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RESEARCH ARTICLE

Active remote sensing for ecology and ecosystem conservation

Benign effects of logging on aerial insectivorous bats in Southeast Asia revealed by remote sensing technologies

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Abstract

1. Logging is the most widespread disturbance in tropical forests, altering ecological communities and functions. However, many species can persist in logged forests, particularly where disturbance is low. Despite a growing understanding of how logging affects wildlife, there remains little information for Southeast Asia's bats—in part due to major challenges in monitoring.
2. We integrated remote sensing data from passive acoustic bat detectors with LiDAR-derived measures of forest structure from a human-modified landscape in Sabah, Borneo. Our appraisal of logging effects benefitted from a semi-automated classifier of bat calls that vastly speeds up the analysis of acoustic recording data. We recorded 105,576 bat passes from 21 phonic groups across a habitat disturbance gradient, comprising old-growth forest, repeatedly logged forest and tree plantations.
3. We show that logging pressure (as depicted by changes to habitat quality, e.g. canopy height or shape) had negligible impact on the acoustic activity of bats. However, bat activity was higher in areas with a greater extent of high-biomass forest, as well as areas with greater topographical ruggedness. Logged forest supported higher levels of activity for several common bat phonic groups compared to old-growth forest. Across the landscape, plantations supported the lowest levels of bat activity, representing a threefold decrease compared to old-growth forest, and several species were not recorded in this habitat.
4. We found different call groups demonstrated different responses to forest disturbance. Sheath-tailed bats (*Emballonura* spp.) were active across all habitat types and were the most resilient to logging. Edge/open foragers were more prevalent in highly forested and topographically rugged areas. Horseshoe and leaf-nosed bats (flutter clutter foragers) demonstrated idiosyncratic responses to logging but were consistently absent from plantations.
5. *Synthesis and applications.* Logged forests can provide an important refuge for many common bat species in Southeast Asia, but do not capture the full breadth of forest-specialist species. Nevertheless, logged forests provide substantially

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better habitat for bats than tree plantations. While aerial insectivorous bats sampled via acoustic methods are poor indicators of forest disturbance overall, several species that respond predictably to logging could be targeted for biodiversity monitoring using acoustic and capture-based methods.

KEYWORDS

acoustic monitoring, biodiversity, Chiroptera, land-use change, remote sensing, Southeast Asia

INTRODUCTION

Tropical forests provide valuable habitat for some of the highest levels of biodiversity in the world, while contributing to the livelihoods of millions of people (Edwards, Tobias, et al., 2014; Meijaard et al., 2005; Putz et al., 2012). Logging is the most widespread disturbance in these globally important ecosystems (Blaser et al., 2011; Costantini et al., 2016). As tropical forests continue to be logged, and often converted for other land uses (primarily agriculture), it is important to understand how these developments could impact biodiversity.

Logged forests are increasingly recognised for their ecological vibrancy and habitat value for wildlife (Malhi et al., 2022). A pan-tropical meta-analysis comprising 48 studies showed lightly logged forests (e.g. $<10\text{m}^3\text{ha}^{-1}$) support more species of mammals, amphibians and invertebrates than old-growth forests (Burivalova et al., 2014). However, logging disturbance is not uniform. The extent of disturbance—and hence impact on biodiversity—depends on the number of logging cycles, logging intensity and extraction techniques (Bicknell et al., 2014). Light Detection and Ranging (LiDAR) remote sensing provides valuable data that can be used to study forest ecosystems and track the degradation caused by logging. Studies utilising LiDAR-derived data have shown how logging impacts the structure of tropical forest by reducing above-ground biomass and canopy height, while increasing canopy gap area (d'Oliveira et al., 2012; Kent et al., 2015; Rangel Pinagé et al., 2019). While logging can be much less detrimental to the ecosystem than the conversion of forest to other land uses (Malhi et al., 2022), it can still cause substantial population declines among specialist taxa (Burivalova et al., 2014; Thorn et al., 2018).

Despite an extensive literature on the effects of logging on biodiversity, there have been relatively few studies on tropical bats (Meyer et al., 2016). This is important because bats represent the second most diverse mammalian order, with over 1400 species globally (Simmons & Cirranello, 2021). In Borneo, bats represent 40% of the mammal diversity (Payne & Francis, 1998). Bats also provide valuable ecosystem services as seed dispersers, pollinators and suppressors of insect populations (Kunz et al., 2011), and are considered important bioindicators of ecosystem health (Jones, Bielby, et al., 2009; Jones, Jacobs, et al., 2009). Presley et al. (2008) outlined three potential demographic responses for bats in logged forests: (1) common species remain common but decrease in abundance; (2) common species decline in abundance, becoming rare in logged

forests; or (3) rare species are locally absent from logged forest. To date, logging-effect studies have found that bat responses to forest change are highly variable between different ensembles of species, particularly dietary guilds (Bicknell et al., 2015; Castro et al., 2021; Castro-Arellano et al., 2009; Clarke et al., 2005; Presley et al., 2008). Small, common phytophagous species (i.e. frugivorous and nectarivorous species) that rely on pioneering plants for foraging opportunities often respond positively to logging disturbance (Clarke et al., 2005; Presley et al., 2008). Larger, insectivorous or animalivorous phyllostomid species are more vulnerable to logging, as well as habitat disturbance more generally, and experience declines in diversity and abundance (Brändel et al., 2020; Clarke et al., 2005; Farneda et al., 2015).

The study of bats in tropical regions has been restricted by limitations in sampling techniques. To fully sample a community and thus avoid biases in taxonomic and ecological coverage, bat surveys require a combination of survey methods (Appel et al., 2021)—a challenge that is amplified in species diverse tropical regions. Live-capture methods (e.g. mist-netting or harp trapping) are most effective for sampling understorey bats, while acoustic methods tend to be better for monitoring those foraging in less cluttered environments, which rely on echolocation for navigation (e.g. above the canopy, in forest gaps). However, to date most logging-effect studies involving tropical bats have relied on live-capture techniques (Meyer et al., 2016). The majority have been undertaken in the American tropics where mist-netting is more effective at capturing a larger portion of the overall bat community (e.g. Bicknell et al., 2015; Castro et al., 2021; Castro-Arellano et al., 2009; Clarke et al., 2005). Far fewer studies have been undertaken in the Asian and African tropics as the bat fauna is dominated by aerial insectivorous species (i.e. those that use ultrasonic calls for orientation and foraging insect prey), which are poorly represented using nets (Castro & Michalski, 2014; Meyer et al., 2016). Capture-based studies in Southeast Asia have demonstrated that logging affects bat community composition, reduces species richness and causes abundance declines (Christine et al., 2013; Danielsen & Heegaard, 1995; Zubaid, 1993). The most comprehensive logging study involving bats in the region used harp traps to characterise bat assemblages across a habitat disturbance gradient, comparing old-growth forest to logged forest areas that had undergone various extraction cycles (Struebig et al., 2013). There was no discernible effect of logging on bat species richness, but species composition differed between old-growth and repeatedly logged forest sites—mirroring patterns observed in the

American tropics (Castro-Arellano et al., 2009; Clarke et al., 2005). Nevertheless, there remain large gaps in our understanding of bat responses to logging simply because many species are poorly represented in traps and nets. More research is needed to determine how different logging disturbances impact echolocating aerial insectivorous species in tropical regions (Meyer et al., 2016).

