



Using passive acoustic monitoring to examine the impacts of ecological restoration on faunal biodiversity in the Western Ghats



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ABSTRACT

Monitoring programs aimed at assessing ecological restoration have often relied on the response of a single taxon owing to the difficulty of sampling multiple taxonomic groups simultaneously. Using passive acoustic monitoring, we examined the impacts of ecological restoration on all vocalizing fauna simultaneously as well as a single indicator taxon, birds. In our study, acoustic recorders were programmed to collect data along a gradient of forest regeneration consisting of actively restored (AR), naturally regenerating (NR), and mature benchmark (BM) sites in a tropical biodiversity hotspot, the Western Ghats of southern India. For all vocalizing fauna, we calculated acoustic space use, a measure that reflects the amount and pattern of sounds within each frequency bin for a given time period. AR and NR sites were not significantly different from each other, and visual examination of the acoustic space showed a lack of sounds between 12 kHz to 24 kHz for AR and NR sites, suggesting limited insect activity. When we considered the response of birds alone (from manually annotated acoustic data), we found significant differences in the proportion of detections of rainforest bird species compared to open-country bird species across all treatment types, with the highest proportion reported in BM sites ($\text{mean} \pm \text{SD}: 0.97 \pm 0.04$), followed by AR sites (0.81 ± 0.12) and NR sites (0.71 ± 0.17). Considering the varied response of different taxa to habitat recovery over two decades, we highlight the need to take a multi-taxon approach while assessing restoration programs. We show that it is now possible to do so in tropical forests using passive acoustic monitoring.

1. Introduction

Deforestation and degradation of tropical forests have become major threats to biodiversity, with over 500 million hectares of land classified as degraded forests worldwide (Burivalova et al., 2014; Dent and Joseph Wright, 2009). Consequently, ecological restoration of degraded forests has emerged as an important method to combat species declines, habitat loss, and habitat fragmentation (Borah et al., 2018; Edwards et al., 2011; Griscom et al., 2017). Restoration practitioners adopt one of two methods to restore habitats: active restoration, in which invasive weeds are removed and native tree species are planted, and passive restoration,

in which vegetation is allowed to regenerate naturally, with little human intervention (Chazdon and Guariguata, 2016). Successful restoration programs have resulted in vegetation recovery, and restored forests have increased canopy cover, tree species richness, and habitat complexity (Crouzeilles et al., 2017; Osuri et al., 2019).

Previous studies have documented many faunal species in these restored forests following floral recovery using traditional survey methods such as point counts or line transects (Catterall et al., 2012; Díaz-García et al., 2020; Hariharan and Raman, 2022). Many of these studies have focused on mobile taxa such as birds, owing to their ability to colonize restored sites and the relative ease with which they can be

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detected (Gould and Mackey, 2015). These animals are also highly vocal, and researchers often rely on auditory cues to detect their presence, especially in tropical forests where it is typically difficult to make visual observations (Celis-Murillo et al., 2012). Past work in the tropics has shown that metrics such as bird species richness, abundance, and community composition vary along a gradient of habitat recovery and that bird species vary in their response to restoration depending on their habitat affiliation (Batisteli et al., 2018; Catterall et al., 2012; Hariharan and Raman, 2022; Latja et al., 2016). However, most of our understanding of the faunal response to restoration comes from studies focusing on a single indicator taxon at a time (but see Díaz-García et al., 2020), and as a result, we do not have a complete picture of how animal communities are impacted by restoration.

Taxon- and species-specific habitat needs and associated ecological traits determine animals' response to habitat restoration (Catterall, 2018; Crouzeilles et al., 2017), and by restricting ourselves to a single group's response, we may have a skewed understanding of the trajectory of change in restored forests (Golet et al., 2011). Most often, challenges associated with a complex topography and vegetation structure (Iknayan et al., 2014; Si et al., 2018) coupled with the scarcity of resources (time, money, and human survey effort) prevent researchers and practitioners from focusing on multiple taxonomic groups (Magurran et al., 2010). Tropical forests, where all these constraints apply, are also notoriously difficult to survey using traditional ecological methods, owing to the presence of large mammals, and challenging field and weather conditions (Gardner et al., 2008).

The emerging field of bioacoustics offers a unique solution to the issues outlined above in the form of passive acoustic monitoring (Pijanowski et al., 2011). Low-cost audio recorders can monitor vocalizing biodiversity across broad spatial scales for extended periods of time (Sueur and Farina, 2015), and the demand on effort and resources is relatively limited (Krause and Farina, 2016). Researchers and conservation practitioners already use recordings to examine and revisit entire soundscapes and the vocalizations of 'indicator' taxa. Soundscapes are composed of biotic (e.g., bird calls and songs) and abiotic (e.g., wind, rain) sounds (Deichmann et al., 2018), while indicator taxa refer to vocalizing groups of interest such as amphibians, birds, insects, and cetaceans. In addition, audio data can be visually observed and verified at the analysis stage, thereby reducing the probability of non-detections and misclassification of species of interest (Burivalova et al., 2021; Deichmann et al., 2018). In the past, soundscape monitoring has been used to assess forest health after selective logging (Burivalova et al., 2019), and compare vocalization patterns across sites that are managed differently to measure acoustic space use (Campos-Cerqueira et al., 2019). Acoustics have also been used to detect rare and endangered species (Zhong et al., 2021), track seasonal movements of migratory taxa (Oliver et al., 2018), and quantify changes in species behavior (Pillay et al., 2019).

