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Hazard, Quentin C.K., Froidevaux, Jérémy S.P., Yoh, Natalie, Moore, Jonathan, Senawi, Juliana, Gibson, Luke and Palmeirim, Ana Filipa (2023) *Foraging guild modulates insectivorous bat responses to habitat loss and insular fragmentation in peninsular Malaysia*. *Biological Conservation*, 281 . ISSN 0006-3207.

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# Foraging guild modulates insectivorous bat responses to habitat loss and insular fragmentation in peninsular Malaysia<sup>1</sup>

**Keywords:** Passive acoustic monitoring; Habitat fragmentation; Hydroelectric dams; Island Biogeography Theory; Land-bridge islands; Tropical forests

## Highlights:

- We assessed the diversity of insectivorous bats in dam-induced islands in Malaysia
- Species persistence was modulated by island size and habitat quality
- Forest foragers activity decreased with island isolation and degradation
- Edge foragers benefited from fragmentation, increasing in activity on smaller islands
- By creating multiple small, isolated, degraded islands, damming erodes bat diversity

## Abstract

Despite mounting evidence on the ecological impacts of damming for biodiversity, little is known regarding its consequences in the hyper-diverse Southeast Asian tropical forests. Here we assess the effects of habitat loss and fragmentation on the diversity and activity of insectivorous bats within the hydroelectric Kenyir Lake in peninsular Malaysia. We surveyed bat assemblages on 26 islands and two mainland continuous forest sites using passive acoustic monitoring. Echolocation calls were classified into sonotypes, each corresponding to either one or multiple species, and grouped into foraging guilds. We then examined bat overall assemblage (sonotype richness, activity, and composition), guild- and sonotype-specific activity. From 9360 hours of recordings, we identified 16 bat sonotypes, including 10 forest (2854 bat passes), three edge (13 703) and three open-space foragers (3651). Sonotype richness increased towards denser canopy structures, as indicated by higher Normalized Difference Vegetation Index values (NDVI). Sonotype composition varied across the gradient of forest area. Forest foragers were positively affected by NDVI and negatively affected by distance to the closest neighbour, whereas edge foragers'

## Abbreviations:

AICc: Akaike Information Criterion corrected for sample size  
 CF: Constant Frequency  
 CI: Confidence Interval  
 FM: Frequency Modulated  
 FMqCF: Frequency Modulated quasi-Constant Frequency  
 LF: Low Frequency  
 LM: Linear Model  
 NDVI: Normalised Difference Vegetation Index  
 NMDS: Non-Metric Multi-Dimensional Scaling  
 QCF: Quasi-constant Frequency

activity increased in smaller islands. Of the six sonotypes analysed, the activity of one forest sonotype increased with forest area, while that of one edge sonotype decreased. Ensuring habitat quality within insular forest remnants, in addition to their functional connectivity, maximises bat diversity, including the persistence of forest foraging species. Future hydropower development should therefore avoid the creation of a myriad of small, isolated, and habitat-degraded islands further characterised by altered levels of bat diversity and guild-level activity.

## 1. Introduction

Humanity currently faces a need to reconcile human population growth, increasing energy demands, and the decarbonization of that energy. In this context, hydropower is an increasingly appealing option, representing 73% of the renewable energy produced in the world (The World Bank, 2016). Yet, river damming is also a major driver of habitat loss and insular fragmentation across lowland forests (Gibson et al., 2017). By flooding the lowland areas, dam construction often creates insular forest fragments matching the previous hilltops that become isolated within an inhospitable aquatic matrix (Jones et al., 2016). Although recent efforts have been made to understand the ecological consequences of hydropower (Palmeirim et al., 2022; Terborgh et al., 2009), few studies have targeted the Southeast Asian forests (Jones et al., 2016). Such understanding is therefore considered a priority for biodiversity conservation in the region (Coleman et al., 2019).

Species diversity persisting in insular forest fragments is typically affected by fragment size and isolation, which limit species population size and colonisation rates respectively (McArthur & Wilson, 1967). Edge effects arising from insularisation, namely increased exposure to windthrows and floristic transition towards light-wooded fast-growing pioneer assemblages, affect habitat quality *within* insular fragments, thereby influencing remaining species diversity (Benchimol & Peres, 2015a). Likewise, further human disturbances, including logging and fires, affect forest structure and thus habitat quality. Altogether, habitat quality can be assessed using the Normalized Difference Vegetation Index (NDVI), distinguishing between forest with denser canopy (higher NDVI values) and sparser canopy (lower NDVI values) (Tovar, 2011).

Species responses to habitat loss and insular fragmentation may further vary between (Palmeirim et al., 2022) and within biological groups (Brändel et al., 2020; Meyer & Kalko, 2008), as influenced by particular species traits (Meyer et al., 2008; Palmeirim et al., 2021). For instance, the persistence of mid-sized mammal species on islands can be related to their swimming capacity (Benchimol & Peres, 2015b), while that of lizard species is dictated by their thermoregulation mode (Palmeirim et al., 2017). Yet, even persisting taxa show general decreases in abundance in insular forest fragments compared to surrounding mainland (e.g., bats: Gorresen & Willig (2004), birds: Yong et al. (2011), and terrestrial and arboreal mammals: Benchimol & Peres (2021)). As such, while certain species able to use non-forest habitats might become overabundant (Moore et al., 2022), forest-dependent species become rarer or locally extinct (Palmeirim et al., 2018). Understanding the drivers of species response to forest insularisation – considering both environmental and intrinsic species characteristics – allows more efficient management actions to be proposed, which is not trivial given the expansion of the hydropower sector across lowland tropical forests (Couto & Olden, 2018).

Although habitat loss and insular fragmentation have been reported as important drivers of bat species' local extinction in the Neotropics (Colombo et al., 2022; Meyer & Kalko, 2008), little is known for Asia. In fact, the only study targeting such effects on insectivorous bats in this region highlighted the importance of island area especially for forest-dependent species in East China (López-Bosch et al., 2021). In addition, in a non-insular matrix setting in peninsular Malaysia, the diversity of insectivorous bats was impacted by forest area, with species-specific responses being modulated by their habitat affinity (Struebig et al., 2008). Insectivorous bats emit echolocation calls to navigate their surroundings and locate food (Schnitzler et al., 2003). The characteristics of the calls produced, e.g., call shape, are adapted to a species' foraging preferences (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). For example, species adapted to foraging in the forest interior (forest foragers) use long constant frequency (CF) calls or very short, broadband, frequency modulated (FM) calls, adapted to particularly cluttered environments. Edge foragers use quasi-constant frequency (QCF) calls, or medium frequency calls (FMqCF) composed of an FM component followed by a short and quasi constant element (qCF), allowing them to locate and navigate between background features (medium frequency FM component), and to locate prey at an intermediate distance (qCF component). Open-space foragers use low frequency (LF) (<30 kHz) FMqCF calls with a narrow FM component and a long QCF component, enabling prey detection in vast empty spaces (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). Within foraging guilds, bat calls are not species specific: the calls of several species have evolved in a convergent way to respond to analogous environmental pressures, resulting in very similar calls in species facing analogous ecological conditions and therefore preventing species-specific identification in certain instances (Gibb et al., 2019; Russo et al., 2017). To overcome this issue, bat calls are commonly classified into sonotypes, i.e., calls of similar shape and peak frequency (Roemer et al., 2021).

Owing to the role of their foraging habitat in modulating their calls, bats of different foraging guilds are expected to respond antagonistically to habitat loss and fragmentation (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). In the aftermath of damming, once continuous forests are lost to smaller insular forest patches harbouring a gradient of vegetation structures: while cluttered forest represent optimal conditions for supporting diverse assemblages of forest bats, the water matrix can pose a serious obstacle to this guild's mobility, thus acting as a morpho-ecological filter (Colombo et al., 2022). On the other hand, the newly created edges and adjacent open water surface might constitute high-quality habitat for edge and open-space foragers, as these vegetation structures are adapted to these guilds' morphological and acoustical adaptations (Denzinger & Schnitzler, 2013; Schnitzler & Kalko, 2001). In this sense, forest-dependent bats, which have been identified as being of conservation priority in SE Asia due to the general decline of forested areas in this region (Kingston, 2010), are expected to be restricted to continuous mainland forest and large, well-connected islands. Differentiating the response of these three guilds is therefore central to the implementation of adapted conservation measures. Notwithstanding, the study of insectivorous bats in Southeast Asia, especially forest and edge foragers, has been largely impaired by the ability of most insectivorous species to avoid live trapping methods, such as harp traps and mist nets (Kingston, 2013). With the increasing affordability of low-cost acoustic devices, insectivorous bat surveys are becoming more accessible and reliable, further allowing for high replication (Gibb et al., 2019; Hill et al., 2018).

