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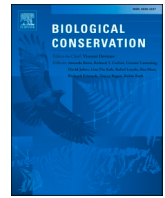
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Tree diversity and liana infestation predict acoustic diversity in logged tropical forests

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ABSTRACT

Logged tropical forests can retain a great deal of biodiversity, but there is substantial variation in the type and severity of habitat degradation caused by logging. Logging-induced habitat degradation can vary significantly at fine spatial scales, with differing effects on plant communities and the growth of lianas, which are woody, climbing vines that proliferate in degraded forests and infest trees by climbing onto them and competing for above and below ground resources. The impacts of such fine-scale variation in habitat structure on faunal diversity is relatively poorly known. We recorded soundscapes and variation in local-scale habitat structure in selectively logged and old-growth primary forests in Malaysian Borneo to examine how changes to logged forest structure predict variation in acoustic diversity indices that are known to correlate with biodiversity indices. We show that acoustic indices relating to higher soundscape diversity increase with liana prevalence but decline with tree species richness and are unaffected by the liana load of adult trees. Our results suggest that acoustic data represent a simple, practicable measure for detecting fine-scale patterns of biodiversity response to post-logging habitat structure. Our findings also suggest that retaining many trees lightly infested by lianas in logged forests is the optimal outcome for biodiversity. This emphasises the need for forest restoration that retains some climbers, rather than blanket-cutting of all stems in projects seeking to return post-logging forest communities towards their primary forest state.

1. Introduction

Over 400 million hectares of natural tropical forest are designated as permanent timber estates (Blaser et al., 2011). Selective logging, a widespread method of logging where only certain tree species and stem sizes are harvested (Edwards et al., 2014b), poses a myriad of environmental threats such as reduced carbon stocks, biodiversity loss, and habitat degradation (Gibson et al., 2011; Putz et al., 2012; Lewis et al., 2015). Yet because selectively-logged forests account for the majority of remaining tree cover in many regions (Blaser et al., 2011; Laurance et al., 2014), and retain high levels of biodiversity and carbon relative to alternative land uses such as agriculture (Gibson et al., 2011; Putz et al.,

2012), they remain vital for conservation.

The conservation value of selectively logged forests varies at different spatial scales. Overall, across the entire selective logging concession, tree community composition is altered and lianas proliferate (Clark and Covey, 2012; Magrach et al., 2016; Hayward et al., 2021). However, varying logging intensities within the selective logging concession generates a heterogeneous habitat matrix composed of heavily logged areas with species-poor tree communities and treefall gaps infested with lianas (Schnitzer and Bongers, 2011; Imai et al., 2012), as well as large interconnected patches of old-growth and lightly logged forest (Edwards et al., 2014b). Thus, when considering finer spatial scales, selective logging concessions still retain relatively

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undisturbed habitat.

As a result, the impact on biodiversity varies across this fine-scale habitat variation. Studies using local logging intensity (i.e. variation in the number of stems or volume cut in one to a few hectares) in Brazil reveal that butterfly abundance peaks at intermediate local logging intensities, yet certain clades benefit disproportionately from the retention of primary forest (Montejo-Kovacevich et al., 2018), while dung beetle species richness and composition are negatively affected by increasing local logging intensity (França et al., 2017). Moreover, in logged forest in Malaysian Borneo, local (transect-level) liana prevalence was positively related to the abundance and species richness of understorey passerines (Ansell et al., 2011), which can be attributed to the provision of fruit, flowers, and foraging and nesting substrates by lianas (Schnitzer et al., 2014; Schnitzer et al., 2020). While these studies show that fine-scale habitat variation can impact biodiversity, such studies only focus on the effects on a single taxonomic group. A key question that remains is how the biodiversity of larger communities is impacted by fine-scale logging-induced habitat variation, such as through the proliferation of lianas.

Acoustic diversity indices have been proposed as highly practicable metrics of biodiversity (Sueur et al., 2014), capable of sampling at much wider spatiotemporal scales than traditional sight-based biodiversity surveys and at a relatively low cost (Darras et al., 2019). Due to the increased diversity of noises produced by a more speciose community of vocal fauna, a more diverse soundscape, as measured by acoustic indices, is positively associated with greater biodiversity, although the strength of this correlation varies between metrics and studies (Sueur et al., 2014; Alcocer et al., 2022). Acoustic indices are also sensitive to anthropogenic change and indicate decreases in acoustic diversity with selective logging (Burivalova et al., 2019; Metcalf et al., 2020; Mitchell et al., 2020). For example, in Indonesian Borneo, soundscape saturation decreased immediately after a second round of selective logging and remained depressed three years after logging (Burivalova et al., 2021).

An important untested question is how fine-scale variation in habitat degradation impacts acoustic diversity, as a biodiversity metric spanning across a range of taxonomic groups. We expect acoustic diversity to increase with local tree species richness due to the greater diversity of resources available for fauna, and to increase with the prevalence and load of lianas on trees due to the increased provisioning of resources by lianas. Here, we investigate how acoustic diversity is impacted by varying levels of selective logging-induced degradation in Sabah,

Malaysian Borneo, a global epicentre of biodiversity and selective logging. We aim to accomplish this by measuring covariation between acoustic diversity and 1) tree species richness and 2) liana infestation. Identifying the optimal levels of tree species richness and liana infestation to maintain biodiversity as measured by acoustic diversity will develop our understanding of how to manage recovering logged tropical forest to retain biodiversity.

2. Methods

2.1. Study area

Sampling was conducted in the selectively logged forests of the Yayasan Sabah logging concession (YS), a ~ 1 million hectare contiguous forest comprised of mostly lowland moist forest dominated by valuable timber species of the family *Dipterocarpaceae* (Newbery et al., 1992; Fisher et al., 2011). Selectively logged forests sites were located in the 141,000 ha Ulu Segama-Malua Forest Reserve (USMFR, Fig. 1), which has been logged twice following a modern uniform system and using tractors and high-lead cable extraction techniques. The area was first logged between 1976 and 1991, when ~120 m³ ha⁻¹ of timber was extracted, and then again between 2001 and 2007, when an additional 15–72 m³ ha⁻¹ of timber was extracted (Edwards et al., 2011).

2.2. Sampling design

Between June and October 2019, soundscapes and habitat structure metrics were sampled at 36 blocks distributed across 3 sites covering 20 km² of twice-logged forest in the USMFR. Soundscape sampling blocks were located every 200 m along a transect, with each transect at least 200 m apart. Two sites contained four 800 m long transects each (Fig. 2). However, due to time constraints, one site could not be as extensively sampled, and thus contained two 400 m long transects. Habitat metrics were collected at 2 to 5 sub-sampling plots of 20 m × 20 m (mean ± SE = 3.83 ± 0.15), distributed randomly within the 100 m × 100 m area of each soundscape sampling block (Fig. 2).