In this study, using passive acoustic monitoring, we aimed to quantify the impacts of ecological restoration on faunal communities in a tropical rainforest, focusing both on the overall acoustic space use (i.e., multiple vocalizing taxonomic groups) and a single indicator taxon, birds. Since 2002, degraded rainforest fragments in the Anamalai hills of the Western Ghats biodiversity hotspot in south India have been either actively restored or allowed to regenerate naturally (Mudappa and Raman, 2007; Raman et al., 2009). These fragments are home to numerous animal species, including many vocalizing taxa such as birds, amphibians, and insects (Raman, 2001; Vasudevan et al., 2006). By analyzing audio data across 43 unique sites along a gradient of comparable forest regeneration consisting of actively restored (AR), naturally regenerating (NR), and undisturbed benchmark (BM) rainforest sites, we asked: (1) how does acoustic space use (ASU) vary along this gradient of forest regeneration? Here, ASU reflects the amount and pattern of sounds within each frequency bin for a given time period (Aide et al., 2017). We expected that the ASU of BM sites would be highest, followed by ASU of AR sites and NR sites respectively (Campos-

Cerqueira et al., 2019). Second, we assessed the response of a single indicator taxon by asking (2) how does the species richness, detection, and composition of birds vary along this gradient of forest regeneration? We expected that avian response to active restoration would vary as a function of species' habitat association. Specifically, rainforest bird species richness and detections would be highest in BM sites, followed by AR sites and NR sites. We expected that the bird community composition of AR sites would be intermediate between that of NR sites and BM sites based on the results of a previous study (Hariharan and Raman, 2022).

2. Materials and methods

2.1. Study area

The Valparai plateau ($10^{\circ}15'$ – $10^{\circ}22'$ N, $76^{\circ}52'$ – $76^{\circ}59'$ E) is a 220 sq. km area located in the Anamalai hills of the Western Ghats (Myers et al., 2000) in south India. The plateau is surrounded by the 958 sq. km Anamalai Tiger Reserve ($10^{\circ}12'$ – $10^{\circ}35'$ N, $76^{\circ}49'$ – $77^{\circ}24'$ E). It largely consists of mid-elevation tropical wet evergreen rainforests (*Cullenia exarillata*-*Mesua ferrea*-*Palaquium ellipticum* type) along an elevational gradient of 700 m to 1500 m above mean sea level (Pascal et al., 2004).

As a result of historical land cover changes from the 1890s to the 1940s, over 51 % of the Valparai plateau is now composed of tea plantations, and 11 % of the area is occupied by shade-grown coffee (Mudappa and Raman, 2007). Such large-scale changes have resulted in the fragmentation of contiguous rainforest tracts, and the plateau currently has >40 rainforest fragments (ranging from 1 ha to 300 ha in size). Despite supporting a high diversity of wildlife, these rainforest fragments have become degraded due to intensive land-use change, weed invasion, and selective tree felling for fuelwood (Muthuramkumar et al., 2006). Since 2002, many of these rainforest fragments have been ecologically restored by the Nature Conservation Foundation, a non-governmental wildlife conservation and research organization, in collaboration with three plantation companies. In active restoration, invasive weeds are removed, and a high diversity of mixed native tree species are planted (Osuri et al., 2019; Raman et al., 2009). While over 100 ha of degraded forests have been restored over the last two decades, plantation companies have also protected several fragments in the plateau from tree felling and other extractive activities, resulting in the natural regeneration or passive restoration of such fragments (Mudappa and Raman, 2007).

2.2. Site selection

We carried out fieldwork across 43 sites along a gradient of forest regeneration: 14 actively restored (AR) sites, 13 naturally regenerating (NR) or passively restored sites, and 16 benchmark (BM) sites that are located within relatively undisturbed tropical rainforest (Fig. 1; Fig. 2; Supporting Information Table S1). AR and NR sites are located within ten rainforest fragments on the Valparai plateau, and the former were restored between 2002 and 2010 (9 to 17 years since restoration, with an average area of 1 ha). AR and NR sites were chosen following a paired study design and are comparable in terms of degradation, topography, flora, physiognomy, and edge distance (Osuri et al., 2019). AR-NR site pairs were located between a minimum distance of ~162 m (see the section below) and a maximum distance of ~1.1 km. BM sites representing undisturbed contiguous rainforest habitat were similar to the restored sites in terms of the vegetation type and climate and were located within the Anamalai Tiger Reserve (Osuri et al., 2019). In addition, there were no significant differences in elevation between AR, NR, and BM sites, and all AR and NR sites were equidistant from roads (Supporting Information Figs. S1, S2).