Utilising such technological advances, here we provide the first assessment of the effects of habitat loss and insular fragmentation on insectivorous bats in a dam-induced landscape in peninsular Malaysia. Using passive acoustic monitoring, we surveyed insectivorous bats in 26 forest islands and two mainland continuous forest sites. Across a gradient of habitat loss and insular fragmentation, we tested the effect of island size, isolation, and habitat quality (island shape and NDVI), at the following levels of bat diversity (1) overall assemblage, considering sonotype richness, activity and assemblage composition, (2) foraging guild, separately considering the activity of forest, edge and open-space foragers, and (3) sonotype, given each sonotype activity. We hypothesise that increased forest size and canopy density (i.e., higher NDVI values), and decreased isolation positively influence sonotype richness and activity. Yet, the different foraging guilds are hypothesised to show contrasting responses. In particular, forest foragers are expected to respond positively to forest size, canopy density, and connectivity to the mainland and surrounding forest patches, while open-space and edge foragers are expected to show opposite responses.

## **2. Material and methods**

### **2.1 Study area**

This study was conducted within the insular fragmented landscape of the Kenyir Lake and its surroundings in peninsular Malaysia. This artificial freshwater reservoir was formed in 1986 by the damming of the Kenyir river. The novel insular landscape occupies 260 000 ha and is composed of >340 islands ranging in size between 0.6 and 1428 ha embedded in the water matrix (Figure 1). Tropical humid forest on the islands and the adjacent mainland continuous forest are characterised by lowland and mid-elevation dipterocarp vegetation. The wide reservoir landscape, including the islands and surrounding mainland continuous forest, was subject to selective logging prior to damming (Muhammad Yusuf, 2005; Qie et al., 2011). This practice is still allowed in some parts of the lake's catchment area, but not in Taman Negara National Park, which borders its south-eastern side (Mariapan et al., 2017). This region experiences a wet season between November and March, and a dry season between May and October. Annual precipitation varies between 2700 and 4000 mm annually (Qie et al., 2011).

### **2.2 Study design and data collection**

We selected 26 islands covering a range of sizes (min-max: 0.45 – 167.3 ha) and distances from the mainland (135 – 2748 m), in addition to two mainland sampling sites. This sampling strategy was set up to study the effects of forest size and isolation independently, i.e. maintaining a low correlation between these variables ( $r = -0.36$  when considering island size and distance to mainland,  $r = -0.49$  when considering log-transformed island size and distance to the mainland). Bat acoustic surveys were carried out between September 8<sup>th</sup> and October 13<sup>th</sup> 2019, using Audiomoth recorders (Hill et al., 2018) set on a sampling rate of 384 kHz and the gain to the second setting (“med”). This sampling period has been selected to avoid the severe monsoons typical of this region, and thus scaping any rain-induced deterioration of the acoustic recording. We deployed one recorder in each sampling

site and recorded for six hours, a sampling effort deemed adequate when aiming to detect bat populations' and assemblages' response to habitat modification (López-Baucells et al., 2021). Recordings were divided into two time periods starting 30 minutes before sunset and ending 30 minutes after sunrise: from 18:00 to 22:00, and from 04:00 to 06:00 (Hayes, 1997), covering the two peaks of bat activity at dusk and dawn (Fenton, 1970). Each recorder was attached to a tree, positioned 2 metres above the ground and, to minimise any uncontrolled impact from edge effects, placed as inland as possible relative to island size, i.e., between 14 and 123 m from the edge (median: 50 m).

## 2.3 Acoustic analysis

Using the software Kaleidoscope Version 5.4.7 (Wildlife Acoustics, 2019), we split the recorded sequences into 5-second recordings (Torrent et al., 2018). The same software was used to filter the sequences containing sounds with a minimum frequency of 10 kHz and a maximum frequency of 250 kHz, and a pulse length between 2 and 500 ms. Among these sequences, only those containing one bat pass, i.e., at least two pulses of the same sonotype were kept for subsequent analysis (Torrent et al., 2018).

Prior to the acoustic analysis, we first compiled a list of all species of insectivorous bat known to occur in peninsular Malaysia (Lim et al., 2014; Nor Zalipah et al., 2019). Secondly, we collated reference calls for these species. We did so by conducting a literature survey using the Web of Science platform, between September and November 2021. We searched for publications by each species' name followed by the country name: we favoured reference calls obtained in our study area in order to avoid any potential geographical variation in the call parameters. For those species we could not find any reference calls, we used the reference calls available in the bat call library Chirovox (Görföl et al., 2022) (Supporting file 1). We therefore matched the call type of the species present in peninsular Malaysia to one of the sonotypes described in Yoh et al. (2022) for bat species in Malaysian Borneo, namely CF, FM, FMqCF1, FMqCF2, FMqCF3, FMqCF4, FMqCF5, QCF and LF sonotypes. Using start and end frequency, frequency of maximum energy, duration and interpulse interval as defined in Russo & Jones (2002), we classified the calls into one of these nine sonotypes. Given their very distinct echolocation parameters, the CF calls belonging to the genera *Rhinolophus* and *Hipposideros* could be identified to the species level.

As the shape of the echolocation calls reflects the physical constraints encountered by the bats, we were able to classify bat sonotypes into three foraging guilds: (1) the constant-frequency and FM calls represent forest foragers, (2) FMqCF4, FMqCF5 and QCF represent edge foragers, and (3) LF, FMqCF2 and FMqCF3 calls represent open-space foragers (Yoh et al., 2022). Social calls could not be identified to the sonotype level and were treated as assemblage-level activity.

## 2.4 Patch variables

Patch variables were obtained from a georeferenced LANDSAT 5 image which was transformed into a land/water matrix using an unsupervised classification on the software ArcGIS (ESRI, 2011). We then used the "landscapemetrics" R package (Hesselbarth et al., 2019) to extract: (1) island size (*area*; ha), (2) shortest Euclidean

distance to the mainland (*dist.main*; m), (3) shortest Euclidean distance to the nearest neighbour island or mainland (*dist.neigh*; m), (4) island shape (*shape*), defined as the ratio between the patch perimeter and the hypothetical minimum perimeter of this patch, i.e. the perimeter of a maximally compact patch (McGarigal & Cushman, 2002), (5) the normalised difference vegetation index (*NDVI*), and (6) distance between the recorder and the forest edge (*dist.edge*; m). Given that the mainland continuous forest sites are characterised by an extensive forest coverage non-isolated area, we attributed these sites with the closest possible values to 'reality'. This included area values of one order of magnitude higher than the largest island (1670 ha) and zero distances to either the mainland or the nearest neighbour. To streamline, we refer to the area of both islands and mainland size as 'forest area'. *NDVI* and *shape* were calculated as for the remaining sampling sites but considering a 1000 m buffer centred in the sampling site and excluding water.

## 2.5 Data analysis

Assemblage-level metrics include sonotype richness, activity, and assemblage composition. Sonotype richness was defined as the number of sonotypes: this measure is representative of the diversity of call traits present at a site. Activity i.e., the number of bat passes, was used as a proxy for abundance. Although activity is widely used as a surrogate for abundance when studying echolocating bats (see for instance Charbonnier et al., 2016; Ellerbrok et al., 2022), this method may overestimate abundance due to the possibility of multiple detection of a single individual (Gibb et al., 2019; Kunz et al., 2009). Yet, it offers an effective tool for the detection of damming effects (e.g., López-Bosch et al., 2021 and Colombo et al., 2022), as well as other human-induced disturbances on bat communities (Mena et al., 2022; Williams-Guillén & Perfecto, 2011). Assemblage composition was summarised as a single variable using a Non-Metric Multi-Dimensional Scaling (NMDS) ordination. This analysis was performed considering sonotype activity and using a Bray-Curtis similarity matrix (stress = 0.130). The scores of the first axis of the NMDS composed the assemblage composition metric. Guild activity was calculated by summing the activity of the individual sonotypes respectively belonging to the forest, open-space and edge guilds (Table 1). Sonotype-level responses were examined for the sonotypes recorded in more than 10 sites and which had more than 50 bat passes. This threshold was intended to ensure a normal distribution of the residuals, as well as homoscedasticity. Social and unidentified calls were only included in the assemblage-level analysis. Among the sonotypes that met the threshold to be analysed, namely FMqCF2, FMqCF3, FMqCF4, FMqCF5, LF, *R. trifolius*, *H. diadema* and QCF, *H. diadema* and FMqCF2 had unequal error variances and were therefore excluded from the analysis.

