

YOUNG VOICES AND VISIONS FOR THE
UN DECADE OF RESTORATION

RESEARCH ARTICLE

Listening for change: quantifying the impact of ecological restoration on soundscapes in a tropical dry forest

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Ecological restoration is crucial to mitigate climate change and conserve biodiversity, and accurately monitoring responses to restoration is imperative to guide current and future efforts. This study examines the impact of ecological restoration of a tropical dry forest in Central India. Here, the state forest department and a nongovernmental organization work with local communities to remove an invasive shrub, *Lantana camara*, in the forest, to assist natural regeneration, primarily for the purpose of improving access to forest resources for forest-dependent people. We used acoustic technology to examine the bird community composition and the acoustic space used (ASU) across comparable restored, unrestored (with *L. camara*), and naturally low *L. camara* density (LLD) sites. We found no significant difference in the cumulative number of bird species detected between the site types (median in restored and LLD = 38, unrestored = 41). We found a significant difference in bird community composition across sites ($r^2 = 0.049, p \leq 0.001$). ASU differs between site types ($r^2 = 0.023, p \leq 0.10$), with restored sites positively associated with ASU compared to unrestored and LLD sites, which could represent a temporary increase in ASU as animal communities are reorganized after the complete removal of *L. camara*. Our results suggest that small-scale restoration efforts that aim to help meet livelihood needs have the potential to contribute to ecological goals in this landscape. However, it is necessary to continue to monitor the regeneration trajectory in restored sites and the possible changes in the ASU.

Key words: acoustic space use, bioacoustics, birds, India, restoration, socio-ecological system, tropical dry forest

Implications for Practice

- Acoustic technology provides the opportunity to study several vocalizing species and sounds in an ecosystem all at once, making it ideal for the long-term monitoring of ecological restoration sites.
- Restoration of tropical dry forests through the removal of invasive species could have the potential to increase the acoustic space used (ASU) in the frequency range of 2–8 kHz. However, given the small temporal scale of this study, it is necessary to monitor the impacts of such interventions closely at several time steps in the future to better understand the association between ASU and restoration.

Introduction

Tropical forests support more than half of the world's biological diversity and are significant carbon reserves (Pimm et al. 1995; Sullivan et al. 2017). Increased tropical forest fragmentation

(Taubert et al. 2018) and loss in recent decades have underscored the need to protect (Cook-Patton et al. 2021) and ecologically restore forests in the human-dominated landscapes of the tropics (Grantham et al. 2020; Cook-Patton et al. 2021). Ecological restoration has the potential to provide a multitude of benefits, such as conserving biodiversity (Crouzeilles et al. 2016; Brancalion et al. 2019), especially specialist species with

Author contributions: PC conceived the research; PC, MA, RD designed the study; PC, SB, DK collected the data; PC, MK, SB, PM analyzed the data; all authors reviewed the results and contributed to writing and revising the article.

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doi: 10.1111/rec.13864

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13864/supinfo>

specific habitat needs (Hariharan & Raman 2021), supporting natural resources-dependent livelihoods (Erbaugh et al. 2020) and, to a limited extent, mitigating climate change (Griscom et al. 2017; Cook-Patton et al. 2021).

In this United Nations' Decade of Restoration, global agreements and sustainable development commitments such as the Bonn Challenge and the United Nations Sustainable Development Goals provide the much needed impetus to restore degraded forests and lands around the world and subsequently contribute to biodiversity conservation and human development goals (CBD 2010; UN 2010). Given the magnitude of ongoing and planned restoration efforts around the world, there is a need for rapid and accurate assessment tools to quantify the impact of restoration on biodiversity at several time steps to guide restoration efforts and realistically forecast the consequences of these efforts in the future. Compared to traditional biodiversity surveys, acoustic surveys are less time- and resource-intensive and, to an extent, eliminate human biases as one can listen to the data as many times as required (Deichmann et al. 2018; Burivalova et al. 2019; Shaw et al. 2021), making them ideal for long-term monitoring of ecological restoration sites.

Based on the premise of the acoustic niche hypothesis (ANH) of ecoacoustics, it is generally inferred that degraded habitats would have fewer acoustic niches occupied in comparison to more intact habitats (Campos-Cerqueira et al. 2020; Rappaport et al. 2022). However, empirical evidence, mainly from humid tropical forests, suggests that this implied linear relationship between acoustic space used (ASU) and habitat intactness may not always hold (Eldridge et al. 2018; Rappaport et al. 2020; Vega-Hidalgo et al. 2021). In the context of using acoustics to monitor ecological restoration, such uncertainties in previous findings present the need for more evidence on ecoacoustic from diverse geographies to better understand changes in landscapes that continue to be restored around the world.

A large proportion of the research on quantification of restoration efforts is from humid tropical forests (Crouzeilles et al. 2016; Osuri et al. 2019) as tropical dry forests remain comparatively understudied and undervalued (Dirzo et al. 2011; Schröder et al. 2021) despite their capacity to sequester carbon and support biodiversity. Tropical dry forests are extensive, historically covering approximately 42% of the tropics (Miles et al. 2006; Morales-Barquero et al. 2014). They are often socio-ecological systems (forests managed by people for subsistence and livelihood needs) supporting millions of people around the world (Schröder et al. 2021). Dry forests remaining today mainly occur in densely populated human-modified landscapes of the world, making them further vulnerable to degradation and, thus, are an important biome to restore (Gillespie et al. 2012).

This study examines passive ecological restoration of a tropical dry forest through the removal of the shrub *Lantana camara* (Linnaeus). The British introduced *L. camara* (Verbenaceae), an invasive woody shrub native to central and southern America, to India in the 1800s (Mungi et al. 2020). *Lantana camara* dominates the understory of forests due to its allelopathic properties and ecological tolerance (Negi et al. 2019). Prior evidence suggests that higher

densities of *L. camara* are associated with lowered densities of sapling and seedlings of native vegetation, often species which may be necessary for wildlife (Wilson et al. 2014b) or of livelihood interest (timber and nontimber forest products [NTFPs]) to local communities (Aravind et al. 2010). Furthermore, *L. camara* can grow in tall dense thickets or can function as a liana (Hiremath 2018), thus becoming a barrier for people to access spaces where *L. camara* is overgrown.