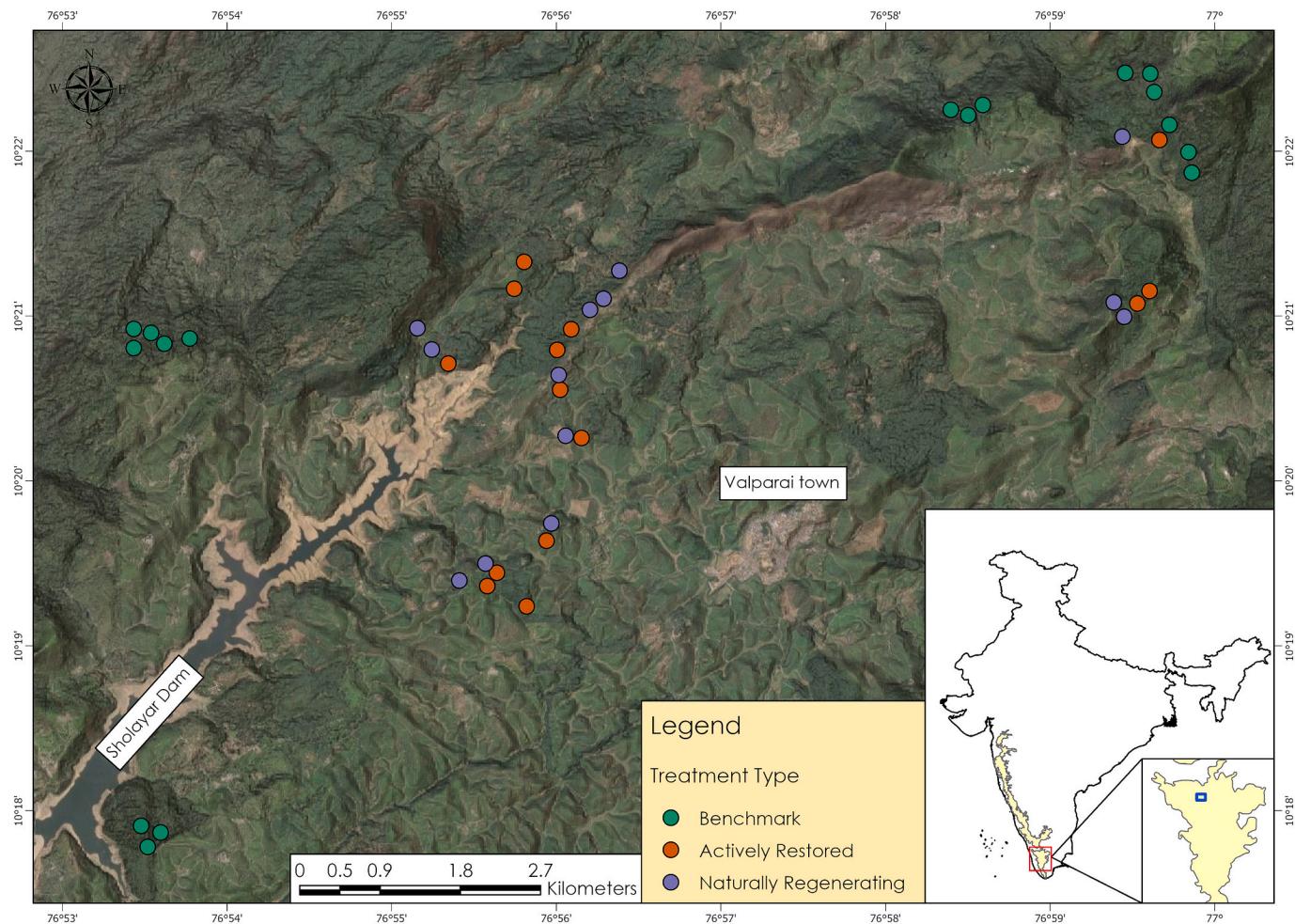


Fig. 1. Sites corresponding to acoustic recorder deployment locations across the Valparai plateau of the Anamalai hills. The above figure showcases a gradient of forest regeneration across the Valparai plateau. Sites in green represent undisturbed benchmark rainforest sites, sites in orange represent actively restored forest sites, and sites in purple represent naturally regenerating forest sites. Ecological restoration is currently being carried out in cooperation with three plantation companies in the Valparai plateau. For more information on the weeding and active restoration protocol, please see the methods in [Haritharan and Raman \(2022\)](#) and [Osuri et al. \(2019\)](#). Over the last two decades, the ecological restoration efforts have resulted in the restoration of over 100 ha of degraded forests. This map was prepared using 30 m resolution SRTM data ([Farr et al., 2007](#)), and ESRI satellite imagery was used as a base map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Acoustic data collection

At each of the 43 sites, we deployed AudioMoth audio recorders to collect acoustic data ([Hill et al., 2019](#)). These passive monitoring devices were placed on trees, approximately 2 m above the ground at each site. Using a sampling rate of 48 kHz and a gain of 40 dB, each recorder was deployed to record data in 4-min segments for every 5-min for seven consecutive days at each site for two seasons (Summer: March 2020 to May 2020 and Winter: November 2020 to January 2021). This recording configuration and schedule were chosen to thoroughly characterize the acoustic environment at each site ([Bradfer-Lawrence et al., 2019](#)). Recorders collected data for seven continuous days twice (in each season), with a gap of two weeks between the cycles. Data could not be collected in April 2020 due to the covid-19 pandemic. In February 2020, we conducted a reconnaissance survey to determine the sound attenuation distance at each site. In order to determine the distance at which a sound is attenuated, we played sounds of varying frequencies (low: 100 Hz to high: 5000 Hz) at a constant volume from a portable speaker and walked a straight-line distance of 150 m from the location where the recorder was deployed. We found that sound attenuation varied between 50 m and 100 m across treatment types. As a result, during recorder deployment, we ensured each recorder was at least 100 m apart.

2.4. Acoustic space use

For any given audio recording, the mathematical premise in calculating acoustic space use (ASU) involves the computation of a short-time discrete Fourier transform (STDFT; [Sueur, 2018](#)). An STDFT is a Fourier transform run on successive sections/windows of the recording instead of the entire audio recording ([Sueur, 2018](#)). To illustrate this further, we shall begin with an audio recording with a sampling rate of $s = 48,000$ Hz and a window length (for the STDFT) $wl = 256$ samples, resulting in a frequency bin size of $z = 187.5$ Hz (where $z = s/wl$). Given the sampling rate s , our Nyquist frequency $f = 24,000$ Hz (where $f = s/2$), and therefore, the total number of frequency bins across which an STDFT was run is $n = 128$ frequency bins ($n = f/z$). The final output of an STDFT corresponds to a matrix of $N * m$ Fourier coefficients ($N = \text{length of the audio recording}$ and $m = \text{number of frequency bins}$). In this study, we computed STDFT across 24 h of audio recordings, which translates to a matrix of 3072 (24 h * 128 bins) Fourier coefficients ([Aide et al., 2017](#); [Campos-Cerqueira et al., 2019](#)). This matrix of coefficients corresponds to ASU (or a measure of space ‘used’ for a frequency bin per unit time). While other studies have estimated ASU as the number of frequency ‘peaks’ above a certain threshold amplitude ([Aide et al., 2017](#); [Campos-Cerqueira et al., 2019](#)), we examined the entire soundscape, and do not