We collected soundscapes using AudioMoths (version 1.0.0; Open Acoustic Devices), which are small, relatively cheap sound recorders. We housed AudioMoths in weatherproof electrical junction boxes with a hole over the microphone that was covered with an e-PTFE, IP67 waterproof acoustic membrane (Voir Tech). Recorders were attached to

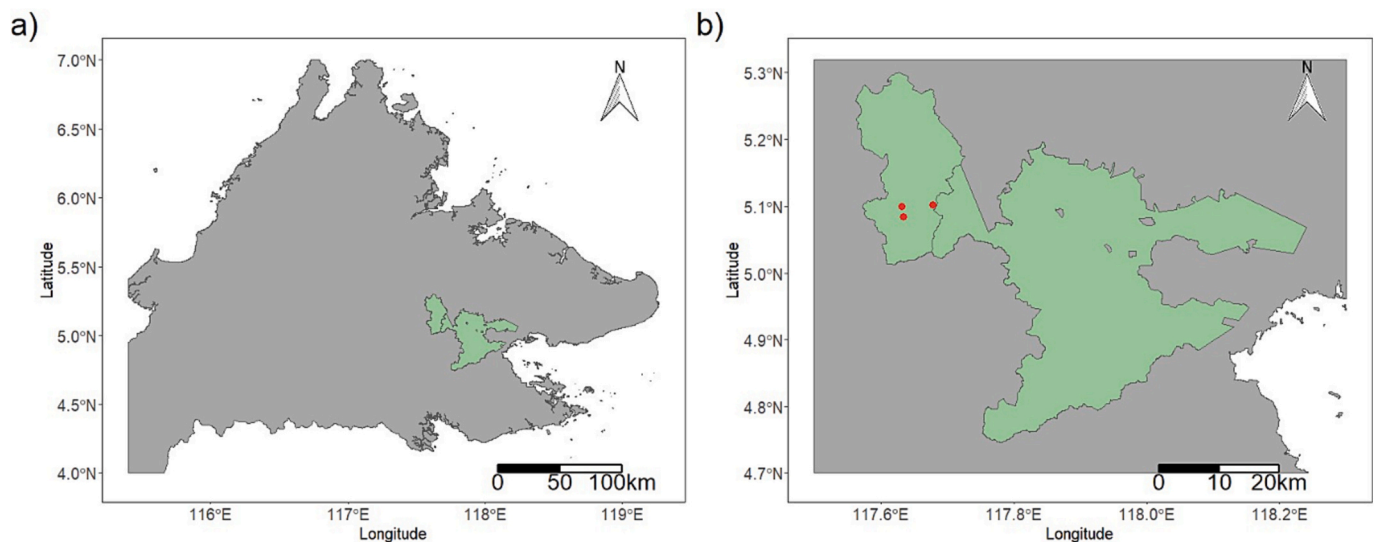


Fig. 1. Maps showing the location of the sampling sites. In (a), the location of the Ulu Segama-Malua Forest Reserve (green) within Sabah is shown, while (b), which shows the location of the three sampling sites (red) within the USMFR. Across these 3 sampling sites are 36 blocks where sampling of soundscapes and habitat metrics took place. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

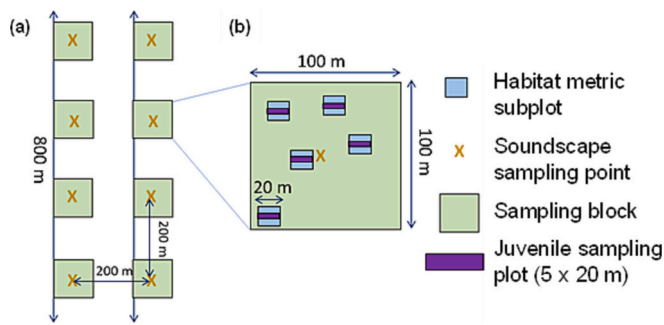


Fig. 2. Soundscape and habitat metric sampling block design. Example of two transects and soundscape sampling point distribution in USMFR (a), and each sampling block with random distribution of five sub-plots (b).

a tree at (or near) the centre of each sampling block, at a height of 1.5 m, with microphones for all recorders facing in the same direction (North) to prevent overlapping recordings of the same noise. If there was an obstruction directly North, the microphone was directed to face as northerly as possible to further minimise overlapping. We configured each AudioMoth to record 10 min every hour between 05:00–08:00 and 18:00–20:00 to capture the dawn and dusk chorus of the bird community as well as the vocalisations of other biota at this time, with a sampling rate of 48 kHz and medium gain, and deployed for a minimum of 4 consecutive days per block. This resulted in 320 to 350 min of soundscape recorded per block. Soundscapes were saved on Secure Digital (SD) cards in Waveform Audio File Format (WAV).

2.3. Habitat metrics

Tree species richness was chosen as a habitat metric because it encompasses changes in both forest structure and resource availability. At our sites, tree species richness was negatively associated with canopy openness and positively associated with tree abundance (Fig. S1). This reflects the transition from unlogged or lightly logged areas characterised by abundant trees, diverse tree species, and a dense canopy, to intensively logged areas with a sparse tree population, limited tree species, and an open canopy. As well as detecting logging-induced changes in forest structure, a greater diversity of tropical trees will reflect an increase in the diversity of tree fruits, nuts, and seeds available (Jansen et al., 2020). Similarly, changes in the level of liana infestation affect both forest structure and resource availability, with liana proliferation resulting in the formation of liana tangles, reduced canopy height, and increased food provisioning (Schnitzer and Bongers, 2002).

To determine whether differences in tree diversity and liana infestation influenced acoustic diversity, we recorded the habitat metrics of 1) tree species richness; 2) liana prevalence, representing the proportion of trees infested by lianas (1 – all trees infested, 0 – no trees infested); and 3) liana load, calculated as the level of liana infestation in the canopy of each tree on an ordinal scale (< 25 % canopy covered by lianas, 26–50 %, 51–75 %, or > 75 % (Muller-Landau et al., 2019)) and then averaged across all trees. These metrics were sampled in subplots within the sampling block, with adult trees (> 10 cm dbh) sampled across a 20 × 20 m subplot while juveniles (≥ 1 cm dbh) were sampled within a nested central 5 × 20 m subplot (Fig. 2).