Here, we explore the effects of logging on bat activity and assemblage structure along a disturbance gradient from old-growth forest through forest logged multiple times and plantations. Our study is based in Sabah, Malaysian Borneo, in a landscape with a long legacy of logging (cumulative extraction rates between 150 and 179 m³ ha⁻¹; Struebig et al., 2013). As 72% of Borneo's bat species are echolocating insectivores (Phillipps & Phillipps, 2016), we use acoustic monitoring coupled with a new classification algorithm as an unintrusive alternative to traditional capture methods. We examine how aerial insectivorous bats respond to landscape changes using airborne LiDAR of forest metrics. Specifically, we sought to use remote sensing technologies to characterise (i) community composition and (ii) bat activity in each disturbance type, while also (iii) assessing possible relationships between habitat extent and quality and bat activity.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

Fieldwork was undertaken within the Kalabakan and Ulu Segama Forest Reserves in and around the Stability of Altered Forest Ecosystems Project (SAFE; www.safeproject.net; 443°N, 117°35'E) in Sabah, Malaysian Borneo (Figure 1). The landscape is characterised by lowland and hill dipterocarp forest, which was initially logged in the 1970s followed by two rotations in the late 1990s and early 2000s. The Ulu Segama forest was left to recover ('twice-logged forest'; 3 sampling blocks; LFE, LF2, LF3; see Table S1 in the Supporting Information). However, in Kalabakan, the forest was subject to salvage logging—the removal of all commercially valuable trees—with the exception of some forest patches set aside for scientific research and conservation purposes ('heavily logged forest'; 6 blocks; A–F). This highly disturbed forest has a high density of roads and skids, few emergent trees and is dominated by pioneer and invasive vegetation (Struebig et al., 2013). The landscape adjoins ca. 1 million ha of continuous forest, including old-growth forest in Maliau Basin Conservation Area ('Old Growth Forest'; 2 blocks; OG2, OG3). The forest is surrounded by a mosaic of tree plantations—mostly oil palm *Elaeis guineensis* Jacq., but also *Acacia mangium* Willd. planted around the year 2000 ('Tree Plantation'; 1 block; AC1).

2.2 | Defining the forest disturbance gradient

Logging activity varied substantially over the landscape. To characterise the resulting structural disturbance to forests, we utilised

airborne light detection and ranging (LiDAR) products to quantify the extent (i.e. habitat quantity) and structure (i.e. habitat quality) of forest, and hence define a disturbance gradient around our sampling sites. LiDAR metrics were produced in November 2014 from a Leica ALS50-II sensor (Jucker et al., 2018). The LiDAR metrics were processed from raw point clouds by Swinfield et al. (2020), who removed noise points, and delineated a digital terrain model from ground points. By subtracting the terrain model, point clouds were normalised and a pit-free canopy height model and plant area density profile was produced. Subsequent LiDAR metrics were then generated from these two models at 30 m resolution.

To delineate forest extent, we utilised information on above-ground vegetation biomass (AGB), which was calculated via a Borneo-specific model (see Jucker et al., 2018 for full details). We applied a threshold to the AGB maps above which cells were classified as Forest, and below which cells were classified as Non-Forest, to estimate *ForestExtent* around sample sites (i.e. a measure of habitat quantity; binary; Forest vs. Non-Forest). This definition of forest excluded areas of plantation and highly degraded young regenerating forest, and was defined as vegetation biomass $\geq 160 \text{ t ha}^{-1}$ (i.e. equivalent to above-ground carbon $\geq 75 \text{ t Cha}^{-1}$; Martin & Thomas, 2011) following the High Carbon Stock Approach (HCS; Rosoman et al., 2017). We chose a more conservative forest categorisation, as areas $< 160 \text{ t ha}^{-1}$ biomass were subject to salvage logging and therefore, more closely resemble areas of scrub.

We also extracted two measures of forest structure as proxies of habitat quality: mean canopy height (*CanopyHeight*; a continuous variable) and shape (*Shape*; continuous; morphological measurement of the ratio of canopy height to the maximum plant area density above ground), an area with a low *Shape* value would be characterised by a dense upper canopy with little understorey (Jucker et al., 2018; Swinfield et al., 2020). There is little research regarding bats and LiDAR metrics, but *Shape* is known to be an important predictor of other forest-dependent mammal species (Deere et al., 2020). In addition to *CanopyHeight*, average topographic ruggedness (*Topography*; continuous) has been shown to be an important predictor for bat occurrence in the project area (Mullin et al., 2020). Therefore, we also included *Topography* using 1 arc-second (ca. 30 m resolution) Shuttle Radar Topography Mission digital elevation model (Farr et al., 2007), converted using a topographic ruggedness index, according to Wilson et al. (2007).

2.3 | Acoustic sampling, processing and bat identification

Bats were recorded using SongMeter-2 automated recorders (Wildlife Acoustics, Maynard, USA) fitted with an omnidirectional ultrasonic SMX-US microphone between April and May 2011 and April and June 2012 (see Supporting Information Table S1). Recorders were stationed across 47 sample points at 1.5–2.0 m height above ground (one per site) and set to record nightly bat activity (18:15–06:15) between one and three consecutive nights.