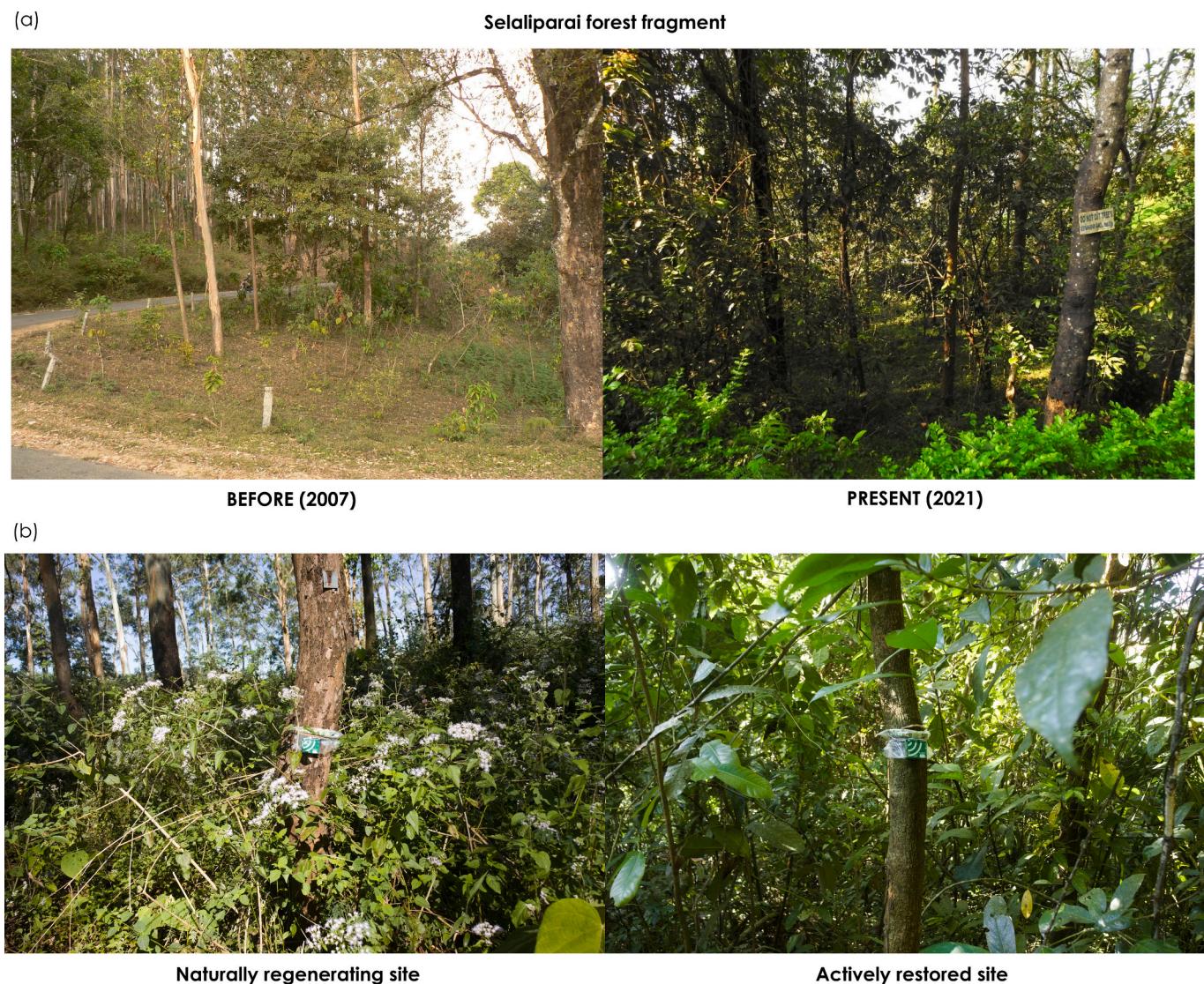


Fig. 2. Ecological restoration across the Valparai plateau of the Anamalai hills. (a) Images of an actively restored forest fragment (Selaliparai) were taken in 2007 and 2021. Habitat and vegetation structure has responded positively to active restoration (Osuri et al., 2019) (Photo credit: T R Shankar Raman). (b) AudioMoth audio recorders were deployed across naturally regenerating, actively restored, and benchmark (not pictured above) sites across the Valparai plateau (Photo credit: first author).

distinguish between biophony, geophony, and anthropophony.

We selected five consecutive days of acoustic data across each site to calculate ASU, excluding deployment and retrieval days, to reduce external bias. To avoid rainy days, we decided to sample these five days of acoustic data from March 2020. In total, across 43 sites, we analyzed ~4128 h of acoustic data to calculate ASU (for each site, this corresponds to 48 min of data per hour across 24 h on each of the five days).

All statistical analyses were conducted within the R programming environment v 4.2.0 (R Core Team, 2022). Analysis of ASU was carried out using functions *readWave* from the package ‘tuneR’, *sspectro* from the package ‘seewave’, and custom functions (Ligges et al., 2022; Sueur et al., 2008). We fitted generalized linear mixed models (GLMMs; Bolker et al., 2009) assuming Gaussian errors to examine the effects of AR, NR, and BM treatment types on ASU. The response variable was the sum of Fourier coefficients, treatment type was the categorical fixed effect, and the AR-NR site pairing was considered a random effect. The GLMM was run using the *glmer* function from the ‘lme4’ package (Bates et al., 2015). We then ran multiple comparison Tukey HSD tests between treatments using the *glht* function from the ‘multcomp’ package (Hothorn et al., 2012). For all the fitted GLMMs, we examined dispersion and patterns in

residuals using the ‘DHARma’ package in R (Hartig, 2022). Overall, the models appeared appropriate and no distinct pattern (over or under-dispersion) in the residuals is likely to have affected our interpretation.

Pairwise dissimilarity in ASU was tested across the 43 sites by first computing a Euclidean distance matrix from ASU values for each site (Faith et al., 1987). These dissimilarity matrices were then used to visualize ASU differences across treatment types (AR, NR, BM) using non-metric multidimensional scaling (NMDS) (Minchin, 1987). We used the functions *vegdist* and *metaMDS* from the ‘vegan’ package to run the above analysis (Oksanen et al., 2013).

Lastly, we visually examined ASU for each of the 128 frequency bins and 24 h across each site and treatment type. Visual examination of the acoustic space was carried out to obtain a clear understanding of the frequency-time combination for which acoustic activity is lower/higher compared to other frequency-time combinations. In this visualization, we estimated the proportion of frequency space occupied by sounds for every hour of recording in a day, using normalized values from 0 to 1.

2.5. Bird community data

We identified all vocalizing bird species at a given site on a subset of the data recorded across each site. First, we randomly selected three non-consecutive days in summer (March 2020 to May 2020) and three non-consecutive days in winter (November 2020 to January 2021) for each site for further analysis. Second, for each day selected, we randomly extracted a continuous 16-min of recording between 6 AM and 10 AM, which is often a time of high avian activity. By subsetting the audio data in the manner described above, we essentially had six ‘visits’ to each site, where each ‘visit’ corresponded to a randomly selected 16-min recording between 6 AM and 10 AM.