Previous studies in India have largely focused on the impact of *L. camara* on vegetation regeneration over the impact of *L. camara* on fauna (Aravind et al. 2010; Wilson et al. 2014a; Ramaswami et al. 2017). This study aims to contribute to closing this gap in our knowledge on the impact of restoration of forests previously invaded by *L. camara* on fauna and, more generally, the soundscape. Furthermore, our work refines our understanding of the outcomes of restoration efforts, primarily carried out for the convenience of local communities and to increase visibility in a forest, of an often undervalued biome (Gillespie et al. 2012).

The objective of this study is to quantify the impact of ecological restoration on soundscapes. We use sites in dry tropical forests of the Central Indian Highlands (CIH) to ask the following questions:

- (1) How does the cumulative number of bird species detected aurally differ between comparable restored, unrestored, and low *Lantana* density sites?
- (2) How does the bird community vary in comparable restored, unrestored, and low *Lantana* density sites according to the habitat preferences of the individual bird species?
- (3) How does the ASU in the frequency range 2–8 kHz in comparable restored, unrestored, and low *Lantana* density sites differ?

Methods

Study Region

This study was carried out in Bichhiya, a subdistrict of Mandla district, Madhya Pradesh, which is part of the CIH, a significant tiger conservation landscape (Jhala & Nayak 2019). The average elevation in the district is 539 m above sea level. Tropical deciduous vegetation dominates this region (Agarwala et al. 2019), and one of the largest populations of constitutionally recognized socio-economically disadvantaged scheduled castes and tribes in India is dependent on timber and NTFPs for livelihoods in this region (Choksi et al. 2021; DeFries et al. 2021). These forests represent classic socio-ecological systems, which have been managed by local communities for their livelihood and subsistence needs for generations (Agarwala et al. 2019). While intensive agricultural expansion is taking place in parts of this region, locals largely engage in subsistence and small-scale market-oriented agriculture, which is primarily rain-fed (Choksi et al. 2021). The region has been experiencing a weakening of the monsoon as well as an increase in the frequency and intensity of heatwaves in recent decades (Choksi et al. 2021).

Restoration Method

In our study area, the state forest department and the local communities, with the support of a local nongovernmental organization, Foundation for Ecological Security (FES), carried out ecological restoration. The restoration used a common strategy of rigorously removing *L. camara* for three consecutive years in the months before the flowering season in October (the plants can have a flowering season in the monsoon months as well) (Negi et al. 2019) and then allowing a site to naturally regenerate. This method of *L. camara* removal involves uprooting the entire rootstock and weeding following the initial removal of *L. camara* is commonly practiced across India for more effective invasive species eradication (Love et al. 2009; Prasad et al. 2018). In these sites, 2017 was the first of the 3 years of *L. camara* removal (Fig. 1).

Site Selection

We selected the study sites through a two-step matching process using propensity score matching, an alternative for true randomization (Luellen et al. 2005) because restoration had already taken place in these sites. We used the package *matchIt* (Ho et al. 2011) to carry out the propensity score match in the R programming environment (R Development Core Team 2019). Communities in villages generally request the state forest department for permission to restore a section of the forests within their village boundaries. Therefore, we started this study by identifying eight “treatment” (restored) villages in the officially designated buffer of Kanha National Park (KNP) in the Bichhiya subdistrict where FES, the state forest department, and local communities had carried out restoration. They restored a demarcated area of a forest (a minimum of 20 ha) within a village’s boundary, which local communities use for their

subsistence and livelihoods (hereafter referred to as sampling site). We selected “control” villages by matching villages (unrestored $n = 8$; references $n = 4$; categories explained below) from the KNP buffer villages in the same subdistrict to the treatment (restored) villages using a propensity score based on socio-economic (Government of India 2011) and remotely sensed geographic variables (Table S1). We classified “control” villages as (1) unrestored (with a high density of *L. camara*) and (2) reference sites representing a low *L. camara* density through site visits. Reference sites, which we refer to as low *Lantana* density (LLD) sites, represent the possible trajectory of restored sites in the event that there is little to no *L. camara* reinvasion in the future. We consulted members of the local community and local forest guards, where possible, about the natural lack of *L. camara* in the last 5 years in forests in LLD villages. We chose LLD sites outside the core area of KNP as the forest department restricts human use inside the park and because KNP has a large focus on plantation forests reflecting its colonial past (Agarwala et al. 2019).

After we matched villages, we identified sampling sites in forests within and adjacent to village boundaries by consulting local community members and the local forest guards. These are areas of the forest where the majority of the local community members extracted firewood and nontimber resources. After this consultation, we drew 20 polygons representing exact sampling sites (restored $n = 8$, unrestored $n = 8$, low *Lantana* density $n = 4$; mean area of polygons: 58.32 ± 30.93 ha) within the forests of villages classified as restored, unrestored, and LLD. To ensure there is no data contamination from sounds and vocalizations outside the sampling sites, we first buffered in the polygon of the treatment or control site by 70 m, to represent the core of the site in which we collected data. To determine exact sampling locations (recorder locations) for vegetation and acoustic data