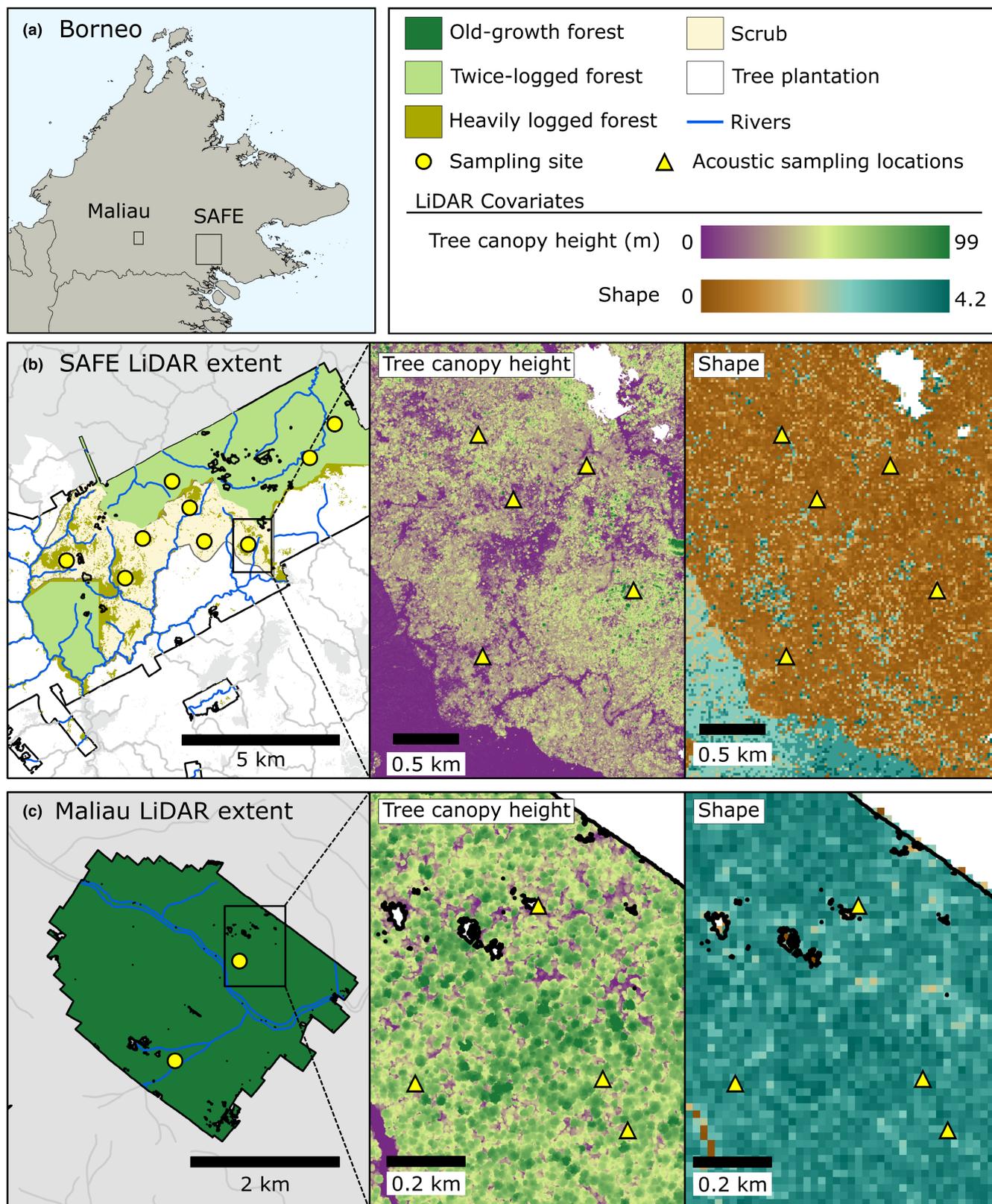


FIGURE 1 Map of the Stability of Altered Forest Ecosystem Project (SAFE) and sampling sites in Maliau Basin, Malaysian Borneo. (a) Location of SAFE and Maliau in Malaysian Borneo, (b) sample blocks across SAFE and examples of two LiDAR variables across multiple survey sites and (c) the two sampling blocks in Maliau with the corresponding LiDAR coverage.

These sample points were designed to target the mid-storey, rather than the cluttered understorey. Each recorder was set to record by triggers of high-frequency sounds appropriate for

echolocating bats in the region (sampling rate 384 kHz, 16-bit resolution; high pass filter 12 kHz (fs/32); trigger level 18 signal to noise ratio; gain 12 dB).

All preprocessing of recordings was undertaken using Kaleidoscope v.5.1.9 g software (Wildlife Acoustics, 2019-05-30) following procedures outlined in Yoh et al. (2022). Files were divided into 5-s long sequences with a minimum of two individual pulses to define a bat pass as a unit of activity, for example, the number of events per time interval (Torrent et al., 2018). While this does not necessarily provide a measure of bat abundance (as it does not determine the number of individual bats), it provides a discrete count of activity which can be compared across sites (Plan, 2014). Calls were automatically assigned to call type, phonic group (a group of species with indistinguishable calls; López-Baucells et al., 2021) or species, and any calls that failed to meet specific confidence thresholds were manually verified (Yoh et al., 2022). Through this process, calls were first identified to one of four call types (see Supporting Information Figure 1): frequency modulated (hereafter referred to as 'active clutter foragers'; FM), constant frequency ('flutter clutter foragers'; CF), frequency-modulated quasi constant frequency ('edge/open foragers'; FMqCF) and quasi-constant frequency ('*Emballonura alecto/monticola*'; QCF; Simmons & Cirranello, 2021). Those identified as edge/open foragers were automatically classified further to one of sixphonic groups. Calls classified as flutter clutter foragers were further differentiated to 17species or phonic groups.

The classifier identified 158,563 files containing bat passes. Of these files, 71,482 included bat passes that required manual verification. All bat passes that did not meet the specified confidence thresholds (26,351 of 71,482), excluding those for active clutter foragers, were manually identified in Kaleidoscope Viewer by a single researcher (NY) to reduce potential bias. Active clutter foragers represented the largest proportion of files to be manually verified (45,131 files). We checked 50% of active clutter forager bat passes and found this call type was easily mistaken for environmental noise at low confidence and fewer than 1% contained true bat passes. Therefore, we discarded active clutter forager calls that did not meet the confidence threshold. Activity (the sum of bat passes per phonic group/species) was averaged by sampling effort (number of nights per site).

2.4 | Statistical analysis

2.4.1 | Bat community composition and habitat association

We used non-metric multidimensional scaling (NMDS) ordinations based on Bray–Curtis dissimilarity coefficients of \log_{10} -transformed bat activity data to determine whether the structure of bat communities reflected the various habitat type or the disturbance gradient. Data were log-transformed to prevent skew from more active species. One phonic group (*Hipposideros cineraceus/dyacorum*) was removed from the analysis as it was only recorded on a single occasion. Ordinations were based on 9999 permutations in the R package VEGAN (Oksanen et al., 2020) specifying two dimensions. We used

PERMANOVA from the package RVAIDEMEMOIRE (Hervé, 2022) to test for differences in bat community composition between habitats.