For bird species identification, each 16-min audio segment was broken down into 10-s audio segments. This was the shortest time period within which a bird species could be identified accurately, as determined by VR and AA. Using Raven Pro (Bioacoustics Research Program, 2014), each 10-s audio recording was both visually inspected as a spectrogram and heard to note the presence/absence of species by AA, who had previously worked on Western Ghats birds and has experience visually and aurally identifying species. In our study, we defined the detection of a bird species if it called or sang in a 10-s audio recording. If a bird was singing or calling for longer than 10-s, the species was marked as detected in each consecutive 10-s recording across the 16-min audio segment. In total, ~69 h of audio data across treatment types were manually annotated by AA.

2.6. Community ecological analyses

Before analysis, birds were classified according to their habitat affiliation as rainforest species and open-country species following (Ali and Ripley, 1983; Hariharan and Raman, 2022; Raman, 2006). Rainforest birds are found in undisturbed wet-evergreen forests, and open-country birds are widespread species that avoid forested areas. A full list of species identified during manual annotation and their habitat affiliation can be found in Supporting Information Table S2.

We estimated bird species richness for each visit by pooling all detections across a 16-min period. Following (Hariharan and Raman, 2022), we computed the first-order jackknife estimates using species richness data to estimate the total number of all, rainforest, and open-country bird species across treatment types using the *specpool* function in the ‘vegan’ package (Brose et al., 2003; Oksanen et al., 2013). We tested for significant differences in jackknife estimates between treatment types for all species, rainforest, and open-country species, by performing an ANOVA and a Tukey HSD.

To better understand differences in the bird community, we calculated a measure of abundance by estimating the proportion of acoustic detections of rainforest and open-country bird species at each site. Since true abundance is difficult to estimate using acoustic data, we estimated the number of detections of each species, which provided us with a measure of vocal activity and habitat use (see Pérez-Granados et al., 2021). For this metric, we first calculated the number of rainforest and open-country bird detections from six visits lasting 16 min each, totaling 96 min at each site. We then calculated the proportion of rainforest and open-country species by dividing the number of detections for each category by the total number of detections at each site, resulting in values ranging from 0 to 1. We could assume that there were no systematic differences in the acoustic detections of rainforest and open-country birds. This is because a previous study, carried out using point counts (Hariharan and Raman, 2022) in the same study area found no differences in the detection rates of rainforest and open-country birds.

Next, we fitted GLMMs assuming Poisson errors with natural log as the link function to examine the effects of treatment types on the first-order jackknife estimates of bird species richness. Jackknife estimate of species richness was the response variable, treatment type was the categorical fixed effect, and the AR-NR site pairing was the random effect. We then ran multiple comparison Tukey HSD tests between

treatments using the *glht* function from the ‘multcomp’ package (Hothorn et al., 2012). We repeated the above analyses to examine the effects of treatment types (AR, NR, and BM) on the proportion of acoustic detections of rainforest and open-country birds. For all the fitted GLMMs, we examined dispersion and patterns in residuals using the ‘DHARma’ package in R (Hartig, 2022). Overall, the models appeared appropriate and no distinct pattern (over or underdispersion) in the residuals is likely to have affected our interpretation.

We used bird detections to compute the pairwise dissimilarity in community composition across treatment types using the Bray-Curtis index (Faith et al., 1987), following which we visualized species compositional differences across treatment types using non-metric multidimensional scaling (Minchin, 1987; Oksanen et al., 2013). We tested for multivariate homogeneity of group dispersions among treatment types using the *betadisper* function from the ‘vegan’ package (Anderson et al., 2006). Finally, we performed a multivariate ANOVA to test if there was a significant difference in species composition among the three treatment types using the *adonis* function from the ‘vegan’ package (Anderson, 2001).

3. Results

3.1. Acoustic space use

Analysis of 4128 h of acoustic data across the three treatment types ($n = 43$ sites) revealed significant differences in acoustic space use between BM-AR and BM-NR sites (Fig. 3a, Tukey HSD $P < 0.05$). ASU was the highest in BM sites (mean \pm SD: 413 ± 103 ; the numbers refer to the sum of Fourier coefficients), followed by AR sites (188 ± 78) and NR sites (182 ± 66) (Fig. 3a). NMDS ordination of ASU (stress = 0.008; Fig. 3b) revealed a loose cluster of benchmark sites, while actively restored and naturally regenerating sites showed tight overlapping clusters. Further, visual examination of ASU across the three treatment types showed limited acoustic activity between 12 kHz to 24 kHz for most AR and NR sites, while BM sites showed high levels of acoustic activity across the same frequency space (Fig. 4).

3.2. Bird species richness, acoustic detections, and community composition

We detected a total of 116 bird species across ~69 h of manual inspection of audio recordings (Supporting Information Table S2). This included 74 rainforest bird species (64 % of all detections) and 42 open-country bird species (36 %). The White-cheeked Barbet *Psilopogon viridis* (11 %), Red-whiskered Bulbul *Pycnonotus jocosus* (7 %), and Crimson-backed Sunbird *Leptocoma minima* (7 %) had the highest number of detections, and five species (Indian scops owl *Otus bakkamoena*, Brown wood-owl *Strix leptogrammica*, Rock pigeon *Columba livia*, Wayanad laughingthrush *Pterorhinus delesserti*, and Jungle nightjar *Caprimulgus indicus*) were detected just once in our dataset.

We observed no significant differences in the first-order jackknife scores when we considered all species together and rainforest bird species separately. The jackknife estimate of open-country bird species varied significantly between BM-AR sites and BM-NR sites (Tukey HSD test, $P < 0.05$). However, when we considered the proportion of acoustic detections, we observed significant differences between treatment types (Tukey HSD test, $P < 0.05$) for both rainforest and open-country bird species. BM sites had the highest proportion of rainforest species detections (mean \pm SD: 0.97 ± 0.04), followed by AR sites (0.81 ± 0.12) and NR sites (0.71 ± 0.17) (Fig. 5a). On the other hand, NR sites had the highest proportion of open-country species detections (mean \pm SD: 0.28 ± 0.17), followed by AR sites (0.18 ± 0.12), and BM sites (0.02 ± 0.04) (Fig. 5b).