2.4. Sound analysis in logged forest

Sound recordings from USMFR were read into R using the package *tuneR* (Ligges et al., 2018). Acoustic diversity of each block was quantified using a range of acoustic indices extracted using the packages *soundecology* and *seewave* (Sueur et al., 2008a; Villanueva-Rivera and Pijanowski, 2018). For each sound file, the function for each acoustic index was applied across the entire ten-minute recording. Recordings

with rain were not removed due to the large number of files (13,816) that would require manual sorting and the time constraints of this study. The following acoustic indices were used due to their relative success as proxies for biodiversity, and are positively correlated with bird species richness (Alcocer et al., 2022):

- 1) Acoustic Entropy Index (H), which measures the evenness of the amplitude among frequency bands and over time (Sueur et al., 2008b; Bradfer-Lawrence et al., 2019). High values can be achieved by an even soundscape, such as similar levels of noisiness across all frequency bands, whether similarly loud or similarly quiet (Bradfer-Lawrence et al., 2019). This can be generated by a more species rich, evenly abundant faunal community, with a wide range of taxonomic groups vocalising in different frequency bands at similar intensities, caused by similarly low or high abundances of individuals in each taxonomic group. H was calculated from *seewave* using default parameters, with a window length for spectral entropy analysis of 512, and utilising a Hilbert amplitude envelope (Sueur et al., 2008a).
- 2) Acoustic Complexity Index (ACI), which is a measure of the variability in sound intensity throughout the soundscape (Pieretti et al., 2011), based on the change in amplitude over time steps and within frequency bands (Bradfer-Lawrence et al., 2019). High ACI values indicate the presence of noises of variable sound intensities occurring in different frequency bands, including biological noises such as bird song (Pieretti et al., 2011). This could be generated by a more abundant and species rich faunal community, generating more noises of variable sound intensity from a diverse range of taxa capable of vocalising at different frequencies. ACI was calculated from *seewave* using default parameters, utilising a Hamming function in the short-term Fourier transform, a window length of 512, and 0 % overlap between successive windows (Sueur et al., 2008a).
- 3) Acoustic Diversity Index (ADI), which measures how evenly distributed sound is across frequency bands. ADI uses the proportion of sound in each frequency band to calculate a Shannon Index value (Villanueva-Rivera et al., 2011), with high ADI values generated by similar levels of noisiness across frequency bands, whether similarly loud or similarly quiet (Bradfer-Lawrence et al., 2019). Similarly to H, this can be generated by a more species rich, evenly abundant faunal community, with a wide range of taxonomic groups vocalising in different frequency bands at similar intensities, caused by similarly low or high abundances of individuals in each taxonomic group. ADI was calculated in *soundecology* using default parameters, utilising ten frequency bands of 1 kHz up to a maximum frequency of 10 kHz (Villanueva-Rivera and Pijanowski, 2018).
- 4) Normalised Difference Soundscape Index (NDSI), which measures the ratio of biological noise to anthropogenic noise, by assigning anthropogenic noise as sounds at a frequency of 1–2 kHz and biological noises typically assigned as occurring at 2–8 kHz, with high NDSI values generated by soundscapes with relatively high levels of biological noise (Kasten et al., 2012; Sueur et al., 2014). These high values could be generated by a more abundant faunal community generating more vocalisations above the 2 kHz threshold. NDSI was calculated using *seewave*, with anthropogenic noise assigned to noises between a frequency of 1–2 kHz, and biotic noise assigned to any noises above a frequency of 2 kHz. This was adjusted from the usual default parameters which assign biotic noise a frequency range of 2–8 kHz as biological noises in tropical habitats are usually not limited to 2–8 kHz (Sueur et al., 2014). Anthropogenic noise present at the study sites included engine noises from vehicles travelling by road, helicopters flying overhead, and forestry machinery such as large excavators with cutting blades deployed to clear an old forestry road.

2.5. Statistical analysis

To assess how changes to these habitat metrics may predict variation

in these acoustic indices, linear mixed-effects models following a Gaussian error structure were constructed using the *lme4* package (Bates et al., 2015). Adult and juvenile trees were modelled separately and then together. Across all models, values for acoustic indices were used as response variables. These values were untransformed due to the robustness of Gaussian linear mixed models to heteroscedasticity and non-normality (Schielzeth et al., 2020; Knief and Forstmeier, 2021), and the inability of natural log and square root transformations to improve normality or homoscedasticity in the dataset. For adult trees, tree species richness, liana load, and liana prevalence were used as fixed effects, with sampling site as a random effect, and hour of day and day of month as nested random effects. Models for juvenile trees were similar but did not have liana load as a fixed effect due to a lack of data.

Models combining adult and juvenile tree data were also constructed, using overall tree species richness across adult and juvenile trees, overall liana prevalence across adult and juvenile trees, and liana load of adult trees as fixed effects. Juvenile liana load could not be included due to the lack of data. Sampling site was used as a random effect, and hour of day and day of month were used as nested random effects except for ADI and ACI analyses which did not include day of month as random effects to prevent convergence errors.

Month could not be added as a random effect as this caused the models to become overfitted. However, this is unlikely to have much of an effect due to the minimal seasonal variation in climate of the study area, especially between June and October (Walsh and Newbery, 1999; Huang et al., 2023). Thus, months with especially high levels of rainfall and wind, or climate-driven phenological patterns are unlikely to occur within the study period and systematically affect the sound analysis.

Model residuals were checked for homoscedasticity and normality. Model fit was compared using Akaike information criterion in the

AICcmodavg package (Anderson, 2008; Mazerolle, 2020), to determine how well habitat metrics explained variation in acoustic index values. The most parsimonious model had the lowest AIC score, which was 2 AIC units lower than the model with the next lowest score. If another model was within 2 AIC units of the most parsimonious model, this was counted as equally parsimonious (Anderson, 2008). The conditional and marginal R^2 of the models, showing the amount of variation explained by the fixed and random effects respectively, were calculated using Nagakawa and Schielzeth's R^2 with the *MuMin* package (Barton, 2020).

A single outlying value with extremely high total, adult, and juvenile tree species richness and an extremely low NDSI value was removed from the analysis.

3. Results

When modelling adult and juvenile trees together, model fit improved for ADI when overall tree species richness, overall liana prevalence, and liana load of adult trees were used as fixed effects, but not for H, ACI or NDSI (Table 1). When modelling adult trees alone, model fit improved for ACI and ADI when tree species richness, liana prevalence, and liana load were used as fixed effects, but not for H or NDSI (Table 2). When modelling juvenile trees alone, model fit improved for NDSI, ACI, and ADI when tree species richness and liana prevalence were used as fixed effects (Table 2).

The null model was the most parsimonious model for H in models across all age classes, for ACI in models combining habitat metrics for adult and juvenile trees, and for NDSI in models containing habitat metrics for adult trees alone as well as when combining both adult and juvenile trees (Table 1, Table 2).