To determine if there were differences in bat activity between forest sites and tree plantations, we first compared activity between habitats using Kruskal–Wallis tests followed by Dunn post hoc tests (Dinno, 2015). Tests were implemented separately for each call type and also for overall levels of bat activity, and all *p*-values were adjusted using the Benjamini–Hochberg method to account for the risk of false positives in call detection (Haynes, 2013).

To determine if there was a relationship between habitat covariates and bat activity, we constructed Generalised Additive Models for Location, Scale and Shape (GAMLSS)—appropriate for the Weibull distribution of the data (goodness-of-fit test for the Weibull distribution correlation=0.984, *p*=0.069; Stasinopoulos et al., 2020)—using the 'GAMLSS' package. We also chose GAMLSS over other models as we expected the response variable to exhibit a nonlinear relationship in response to predictor variables (Stasinopoulos et al., 2020). LiDAR datasets were not available for tree plantation sites and so were omitted from these analyses. All covariates (*ForestExtent*, *CanopyHeight*, *Shape* and *Topography*) were extracted from a 100 m circular buffer around each site location. Habitat type (*HabitatType*; categorical; three levels) was also included to assess if there were differences in activity not explained by the other measures of habitat quality or extent. We centred and scaled continuous covariates to one unit standard deviation and assessed for collinearity using Pearson correlation coefficient. This revealed a high level of correlation among covariates (Pearson $r = \geq 0.7$), and we therefore excluded highly correlated covariates from appearing in the same model. We specified GAMLSS with an effect parameterisation, specifying old-growth forest as the fixed intercept and reference class from which to compare twice-logged forest and heavily logged forest. We fitted separate global models for total bat activity, call type and the four dominant phonic types. We then used the dredge function from the MUMIN package to fit all possible model combinations. After inspecting the final models for goodness of fit using residual diagnostics (Burnham & Anderson, 2002), we then model-averaged coefficient values across the best performing models ($\Delta AIC < 2$; Supporting Information Table S2). All analysis was performed using R version 4.1.1 (2021-08-10) statistical software (R Core Team, 2017). Ethical approval for this research was granted by the School of Anthropology and Conservation Research Ethics Committee, University of Kent (2011). The research was carried out under permit number UPE: 40/200/19/2723, granted by the Economic Planning Unit of the Malaysian Government and the Sabah Biodiversity Council under Matthew J. Struebig.

3 | RESULTS

From our data of remotely sensed bat activity, we identified 105,576 bat passes from 21 phonic types across the landscape. More than 76%

of all bat activity was represented by five phonic groups: *Emballonura alecto/monticola* (18.6% of calls), Sonotype 6 (17.3%), *Rhinolophus sedulus* (15.1%), Sonotype 5 (13.2%) and *Rhinolophus trifolius* (12.2%; Table 1). Two phonic groups (*H. cineraceus/dyacorum* and *Rhinolophus philippinensis*) were only recorded in heavily logged forest, once and on three occasions, respectively. For activity, the composition of the top five phonic groups was similar across habitats, consisting mostly of common generalist species. Sonotype 6 and *E. alecto/monticola* were among the top five most active phonic groups across all habitat types (Table 1).

3.1 | Bat community composition and association with habitats

The NMDS ordination of bat activity revealed substantial variation in taxonomic composition across the landscape and overlap between

the various habitat types (Figure 2). The greatest variation occurred among twice-logged sites and the least among tree plantation sites. Across the landscape, there was a significant difference in bat community composition between habitats (PERMANOVA: $R^2=0.17$, $p=0.003$), driven by differences between the heavily logged forest and the twice-logged forest (pairwise comparisons $p=0.02$).

We found significant differences in bat activity between habitats, for total activity ($H(3)=10.126$, $p=0.018$) and for each call type (active clutter foragers— $H(3)=25.483$, $p<0.001$; flutter clutter foragers— $H(3)=45.251$, $p<0.001$; edge/open foragers— $H(3)=15.763$, $p=0.001$; *Emballonura* spp. activity— $H(3)=10.039$, $p=0.018$; Figure 3). Activity for all call types was lower in the plantations compared to forest (Supporting Information Table S3 and Figure 3). GAMLSS analyses revealed that bat activity levels were similar among the three forest types (old-growth forest, twice-logged forest, heavily logged forest; Figures 3 and 4). Overall bat activity was positively

TABLE 1 Total bat passes per sonotype or species in each habitat along the disturbance gradient. For each habitat type, relative bat passes (total bat passes/total nights surveyed) are provided in brackets for comparison. Detection range represents the distance at which a bat pass is likely to be detected and is represented by three classes, Short (1–3 m), Intermediate (3–10 m) or Long (10–20 m). Detection range is determined by call shape, call frequency and call intensity.

	Detection range	Bat activity			
		Old-growth forest	Twice-logged forest	Heavily logged forest	Tree plantation
Total nights surveyed		23	36	73	12
Total detector sites		8	12	23	4
Active clutter foragers (FM) (e.g. <i>Kerivoula</i> spp.)	Short	628 (27.3)	1988 (55.2)	2556 (35.0)	49 (4.1)
Flutter clutter bats (CF)					
<i>Hipposideros cineraceus/dyacorum</i>	Short	0	0	1 (<0.1)	0
<i>Hipposideros cervinus</i>	Short	5 (0.2)	54 (1.5)	9 (0.1)	22 (1.8)
<i>Hipposideros diadema</i>	Short	248 (10.8)	36 (1.0)	33 (0.5)	7 (0.6)
<i>Hipposideros galeritus</i>	Short	37 (1.6)	162 (4.5)	36 (0.5)	5 (0.4)
<i>Hipposideros ridleyi</i>	Intermediate	3 (0.1)	3 (0.1)	0	0
<i>Rhinolophus acuminatus</i>	Intermediate	229 (10.0)	165 (4.6)	262 (3.6)	91 (7.6)
<i>Rhinolophus affinis</i>	Intermediate	0	0	2 (<0.1)	2 (0.2)
<i>Rhinolophus borneensis</i>	Intermediate	68 (3.0)	822 (22.8)	143 (2.0)	1 (0.1)
<i>Rhinolophus creaghi</i>	Intermediate	1 (<0.1)	443 (12.3)	4 (0.1)	8 (0.1)
<i>Rhinolophus luctus</i>	Intermediate	503 (21.9)	80 (2.2)	181 (2.5)	5 (0.4)
<i>Rhinolophus philippinensis</i>	Intermediate	0	0	3 (<0.1)	0
<i>Rhinolophus sedulus</i>	Intermediate	196 (8.5)	9558 (265.5)	6069 (83.1)	86 (7.2)
<i>Rhinolophus trifolius</i>	Intermediate	1703 (74.0)	1611 (44.8)	9542 (130.7)	42 (3.5)
Edge/open foragers (FMqCF)					
Sonotype 1	Intermediate	10 (0.4)	39 (1.1)	271 (3.7)	95 (7.9)
Sonotype 2 (e.g. <i>Hesperoptenus blanfordi</i>)	Intermediate	241 (10.5)	6151 (170.9)	980 (1.3)	108 (9.0)
Sonotype 3 (e.g. <i>Pipistrellus stenopterus</i>)	Long	2373 (103.2)	504 (14.0)	2053 (28.1)	100 (8.3)
Sonotype 4 (e.g. <i>Glischropus tylopus</i>)	Intermediate	770 (3.3)	302 (8.9)	499 (6.8)	534 (44.5)
Sonotype 5 (e.g. <i>Myotis muricola</i>)	Intermediate	3911 (170.0)	2883 (80.1)	6180 (84.7)	961 (80.1)
Sonotype 6 (e.g. <i>Chaerephon plicatus</i>)	Long	9249 (402.1)	775 (21.5)	7019 (96.2)	1256 (104.7)
<i>Emballonura alecto/monticola</i> (QCF)	Intermediate	2590 (112.6)	4634 (128.7)	12,410 (170.0)	463 (38.6)