NMDS ordination of bird species detections (stress = 0.001; Fig. 5c) revealed distinct clusters of BM sites but overlapping clusters for AR and NR sites. However, AR sites occupied an intermediate position between

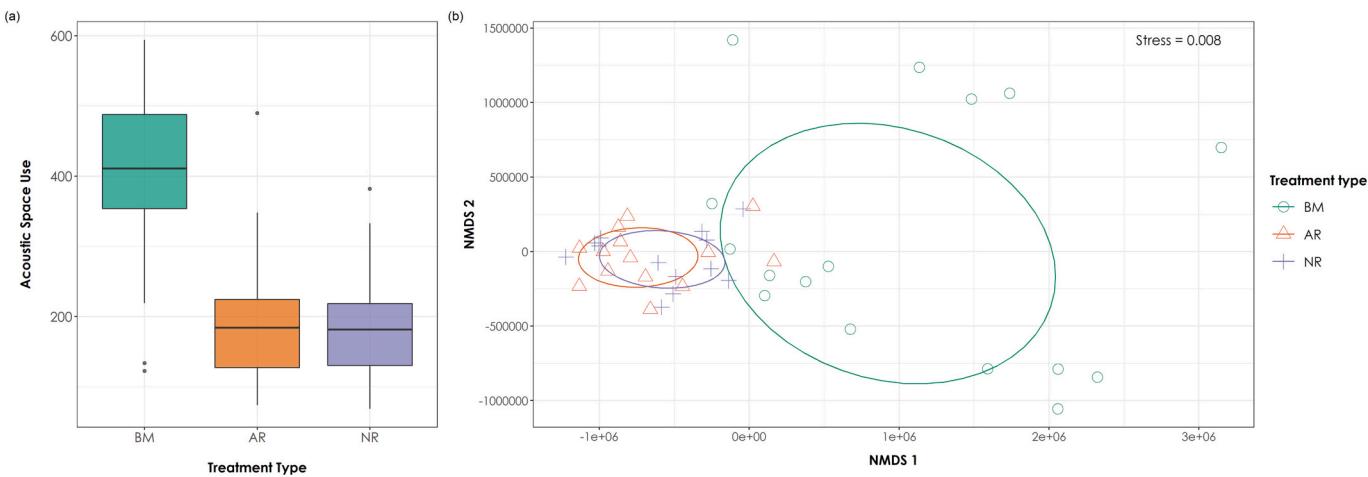


Fig. 3. Acoustic space use across treatment types. (a) Analysis of ~4128 h of acoustic data across treatment types (for the 43 sites) revealed significant differences in ASU between BM-AR and BM-NR sites (Tukey HSD $P < 0.05$). ASU was the highest in BM sites (mean \pm SD: 413 ± 103), followed by AR sites (mean \pm SD: 188 ± 78) and NR sites (mean \pm SD: 182 ± 66). (b) NMDS ordination of ASU (stress = 0.008) revealed a loose cluster of benchmark sites, while actively restored and naturally regenerating sites showed tight overlapping clusters. In the above figure, BM = undisturbed benchmark rainforest sites, AR = Actively restored forest sites, and NR = Naturally regenerating forest sites.

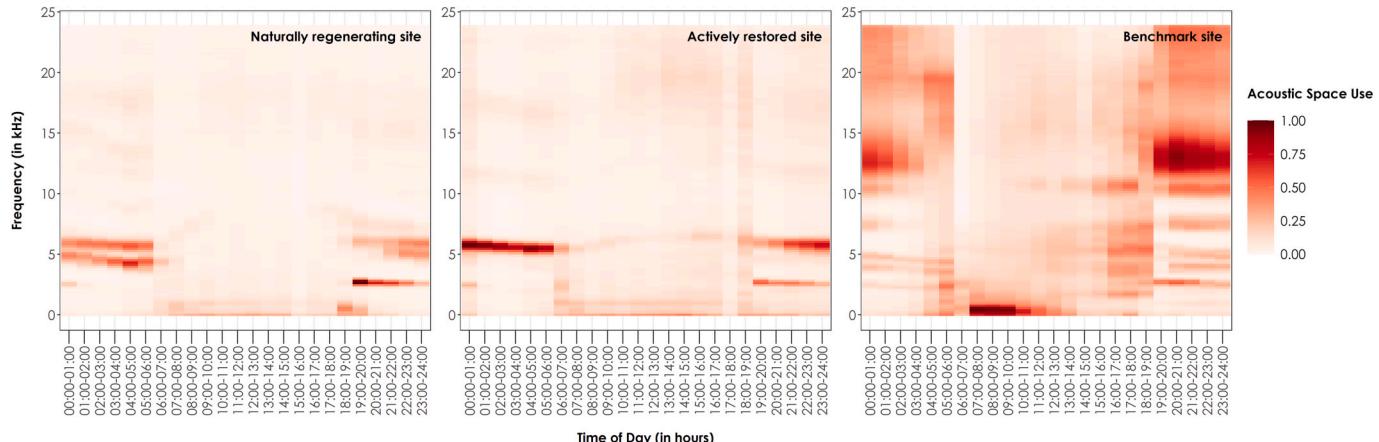


Fig. 4. Visual examination of acoustic space use across a naturally regenerating, actively restored, and benchmark site. In this figure, we visually examined ASU for each of the 128 frequency bins and 24 h across each site and treatment type. Shown here are representative figures for an NR, AR, and BM site. In this visualization, we estimated the proportion of frequency space (values between 0 and 1) occupied by sounds above 0.003 dB for every single hour of recording across 24 h a day. We observed largely empty frequency bins between 12 kHz to 24 kHz for the majority of AR and NR sites. For the sake of this representative figure, we show the average ASU calculated across five days for each site. However, the patterns described here are broadly consistent across days and sites (Supporting Information). In the above figure, BM = undisturbed benchmark rainforest sites, AR = Actively restored forest sites, and NR = Naturally regenerating forest sites. All three panels visualize acoustic data that was recorded simultaneously.

BM and NR sites, indicating the direction of change in bird community composition from NR sites toward BM sites. We found that bird community composition was significantly different between the three treatment types (adonis $R^2 = 0.27$, $P = 0.001$), as revealed by the permutational multivariate analysis of variance.