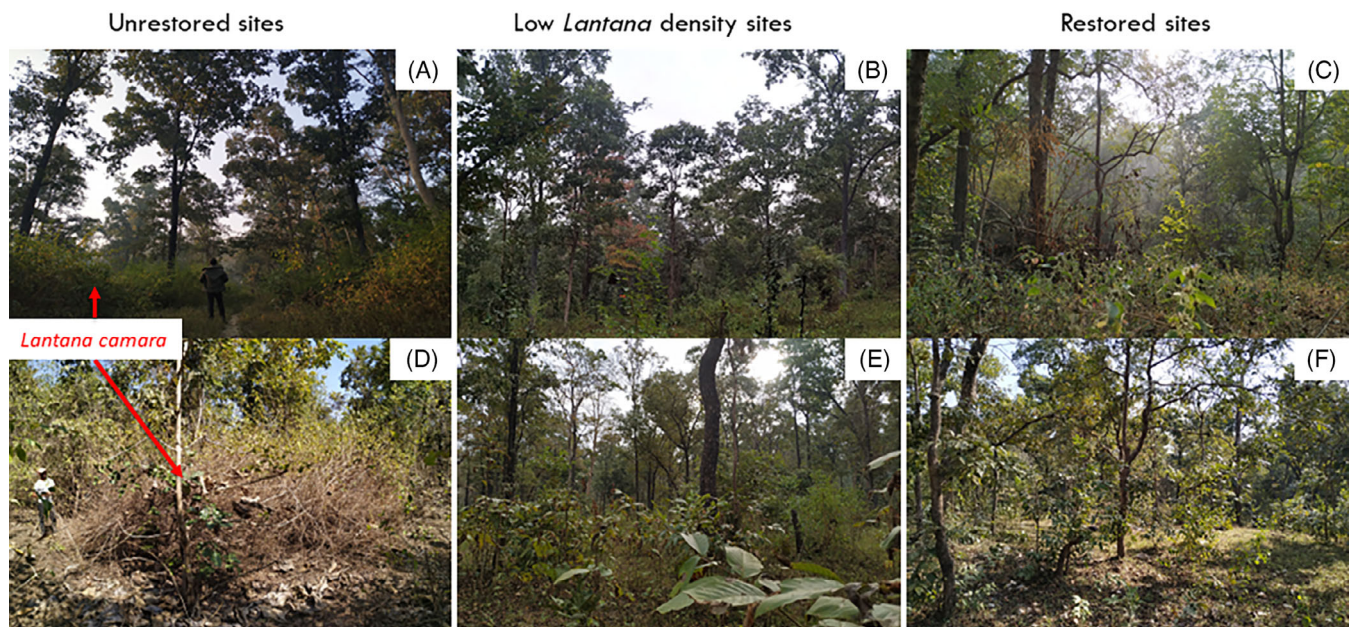


Figure 1. Pictures from unrestored (A, D), low *Lantana* density (B, E), and restored (C, F) sites. The red arrows point to the *Lantana camara* in the understory.

collection, we then used a random point generator in QGIS 3.6.1 (QGIS Development Team 2022) to establish two or more locations (depending on the size of the polygon) between 380 and 500 m apart to set up acoustic recorders within the core of a site. In each sampling site, we had 3 (± 1) sampling locations.

Vegetation Data Collection

Between January and early April 2021, at every sampling location (recorder location), we established a circular 314.2-m² plot (10-m radius plot) to sample the vegetation. Within the 1-m radius, we (authors PC and DK) noted the diversity of identifiable grasses. In the 3-m radius, we identified and counted all seedlings and saplings, the number of *L. camara* saplings (single stems below 1 m in height) and mature *L. camara* plants (>1 m in height). In the 10-m radius, we measured the diameter at breast height and visually estimated the height of all trees above the height of 2 m (refer to Tables S2 & S3 for more details on the vegetation in sites). At four sampling locations in two restored sampling sites, due to COVID-19 related travel restrictions, we were abruptly unable to return to the site collect data and have used vegetation metrics from the closest sampling locations (approximately 400 m away) within the sampling site.

After vegetation sampling, we performed a secondary match (an optimal full match using the *matchIt* R package) for all the sampling locations ($n = 55$; Fig. 2) for all the restored, unrestored, and LLD sampling locations to ensure a balanced sample based on vegetation composition and structure (of the

overstory), socio-economic and geographic variables that previous studies have found to be important for quantifying people's forest-resource use (DeFries et al. 2021) (Table 1).

Acoustic Data Collection and Analysis

At each sampling location ($n = 55$), we tied acoustic recorders at approximately 2 m aboveground on tree trunks. We used Audio moth 1.0.0 (sampling rate = 48 kHz, gain = medium) (Hill et al. 2018) and sampled every 1 minute in 5 minutes for 24 hours in a day for a period of 7–10 days (Bradfer-Lawrence et al. 2019) during the winter seasons (December–early March) in 2020 and 2021. We were unable to record over spring and summer due to increased COVID-19 infections through the peaks of different waves. In total, we recorded 30.44 ± 8.27 hours in 2020 and 42.24 ± 12.05 hours in 2021 across all sampling locations. At four instances (at three sampling locations in a single year), we experienced recorder malfunctions, and had to remove those recordings from the analysis. For example, for 55 sampling locations over 2 years, for any outcome variable, instead of a total of 110 observations, we have only 106 observations.

Bioacoustics: Bird Community

We randomly selected 45 minutes in the morning hours (05:30–09:30 hours) per year (Table S4) from each sampling location ($n = 55$) to be manually annotated for all avian species