Table 1

Model selection of linear mixed-effects models combining data for adult and juvenile trees. Models were selected for all acoustic metrics in relation to environmental gradient variables based on their AIC values. Fixed effects are liana load of adult trees, overall liana prevalence across adult and juvenile trees, and overall tree species richness across adult and juvenile trees. Null models only contain the random effects of site, hour of day, and day of month, except for NDSI which only contains site and hour of day as random effects, and ACI which only contains site as a random effect. The most parsimonious models are highlighted in bold. AIC, Akaike information criterion; Δ AIC, the AIC difference between the best model and the stated model; Marginal R^2 , variation explained by fixed effects; Conditional R^2 , variation explained by the model.

Response variable	Model	AIC	Δ AIC	Marginal R^2	Conditional R^2
Acoustic Entropy Index (H)	NULL	-29,284.23	0.00	0.00	0.35
	richness	-29,283.40	0.83	0.00	0.35
	load+richness	-29,282.86	1.37	0.01	0.35
	prevalence+richness	-29,282.55	1.68	0.01	0.35
	prevalence	-29,282.44	1.79	0.00	0.35
	load	-29,282.36	1.87	0.00	0.35
	load+prevalence+richness	-29,281.23	3.00	0.01	0.35
	load+prevalence	-29,280.46	3.77	0.00	0.35
	NULL	37,821.58	0.00	0.00	0.21
	richness	37,821.69	0.11	0.00	0.21
Acoustic Complexity Index (ACI)	prevalence	37,822.52	0.93	0.00	0.21
	load	37,822.73	1.15	0.00	0.21
	prevalence+richness	37,823.46	1.88	0.00	0.21
	load+richness	37,823.66	2.07	0.00	0.21
	load+prevalence	37,824.35	2.77	0.00	0.21
	load+prevalence+richness	37,825.46	3.88	0.00	0.21
	prevalence + richness	6074.23	0.00	0.06	0.33
	load + prevalence + richness	6076.05	1.82	0.07	0.34
	richness	6076.63	2.40	0.04	0.33
	load+richness	6076.99	2.77	0.05	0.34
Acoustic Diversity Index (ADI)	load+prevalence	6079.52	5.29	0.07	0.36
	prevalence	6079.70	5.47	0.07	0.36
	load	6081.51	7.28	0.06	0.37
	NULL	6088.49	14.26	0.00	0.36
	prevalence	-268.38	0.00	0.06	0.62
	load	-267.39	0.98	0.04	0.62
	prevalence+richness	-267.12	1.25	0.08	0.63
	load+prevalence	-266.84	1.53	0.06	0.62
	NULL	-266.47	1.91	0.00	0.62
	load+richness	-265.73	2.65	0.04	0.63
Normalised Difference Soundscape Index (NDSI)	load+prevalence+richness	-265.42	2.96	0.08	0.64
	richness	-265.03	3.34	0.01	0.62

Table 2

Model selection of linear mixed-effects models for adult and juvenile trees separately. Models were selected for all acoustic metrics in relation to habitat metrics based on their AIC values. Fixed effects are liana load, liana prevalence, and tree species richness. Null models only contain the random effects of site, hour of day, and day of month. The most parsimonious models are highlighted in bold. AIC, Akaike information criterion; Δ AIC, the AIC difference between the best model and the stated model; Marginal R^2 , variation explained by fixed effects; Conditional R^2 , variation explained by the model.

Response variable	Model	AIC	Δ AIC	Marginal R^2	Conditional R^2
Acoustic Entropy Index (H) (Adult)	NULL	-29,284.23	0.00	0.00	0.35
	richness	-29,283.80	0.43	0.00	0.35
	load+richness	-29,283.68	0.55	0.01	0.35
	prevalence+richness	-29,282.84	1.39	0.01	0.35
	prevalence	-29,282.81	1.42	0.00	0.35
	load	-29,282.36	1.87	0.00	0.35
	load+prevalence+richness	-29,281.77	2.46	0.01	0.35
	load+prevalence	-29,280.82	3.41	0.00	0.35
	NULL	-29,284.23	0.00	0.00	0.35
	richness	-29,282.96	1.27	0.00	0.35
Acoustic Entropy Index (H) (Juvenile)	prevalence	-29,282.34	1.89	0.00	0.35
	prevalence+richness	-29,281.28	2.95	0.00	0.35
	prevalence + richness	36,516.65	0.00	0.02	0.40
	richness	36,517.95	1.30	0.02	0.40
	load + prevalence + richness	36,518.65	2.00	0.02	0.40
	load+richness	36,518.84	2.19	0.02	0.41
	load	36,520.51	3.86	0.02	0.41
	load+prevalence	36,521.59	4.94	0.01	0.41
	prevalence	36,522.12	5.47	0.01	0.40
	NULL	36,524.50	7.85	0.00	0.40
Acoustic Complexity Index (ACI) (Adult)	richness	36,515.21	0.00	0.01	0.40
	prevalence + richness	36,516.66	1.45	0.01	0.40
	NULL	36,524.50	9.30	0.00	0.40
	prevalence	36,524.55	9.34	0.01	0.41
	prevalence + richness	5661.57	0.00	0.07	0.40
	richness	5662.71	1.14	0.06	0.41
	load + prevalence + richness	5663.56	1.99	0.07	0.41
	load+richness	5663.85	2.28	0.07	0.41
	load	5668.31	6.74	0.05	0.42
	load+prevalence	5669.65	8.08	0.04	0.42
Acoustic Complexity Index (ACI) (Juvenile)	prevalence	5670.99	9.42	0.02	0.41
	NULL	5673.39	11.82	0.00	0.41
	prevalence + richness	5663.14	0.00	0.05	0.40
	richness	5665.23	2.09	0.03	0.40
	prevalence	5668.96	5.82	0.05	0.42
	NULL	5673.39	10.25	0.00	0.41
	load	-267.39	0.00	0.04	0.62
	richness	-267.07	0.33	0.03	0.62
	load+richness	-266.93	0.47	0.06	0.62
	prevalence+richness	-266.50	0.89	0.05	0.62
Normalised Difference Soundscape Index (NDSI) (Adult)	NULL	-266.47	0.93	0.00	0.62
	load+prevalence	-265.85	1.54	0.04	0.63
	prevalence	-265.20	2.19	0.01	0.63
	load+prevalence+richness	-264.93	2.46	0.05	0.63
	prevalence	-269.02	0.00	0.08	0.62
	prevalence + richness	-268.56	0.46	0.09	0.63
	NULL	-266.47	2.55	0.00	0.62
	richness	-264.95	4.06	0.01	0.63