4. Discussion

In this study, we used a cost-effective method to assess the response of faunal communities to ecological restoration in a tropical biodiversity hotspot, the Western Ghats. Passive acoustic monitoring of restored, unrestored, and undisturbed forests in this landscape allowed us to consider the response of all vocalizing biodiversity at once while also enabling close examination of one indicator taxon, birds. The data we collected over the course of this study can be repeatedly analyzed in the future to verify the patterns we report here and single out other vocalizing taxa of interest, such as insects, amphibians, and mammals.

4.1. Acoustic space use

We found few differences in the overall acoustic space use patterns of actively restored and naturally regenerating sites, despite intensive tree planting drives in the former, which have resulted in a significant difference in the habitat structure between these sites (Osuri et al., 2019; Supplementary material). However, our analysis showed that undisturbed rainforests significantly differed from restored forests even after two decades of restoration.

When we visually examined the soundscape in the three treatment types, we found limited acoustic activity between 12 kHz and 24 kHz in NR and AR sites, while the same frequency range was occupied in BM sites (Fig. 4). Higher frequencies are often occupied by insect vocal activity (Ferreira et al., 2018; Gasc et al., 2018), and insects, which are sensitive to changes in microhabitat conditions, could be avoiding structurally simpler AR and NR sites (Jain and Balakrishnan, 2011). While true crickets (family: Gryllidae) are well represented between 3

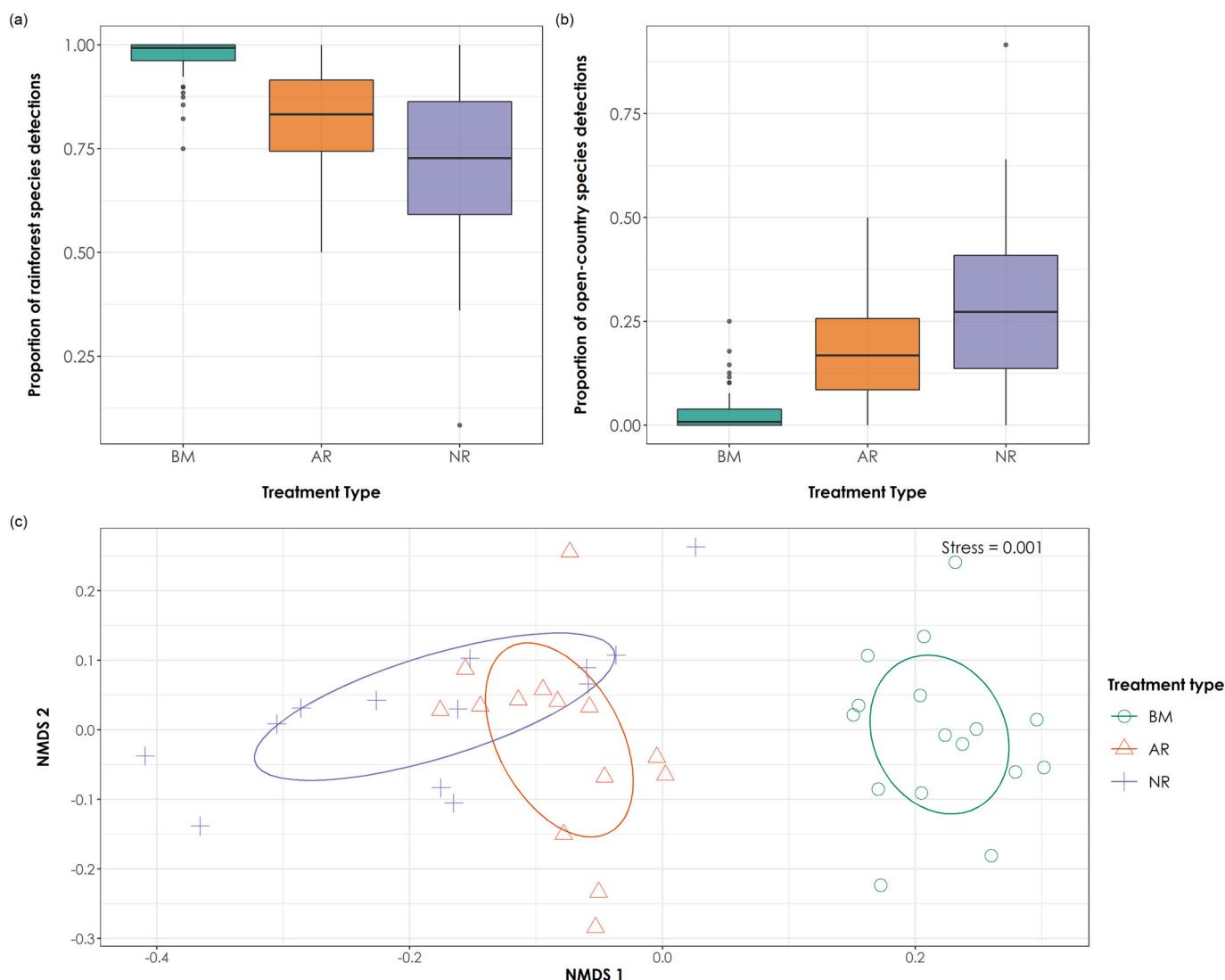


Fig. 5. Proportion of acoustic detections of rainforest and open-country bird species and NMDS ordination results of bird species detections. (a) We observed significant differences in the proportion of rainforest bird species detections across each of the three treatment types (Tukey HSD test, $P < 0.05$). BM sites had the highest proportion of rainforest bird species detections (mean \pm SD: 0.97 ± 0.04), followed by AR sites (mean \pm SD: 0.81 ± 0.12) and NR sites (mean \pm SD: 0.71 ± 0.17). (b) We observed significant differences in the proportion of open-country bird species detections across each of the three treatment type (Tukey HSD test, $P < 0.05$). NR sites had the highest proportion of open-country bird species detections (mean \pm SD: 0.28 ± 0.17), followed by AR sites (mean \pm SD: 0.18 ± 0.12) and BM sites (mean \pm SD: 0.02 ± 0.04). (b) The ordination analysis of bird detections data (stress = 0.001) revealed distinct clusters of BM sites but relatively loose clusters for AR and NR sites. However, AR sites occupied an intermediate position between BM and NR sites, indicating a direction of change in bird community composition toward BM sites. In the above figure, BM = undisturbed benchmark rainforest sites, AR = actively restored forest sites, and NR = naturally regenerating forest sites.