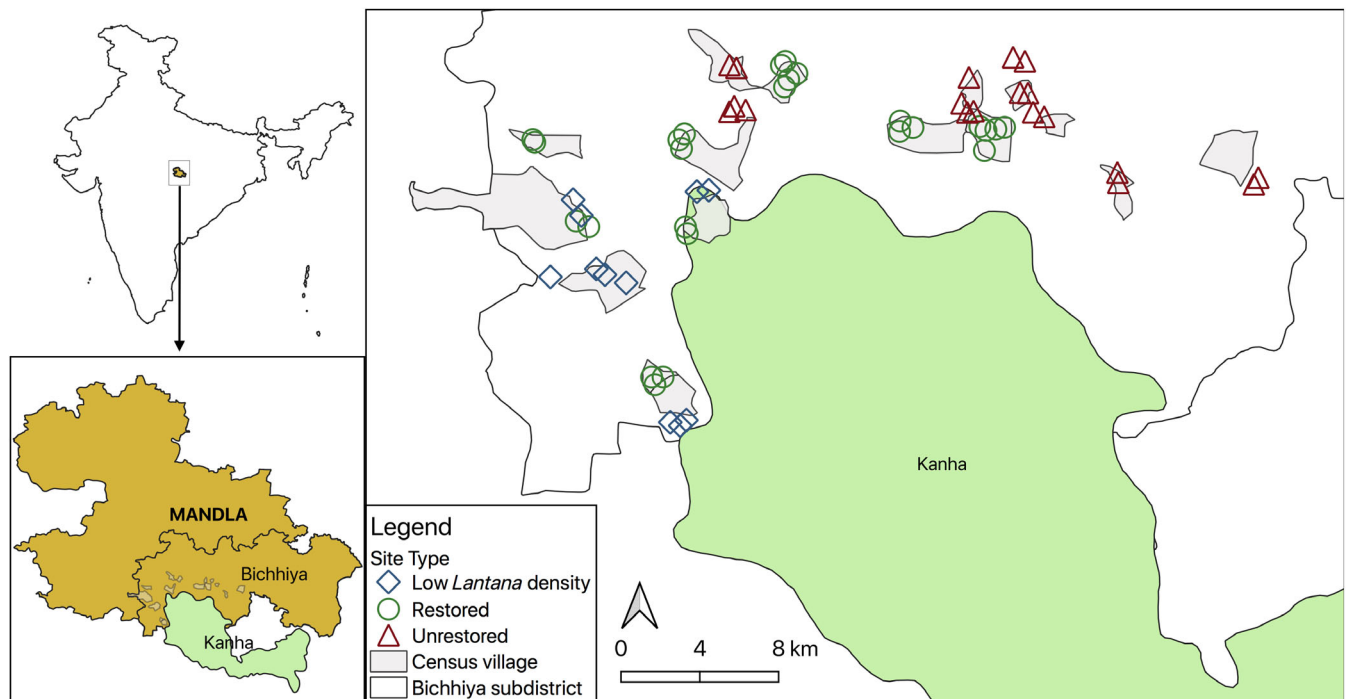


Figure 2. Map of restored, unrestored, and low *Lantana* density sites in Mandla District (subdistrict Bichhiya). Acoustic recorder locations in restored, unrestored, and low *Lantana* density forest sites are represented by the circle, triangles, and diamond symbols, respectively, around the census villages (in gray) that use the particular forests for subsistence. The sampling locations are approximately 400 m apart from one another, avoiding any possible overlap in acoustic data collection.

Table 1. Summary of the mean and standard deviations of matching (and statistical model predictor) variables of sites. The standard deviation for variables is provided in parenthesis.

Treatment Type	Restored	Unrestored	Low Lantana Density	
Definition of treatment	Sites where restoration by way of <i>Lantana camara</i> removal has taken place in the last 5 years	Sites with high density of <i>L. camara</i> where no restoration has taken place in the last 5 years	Sites which naturally have very few <i>L. camara</i> plants or no <i>L. camara</i> plants in the last 5 years	
Variable for Matching	Definitions of Variable and Source of Data	Mean of Variables in Treatment (Restored) Sites	Means of Variables in Control (Unrestored) Sites	Means of Variables in Control (Low Lantana Density) Sites
Tree density	Number of small, medium, and large trees in a 10-m radius plot Source: Vegetation survey	29.56 (25.82)	26.98 (11.60)	22.32 (10.50)
Large trees density	Number of large trees (>10 cm diameter at breast height) density in 10 m radius plot Source: Vegetation survey	16.20 (7.45)	17.93 (6.85)	12.96 (5.85)
Plot Simpson diversity index	Simpson diversity index of all tree in 10-m radius plot Source: Vegetation survey	0.69 (0.19)	0.62 (0.28)	0.76 (0.11)
% Forest cover in 3 km buffer	Source: (Khanwilkar et al. 2021)	46 (23.00)	44 (13.11)	65 (6.09)
% Farm land in 3 km buffer	Source: Khanwilkar et al. 2021	9 (6.95)	15 (6.12)	7.3 (5.87)
Total population (Census 2011) in 3 km buffer	Source: (Government of India 2011)	5,251 (2145)	6,628 (5505)	4,018 (2123)
Total sampling sites (recorder locations) matched		25	19	11

detected (Table S5 provides a list of all species heard in the manually annotated data). Our choice of morning hours was based on two factors: (1) although the sunrise hours are when the birds are most vocal, we chose a larger range of hours to annotate data because these forests are actively used by local communities in the mornings, and this human activity could affect temporal trends in bird vocalizations and (2) it is often difficult to hear all the species calling and distinguish between them correctly with a lot of background vocalizations during the dawn chorus. In some cases, (mainly unrestored sites) we annotated additional minutes over 2 years to compensate for recorder malfunctions, bad weather, and fewer sampling locations (Table S4). Authors (SB and PM) annotating this data are also eBird (Sullivan et al. 2014) reviewers for Central India and possess knowledge of the natural history and the wide repertoire of vocalizations of birds in this region. To make annotation easier, the audio data, which were minute-long, were split into 10-second clips and used a presence/absence matrix to note whether a particular avian species was heard in a 10-second clip or not. We used Raven Pro (version 1.5) (Cornell Lab of Ornithology 2021) to visualize each 10-second file and then note the presence or absence of a species in a matrix. In the event there was uncertainty about the identity of an avian species, the specific 10-second clip, and the larger minute-long clip it belonged to was sent to other bird call experts, mainly other eBird reviewers for Central India. We then finalized the identity of the species

based on the majority consensus among the experts. We classified all the bird species identified through manual analysis as generalist or forest- and woodland-affiliated species based on the classifications by State of India's Birds (SoIB) (The SoIB Partnership 2020). We considered only these two categories of habitat preferences as our study sites are tropical deciduous forests and all the other categories of habitat preferences as per the SoIB (grassland, scrub, and wetland) accounted for only 2–5% of the species across all our sites. In the rare event (three species; Table S5) that a species fell into two habitat categories in the SoIB, we classified the predominant habitat specialization based on the experiences of authors.