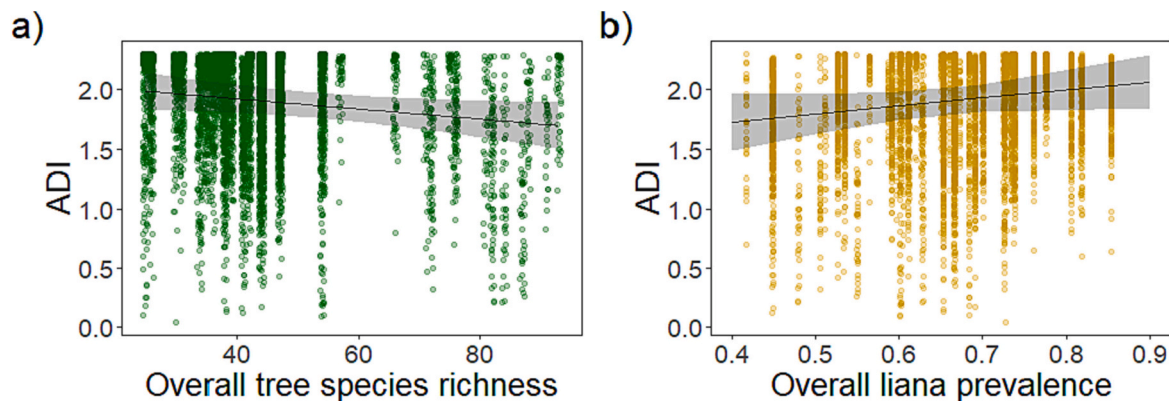


Fig. 3. Graphs showing how the Acoustic Diversity Index (ADI) varies with the (a) tree species richness and (b) liana prevalence of both adult and juvenile trees combined, with a 95 % confidence limit.

3.1. Tree species richness and acoustic diversity

As overall tree species richness increased, ADI decreased (Fig. 3a). Modelling adult and juvenile trees separately also showed similar impacts on acoustic indices (Fig. 4). ADI (Fig. 4ab) was also negatively related to adult and juvenile tree species richness when modelled separately, however ACI displayed only a slightly negative relationship to adult and juvenile tree species richness. NDSI also showed only a slight negative relationship to juvenile tree species richness alone. For indices where models containing habitat metrics were not the most parsimonious, no clear direction was observed in the relationship between the acoustic index and tree species richness (Figs. S2, S3).

3.2. Liana infestation and acoustic diversity

As the overall liana prevalence increased, so did ADI (Fig. 3b). Modelling the liana prevalence of adult and juvenile trees separately also showed similar impacts on acoustic indices (Fig. 5). ADI (Fig. 5ab) was positively related to the liana prevalence of adult and juvenile trees, whereas ACI (Fig. 5cd) showed only a slightly positive relationship with the liana prevalence of both adult and juvenile trees. NDSI was positively associated with the liana prevalence of juvenile trees only (Fig. 5e). However, liana load showed a mostly flat relationship with ADI and ACI (Fig. 6). For indices where models containing habitat metrics were not the most parsimonious, no clear direction was observed in the relationship between the acoustic index and liana prevalence (Figs. S2, S4) or liana load (Fig. S5).

4. Discussion

We address the issue of understanding the impacts of fine-scale habitat degradation from selective logging on faunal communities, focussing specifically on vocal fauna. Using acoustic indices, we find that tropical forest soundscapes tend to be more acoustically diverse in logged forests that have lower tree species richness and high liana prevalence, with the liana load of adult trees having mixed effects on the soundscape. With this increased soundscape diversity associated with an increase in biodiversity, particularly bird species richness, our results highlight the need to retain climbers in restored forests.

4.1. Limitations of individual soundscape metrics in this study

The Acoustic Entropy Index (H) was not correlated with the degree of habitat degradation. The lack of relationship may be caused by the limitations of this index for our study context. By default, the ADI function in *soundecology* eliminates sounds quieter than -50dBFS, whereas sound analysis with H does not include a minimum noise threshold and as a result values of H may be more influenced by faint non-biological noises such as constantly occurring microphone self-noise and light wind in the environment. NDSI accounts for the presence of anthropogenic noise between 1 and 2 kHz produced by mechanical sounds (Kasten et al., 2012), such as the occasional sounds of vehicles, helicopters, and forestry machinery around our study site, whereas H does not distinguish between biological and non-biological sounds. ACI captures the intrinsic variability of intensity over time present in biotic noise that is missing in the constant intensity of

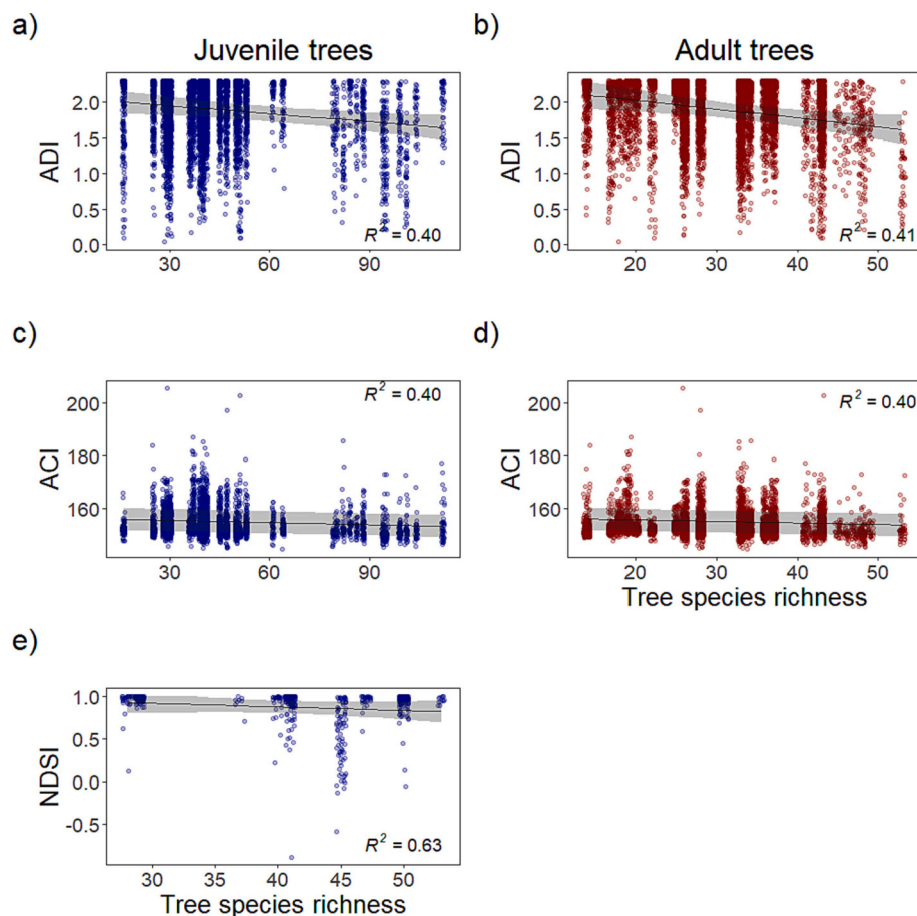


Fig. 4. Graphs showing how different acoustic indices vary with the species richness of juvenile trees (a, c, e) and adult trees (b, d). Shown are the relationships between Acoustic Diversity Index (ADI) (a, b) and Acoustic Complexity Index (ACI) (c, d) and the species richness of both adult and juvenile trees with a 95 % confidence limit. Normalised Difference Soundscape Index (NDSI) (e) is shown only against the species richness of juvenile trees.