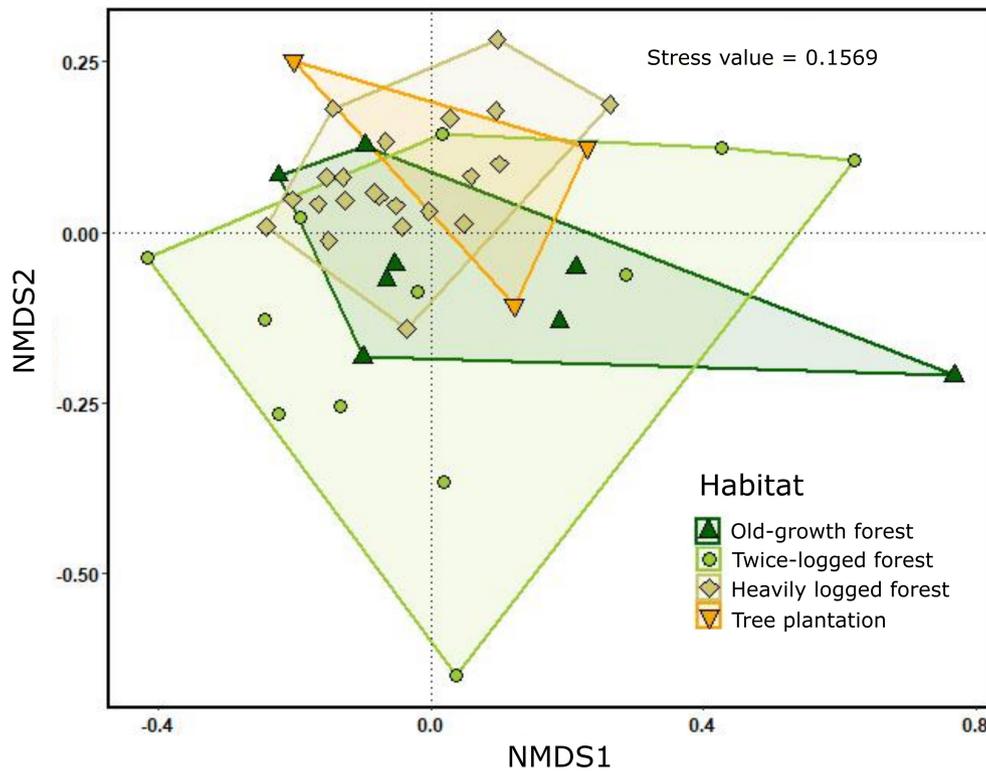


FIGURE 2 Nonmetric multi-dimensional scaling showing the (dis)similarities between bat communities across the four habitat types.

associated with *ForestExtent* but was not associated with any measure of habitat quality or *Topography* (Figure 4). The activity of edge/open foragers was also positively associated with *ForestExtent* as well as *Topography*. Both edge/open foragers and active clutter foragers were positively associated with *Topography*. Active clutter foragers were the only call type to show a significant difference between habitat types, and neither flutter clutter forager activity nor *Emballonura* spp. activity exhibited a response to any habitat covariate. We found differences between the responses of individual phonic groups and these did not reflect responses at the call type level (Figure 5).

4 | DISCUSSION

Pairing a semi-automated classifier of bat calls with LiDAR-derived forest structural metrics, we found little evidence that logging disturbance negatively affected the composition of aerial insectivorous bat communities. Although we observed some differences in the bat community between twice-logged forest and heavily logged forest, neither of these disturbed forests differed significantly from old-growth forest in terms of bat composition. Although bats persisted in highly disturbed logged forests, bat activity declined in tree plantations and several species/phonic groups were not recorded in this habitat. These findings support previous studies of other vertebrate groups that show logged forests support many forest species compared to tree plantations, such as oil palm and acacia (Edwards, Magrach, et al., 2014; Gibson et al., 2011). Species most

adversely affected by logging tend to have narrow niche breadth and are adapted to the stable conditions usually found in the forest interior—as exemplified for animalivorous bats (Presley et al., 2008) and understorey birds (Hamer et al., 2014). These include species dependent on old-growth trees for feeding or nesting (including cavity-nesting birds and saproxylic insects), large-bodied/long-lived species with low fecundity, insectivorous/animalivorous species or target species for poachers (Bicknell & Peres, 2010; Costantini et al., 2016; Edwards, Magrach, et al., 2014; Thorn et al., 2018).