Ecoacoustics: Acoustic Space Use Quantification

We followed the method of calculating ASU from Campos-Cerqueira et al. (2020). The proportion of acoustic space could represent the abundance or diversity of species at a point of time. First, we created a mean spectrum for each 1-minute recording by computing a short-time Fourier transform ($f = 48,000$, $wl = 512$, $wn =$ "hanning," $norm = FALSE$) using the *mean-spec* function from the *seewave* package in the R programming environment (R Development Core Team 2019). This resulted in a two-column matrix of frequency and amplitude values for 256 frequency bins, with the minimum absolute amplitude over all files at 0.073 dB and the maximum at 12,104.95 dB. We then

used the *fpeaks* function in the same R package to detect the peaks of the frequency spectrums. We scaled these amplitude values in the *fpeaks* output from -1 to 1 . To separate biophony from background noise, we applied a scaled amplitude threshold of 0.003 and selected only the frequency peaks above the threshold (frequency distance threshold set to zero). This selection resulted in a two-column matrix of frequency and scaled amplitude values above the threshold. Thus, effectively, if there was a peak in a particular frequency/time bin, it was considered as an acoustic niche that is “occupied.” We then aggregated the selected frequency peaks between 0 and 24 kHz for each audio recording into $3,072$ bins (128 frequency bins of 187.5 Hz \times 24 time bins). For our analysis, we filtered the frequency bins of interest, between $2,000$ and $8,000$ Hz (a total 768 frequency/time bins), to focus largely on biophony in the frequency range audible to humans (Kasten et al. 2012). We calculated the proportion of ASU in a frequency/time bin by aggregating the number of recordings when the scaled amplitude threshold of 0.003 (Campos-Cerqueira et al. 2020) was crossed in each bin and dividing it by the total number of recordings in each hour (we recorded 1 minute for every 5 minutes, giving us a maximum of 12 recordings in an hour).

Predictor Variables

We included the variables that were used to match the sites for a pairwise comparison as predictor variables in our statistical models (correlation plot of matching variables in Fig. S1). Table 1 shows the summary statistics of the predictor variables across all the sites. All continuous variables were scaled and centered to create the z -score to estimate the statistical model described below.

Statistical Tests and Models

We tested the significance of associations between restoration efforts and the bio- and ecoacoustics using parametric and non-parametric approaches. We performed a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function in the R *vegan* package (Oksanen et al. 2019) to determine whether there was a significant difference in the bird community across the sites based on their type (restored, unrestored, and Low *Lantana* density) (n permutations = 999). We also fit generalized linear mixed models (GLMMs) for the following outcome variables at the level of the sampling location: (1) cumulative number of bird species, (2) cumulative number of forest- and woodland-affiliated species, and (3) cumulative number of generalist species detected aurally. For the GLMMs, we used a *poisson* distribution and included predictor variables listed in Table 1 as fixed effects, and the sampling sites ($n = 20$) as a categorical random effect to account for the variation in space. We added the year of data collection (2020 and 2021) as a categorical fixed effect in our model. Additionally, for these three outcome variables mentioned above, we also performed a Wilcoxon test of significance to determine whether the medians of site types are significantly different from each other across the years and in each year.

For the ecoacoustics analysis, we similarly performed a PERMANOVA analysis to test the differences in ASU between the three types of sites (n permutations = 999). For the PERMANOVA analyses, we used the predictor variables listed in Table 1. For these tests we used the matrix of the proportion of ASU in each frequency/time bin in the range $2,000$ – $8,000$ Hz (768 frequency/time bins in total) for each day of recording at each sampling location. To estimate a GLMM (using a binomial distribution), we aggregated the frequency bins between $2,000$ and $8,000$ Hz to compute the ASU across the frequency range at a given time in 24 hours as the outcome variable. Thus, we have a single value representing the total proportion of ASU (count of all recordings when the amplitude threshold was crossed divided by the total number of recordings in an hour) at every hour in 24 hours. The predictor variables listed in Table 1 and the year (2020 and 2021) were fixed effects in this model. We accounted for variation in space by including the sampling site ($n = 20$) as a categorical random variable. To account for the variation in time, we used the Julian date of recording ($n = 100$), the time in 24 hours ($n = 24$) as random effects. Additionally, to determine whether the day time ($06:00$ – $18:00$ hours) ASU is significantly different from the night time ($18:00$ – $06:00$ hours), we performed a Wilcoxon test.

We estimated all the GLMMs using the R package *lme4* (Bates et al. 2015). Further, for all our models, using an inflation threshold of 5 , we ran a variance inflation factor test, using the R package *car* (Fox & Weisberg 2019), to ensure there is no collinearity in the predictor variables. None of the models displayed variance inflation, and we have thus presented the full models controlling for all the propensity score-matching variables with alternative models for reference. Alternative models do not include correlated predictor variables in the same model. We then validated the model results using the residuals of the GLMMs (Zuur & Ieno 2016).

Expectations

We expect significant differences in the cumulative number of species detected across the sites as well as in the bird community composition based on prior research (Jayapal et al. 2009). Furthermore, we expect restored sites to have lower ASU (or fewer “occupied” acoustic niches) compared to LLD and unrestored sites, where no such sudden structural changes have occurred (Burivalova et al. 2021). Further, based on the premise of the ANH, we expect LLD sites, which are the least “disturbed” sites (as no sudden structural changes have taken place and they are not dominated by *L. camara*), to display highest ASU.

