Marathe K., Sarkar V., Simon C., et al. (2016). The cicadas (Hemiptera: Cicadidae) of India, Bangladesh, Bhutan, Myanmar, Nepal and Sri Lanka: An annotated provisional catalogue, regional checklist and bibliography. Biodiversity Data Journal. 4: e8051. https://doi.org/10.3897/BDJ.4.e8051.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/. January 2017.

Raman T. R. S. (2006). Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. Biodiversity & Conservation. 15 (4): 1577–1607. https://doi.org/10.1007/s10531-005-2352-5.

Rychtáriková M. and Vermeir G. (2013). Soundscape categorization on the basis of objective acoustical parameters. Applied Acoustics. 74 (2): 240–247. https://doi.org/10.1016/j.apacoust.2011.01.004.

Sidhu S., Raman T. R. S., and Goodale E. (2010). Effects of plantations and home-gardens on tropical forest bird communities and mixed-species bird flocks in the southern Western Ghats. Journal of the Bombay Natural History Society. 107: 91–108.

Stem C., Margoluis R., Salafsky N., and Brown M. (2005). Monitoring and evaluation in conservation: A review of trends and approaches. Conservation Biology. 19: 295–309. https://doi.org/10.1111/j.1523-1739.2005.00594.x.

Sueur J., Aubin T., and Simonis C. (2008a). Seewave: A free modular tool for sound analysis and synthesis. Bioacoustics. 18 (2): 213–226. https://doi.org/10.1080/09524622.2008.9753600.

Sueur J. and Farina A. (2015). Ecoacoustics: The ecological investigation and interpretation of environmental sound. Biosemiotics. 8 (3): 493–502. https://doi.org/10.1007/s12304-015-9248-x.

Sueur J., Farina A., Gasc A., Pieretti N., and Pavoine S. (2014). Acoustic indices for biodiversity assessment and landscape investigation. Acta Acustica. 100 (4): 772–781. https://doi.org/10.3813/AAA.918757.

Sueur J., Pavoine S., Hamerlynck O., and Duvail S. (2008b). Rapid acoustic survey for biodiversity appraisal. PLoS One. 3 (12): e4065. https://doi.org/10.1371/journal.pone.0004065.

Sutherland W. J., Broad S., Caine J., Clout M., Dicks L. V., et al. (2016). A horizon scan of global conservation issues for 2016. Trends in Ecology & Evolution. 31: 44–53. https://doi.org/10.1016/j.tree.2015.11.007.

Torija A. J., Ruiz D. P., and Ramos-Ridao A. F. (2013). Application of a methodology for categorizing and differentiating urban soundscapes using acoustical descriptors and semantic-differential attributes. The Journal of the Acoustical Society of America. 134: 791–802. https://doi.org/10.1121/1.4807804.

Towsey M., Wimmer J., Williamson I., and Roe P. (2014). The use of acoustic indices to determine avian species richness in audio-recordings of the environment. Ecological Acoustics. 21: 110–119. https://doi.org/10.1016/j.ecoinf.2013.11.007.

Tucker D., Gage S. H., Williamson I., and Fuller S. (2014). Linking ecological condition and the soundscape in fragmented Australian forests. Landscape Ecology. 29 (4): 745–758. https://doi.org/10.1007/s10980-014-0015-1.

Villanueva-Rivera L., Pijanowski B., Doucette J., and Pekin B. (2011). A primer of acoustic analysis for landscape ecologists. Landscape Ecology. 26: 1233–1246. https://doi.org/10.1007/s10980-011-9636-9.