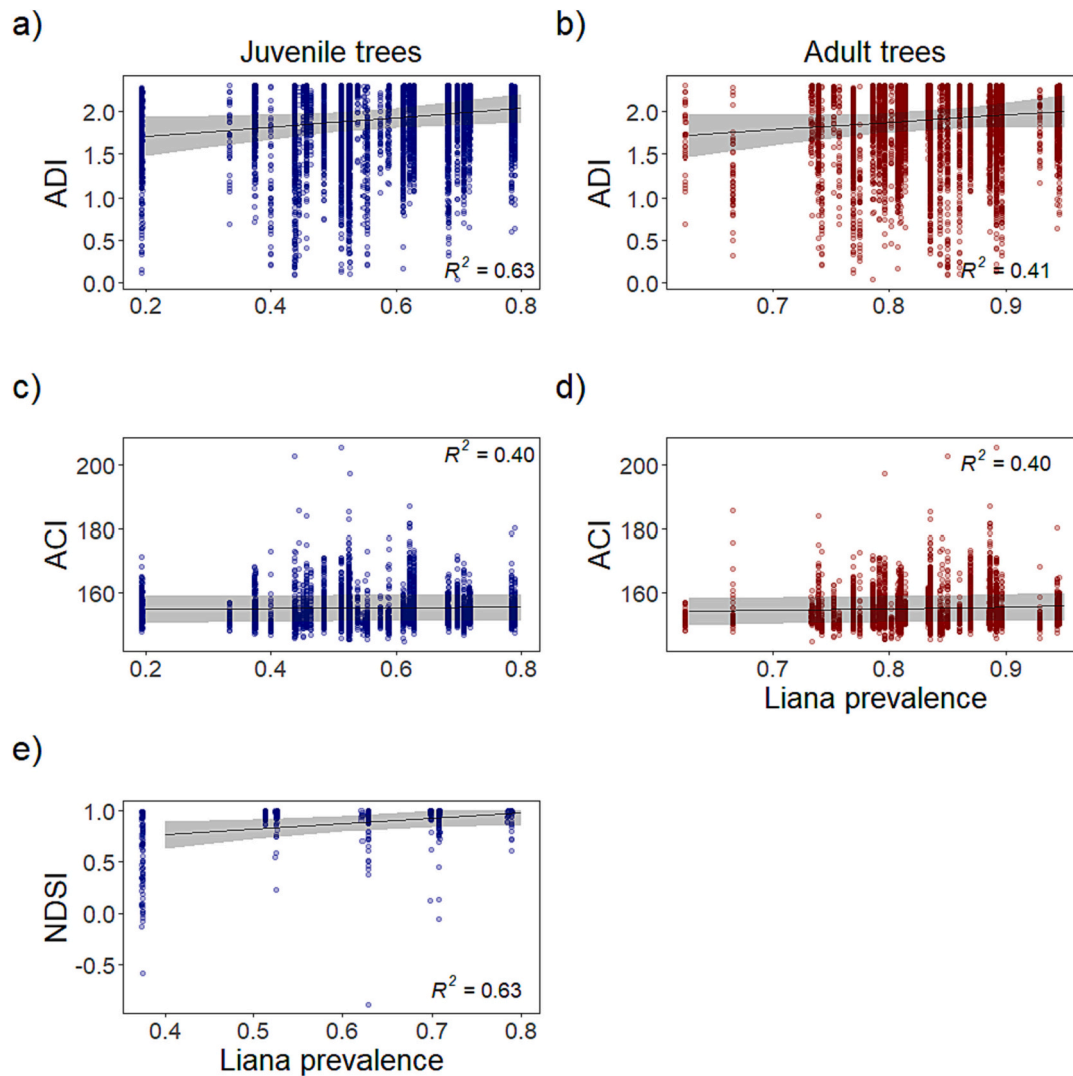


Fig. 5. Graphs showing how different acoustic indices vary with the liana prevalence of juvenile trees (a, c, e) and adult trees (b, d). Shown are the relationships between Acoustic Diversity Index (ADI) (a, b) and Acoustic Complexity Index (ACI) (c, d) and the liana prevalence of both adult and juvenile trees with a 95 % confidence limit. Normalised Difference Soundscape Index (NDSI) (e) is shown only against the liana prevalence of juvenile trees.

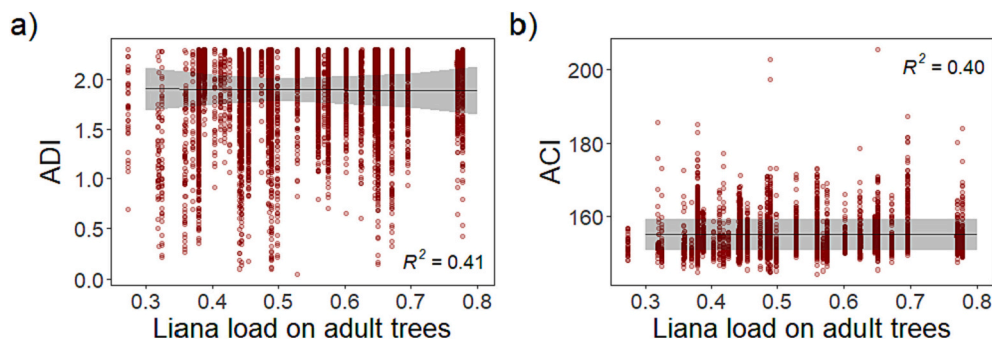


Fig. 6. Graphs showing how different acoustic indices vary with liana load of adult trees. Changes in the Acoustic Diversity Index (ADI) (a) and Acoustic Complexity Index (ACI) (b) are shown against changes in the liana load of adult trees with a 95 % confidence limit.

geophony such as wind or rain (Pieretti et al., 2011), however despite H having a similar purpose to ACI, high values in H can also be achieved by an amplitude with almost no variation (Bradfer-Lawrence et al., 2019). Thus, values generated by H may be more easily influenced by faint, non-biological noises of anthropogenic, geophonic, and technological origins occurring during our study.