Results

Bioacoustics: Bird Community Composition

There are no significant differences in the cumulative number of aurally identified species (median number of species at restored and LLD sites = 38 , unrestored sites = 41) between the sites (Tables S6 & S7). Furthermore, we did not find significant differences in the cumulative number of forest- and woodland-

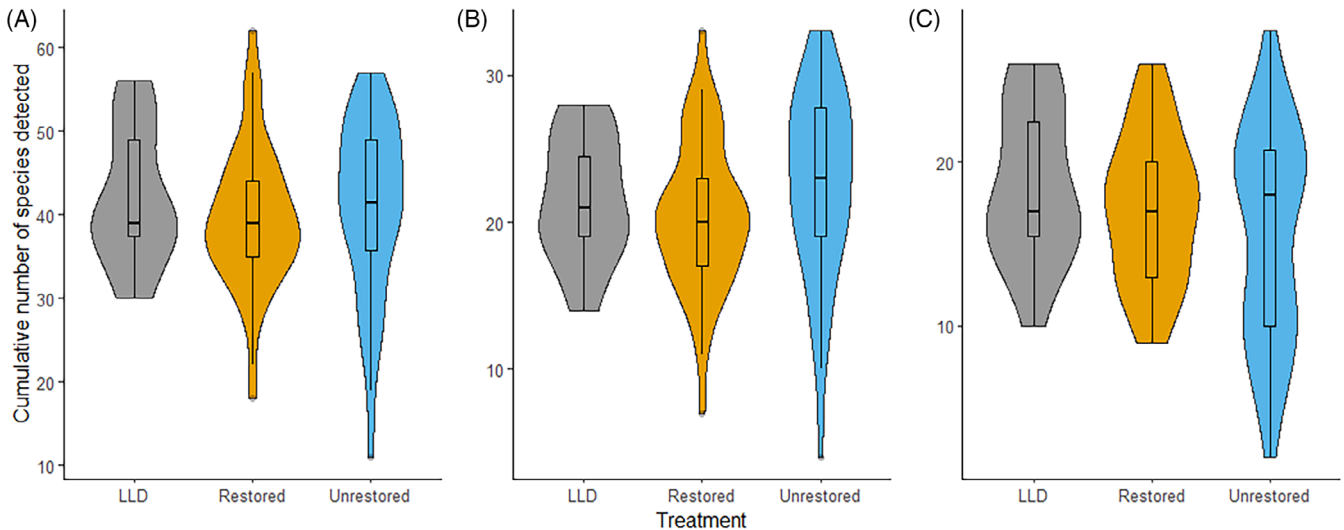


Figure 3. Violin plots displaying (A) the cumulative number of bird species detected, (B) the cumulative number of generalist species detected, and (C) cumulative number of forest- and woodland-affiliated species detected across the sites. Refer to Tables S6 and S7 for the Wilcoxon test of significance results.

affiliated and generalist species in the three types of sites (Table S6 & S7; Fig. 3). However, there is a significantly lower number of generalist species in restored sites compared to unrestored sites (median restored = 20, unrestored = 23; Table S6). Also, we found that in 2021 compared to the year 2020, in the case of unrestored and LLD sites there was a decrease in the cumulative number of birds and subsequently the cumulative number of generalist and specialist species detected (Table S7). In the case of restored sites, we found an increase in the cumulative number of birds and generalists detected between 2020 and 2021 (Table S7).

We found that there is a significant difference in the species community across the sites (PERMANOVA $r^2 = 0.049$, $p \leq 0.001$). The sites have 100 species in common, with a majority of generalist birds across all sites (Table S5). Thirteen species were unique to restored sites, of which only two were forest-affiliated species such as the Scarlet minivet (*Pericrocotus speciosus*) that tends to prefer the canopy over the understory. Eleven species, predominantly forest-affiliated, were unique to unrestored sites, and only three species were unique to LLD sites. Restoration is negatively associated with the cumulative number of species (GLMM coefficient = -0.126 , SE = 0.074 , $p = 0.089$) and significantly negatively associated with the number of generalists detected aurally per year (GLMM coefficient = -0.092 , SE = 0.105 , $p = 0.036$; Table S9A; alternative models in Tables S10–S12). Restoration also has the largest negative effect, albeit with large variation, on the number of species detected aurally among all the predictor variables (Table S9A).

Ecoacoustics: Acoustic Space Use

We found a difference (approaching significance) in the ASU between sites (PERMANOVA $r^2 = 0.023$, $p = 0.052$) (Table S13). Figure 4 shows the outcome variable for the GLMM, the aggregated proportion of ASU for every 1-hour

bin over 24 hours. The results indicate that restored sites have significantly higher ASU than LLD and unrestored sites, but ASU in restored and LLD sites is more similar to each other in comparison to unrestored sites (Table S14). With the exception of day time hours (06:00–18:00 hours), when restored sites have a marginally higher ASU than LLD sites (median ASU in restored = 0.148 , LLD = 0.139) (Table S14). Overall, across sites, ASU is higher in the night hours (18:00–06:00 hours) compared to the day time hours (06:00–18:00 hours), and thus, we conclude that ASU across all sites is largely driven by nighttime acoustic activity, often dominated by insects. The first and third quantiles of ASU reported for each type of site in Table S14 indicate that there is considerable variation between sampling locations. Restoration is positively, but not significantly, associated with ASU (GLMM coefficient = 0.056 , SE = 0.045 , $p = 0.180$) (Table S15; alternative models in Table S16). When we examine the effect size, it has a relatively smaller association with ASU with large variation compared to predictors such as tree density (GLMM coefficient = 0.082 , SE = 0.006 , $p < 0.001$; Table S15) and large tree density (GLMM coefficient = -0.109 , SE = 0.006 , $p < 0.001$; Table S15). While LLD sites have significantly higher ASU than unrestored sites (Table S14), there is no significant association between LLD sites and the outcome variable, ASU (GLMM coefficient = -0.001 , SE = 0.056 , $p = 0.986$; Table S15) indicating that we could attribute the ASU to other highly significant predictors, such as the vegetation structure and composition.