Logging pressure (e.g. as reflected by timber extraction rate) is an important determinant of logging impacts on biodiversity (Bicknell et al., 2014; Burivalova et al., 2014). Although high numbers of species are reported from twice-logged tropical forests (Putz et al., 2012), further logging deteriorates habitat conditions to such an extent that forest-specialist species decline and taxa associated with forest edges or gaps proliferate to take their place (Cleary et al., 2007; Edwards, Magrach, et al., 2014). In contrast, we found no relationship between the forest quality (*Shape*, *CanopyHeight*) and bat activity, suggesting that the logging pressure in our study system did not reduce habitat value, at least for common bat phonic groups. Unlike previous studies of riparian forest remnants in the landscape (Mullin et al., 2020), we found habitat extent was more important than measures of habitat quality for determining bat activity. However, we utilised a more conservative measure of forest extent based on LiDAR data that represents high-quality forest and as such, excludes young regenerating forests in the landscape. Therefore, our findings suggest forest management should aim to maintain forest with above-ground carbon ≥ 75 tCha⁻¹ to ensure sufficient

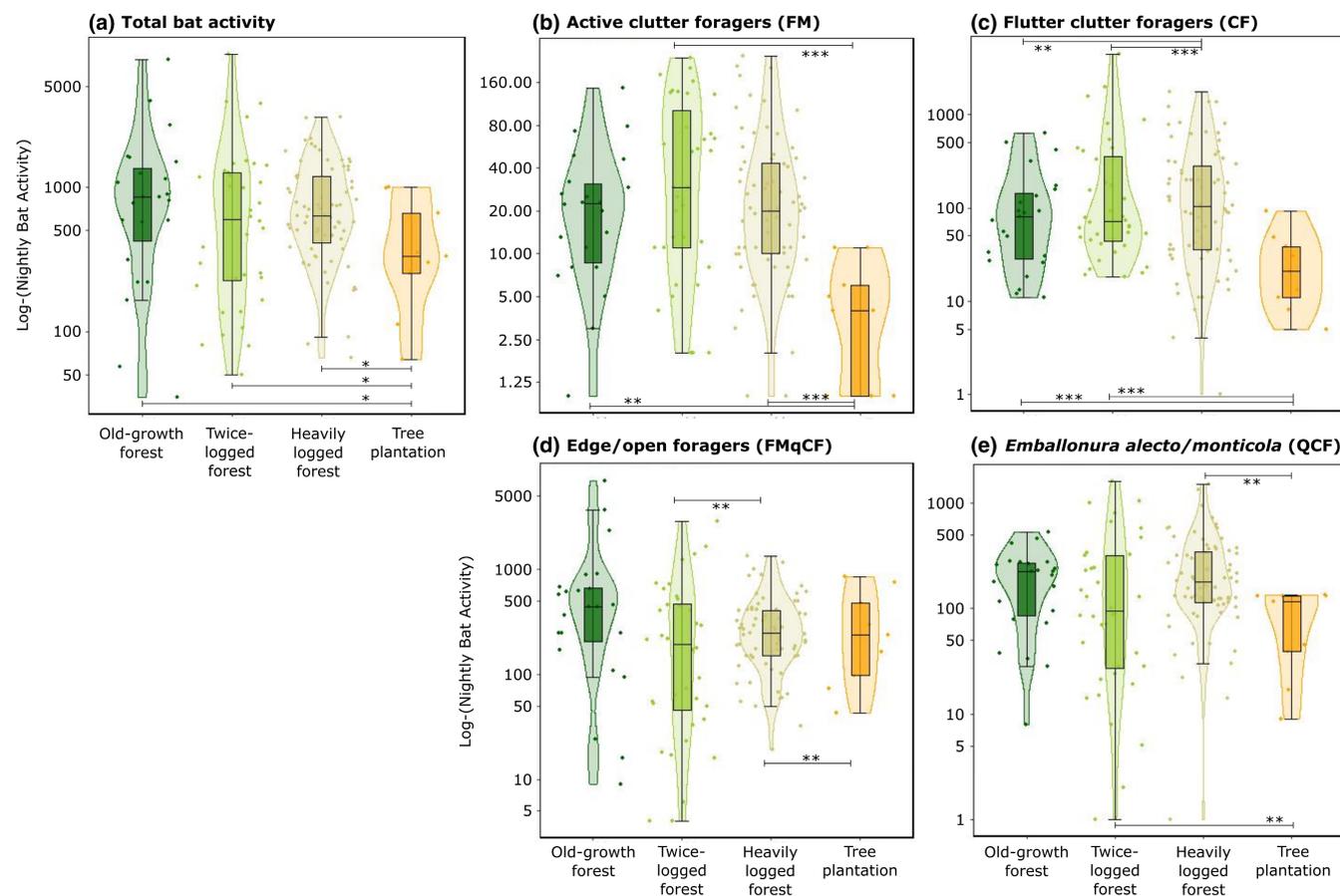


FIGURE 3 A comparison of overall nightly bat activity across each of the four habitat types. Each point represents an individual recording location. (a) Total bat activity, (b) active clutter forager activity, (b) flutter clutter forager activity, (c) edge/open forager activity and (d) *Emballonura alecto/monticola* activity. Horizontal lines are median values, the boxes are between the 25th and 75th percentiles and the whiskers represent the interquartile range. Statistical significance of the comparisons is according to the Dunn test results * < 0.05, ** < 0.01, *** < 0.001.

habitat quality to support Southeast Asian bat communities. More fine-scale research is needed to better assess the relationship between changes to understorey structure and bat activity, particularly for forest specialists.

Species adapted to foraging in more open spaces, such as sheath-tailed bats (*E. alecto/monticola*), were the most resilient to disturbance, as reflected by comparable levels of activity within plantations and old-growth forest. Edge/open foragers also maintained similar activity levels in plantations, but were positively associated with the availability of good quality habitat, as determined by greater forest extent. Bats of all other call types declined substantially in tree plantations or were not detected at all in this habitat. We observed one of the demographic responses outlined by Presley et al. (2008)—the decline of rare species in logged forests. For example, *H. ridleyi* (a forest specialist species classified as Vulnerable by the IUCN, 2022) was absent from both the heavily logged forest and tree plantations, though persisted in twice-logged forest. However, we also observed positive demographic responses to logging. Several common phonic groups were recorded much more frequently and at higher activity levels in logged forest compared to old growth, in line with findings from peninsular Malaysia (Christine et al., 2013). Positive responses

to logging have also been observed for terrestrial mammals in the same study system (Wearn et al., 2017). We, therefore, suggest an additional demographic response—namely that common species remain common and increase in abundance.