We first accounted for spatial autocorrelation by applying Mantel tests using the R package "ade4" (Dray & Dufour, 2007). These tests correlate geographic distance between sampling sites and each response variable as well as the residuals of each model introduced in the subsequent section. We found no spatial autocorrelation ( $p > 0.05$ ) in all instances. We also examined the pairwise correlation between patch variables using Pearson correlation coefficients. *Shape* and *area* ( $\log_{10} x$ ) ( $r = 0.720$ ), as well as *area* ( $\log_{10} x$ ) and *NDVI* were highly correlated ( $r = 0.800$ ). Given the overall importance of area explaining biodiversity patterns in insular forest fragments (Jones et al., 2021), we preferred to keep this metric to enable comparisons with other studies, whereas *shape* was excluded from

subsequent analysis. Due to the lack of knowledge on the effects of canopy closeness on bats in this region, we chose to also keep *NDVI* in subsequent analyses. However, *area* ( $\log_{10} x$ ) and *NDVI* were not included together in a model. Collinearity between predictor variables was also examined using Variance Inflation Factors (VIFs), with no variable showing substantial collinearity ( $VIF > 5$ ) (Dormann et al., 2013).

We then analysed the combined effects of patch variables – *area*, *dist.main*, *dist.neigh* and *NDVI* – on (1) sonotype richness, activity and assemblage composition; (2) activity of forest, edge, and open-space sonotypes, and (3) the individual activity of eight sonotypes. To do so, we applied Linear Models (LMs) to each of these response variables, whose distribution was scrutinised prior to the analysis. The response variables regarding overall assemblage, guild and sonotype level activity, as well as forest area were log-transformed. Although all models were run with a gaussian error distribution, we initially considered a negative binomial distribution for the overall, guild-level and sonotype-level activity responses. Given that none of the models addressing individual sonotypes activity nor forest guild activity converged with a negative binomial error distribution, and that the distribution of these variables' residuals was closer to a normal distribution when using a log-transformation with a gaussian error structure, we chose to retain that transformation and error structure in the models. We further considered *dist.edge* as a covariate in each model, aiming to control for any eventual effect of distance to the forest edge.

A candidate model set including all possible combinations of patch variables (including the covariate *dist.edge*), except combinations involving *area* ( $\log_{10} x$ ) and *NDVI* in the same model, was generated using the dredge function of the “MuMIn” R package (Barton, 2022). All models were ranked by Akaike Information Criteria corrected for small sample sizes (AICc: Burnham & Anderson (2002)). To account for model uncertainty in multi-model inference, we used a model-averaging approach considering the most parsimonious models, i.e. those having the lowest AICc within a  $\Delta AICc < 2$  ( $\Delta AICc = AICc_i - AICc_{min}$ ,  $i$  being the  $i^{th}$  model derived from the dredge) (Froidevaux et al., 2022). We report model average estimates along with their 95% confidence intervals (CIs) which were considered significant if not overlapping zero (Nakagawa & Cuthill, 2007). Assumptions about the normal distribution of the variables and their residuals were verified using the R packages “performance” (Lüdtke et al., 2021) and “Dharma” (Hartig, 2022). All data analyses were performed using R (R Core Team, 2022).

### 3. Results

In total, we recorded 21 197 bat passes from 16 different sonotypes: 10 forest, three edge and three open-space foragers (Table 1). Sonotype richness varied between 4 and 13 sonotypes per site, activity varied between 43 and 3351 bat passes per six hours recording. Activity varied greatly across sampling sites ( $43 - 3351$ ,  $757.03 \pm 744.18$ ), and among foraging guilds ( $0 - 689$ ,  $101.89 \pm 174.73$  for forest foragers,  $2 - 2923$ ,  $489.39 \pm 698.75$  for edge foragers, and  $11 - 641$ ,  $130.39 \pm 144.01$  for open-space foragers). While the edge forager FMqCF4 and the open-space forager LF were present at every site, the following forest foragers were found at only one site: *Rhinolophus refulgens* (island 13), CF.46 (island 25), *Hipposideros cervinus*, *H. kunzi* and *H. bicolor* (CF A) (Tables 1 and S1). According to the NMDS, low values in the first axis were mostly associated with larger forest sites and forest foragers (*H. cervinus*, *H. kunzi*, *H. bicolor*, FM), while high values were associated with smaller



islands, as well as with edge (FMqCF4, FMqCF5), open-space (FMqCF3), and forest foragers (*R. refulgens*, *R. affinis*) (Figure 2). Overall, 988 bat passes could not be identified to either the guild or to the sonotype level, including 981 bat passes corresponding to social calls (Table 1). *R. trifolius* was likely greatly influential on the response of the forest guild: being present in less than half the forest sites, it accounted for nearly 80% of the forest guild's activity (Table 1). Most of the FM sonotype activity (71.42%) was recorded on the mainland sites.

### 3.1 Overall assemblage responses

Sonotype richness increased with NDVI ( $\beta = 0.819 \pm 0.409$ ,  $p = 0.045$ ,  $CI_{\min} = 0.017$ ,  $CI_{\max} = 1.620$ ), while total bat activity was unaffected by the patch variables considered (Table S2). Assemblage composition varied among sites based on their size ( $\beta = -0.536 \pm 0.137$ ,  $CI_{\min} = -0.817$ ,  $CI_{\max} = -0.254$ ),  $p < 0.001$ ) (Table S2, Figure 3D, I and Figure 4).

### 3.2 Guild-level responses

Forest sonotypes were more active at sites with higher NDVI ( $\beta = 1.476 \pm 0.439$ ,  $p = 0.002$ ,  $CI_{\min} = 0.616$ ,  $CI_{\max} = 2.335$ ). The activity of forest sonotypes also increased with decreasing distance to the closest neighbouring forest site ( $\beta = -1.468 \pm 0.439$ ,  $p = 0.002$ ,  $CI_{\min} = -2.328$ ,  $CI_{\max} = -0.608$ ), while edge sonotypes activity decreased with increasing both island size ( $\beta = -1.050 \pm 0.366$ ,  $p = 0.004$ ,  $CI_{\min} = -1.768$ ,  $CI_{\max} = -0.332$ ) and distances to edge ( $\beta = -1.045 \pm 0.355$ ,  $p = 0.003$ ,  $CI_{\min} = -1.741$ ,  $CI_{\max} = -0.350$ ). None of the tested variables had a significant effect on open-space sonotypes (Table S2, Figure 3O – Q and Figure 4). Unlike all other response variables, only one model was selected for the activity of forest foragers (*Dist.neigh*, NDVI, AICc = 132.129) (Table S3).

### 3.3 Sonotype-level responses

Among all the six individual sonotypes, only FMqCF4 and *R. trifolius* showed a significant response to the tested patch variables. FMqCF4 sonotype showed higher activity in smaller islands ( $\beta = -1.127 \pm 0.365$ ,  $p = 0.002$ ,  $CI_{\min} = -1.841$ ,  $CI_{\max} = -0.412$ ), while *R. trifolius* was more active on larger forest sites ( $\beta = 1.487 \pm 0.446$ ,  $p = 0.001$ ,  $CI_{\min} = 0.614$ ,  $CI_{\max} = 2.361$ ) (Table S2, Figure 4 and S1).

## 4. Discussion

A number of studies have demonstrated that habitat loss and insular fragmentation cause species local extinctions across lowland tropical forests (Gibson et al., 2013; Moore et al., 2022; Palmeirim et al., 2022; Pinto Henriques et al., 2021). Here, we contribute to fill an important knowledge gap by accordingly demonstrating overall negative bats response to dam-induced disturbance across an insular fragmented landscape in Southeast Asia. Our results highlight the role of canopy density driving the number of sonotypes, whereas forest area dictated which sonotypes were able to persist. Our guild-level analysis revealed that forest foragers were associated with denser forest structures, likely representing higher habitat quality for this guild, and were negatively affected by increasing isolation from neighbouring landmasses. In contrast, edge foragers seemed to benefit from island shrinkage. Fragmentation effects were not so clearly observed at the sonotype-level, with only two of the six

sonotypes analysed responding to patch variables, namely to forest area which had a positive effect on the forest forager *R. trifolius* and a negative effect on the edge sonotype FMqCF4.