kHz to 6 kHz across AR and NR sites, high-frequency katydids (family: Tettigoniidae; (Tiwari and Diwakar, 2023)) are missing in actively restored and naturally regenerating sites. Studies from Central and South America have also shown that ASU is positively associated with insect species richness (Aide et al., 2017), and this association may directly explain significant differences between managed and primary forests (Campos-Cerqueira et al., 2019). In our study site, the relatively empty frequency bins at higher frequencies potentially corresponding to katydid activity in restored sites could be driving the pattern of differentiation between these disturbed forests and undisturbed BM sites.

Soundscapes may take longer than individual taxa to recover (Vega-Hidalgo et al., 2021), and novel approaches such as playing soundscapes in restored and naturally regenerating areas can potentially increase the pace of faunal recolonization (Znidarsic and Watson, 2022). While our examination of ASU provides only a snapshot of overall acoustic activity and may not reflect long-term patterns, it is clear that undisturbed tropical forests are acoustically unique and largely irreplaceable.

4.2. Bird species richness, acoustic detections, and community composition

Besides harboring a unique soundscape, benchmark sites are also vital for rainforest bird species (Hariharan and Raman, 2022). We find that the proportion of acoustic detections of rainforest bird species was highest in BM sites, followed by AR sites and NR sites, while for open-country bird species, NR sites had the highest proportion of acoustic detections, followed by AR and BM sites. Our measure of acoustic detections is similar in principle to the vocal activity rate index, which estimates the number of songs/calls of a species for a given time period, and is positively associated with species abundance (Nelson and Graves, 2004; Oppel et al., 2014; Pérez-Granados et al., 2021). A recent study conducted in the same landscape provides support for these patterns in bird species richness and abundance, showing that active restoration aids in the recovery of rainforest bird species (Hariharan and Raman, 2022). Closely mirroring what (Hariharan and Raman, 2022) found,

when we analyzed the community composition of bird species, we found that bird communities in AR sites were in transition from those in NR sites to BM sites. Other monitoring programs in the tropics using acoustics to understand the avian response to restoration have found similar shifts in community structure within comparable time frames, with forest specialists returning to maturing forests later than other species (Owen et al., 2020).

Point counts and passive acoustic recording methods produce similar estimates of avian species richness and community composition, but recorders may be more resource-efficient for long-term and/or large-scale studies and aid in detecting unique species (Klingbeil and Willig, 2015; Leach et al., 2016). Nocturnal birds, which are often difficult to survey, and amphibians, which need to be surveyed during challenging monsoon conditions, may benefit from the method we have outlined here (Knight et al., 2022). Similarly, soundscape saturation metrics may be a valuable tool to detect species in tropical forests alongside existing tools such as camera trapping (Zwerts et al., 2022). In the future, a cross-disciplinary approach with field methods led by passive acoustic monitoring that relies on the expert knowledge of natural scientists may allow us to understand the response of all vocalizing taxa to restoration and land-use change. By using this effective and efficient method for data collection, it may be possible to overcome some of the challenges associated with conducting long-term studies in ecology and evolution and contribute data from historically understudied regions (Kuebbing et al., 2018). Data collected during the course of such studies can be instrumental in building training data for automated recognition algorithms, further opening up opportunities for collaboration across fields to conduct rapid species assessments (Kahl et al., 2021; Zhong et al., 2020).

5. Conclusions

Actively restored and naturally regenerating sites are more similar in acoustic space use compared to benchmark sites. Acoustic space use measures provided a snapshot of the overall acoustic environment corresponding to the vocal activity of multiple taxonomic groups. Moving beyond single indicator taxon studies, we found that sounds at higher frequencies (potentially corresponding to katydid vocalizations) were largely missing from AR and NR sites. Encouragingly, we find that rainforest bird species return to actively restored forest sites, as revealed through our measure of species acoustic detections. However, despite 20 years of active restoration, we find that benchmark sites are irreplaceable in their acoustic and species diversity. Such sites need continued protection to sustain existing levels of biodiversity.

Over the past decade, novel remote monitoring tools such as live cameras and underwater microphones have aided in the monitoring of biodiversity, supplementing traditional field ecological methods on the ground ((Blumstein et al., 2011; Wood et al., 2020)) Acoustic monitoring has been used in several logically challenging habitats such as ponds (Greenhalgh et al., 2021), reed beds (Stermin et al., 2013), temperate forests (Depraetere et al., 2012), to assess the recovery of individual species (Kahl et al., 2021; Wood et al., 2022)) and to determine anthropogenic pressure on natural habitats (Burivalova et al., 2021) However, the majority of long-term monitoring programs rely almost entirely on traditional surveys. While the use of passive acoustic monitoring has its limitations, we strongly recommend supplementing traditional ecological survey methods with this technique to assess the impacts of conservation intervention programs. As a first step, we encourage the use of passive acoustic monitoring techniques to assess the response of faunal biodiversity to ecological restoration especially in biodiverse tropical forests.

CRediT authorship contribution statement

Vijay Ramesh, VV Robin, and Ruth DeFries conceived the ideas; Vijay Ramesh and Priyanka Hariharan designed the methodology; Vijay

Ramesh and VA Akshay collected the data; Vijay Ramesh analyzed the data; Vijay Ramesh and Priyanka Hari Haran led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This study brings together authors from multiple countries and includes scientists based in the country where the study was carried out. Our study design brought together a diverse perspective from multiple stakeholders in the landscape.

Declaration of competing interest

Authors have no conflict of interest to declare.

Data availability

The complete analysis and associated supplementary material are available on GitHub (<https://github.com/vijjan91/acoustics-Restoration>) and is archived on Zenodo (<https://doi.org/10.5281/zenodo.7036137>).

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Appendix A. Supplementary data

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