The relationships between the Acoustic Complexity Index (ACI) and the habitat metrics are much flatter than those with ADI and NDSI. While slightly negative relationships between tree species richness and ACI can be seen, relationships with liana infestation metrics are even flatter. This may be because of the susceptibility of ACI to the influence of cicada calls, as the constant intensity of cicada calls generates low ACI

values (Bradfer-Lawrence et al., 2019). As cicada calls can travel vast distances (O'Toole, 2002), and with Bornean cicada calls occurring throughout much of the dawn and dusk chorus (Gogala and Riede, 1995; Riede, 1997; Prešern et al., 2004), these calls may depress ACI values throughout our forest site regardless of local habitat structure and at all of our recording times.

ADI showed relationships with tree species richness and liana prevalence despite a recent meta-analysis showing this index has a weaker correlation with biodiversity than H and ACI (Alcocer et al., 2022). In the analysis by Alcocer et al. (2022), ADI was positively correlated with biodiversity indices, particularly bird species richness. This corresponds to the theoretical understanding that a more speciose assemblage of vocalising fauna will produce a greater diversity of sounds across a range of frequency bins, increasing the evenness of occupancy of frequency bins and therefore the ADI (Villanueva-Rivera et al., 2011; Bradfer-Lawrence et al., 2019). However, given that individual studies in the Neotropics have found negative relationships between ADI and bird species richness (Jorge et al., 2018; Bradfer-Lawrence et al., 2020), region-specific studies testing this relationship may be valuable given this inter-study variability. While our study focusses on smaller-scale gradients within a land-use, another example from Malaysian Borneo found no relationship between bird species richness and ADI across a gradient of land-uses with varying levels of habitat degradation (Mitchell et al., 2020). This may be caused by the non-linear relationship between biodiversity and acoustic indices, where doubling the number of vocalising species does not double the value of an acoustic index (Bradfer-Lawrence et al., 2023). As a result, variation in acoustic indices may not reflect the full disparity in biodiversity between extremely species-rich and species-poor habitats such as primary lowland dipterocarp forest and oil palm plantations respectively (Edwards et al., 2014a), but may be more sensitive to smaller-scale intra-habitat variation in biodiversity. Further testing of the relationship between biodiversity and acoustic diversity within Bornean selectively logged forests will help clarify the accuracy of our conclusions.

While high ADI values can be driven by an empty soundscape across all frequency bands, this is unlikely to be the case in our study. Visualising spectrograms for a random sample of 30 recordings in ARBIMON (<https://arbimon.rfcx.org>) showed that our recordings were densely packed with distinct sonotypes across a wide range of frequencies from 0 to 24 kHz.

Similar to ADI, in Alcocer et al. (2022), NDSI was also found to positively correlate with bird species richness. While increased NDSI values could be derived without any increase in biological noise should anthropogenic noise have increased instead, this is highly unlikely in our study because there was no overall increase in human activity over time, with logging operations ceased in 2007. Furthermore, given the cessation of logging and the infrequent use of the nearby, dirt-based, former logging road, there will be a relatively low level of anthropogenic noise to affect the index, allowing us to attribute changes in NDSI to changes in biological noise.

Although our study focusses on capturing the dawn and dusk chorus of birds, other animals call at low frequencies close to or within the anthropogenic noise range of 1–2 kHz, such as frogs or gibbons (Sanchez-Herraiz et al., 1995; Clink et al., 2020). Hence, a decrease in noise in the 1–2 kHz range due to fewer frogs/gibbons could also explain the increase in NDSI with liana prevalence. However, as amphibians and mammals make relatively small contributions to the dawn and dusk chorus in Bornean forests compared to birds (Burivalova et al., 2022), and since links between the diversity of other non-avian taxa and acoustic indices remain little tested (Alcocer et al., 2022), we anticipate that changes in NDSI are driven by changes in frequency bands above 2 kHz.

4.2. Tree species richness and acoustic diversity

Increased tree species richness was associated with a decline in

soundscape diversity, as shown by the clear decrease in ADI across adult, juvenile, and overall tree species richness, and the slight decline in NDSI with juvenile tree species richness.

This decreased ADI and NDSI in areas of high tree species richness, which is associated with decreased bird species richness (Alcocer et al., 2022), could be attributed to the effects of fine-scale changes in habitat structure and post-logging shifts in community composition (Osazuwa-Peters et al., 2015; Senior et al., 2018; Hayward et al., 2021). Logged forest areas with higher tree species richness have a greater abundance of trees, indicating that the area was less intensely logged, with fewer, smaller logging gaps. This contrasts with areas of lower tree species richness that have fewer trees, indicating more intensely logged areas with more, larger logging gaps (Berry et al., 2008; Imai et al., 2012).

Consequently, while all logged forest areas will lose disturbance-sensitive forest fauna, such as forest-interior specialists (Edwards et al., 2014b), intensively logged areas low in tree species and with larger logging gaps could compensate for the loss in acoustic diversity of forest fauna with an invasion of edge-tolerant, generalist faunal species. This may include avian understorey insectivores such as *Orthotomus sericeus* utilising the pioneer saplings and lianas that proliferate in logging gaps, and avian nectarivores such as *Dicaeum trigonostigma* and *Arachnothera longirostra* exploiting the flowers of pioneering plants in regenerating logging gaps (Cleary et al., 2007; Costantini et al., 2016), which drives the increase in bird species richness associated with greater acoustic diversity (Alcocer et al., 2022). This is corroborated by a previous study in Malaysian Borneo, which found that more intensively logged forests had greater dung beetle and bird species richness and abundance than less intensively logged forests, but had an altered community composition (Edwards et al., 2011).

The greater acoustic diversity associated with more intensively logged forest occurs despite the likely comparable levels of sound attenuation across the entire logging concession. Intact patches of logged forest contain a high abundance of tree trunks and little leafy understorey vegetation. In contrast, more intensively logged areas of forest have a low abundance of tree trunks and a high density of leafy understorey vegetation (Heydon and Bulloh, 1997). As sound-absorbing foliage prevalent in intensively logged forest attenuates noises above 1 kHz to a similar degree or even better than sound-scattering tree trunks prevalent in lightly logged forest (Aylor, 1972; Gaudon et al., 2022), including biological noises such as passerine bird song as well as anthropogenic sounds (Sueur et al., 2014; Mikula et al., 2021), our results suggest that the increase in acoustic diversity in intensively logged forest surpasses the effects of sound attenuation.