#### Effects of forest area

Forest area did not predict sonotype richness at our study site. Owing to their high correlation, habitat quality and forest area were precluded from being combined in models, and models including habitat quality were more parsimonious than those including area: the absence of area effects is therefore more likely a consequence of the study design rather than a proper lack of area effects. In fact, a large body of evidence reports that area affects bat richness in fragmented insular (Luypaert et al., 2023), and non-insular systems (Rocha et al., 2017). This pattern holds true for several taxa on reservoir islands (Palmeirim et al., 2022), including dung-beetles (Qie et al., 2011), primates and ungulates (Yong, 2015), and birds (Yong et al., 2011) surveyed in nearly the same islands in Kenyir. Notwithstanding, bat assemblage composition varied along the gradient of forest area, with edge foragers being particularly active on smaller islands. This trend was further reflected at the sonotype level by the edge forager FMqCF4 and the forest forager *R. trifolius*, both of whom displayed contrasting responses to forest area, the former being negative, and the latter being positive. These responses were expected given that small islands tend to be edge-dominated. The extensive variation in species-specific home-range size may have further influenced the ability of some species to use the smaller fragments: while that of most edge foragers (5 – 210 ha) and *R. trifolius* (5 ha) are notably small, the majority of forest foragers have a vast home-ranges, reaching up to 2199 ha for some species (Wilson et al., 2010). Given their tendency to avoid flying across the water matrix (Meyer & Kalko, 2008), forest foraging species, mostly belonging to the FM sonotype, were therefore rarely recorded on smaller islands. Yet, as a caveat to this study, in small islands, detectors had to be placed closer to edges given the lack of forest interior. It is therefore possible that the detectors on small islands, being mechanically closer to forest edges, recorded a higher activity of edge foragers. This is further supported by the negative relationship between edge foragers activity and the *Dist.edge*. In any case, this would still demonstrate the preferential use of edges by this bat guild (López-Bosch et al., 2021). In contrast, our results show that the forest forager *R. trifolius* responds positively to forest area, suggesting that this sonotype requires greater habitat complexity associated with larger areas of forest (Benchimol & Peres, 2015a).

#### Effects of habitat quality

Despite the absence of clear effects of forest size, canopy closeness, as indicated by the NDVI, promoted an increase in the number of bat sonotypes and forest foragers activity across the Kenyir landscape. A bat species' response to habitat quality is likely influenced by the intrinsic habitat characteristics such as 3D forest structure or canopy ruggedness, ultimately impacting which species are able to use each site (Froidevaux et al., 2016). Our study landscape has been subject to intensive selective logging prior to the construction of the dam (Qie et al., 2011). Indeed, evidence for previous logging is still noticeable in the area, with logging trails and canopy holes being observed *in-situ*, resulting in a low but variable overall NDVI on the islands and surrounding continuous forest sites. Whilst the effects of logging on bat species richness seem to be limited both in the Neotropics (Meyer et al., 2016) and in the Paleotropics (Struebig et al., 2013), logging appears to strongly influence

assemblage composition, edge species being indicative of repeatedly logged sites (Peters et al., 2006). Yet, the effects of logging on biodiversity depend on the intensity and extraction methods (Burivalova et al., 2014), and further investigations regarding the effects of logging intensity in the context of insular forest fragments are needed to further our understanding of how logging may drive bat sonotype richness. Notwithstanding the potential effects of logging, forest insularisation led to the creation of edges, whose deleterious effects on vegetation include increased exposure to wind-throws, culminating in shifts towards disturbance-adapted pioneer trees (Benchimol & Peres, 2015a; Santo-Silva et al., 2021). While sites with low canopy closeness can be widely used by edge foragers, only those sites harbouring increased NDVI may represent suitable habitat for manoeuvrable forest dependent species that are further adapted to echolocate in more cluttered environments (Froidevaux et al., 2016; Suarez-Rubio et al., 2018). By allowing forest foragers to persist, habitat quality contributes to maintain bat diversity, as also observed for other biological groups, e.g., large-sized mammals and reptiles (Oliveira et al., 2020; Silva et al., 2022). This is further supported by the increase in forest bat activity we observed in denser canopies. Higher NDVI values may also be associated with higher availability of mature trees that provide roosting sites for species such as *R. trifolius*, *R. sedulus*, *K. papillosa* and *K. pellucida*, all of which depend on these structures to rest and thus to persist. For instance, in Malaysia, the absence of tree cavities due to forest disturbance was associated with the decline of the forest foragers *Kerivoula* sp. (Struebig et al., 2013). Our findings reiterate the importance of habitat quality as a key driver of species diversity in fragmented landscapes (Armstrong et al., 2022; Poniatowski et al., 2018).

#### Effects of isolation

Contrary to our expectations, isolation was not an important variable explaining bat assemblage-level responses. These results contrast with an insular fragmented landscape in Panama, where isolation to the mainland was the main predictor of bat richness (Meyer & Kalko, 2008). However, our results are in agreement with findings from a non-insular Malaysian fragmented landscape, where isolation has also been found to be a poor prediction of bat richness (Brändel et al., 2020). The lack of isolation effects may be related to the overall small distance separating most of the sampling sites, and the overall size of the lake, as the home ranges for most local species exceed the distance separating most of the study sites (Wilson et al., 2010). Nevertheless, forest foragers were more active in sites less isolated from neighbouring landmasses, which might be due to morphological constraints (Norberg & Rayner, 1987). Indeed, forest foragers have a wing morphology characterised by a low aspect ratio ( $\text{wingspan}^2/\text{wing area}$ ) and a low wing loading ( $\text{body mass}/\text{wing area}$ ) (Norberg & Rayner, 1987). Although this characteristic allows them to have a slow and highly manoeuvrable flight, it also makes flight over open spaces particularly energetically demanding (Altringham, 2011; Bader et al., 2015). Furthermore, the absence of distance-to-mainland effects in favour of distance-to-neighbour effects for forest foragers underlines the value of intermediary islands to act as stepping-stones for forest bats to cross the water matrix and reach more remote islands. This idea is supported by Saura et al. (2014) who also stress that these intermediate islands need to be sufficiently large and of high quality in order to act as stepping-stones.

#### Limitations and potential caveats

Our results emphasise the valuable use of passive acoustic monitoring techniques to survey bat assemblages, further allowing us to examine bat responses at multiple levels. However, the use of sonotype richness instead of species richness likely biased the estimated sonotype richness towards forest species. Indeed, while the CF calls produced by forest foragers could be identified to the species level, other sonotypes including FMqCF, QCF and LF contained multiple species. Likewise, given the similarity of the ecological constraints faced by edge foragers, the calls produced by the species belonging to this guild can only be separated between three sonotypes (FMqCF4, FMqCF5 and QCF). For this reason, our results might underestimate the effects of habitat loss and insular fragmentation on insectivorous bats, which is further enhanced by the fact that larger forest sites – expected to harbour higher species diversity – were proportionally less sampled. In addition, as species detectability is a function of call intensity (Hayes, 2000), forest bats producing low-intensity FM calls such as Vespertilionidae (e.g., *Kerivoula* and *Myotis* spp.) tend to be under-detected (Waters & Jones, 1995). This might further explain the relatively weak responses observed at the sonotype-level, which should therefore be interpreted with caution. Likewise, even the most commonly used devices in bat detection, including Audiomoths, tend to lack the sensitivity required to detect some of the high intensity calls emitted by smallest-bodied bats such as *H. cervinus*, *H. larvatus* and *H. bicolor* (Kingston, 2010): although common in Peninsular Malaysia (Lim et al., 2014), these species have probably been under detected in our study. Live trapping remains the most efficient method to monitor these species (Kingston, 2013), and still, studies using these trapping methods have highlighted the high sensitivity of these forest genera to forest disturbance (Huang et al., 2019).

#### Conservation implications

SE Asia may lose over 74% of its original forest cover by the end of the century, putting forest-dependent species at tremendous risk (Sodhi et al., 2004). Forest foragers from the Kenyir lake are no exception: being absent from the smallest islands, they showed low activity in isolated and degraded forest patches, which nevertheless make up the majority of the landscape of Lake Kenyir. Additionally, three forest species, namely *H. bicolor*, *H. cervinus* and *H. kunzi*, were only found on the mainland. Our results suggest that conservation efforts should target forest bats which, given their forest-adapted morphology and the rapid vanishing of their foraging habitat, are particularly extinction prone (Jones et al., 2003; Safi & Kerth, 2004). The FM sonotype, of which most potential representatives such as *Kerivoula intermedia*, *K. pellucida* or *Nycteris tragata* are listed as near threatened (Senawi & Ahmad, 2021), was mostly active in the mainland, and completely absent from 21 islands. We therefore stress that bats highly dependent on forest can only persist in large undisturbed forest tracts. The independent presence of dense canopies and connection to nearby landmasses does not guarantee the use by forest bats. Indeed, only patches that are large, well connected to the mainland, and harbouring a high habitat quality can serve as stepping-stones, and therefore allow less vagile species to commute over the water matrix (Saura et al., 2014). In insular forest patches, species are lost in a sustained and delayed manner according to the time elapsed since isolation, a process referred to as an “extinction debt” (Jones et al., 2016). Furthermore, these islands suffer an inevitable vegetation decay (Benchimol & Peres, 2015a). In line with (Jones et al., 2016), our results suggest that islands

should not be used as conservation units for mitigation purposes due to the imminent extinction debt. Instead, conservation efforts should prioritise maintaining mainland habitat quality, for instance by minimising logging activity in these highly forested areas (Hari Poudyal et al., 2018; Harvey & Brais, 2011). This can be achieved by legally protecting the islands and surrounding mainland continuous forest/wider reservoir landscape as to minimise disturbances. Such measures have successfully helped minimising further human activities in a Brazilian Biological reserve encompassing part of a mega-dam (Benchimol & Peres, 2015a, 2015b). In addition, future hydropower developments should consider how dam placement is likely to affect the creation of different island systems. These developments should aim to reduce the creation of a myriad of small, isolated, and habitat-degraded forest fragments, for instance by targeting craggy locations over flat areas, therefore drastically minimising the flooded area. The biological impacts of damming tend to be largely underestimated, as current environmental impact assessment methods poorly predict the extent and location of dam-induced flooding, possibly leading to a 64.5 % increase of the flooded surface compared to initial predictions (Cochrane et al., 2017). Working towards a more accurate planning is therefore essential to minimise the flooding area, avoid the flooding of ecologically valuable zones, and adequately locate future dams.