Discussion

Large-scale ecological restoration projects require quick and frequent biodiversity appraisals. In this study, we provide an example of how bio- and ecoacoustics may be combined to gain insights on the impact of restoration on fauna and soundscapes. While we found no significant difference in the cumulative

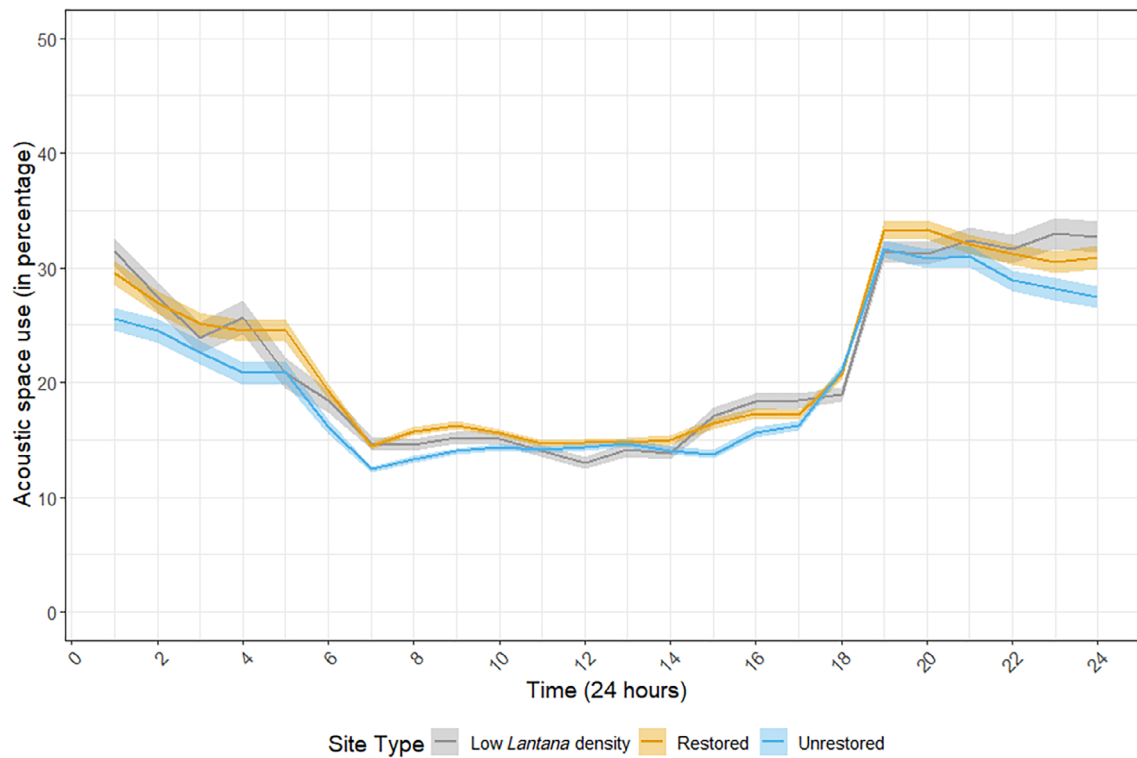


Figure 4. Acoustic space used over time in 24 hours (frequency range: 2000-8000 Hz) averaged across all days of data collection across all sampling locations (based on raw data). The transparent bands represent the standard deviations of the means represented by the solid line.

number of species at a site, it is noteworthy that there is a significant difference in community composition across the sites. Our results align to a limited degree with other evidence on ecological restoration, for example, from southern India, where restoration interventions are associated with a significant turnover in species richness and composition after two decades (Hariharan & Raman 2021). However, we did not find a significant difference in the total number of species detected. Further, while the difference in the site types was small and insignificant, unrestored sites had a marginally higher number of species, which may be indicative of the availability of more food sources (*Lantana camara* berries) in a *L. camara* dominated understory (Aravind et al. 2010; Ramaswami et al. 2017). However, we expect that as restored sites naturally regenerate in the coming years, there will be species turnover associated with the forest age (Owen et al. 2020). Moreover, we also hypothesize that a change in the understory may change the abundances of different birds, which we did not quantify in this study. Last, there are differences in the number of species detected aurally from 1 year to the next. The only change over the 2 years of data collection was a temporary lockdown due to COVID-19 and we are unable to attribute these small changes between 2020 and 2021 to any concrete reason.

Although we matched the sites on several factors, small differences in predictor variables impact the bird community composition and ASU. For example, having a higher proportion of forest cover in a 3 km buffer, which is often a significant predictor of bird diversity (Shoffner et al. 2018), did not significantly

increase ASU and the total number of species detected, but is significantly associated with a greater number of forest- and woodland-affiliated species. Furthermore, human-modified land covers, such as the percent farm cover in a 3 km buffer, positively impact the total number of species detected at sites, but negatively impact ASU. We speculate that this could be because a majority of the bird species in this study are generalists and may benefit from farms as potential food sources. ASU is most likely driven by insects at our sites as previous studies have found and not birds (Aide et al. 2017; Campos-Cerqueira et al. 2020).

Overall, restored and LLD sites displayed marginally higher (statistically significant) ASU than unrestored sites. However, the lack of significant association of ASU with the site types indicates that the small differences in the geographic and vegetation composition and structure are driving the results in that the overstory matters more than the understory for ASU in the Central Indian landscape. We postulate that this result is also in part because (1) tropical dry forests are slow-growing (Murphy 1986) and it may take some time to see significant differences due to restoration, if any or (2) changes in the understory may impact other facets of species' behavior and not the vocalizations. Restored sites had marginally higher ASU than LLD sites. This result is supported by another study on ecological restoration in Costa Rica (Vega-Hidalgo et al. 2021), which finds a lower acoustic energy of broadband insects in reference sites compared to restored sites, possibly due to a robust or more diverse predator community of bats (Vega-Hidalgo et al. 2021).