Overall levels of bat activity provided a poor representation of how each call type and taxon responded to habitat disturbance. Edge/open forager activity was dominated by two phonic groups (Sonotype 5 and 6) which together constitute 67% of activity for this call type. Overall, edge/open forager activity was positively associated with increased habitat extent and topography ruggedness. However, it is unclear which phonic group drives the relationship at the call type level as neither phonic group exhibited a relationship between habitat extent and topography. Different flutter clutter forager species indicated different susceptibility to logging disturbance, as indicated by changes in their activity. This aligns with the known ecology of this group. Unlike edge/open foragers, flutter clutter foragers include forest specialist taxa, as well as species adapted to more disturbed areas, such as forest edge/gaps (Furey & Racey, 2016; Kingston, 2013; Table S4). Therefore, it is to be expected that there would be more heterogeneity between the responses of species in this call type compared to more ecologically similar species

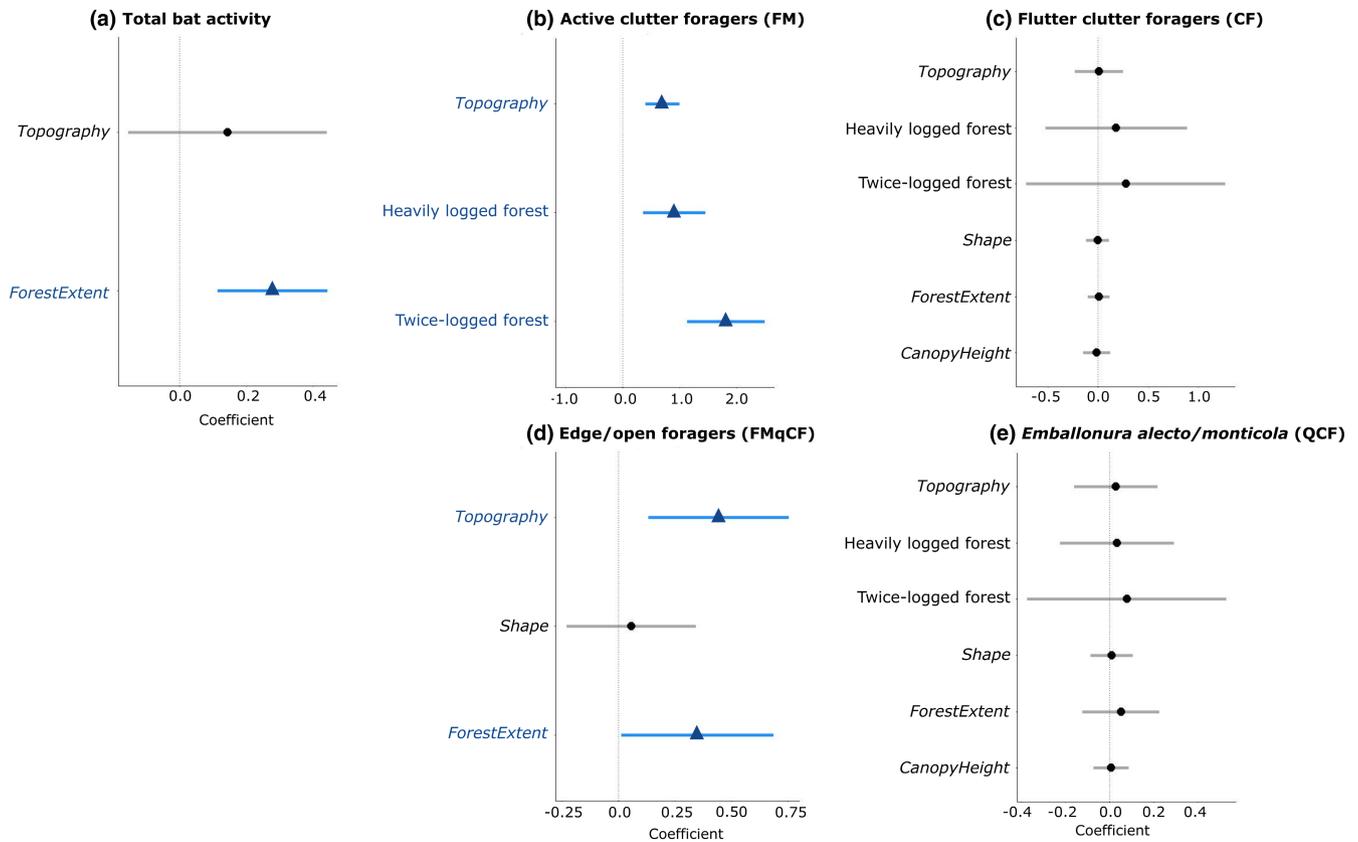


FIGURE 4 Caterpillar plots from the General Additive Models for location, shape and space (including 95% confidence interval) for each call type. (a) Total activity, (b) active clutter forager activity, (c) flutter clutter forager activity, (d) edge/open forager activity and (e) *Emballonura alecto/monticola* activity. Significant associations are shown with a triangle point and highlighted in blue. Models are listed in Supporting Information Table S2.

in the other call types. *Rhinolophus sedulus* and *R. trivoliatus* collectively represented 89% of activity for this call type and exhibited contrasting responses to logging, consistent with those observed by Struebig et al. (2013). Repeated logging cycles reduce roosting opportunities for some forest species, such as woodpeckers, squirrels and bats. As such, forest-roosting species are considered to be more susceptible to logging disturbance than those that dwell elsewhere (Costantini et al., 2016; Struebig et al., 2013). When interpreting the results of our study, it is important to consider that there are several factors that can influence the likelihood of detecting species acoustically. These include differences in environmental conditions (e.g. structural clutter, microclimate) and call characteristics between species (e.g. call intensity, peak frequency; Russo et al., 2018; Table 1). Therefore, the relative sampling area will differ between sites and species. Low-intensity, high-frequency calls typical of active clutter foragers (e.g. woolly bats *Kerivoula* spp.) remain difficult to detect and record, particularly in complex, understory vegetation (Kingston, 2013; Russo et al., 2018). Considering only acoustic surveys, we found that logging appeared to positively influence the activity of forest-specialist, active clutter foragers. However, capture studies using harp traps demonstrate that these same taxa are highly sensitive to logging and forest fragmentation (Kingston et al., 2003; Struebig et al., 2008, 2013). We are therefore mindful that our

study alone does not fully capture the responses of all bats in the study system to habitat change. However, we demonstrate acoustic monitoring and semi-automated classification of calls to be effective at surveying a large subset of the overall bat community that cannot be reliably sampled with capture methods, but ultimately data from both trapping and acoustic monitoring should be used to account for biases across survey methods.