## **5. Conclusions**

Hydropower development is set to massively expand across Southeast Asian forests, with energy production expected to increase threefold by 2035 (Petinrin & Shaaban, 2015; Tang et al., 2019). In Malaysia alone, at least four additional major dams will soon be constructed (> 34 000 MW) (Foo, 2015). Coupled with a steadily declining share of forest in this region, these threats put insectivorous bat assemblages at risk, especially for forest-dependent species. Here, we showed that canopy density played a central role in promoting both sonotype richness, persistence and activity of forest foragers, while this guild was negatively impacted by isolation to neighbouring forest patches. Forest area further affected the assemblage composition, larger forest patches being associated with forest-dominated assemblages, and smaller patches being associated with edge-foragers. Large, dense, well connected forest fragments still supported a subset of the mainlands' assemblage diversity. Yet, our results suggested that preserving a high canopy density, especially in the mainland, is essential to serve the preservation of forest-dependent species. Keeping forest disturbances such as logging minimum and developing more efficient tools to predict the spatial extent of future dam's effects is therefore a priority for the preservation of bat assemblages in SE Asia.

## **Acknowledgements:**

We are grateful for the fieldwork assistance of David L´opez-Bosch and Ahmad Faizul Bin Zulkifli during data collection. We thank the Economic Planning Unit, Department of Prime Minister, Malaysia for permission to conduct research and Department of Wildlife and National Parks Peninsular Malaysia for permission to work in Kenyir (JPHL&TN (IP):100-34/1.24 Jld 14(57). AFP was supported by the Outstanding Postdoctoral Fellowship of the Southern University of Science and Technology (SUSTech), and is currently funded by the European Union's Horizon 2020 research and innovation programme under grant agreement

No. 854248. L.G. was supported by the China Thousand Young Talents Program (K18291101), as a Guangdong Government distinguished expert (K20293101), and by the Shenzhen Government (Y01296116). JSPF is funded by the Leverhulme Trust through an earlycareer fellowship (Award Reference: ECF-2020-571). NY was supported by the UK's Natural Environmental Research Council (NERC) via a EnvEast DTP scholarship (NE/L002582/1). JS was supported by National Science Fund - USA through Texas Tech University (ST-2019-006) and Malaysia Ministry of Higher Education (FRGS/1/2020/WAB11/UKM/02/3).

## Bibliography:

- Altringham, J. D. (2011). Bats: From Evolution to Conservation. In *Bats: From Evolution to Conservation*.  
<https://doi.org/10.1093/acprof:osobl/9780199207114.001.0001>
- Armstrong, D. P., Boulton, R. L., McArthur, N., Govella, S., Gorman, N., Pike, R., & Richard, Y. (2022). Using experimental reintroductions to resolve the roles of habitat quality and metapopulation dynamics on patch occupancy in fragmented landscapes. *Conservation Biology*, 36(3), e13843.  
<https://doi.org/10.1111/COBI.13843>
- Bader, E., Jung, K., Kalko, E. K. V., Page, R. A., Rodriguez, R., & Sattler, T. (2015). Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biological Conservation*, 186, 97–106. <https://doi.org/10.1016/j.biocon.2015.02.028>
- Barton, K. (2022). *Package “MuMIn” Title Multi-Model Inference*.
- Benchimol, M., & Peres, C. A. (2015a). Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*, 103(2), 408–420.  
<https://doi.org/10.1111/1365-2745.12371>
- Benchimol, M., & Peres, C. A. (2015b). Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. *Biological Conservation*, 187, 61–72. <https://doi.org/10.1016/j.biocon.2015.04.005>
- Benchimol, M., & Peres, C. A. (2021). Determinants of population persistence and abundance of terrestrial and arboreal vertebrates stranded in tropical forest land-bridge islands. *Conservation Biology*, 35(3), 870–883.  
<https://doi.org/10.1111/cobi.13619>
- Brändel, S. D., Hiller, T., Halczok, T. K., Kerth, G., Page, R. A., & Tschapka, M. (2020). Consequences of fragmentation for Neotropical bats: The importance of the matrix. *Biological Conservation*, 252.  
<https://doi.org/10.1016/j.biocon.2020.108792>
- Burivalova, Z., Şekercioğlu, Ç. H., & Koh, L. P. (2014). Thresholds of Logging Intensity to Maintain Tropical Forest Biodiversity. *Current Biology*, 24(16), 1893–1898. <https://doi.org/10.1016/J.CUB.2014.06.065>

- Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference. In *Model Selection and Inference*. Springer New York.  
<https://doi.org/10.1007/978-1-4757-2917-7>
- Charbonnier, Y. M., Barbaro, L., Barnagaud, J. Y., Ampoorter, E., Nezan, J., Verheyen, K., & Jactel, H. (2016). Bat and bird diversity along independent gradients of latitude and tree composition in European forests. *Oecologia*, 182(2), 529–537. <https://doi.org/10.1007/s00442-016-3671-9>
- Cochrane, S. M. V., Matricardi, E. A. T., Numata, I., & Lefebvre, P. A. (2017). Landsat-based analysis of mega dam flooding impacts in the Amazon compared to associated environmental impact assessments: Upper Madeira River example 2006–2015. *Remote Sensing Applications: Society and Environment*, 7, 1–8. <https://doi.org/10.1016/j.rsase.2017.04.005>
- Coleman, J. L., Ascher, J. S., Bickford, D., Buchori, D., Cabanban, A., Chisholm, R. A., Chong, K. Y., Christie, P., Clements, G. R., dela Cruz, T. E. E., Dressler, W., Edwards, D. P., Francis, C. M., Friess, D. A., Giam, X., Gibson, L., Huang, D., Hughes, A. C., Jaafar, Z., ... Carrasco, L. R. (2019). Top 100 research questions for biodiversity conservation in Southeast Asia. *Biological Conservation*, 234, 211–220.  
<https://doi.org/10.1016/J.BIOCON.2019.03.028>
- Colombo, G. T., di Ponzio, R., Benchimol, M., Peres, C. A., & Bobrowiec, P. E. D. (2022). Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. *Functional Ecology*.  
<https://doi.org/10.1111/1365-2435.14118>
- Couto, T. B. A., & Olden, J. D. (2018). Global proliferation of small hydropower plants – science and policy. *Frontiers in Ecology and the Environment*, 16(2), 91–100. <https://doi.org/10.1002/FEE.1746>
- Denzinger, A., & Schnitzler, H. U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4(164).  
<https://doi.org/10.3389/fphys.2013.00164>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/J.1600-0587.2012.07348.X>
- Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22(4), 1–20.  
<https://doi.org/10.18637/JSS.V022.I04>
- Ellerbrok, J. S., Delius, A., Peter, F., Farwig, N., & Voigt, C. C. (2022). Activity of forest specialist bats decreases towards wind turbines at forest sites. *Journal of Applied Ecology*, 59(10), 2497–2506.  
<https://doi.org/10.1111/1365-2664.14249>