We speculate that our results too may be an indication of a potentially larger presence of a predatory insectivorous bird abundance (which we did not quantify) in LLD sites in comparison to restored and unrestored sites, for which there is some prior evidence from this landscape (Aravind et al. 2010). Another reason for the marginally lower ASU in the LLD sites may be that species, for example, birds, may rely less on vocal communication and instead have more visual communication when using these particular sites in the forest.

When evaluating our results using the lens of the ANH, we find that across restored, unrestored and LLD sites, all acoustic niches in our frequency range of interest (768 frequency/time bins) were “occupied” as such. Contrary to our expectations, the removal of *L. camara*, which we expected would decrease forest structural diversity, thereby possibly decreasing structural niches (Holmes et al. 1979; Jayapal et al. 2009), did not display empty acoustic niches or a reduction in ASU. Therefore, following the ANH, we interpret the association of restoration and ASU as a positive indication of the ecological health of the restored sites. Further, we speculate that we see no reduction in ASU in restored sites due to three reasons: (1) species largely dependent on this shrub may easily and quickly adapt to a new vegetation structure following the complete removal of *L. camara* and thus, acoustic niches never become empty; (2) structural niches may not have a linear relationship with acoustic niches in this landscape, or (3) a, possibly temporary, influx of species contributing to different acoustic niches as a response to a change in the forest structure. We find that the second and third reason may be the most reasonable assumptions for our study. In the Brazilian Amazon, a study found similar nonlinearity in structural complexity (represented by biomass) and acoustic niches, where patterns in ASU in logged and previously burned and reference forests were similar (Rappaport et al. 2022). As the ANH is tested in more places around the world, a better understanding of the relationship between ecological health and acoustic niche occupancy will emerge.

This study has a few limitations. We focused on vocalizing diversity in this study. However, non-vocalizing invertebrates are critical to restoration because of soil health and ecosystem functions and are equally important to measure (Schowalter et al. 2018). Also, we used a space-for-time approach for site selection; we accounted for various vegetation, geographic, and human resource use differences across sites, there is always a possibility that we have not captured some underlying unknown variation in the sites, which may impact vocalizing biodiversity.

In sum, our results indicate that people-centric restoration, carried out to improve access and visibility for local communities and not intended to increase faunal diversity, has a marginal biodiversity cobenefit over short timescales. Monitoring these sites over the long term to understand ASU and faunal responses to changes in vegetation can further guide restoration efforts. For such future monitoring efforts, our data and study act as a “time capsule,” providing a baseline for acoustic studies. We also note that these positive associations between ASU and restoration exist at small spatial scales and it is necessary to carry

out such a study at a larger scale for a better understanding of the relationship between ASU and restoration.

Acknowledgments

The authors are grateful to the Madhya Pradesh Forest Department for the necessary research permission. PC thanks the former Field Director of Kanha National Park, K. Krishnamoorthy, for his valuable suggestions on the study design. PC thanks the members of the local community, especially B. Jhariya and R. L. Nareti, who provided context on the *Lantana camara* invasion over time in study sites. Foundation for Ecological Security members I. Agrawal, D. Lalai, and M. Pawar assisted in identifying sites for research, for which we are thankful. PC is grateful for the feedback from A. Krishnan and the Krishnan Lab at the preliminary stages of the study. PC is thankful to the Marawi family for their hospitality through the duration of data collection for this project. PC received funding from the National Geographic Society, Center for Environmental Economics and Policy (CEEP), and the Advanced Consortium on Cooperation, Conflict and Complexity (AC4) to carry out this research. The authors thank M. C. Cerqueira for his guidance on ASU methods. The authors thank two anonymous reviewers for their comments that greatly helped improve the current draft of this manuscript. The R code used for this study is provided on GitHub and the data is available on Zenodo.

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Supporting Information

The following information may be found in the online version of this article:

Table S1: Summary of the mean and standard deviations of variables used for preliminary match of villages within which restored, unrestored, and low *Lantana* density sites were used for this study.

Table S2: *Lantana camara* density categories within 3-m radius plot.

Table S3: Wilcoxon test results for vegetation composition and structure variables across restored, unrestored, and low *Lantana* density sites.

Table S4: Summary of the number of minutes manually analyzed for each sampling site and sampling location.

Table S5: List of avian species detected aurally across 2 years of data collection.

Table S6: Wilcoxon test results for bird species composition variables.

Table S7: Wilcoxon test results of the (A) total number of bird species, (B) total number of forest- and woodland-affiliated birds, and (C) total number of generalist birds detected aurally across all sampling locations presented according to the treatment types.

Table S8: PERMANOVA analysis of bird community composition (N permutations = 999).

Table S9: Coefficients and standard errors for predictor variables and the treatment (restoration) or control (*Lantana*-free sites) of generalized linear mixed models.

Table S10: Alternative models without collinear variables for the total number of species detected aurally over each year of acoustic data collection.

Table S11: Alternative models without collinear variables for the total number of forest- and woodland-affiliated species detected aurally over each year of acoustic data collection.

Table S12: Alternative models without collinear variables for the total number of generalist species detected aurally over each year of acoustic data collection.

Table S13: PERMANOVA analysis of the acoustic space use.

Table S14: Wilcoxon test results for acoustic space use in the frequency range 2,000–8,000 Hz aggregated over 1-hour time intervals across 2 years of data collection.

Table S15: Coefficients and standard errors for predictor variables and the treatment (restoration) or control (*Lantana*-free sites) of generalized linear mixed models.

Table S16: Alternative models without collinear variables for proportion of acoustic space used (%) over time (in hours) in the 2,000–8,000 Hz frequency range.

Figure S1: Correlation plot of variables used for sampling site match.

Guest Coordinating Editor: Courtney Stuart

Received: 12 June, 2022; First decision: 1 July, 2022; Revised: 3 January, 2023; Accepted: 3 January, 2023