4.3. Liana prevalence and acoustic diversity

Increased liana prevalence was associated with increased soundscape diversity and increased biophony. The increased ADI, which relates to increased bird species richness (Alcocer et al., 2022), associated with increased liana prevalence of trees, reflects the wide range of benefits that lianas provide for birds. Birds throughout the tropics feed on the fruit, nectar, and arthropods associated with lianas, and utilise lianas as nesting substrate and antipredator shelter (Schnitzer et al., 2014; Schnitzer et al., 2020). The increased liana prevalence widens the distribution of these resources in the local area, benefitting the vocal fauna in the area, such as birds, and increasing acoustic diversity.

The increase in NDSI, which relates to increased bird species richness and insect biophony (Bradfer-Lawrence et al., 2019; Alcocer et al., 2022), was found to be associated specifically with the liana prevalence of juvenile trees. This may be due to the value of lianas for understorey birds in particular. The young, small, trees comprising the understorey of lowland dipterocarp forests form a dense habitat (Newbery et al., 1999), similar to the dense liana tangles in the understorey created by lianas. This provides a suitable substrate for the shelter and movement of understorey birds evading predators, as well as supporting arthropod communities for understorey insectivores to feed on (Schnitzer et al.,

2014).

4.4. Liana load and acoustic diversity

ADI and ACI had largely flat relationships with liana load, which measures the amount of liana cover in trees with lianas already present, excluding trees without lianas from the calculation. In contrast, liana prevalence measures the proportion of trees with lianas present throughout the sample (Muller-Landau et al., 2019). Thus, our results suggest having many liana-infested adult trees increases soundscape diversity, but increasing the degree of liana infestation on liana-infested trees does not further increase soundscape diversity.

This may be caused by liana infestation suppressing the production of fruits by trees, which occur as lianas compete with trees for light and below-ground resources such as water (García León et al., 2017; Estrada-Villegas and Schnitzer, 2018). While simply having lianas present may provide additional food for bird species without substantially harming the fruit production of trees, further increases in the magnitude of liana infestation may correspond with further declines in fruit production from the tree, which may result in little overall change in food availability for birds.

4.5. Future directions

Our hypotheses are heavily linked to resource availability, with our initial expectations of the relationship between acoustic indices and tree species richness based on the diversity of resources provided by more tree species, and our explanation of the relationship between acoustic diversity and liana prevalence and load based on the overall level of resource provisioning, especially food. To further prove our conclusions, future studies of acoustic diversity could record the resources available in the vicinity, such as the number of fruiting trees nearby, the presence of liana fruits, or detecting folivory on liana leaves.

Tree species richness, liana prevalence, and liana load may be correlated, particularly with low tree species richness areas with large logging gaps potentially also being heavily liana infested, with high liana prevalence and liana load (Schnitzer and Bongers, 2011). Hence, it is difficult to determine whether low tree species richness or high liana prevalence alone are driving the change in acoustic diversity. Adding interactive terms between habitat variables to models would help account for this correlation, while including structural and directly logging-related variables such as canopy cover, local logging intensity, and distance to logged areas would further develop a better understanding of exactly what forest conditions help generate high acoustic diversity.

As guidelines for studying soundscapes continue to develop, low-frequency microphone self-noise is an issue to consider (Bradfer-Lawrence et al., 2023), with individual studies choosing whether or not to filter their recordings by restricting noise below a specific frequency (Hyland et al., 2023). However, proposed filters can affect a substantial proportion of the soundscape, with one example filter of 500 Hz removing half of one of the ten frequency bins in an ADI analysis (Villanueva-Rivera and Pijanowski, 2018; Bradfer-Lawrence et al., 2019; Hyland et al., 2023), and would affect any Bornean gibbon calls in our analysis (Clink et al., 2020).

4.6. Management implications and conclusions

Variation in acoustic diversity provides valuable insights into habitat management. Changes in acoustic diversity in locally heavily logged sites may show a greater invasion of edge-tolerant species, indicating the need for forest restoration schemes to enable disturbance-sensitive species such as forest-interior specialists to return to degraded forests and reclaim their acoustic niches by restoring forests to a primary forest-like state. Additionally, liana growth on juvenile trees should be encouraged, due to the increase in food availability and shelter

provisioning without drastically affecting the habitat structure of the understory.

Of particular note are the implications of our findings for liana cutting on adult trees, which is a commonly used silvicultural technique (Cerullo et al., 2019; Finlayson et al., 2022). Our findings further emphasise arguments for the need for liana cutting practices to retain a small number of climbers across a large area, rather than blanket cutting of all stems (Ansell et al., 2011; Cosset and Edwards, 2017). This is particularly important in restoration projects that seek to return post-logging forests towards their primary forest state. Given the sheer scale of logged tropical forests pan-tropically and their retention of high values for conservation values, the retention of some lianas in these timber production forests would also seem pertinent.

CRediT authorship contribution statement

Zachary Chu: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Cindy C.P. Cosset:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Catherine Finlayson:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Patrick G. Cannon:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Robert P. Freckleton:** Writing – review & editing, Methodology, Conceptualization. **Kalsum M. Yusah:** Conceptualization, Writing – review & editing. **David P. Edwards:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

The authors have no conflicts of interest to disclose.

Data availability

The data that has been used is confidential.

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Z.C., C.C.P.C, C.F, P.G.C, R.P.F, D.P.E. conceived the ideas and designed the methodology; C.F., P.G.C. collected the data; Z.C., C.C.P.C. analysed the data; ZC led the writing of the manuscript. K.M.Y contributed to the original proposal of the research and acted as a local collaborator for the project. All authors contributed critically to the drafts and gave final approval for publication. Financial support for C.F. and P.G.C. was provided by NERC (Ref: NE/L002450/1) and a PhD studentship from the Leverhulme Trust's Centre for Advanced Biological Modelling (CABM), and additional fieldwork funding was provided by the Rufford Foundation. We thank all staff at the Malua Research Station, and members of the South East Asia Rainforest Research Program (SEARRP) for logistical support; and Remmy Murinus, Udin Jaga, Bernadus Bala Ola, Jude, Ridly, Eglie, Japin Rasiun, Vendi Vens Aishiteru, Viddi Saidi, Mohammad Fauzi Osman, Gianluca Cerullo, Yvonne Koid Qian Qun, Emma Watson, Lingxin Tiyo, Cheok Tze Ning, Gillian Gabriel Gallus Gawis, Grace Juman, Rui Wong Yu, and Frolyin Felix for field assistance. We also extend our thanks to the Sabah Biodiversity Council, Yayasan Sabah, Sabah Forestry Department, Danum Valley Management Committee, the State Secretary, and Sabah Chief Minister's Department for site access and research permissions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110488>.

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