Logging intensity across our logged sites was highly variable (e.g. the cumulative extraction rate for the twice logged forest = $150\text{m}^3\text{ha}^{-1}$ and heavily logged forest = $179\text{m}^3\text{ha}^{-1}$; Struebig et al., 2013). However, these rates are very high compared to those found in logging impact studies from the African and American tropics (Burivalova et al., 2014). Therefore, both logging categories represent high-intensity logging regimes. Further research could investigate the potential for conservation initiatives, such as reduced-impact logging, to benefit forest-specialist bats in these landscapes. While there were 2–3 years between the acoustic sampling (2011/2012) and the LiDAR coverage (2014), there was no logging disturbance in the forests in that period. So, while we cannot rule out other potential influences to the forest or bat community in that interval (e.g. inter-annual climatic variation), we assume that structural changes (e.g. through plant growth etc.) were experienced at broadly consistent rates across the landscape. Even if this

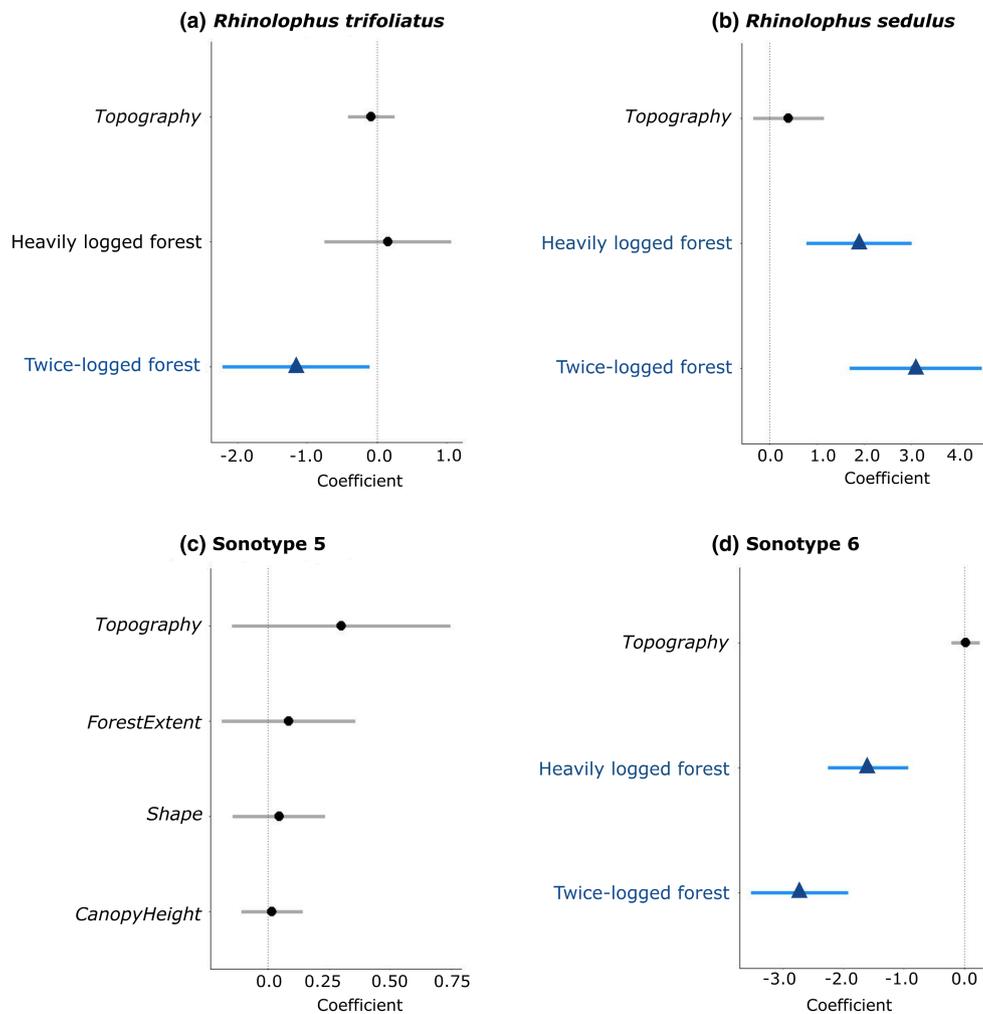


FIGURE 5 Caterpillar plots from the general additive models for location, shape and space (including 95% confidence interval) for the dominant phonic group/species (*Emballonura* spp. are represented in Figure 5). (a) *Rhinolophus trifoliatus*, (b) *Rhinolophus sedulus*, (c) Sonotype 5, and (d) Sonotype 6. Significant associations are highlighted in blue. Models are listed in Supporting Information Table S2.

assumption was not fully met, we should expect the potential influence of forest changes due to logging to be greater than any changes over 2–3 years of forest recovery. Nevertheless, future survey efforts could use time-series analyses to investigate how forest recovery over time impacts bat activity and species' long-term persistence following logging disturbance.

5 | CONCLUSIONS

Logging continues to be the most extensive disturbance affecting tropical forests worldwide. Using remote sensing technologies, we show that even heavily logged forest areas can support comparable levels of Southeast Asian bat activity to old-growth forest. However, old-growth forest remains an important habitat for several rarer, forest-specialist species, which do not persist in disturbed habitats. Neighbouring old-growth forests are also likely to provide resources to more mobile species, for example, roost sites, that would otherwise be absent from logging concessions. Therefore, our results suggest

heterogeneity is key to maintaining bat diversity in human-modified tropical landscapes. We demonstrate how acoustic monitoring methods can be used to incorporate aerial insectivores into bat biodiversity studies and help identify species for monitoring. Combining acoustic data with live-trapping information could help better evaluate the more subtle, species-specific impacts of logging disturbance.

AUTHOR CONTRIBUTIONS

Matthew J. Struebig, Henry Bernard and Jake E. Bicknell conceived and designed the study. Matthew J. Struebig led the fieldwork. Natalie Yoh processed the bat calls. Natalie Yoh, Dave J. I. Seaman and Nicolas J. Deere performed the statistical analysis. Natalie Yoh, Jake E. Bicknell and Matthew J. Struebig wrote the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Matthew J. Struebig is an Associate Editor of the Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Bat count data are available from Zenodo <https://doi.org/10.5281/zenodo.7740421> (Yoh et al., 2023). LiDAR structural data are available at <https://doi.org/10.5281/zenodo.4020697> (Swinfield et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Site descriptions for each of the acoustic survey points in Sabah, Borneo. Block refers to the Stability of Altered Forest Ecosystem's (SAFE) site codes during 2011–2012.

Table S2. Candidate models used to characterise bat activity at the 100 m scale. Shading represents the top models.

Table S3. Table outlining the results of the post-hoc Dunn test comparing bat activity between the four habitat types for overall activity and for each of the call types. Significance * <0.05 , ** <0.01 , *** <0.001 .

Table S4. Table outlining the results of the similarity percentages in bat activity between the four habitat types. Significance * <0.05 , ** <0.01 , *** <0.001 .

Table S5. Morphological and ecological characteristics of species known to be included in the Borneo Bat Classifier used for processing the acoustic data. Adult body mass and adult forearm represent averages across sexes. Roost specialism^{C,D} includes three classes (forest, flexible, cave). Vertical stratification^D includes two classes (U–understorey; C–canopy).

Figure S1. Example sonograms for each of the four call types used in the study. Call amplitude has not been standardized between species and therefore this image is for illustrative purposes only and should not be used for call identification.

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