- ESRI. (2011). *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.
- Fenton, M. B. (1970). A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Canadian Journal of Zoology*, 48(4), 847–851. <https://doi.org/10.1139/Z70-148>
- Foo, K. Y. (2015). A vision on the opportunities, policies and coping strategies for the energy security and green energy development in Malaysia. *Renewable and Sustainable Energy Reviews*, 51, 1477–1498. <https://doi.org/10.1016/J.RSER.2015.07.041>
- Froidevaux, J. S. P., Laforge, A., Larrieu, L., Barbaro, L., Park, K., Fialas, P. C., & Jones, G. (2022). Tree size, microhabitat diversity and landscape structure determine the value of isolated trees for bats in farmland. *Biological Conservation*, 267, 109476. <https://doi.org/10.1016/J.BIOCON.2022.109476>
- Froidevaux, J. S. P., Zellweger, F., Bollmann, K., Jones, G., & Obrist, M. K. (2016). From field surveys to LiDAR: Shining a light on how bats respond to forest structure. *Remote Sensing of Environment*, 175, 242–250. <https://doi.org/10.1016/j.rse.2015.12.038>
- Gibb, R., Browning, E., Glover-Kapfer, P., & Jones, K. E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. In *Methods in Ecology and Evolution* (Vol. 10, Issue 2, pp. 169–185). John Wiley & Sons, Ltd. <https://doi.org/10.1111/2041-210X.13101>
- Gibson, L., Lynam, A. J., Bradshaw, C. J. A., He, F., Bickford, D. P., Woodruff, D. S., Bumrungsri, S., & Laurance, W. F. (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, 341(6153), 1508–1510. <https://doi.org/10.1126/SCIENCE.1240495>
- Gibson, L., Wilman, E. N., & Laurance, W. F. (2017). How Green is ‘Green’ Energy? In *Trends in Ecology and Evolution* (Vol. 32, Issue 12, pp. 922–935). Elsevier Ltd. <https://doi.org/10.1016/j.tree.2017.09.007>
- Görföl, T., Huang, J. C. C., Csorba, G., Gyorössy, D., Estók, P., Kingston, T., Szabadi, K. L., McArthur, E., Senawi, J., Furey, N. M., Tu1, V. T., Thong, V. D., Khan, F. A. A., Jinggong, E. R., Donnelly, M., Kumaran, J. V., Liu, J. N., Chen, S. F., Tuanmu, M. N., ... Zsebok, S. (2022). ChiroVox: A public library of bat calls. *PeerJ*, 10, e12445. <https://doi.org/10.7717/PEERJ.12445/FIG-2>
- Gorresen, P. M., & Willig, M. R. (2004). Landscape Responses of Bats to Habitat Fragmentation in Atlantic Forest of Paraguay. *Journal of Mammalogy*, 85(4), 688–697. <https://doi.org/10.1644/BWG-125>
- Hari Poudyal, B., Maraseni, T., & Cockfield, G. (2018). Evolutionary dynamics of selective logging in the tropics: A systematic review of impact studies and their effectiveness in sustainable forest management. *Forest Ecology and Management*, 430, 166–175. <https://doi.org/10.1016/J.FORECO.2018.08.006>



- Hartig, F. (2022, January 16). *DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models*. <https://cran.r-project.org/web/packages/DHARMA/vignettes/DHARMA.html>
- Harvey, B., & Brais, S. (2011). Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. *Https://Doi.Org/10.1139/X02-006*, 32(4), 653–666. <https://doi.org/10.1139/X02-006>
- Hayes, J. P. (1997). Temporal Variation in Activity of Bats and the Design of Echolocation-Monitoring Studies. *Journal of Mammalogy*, 78(2), 514–524. <https://doi.org/10.2307/1382902>
- Hayes P., J. (2000). Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*, 2(2). [https://www.researchgate.net/publication/281335545\\_Assumptions\\_and\\_practical\\_considerations\\_in\\_the\\_design\\_and\\_interpretation\\_of\\_echolocation-monitoring\\_studies](https://www.researchgate.net/publication/281335545_Assumptions_and_practical_considerations_in_the_design_and_interpretation_of_echolocation-monitoring_studies)
- Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42(10), 1648–1657. <https://doi.org/10.1111/ECOG.04617>
- Hill, A. P., Prince, P., Piña Covarrubias, E., Doncaster, C. P., Snaddon, J. L., & Rogers, A. (2018). AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution*, 9(5), 1199–1211. <https://doi.org/10.1111/2041-210X.12955>
- Huang, J. C. C., Rustiati, E. L., Nuslawo, M., & Kingston, T. (2019). Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture. *Biotropica*, 51(5), 757–768. <https://doi.org/10.1111/BTP.12694>
- Jones, I. L., Bueno, A. S., Benchimol, M., Palmeirim, A. F., Storck-Tonon, D., & Peres, C. A. (2021). Using relict species-area relationships to estimate the conservation value of reservoir islands to improve environmental impact assessments of dams. *The Species–Area Relationship*, 417–437. <https://doi.org/10.1017/9781108569422.023>
- Jones, I. L., Bunnefeld, N., Jump, A. S., Peres, C. A., & Dent, D. H. (2016). Extinction debt on reservoir land-bridge islands. *Biological Conservation*, 199, 75–83. <https://doi.org/10.1016/J.BIOCON.2016.04.036>
- Jones, K. E., Purvis, A., & Gittleman, J. L. (2003). Biological Correlates of Extinction Risk in Bats. *Https://Doi.Org/10.1086/368289*, 161(4), 601–614. <https://doi.org/10.1086/368289>
- Kingston, T. (2010). Research priorities for bat conservation in Southeast Asia: A consensus approach. *Biodiversity and Conservation*, 19(2), 471–484. <https://doi.org/10.1007/S10531-008-9458-5>
- Kingston, T. (2013). Response of bat diversity to forest disturbance in Southeast Asia: Insights from long-term research in Malaysia. In *Bat Evolution*,

- Ecology, and Conservation* (pp. 169–185). Springer, New York, NY.  
[https://doi.org/10.1007/978-1-4614-7397-8\\_9](https://doi.org/10.1007/978-1-4614-7397-8_9)
- Kunz, T. H., Betke, M., Hristov, N. I., & Vonhof, M. J. (2009). Methods for assessing colony size, population size, and relative abundance of bats. In T. H. Kunz & S. Parsons (Eds.), *Ecological and behavioral methods for the study of bats* (pp. 133–157). Johns Hopkins University Press.
- Lim, L. S., Mohd-Adnan, A., Zubaid, A., Struebig, M. J., & Rossiter, S. J. (2014). Diversity of Malaysian insectivorous bat assemblages revisited. *Journal of Tropical Ecology*, 30(2), 111–121.  
<https://doi.org/10.1017/S0266467413000874>
- López-Baucells, A., Yoh, N., Rocha, R., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2021). Optimizing bat bioacoustic surveys in human-modified Neotropical landscapes. *Ecological Applications*, 31(6).  
<https://doi.org/10.1002/EAP.2366>
- López-Bosch, D., Rocha, R., López-Baucells, A., Wang, Y., Si, X., Ding, P., Gibson, L., & Palmeirim, A. F. (2021). Passive acoustic monitoring reveals the role of habitat affinity in sensitivity of sub-tropical East Asian bats to fragmentation. *Remote Sensing in Ecology and Conservation*, rse2.237.  
<https://doi.org/10.1002/rse2.237>
- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, 6(60), 3139. <https://doi.org/10.21105/JOSS.03139>
- Luypaert, T., Bueno, A. S., Haugaasen, T., & Peres, C. A. (2023). *Extending species-area relationships into the realm of ecoacoustics: The soundscape-area relationship*. <https://doi.org/10.1101/2023.02.08.527658>.
- Mariapan, M., Lin, E. L. A., Isa, S. S., Karim, M. S., & Hakeem, K. R. (2017). *Ecotourism Potentials in Malaysia*.  
[https://www.researchgate.net/publication/332461983\\_ECOTOURISM\\_POTENTIALS\\_IN\\_MALAYSIA](https://www.researchgate.net/publication/332461983_ECOTOURISM_POTENTIALS_IN_MALAYSIA)
- McArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
- McGarigal, K., & Cushman, S. A. (2002). Comparative Evaluation of Experimental Approaches to the Study of Habitat Fragmentation Effects. *Ecological Applications*, 12(2), 335. <https://doi.org/10.2307/3060945>
- Mena, J. L., Rivero, J., Bonifaz, E., Pastor, P., Pacheco, J., & Aide, T. M. (2022). The effect of artificial light on bat richness and nocturnal soundscapes along an urbanization gradient in an arid landscape of central Peru. *Urban Ecosystems*, 25(2), 563–574. <https://doi.org/10.1007/S11252-021-01163-X/METRICS>
- Meyer, C. F. J., Fründ, J., Lizano, W. P., & Kalko, E. K. V. (2008). Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45(1), 381–391. <https://doi.org/10.1111/j.1365-2664.2007.01389.x>

- Meyer, C. F. J., & Kalko, E. K. V. (2008). Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, 35(9), 1711–1726.  
<https://doi.org/10.1111/j.1365-2699.2008.01916.x>
- Meyer, C. F. J., Struebig, M. J., & Willig, M. R. (2016). Responses of tropical bats to habitat fragmentation, logging, and deforestation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 63–103). Springer International Publishing. [https://doi.org/10.1007/978-3-319-25220-9\\_4](https://doi.org/10.1007/978-3-319-25220-9_4)
- Moore, J. H., Palmeirim, A. F., Peres, C. A., Ngoprasert, D., & Gibson, L. (2022). Invasive rat drives complete collapse of native small mammal communities in insular forest fragments. *Current Biology*, 32(13), 2997–3004.e2. <https://doi.org/10.1016/J.CUB.2022.05.053>
- Muhammad Yusuf, S. (2005). Environmental Issues in a Federation : The Case of Malaysia. *Intellectual Discourse*, 13(2), 201–212.  
[https://www.researchgate.net/publication/277125893\\_Environmental\\_Issues\\_in\\_a\\_Federation\\_The\\_Case\\_of\\_Malaysia](https://www.researchgate.net/publication/277125893_Environmental_Issues_in_a_Federation_The_Case_of_Malaysia)
- Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biological Reviews*, 82(4), 591–605. <https://doi.org/10.1111/J.1469-185X.2007.00027.X>
- Nor Zalipah, M., Roslan, A., Senawi, J., Jayaraj, V. K., Azhar, M. I., Abdullah, M. T., & Lim, B. L. (2019). Checklist of small mammals of Hulu Terengganu, Terengganu. In *Greater Kenyir Landscapes: Social Development and Environmental Sustainability: From Ridge to Reef* (pp. 191–200). Springer, Cham. [https://doi.org/10.1007/978-3-319-92264-5\\_18](https://doi.org/10.1007/978-3-319-92264-5_18)
- Norberg, Ulla. M., & Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 316(1179), 335–427.  
<https://doi.org/10.1098/rstb.1987.0030>
- Oliveira, R. F., de Moraes, A. R., & Terribile, L. C. (2020). Effects of landscape and patch attributes on the functional diversity of medium and large-sized mammals in the Brazilian Cerrado. *Mammal Research*, 65(2), 301–308.  
<https://doi.org/10.1007/S13364-019-00471-0/TABLES/3>
- Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A. (2018). Small mammal responses to Amazonian forest islands are modulated by their forest dependence. *Oecologia*, 187(1), 191–204.  
<https://doi.org/10.1007/S00442-018-4114-6/FIGURES/5>
- Palmeirim, A. F., Emer, C., Benchimol, M., Storck-Tonon, D., Bueno, A. S., & Peres, C. A. (2022). Emergent properties of species-habitat networks in an insular forest landscape. *Science Advances*, 8(34), 397.  
<https://doi.org/10.1126/sciadv.abm0397>
- Palmeirim, A. F., Farneda, F. Z., Vieira, M. V., & Peres, C. A. (2021). Forest area predicts all dimensions of small mammal and lizard diversity in

Amazonian insular forest fragments. *Landscape Ecology*, 36(12), 3401–3418. <https://doi.org/10.1007/S10980-021-01311-W/FIGURES/6>

Palmeirim, A. F., Vieira, M. V., & Peres, C. A. (2017). Non-random lizard extinctions in land-bridge Amazonian forest islands after 28 years of isolation. *Biological Conservation*, 214, 55–65. <https://doi.org/10.1016/J.BIOCON.2017.08.002>

Peters, S. L., Malcolm, J. R., & Zimmerman, B. L. (2006). Effects of selective logging on bat communities in the southeastern Amazon. *Conservation Biology: The Journal of the Society for Conservation Biology*, 20(5), 1410–1421. <https://doi.org/10.1111/J.1523-1739.2006.00526.X>

Petinrin, J. O., & Shaaban, M. (2015). Renewable energy for continuous energy sustainability in Malaysia. *Renewable and Sustainable Energy Reviews*, 50, 967–981. <https://doi.org/10.1016/J.RSER.2015.04.146>

Pinto Henriques, L. M., Dantas, S., Santos, L. B., Bueno, A. S., & Peres, C. A. (2021). Avian extinctions induced by the oldest Amazonian hydropower mega dam: Evidence from museum collections and sighting data spanning 172 years. *PeerJ*, 9. <https://doi.org/10.7717/PEERJ.11979/SUPP-2>

Poniatowski, D., Stuhldreher, G., Löffler, F., & Fartmann, T. (2018). Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity. *Biological Conservation*, 225, 237–244. <https://doi.org/10.1016/J.BIOCON.2018.07.018>

Qie, L., Lee, T. M., Sodhi, N. S., & Lim, S. L. H. (2011). Dung beetle assemblages on tropical land-bridge islands: Small island effect and vulnerable species. *Journal of Biogeography*, 38(4), 792–804. <https://doi.org/10.1111/j.1365-2699.2010.02439.x>

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rocha, R., López-Baucells, A., Farneda, F. Z., Groenenberg, M., Bobrowiec, P. E. D., Cabeza, M., Palmeirim, J. M., & Meyer, C. F. J. (2017). Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology*, 32(1), 31–45. <https://doi.org/10.1007/s10980-016-0425-3>

Roemer, C., Julien, J. F., & Bas, Y. (2021). An automatic classifier of bat sonotypes around the world. *Methods in Ecology and Evolution*, 12(12), 2432–2444. <https://doi.org/10.1111/2041-210X.13721>

Russo, D., Ancillotto, L., & Jones, G. (2017). Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification1. <https://doi.org/10.1139/Cjz-2017-0089>, 96(2), 63–78. <https://doi.org/10.1139/CJZ-2017-0089>

Russo, D., & Jones, G. (2002). Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology*, 258(1), 91–103. <https://doi.org/10.1017/S0952836902001231>

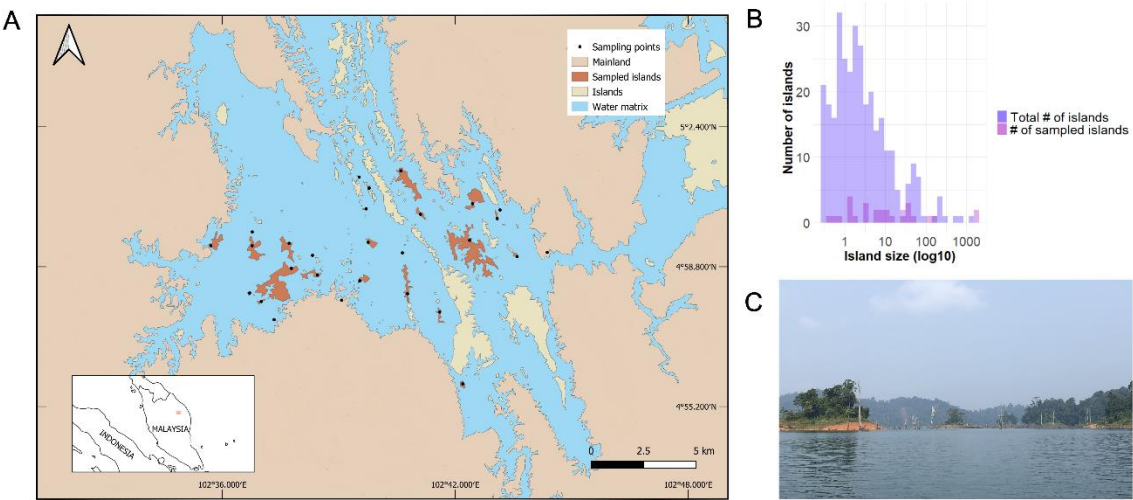
- Safi, K., & Kerth, G. (2004). A Comparative Analysis of Specialization and Extinction Risk in Temperate-Zone Bats. *Conservation Biology*, 18(5), 1293–1303. <https://doi.org/10.1111/J.1523-1739.2004.00155.X>
- Santo-Silva, E. E., Benchimol, M., & Peres, C. A. (2021). Phylogenetic homogenization of Amazonian tree assemblages in forest islands after 26 years of isolation. *Applied Vegetation Science*, 24(3). <https://doi.org/10.1111/AVSC.12601>
- Saura, S., Bodin, Ö., & Fortin, M. J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51(1), 171–182. <https://doi.org/10.1111/1365-2664.12179>
- Schnitzler, H. U., Moss, C. F., & Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology & Evolution*, 18(8), 386–394. [https://doi.org/10.1016/S0169-5347\(03\)00185-X](https://doi.org/10.1016/S0169-5347(03)00185-X)
- Schnitzler, H.-U., & Kalko, E. K. v. (2001). Echolocation by Insect-Eating Bats. *BioScience*, 51(7), 557–569. [https://doi.org/10.1641/0006-3568\(2001\)051\[0557:EBIEB\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2)
- Senawi, J., & Ahmad, N. (2021). *Kelawar Malaysia*. Kementerian Tenaga & Sumber Asli. <https://www.mybis.gov.my/pb/4507>
- Silva, D. J., Palmeirim, A. F., Santos-Filho, M., Sanaiotti, T. M., & Peres, C. A. (2022). Habitat Quality, Not Patch Size, Modulates Lizard Responses to Habitat Loss and Fragmentation in the Southwestern Amazon. *Journal of Herpetology*, 56(1), 75–83. <https://doi.org/10.1670/20-145>
- Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. L. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, 19(12), 654–660. <https://doi.org/10.1016/j.tree.2004.09.006>
- Struebig, M. J., Kingston, T., Zubaid, A., Mohd-Adnan, A., & Rossiter, S. J. (2008). Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation*, 141(8), 2112–2126. <https://doi.org/10.1016/j.biocon.2008.06.009>
- Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., & Bell, D. (2013). Quantifying the Biodiversity Value of Repeatedly Logged Rainforests. Gradient and Comparative Approaches from Borneo. In *Advances in Ecological Research* (Vol. 48, pp. 183–224). Academic Press Inc. <https://doi.org/10.1016/B978-0-12-417199-2.00003-3>
- Suarez-Rubio, M., Ille, C., & Bruckner, A. (2018). Insectivorous bats respond to vegetation complexity in urban green spaces. *Ecology and Evolution*, 8(6), 3240–3253. <https://doi.org/10.1002/ECE3.3897>
- Tang, S., Chen, J., Sun, P., Li, Y., Yu, P., & Chen, E. (2019). Current and future hydropower development in Southeast Asia countries (Malaysia, Indonesia, Thailand and Myanmar). *Energy Policy*, 129, 239–249. <https://doi.org/10.1016/J.ENPOL.2019.02.036>
- Terborgh, J., Pitman, N., Silman, M., Schichter, H., & Núñez V., P. (2009). Maintenance of tree diversity in tropical forests. In *Seed dispersal and*

- frugivory: ecology, evolution and conservation. *Third International Symposium-Workshop on Frugivores and Seed Dispersal, São Pedro, Brazil, 6-11 August 2000* (pp. 1–17).  
<https://doi.org/10.1079/9780851995250.0001>
- The World Bank. (2016). *Electricity production from renewable sources, excluding hydroelectric*. World Bank Indicators.  
<http://data.worldbank.org/indicator/EG.ELC.RNWX.KH>
- Torrent, L., López-Baucells, A., Rocha, R., Bobrowiec, P. E. D., & Meyer, C. F. J. (2018). The importance of lakes for bat conservation in Amazonian rainforests: an assessment using autonomous recorders. *Remote Sensing in Ecology and Conservation*, 4(4), 339–351.  
<https://doi.org/10.1002/rse2.83>
- Tovar, C. L. M. (2011). NDVI as indicator of degradation. *Unasylva*, 62, 39–46.  
[https://www.researchgate.net/publication/292666603\\_NDVI\\_as\\_indicator\\_of\\_degradation](https://www.researchgate.net/publication/292666603_NDVI_as_indicator_of_degradation)
- Waters, D. A., & Jones, G. (1995). Echolocation call structure and intensity in five species of insectivorous bats. *The Journal of Experimental Biology*, 198(Pt 2), 475–489. <https://doi.org/10.1242/JEB.198.2.475>
- Wildlife Acoustics. (2019). *Kaleidoscope Pro Analysis Software*.  
<https://www.wildlifeacoustics.com/products/kaleidoscope-pro>
- Williams-Guillén, K., & Perfecto, I. (2011). Ensemble Composition and Activity Levels of Insectivorous Bats in Response to Management Intensification in Coffee Agroforestry Systems. *PLOS ONE*, 6(1), e16502.  
<https://doi.org/10.1371/JOURNAL.PONE.0016502>
- Wilson, K. A., Meuaard, E., Drummond, S., Grantham, H. S., Boitani, L., Catullo, G., Christie, L., Dennis, R., Dutton, I., Falcucci, A., Maiorano, L., Possingham, H. P., Rondinini, C., Turner, W. R., Venter, O., & Watts, M. (2010). Conserving biodiversity in production landscapes. *Ecological Applications*, 20(6), 1721–1732. <https://doi.org/10.1890/09-1051.1>
- Yoh, N., Kingston, T., McArthur, E., Aylen, O. E., Huang, J. C. C., Jinggong, E. R., Khan, F. A. A., Lee, B. P. Y. H., Mitchell, S. L., Bicknell, J. E., & Struebig, M. J. (2022). A machine learning framework to classify Southeast Asian echolocating bats. *Ecological Indicators*, 136, 108696.  
<https://doi.org/10.1016/j.ecolind.2022.108696>
- Yong, D. L. (2015). Persistence of primate and ungulate communities on Forested Islands in Lake Kenyir in Northern peninsular Malaysia. *Natural History Bulletin of the Siam Society*, 61(1), 7–14.  
[https://www.researchgate.net/publication/285593139\\_Persistence\\_of\\_primate\\_and\\_ungulate\\_communities\\_on\\_forested\\_islands\\_in\\_Lake\\_Kenyir\\_northern\\_Peninsular\\_Malaysia](https://www.researchgate.net/publication/285593139_Persistence_of_primate_and_ungulate_communities_on_forested_islands_in_Lake_Kenyir_northern_Peninsular_Malaysia)
- Yong, D. L., Qie, L., Sodhi, N. S., Koh, L. P., Peh, K. S. H., Lee, T. M., Lim, H. C., & Lim, S. L. H. (2011). Do insectivorous bird communities decline on land-bridge forest islands in Peninsular Malaysia? *Journal of Tropical Ecology*, 27(1), 1–14. <https://doi.org/10.1017/S0266467410000520>

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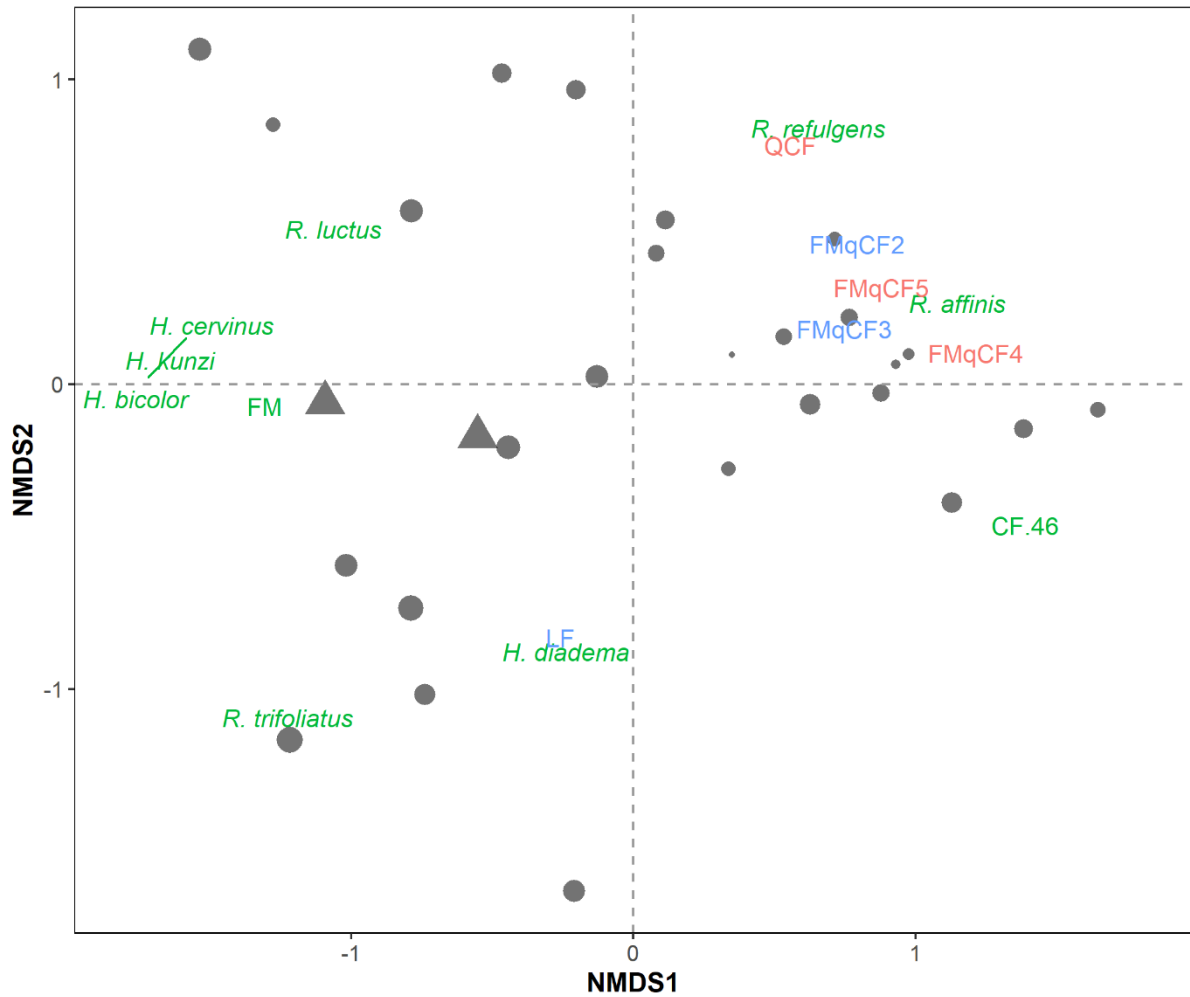
942 **Figures and Tables:**

943 *Colour should be used for figures 1, 2, 3, 4 and S1*



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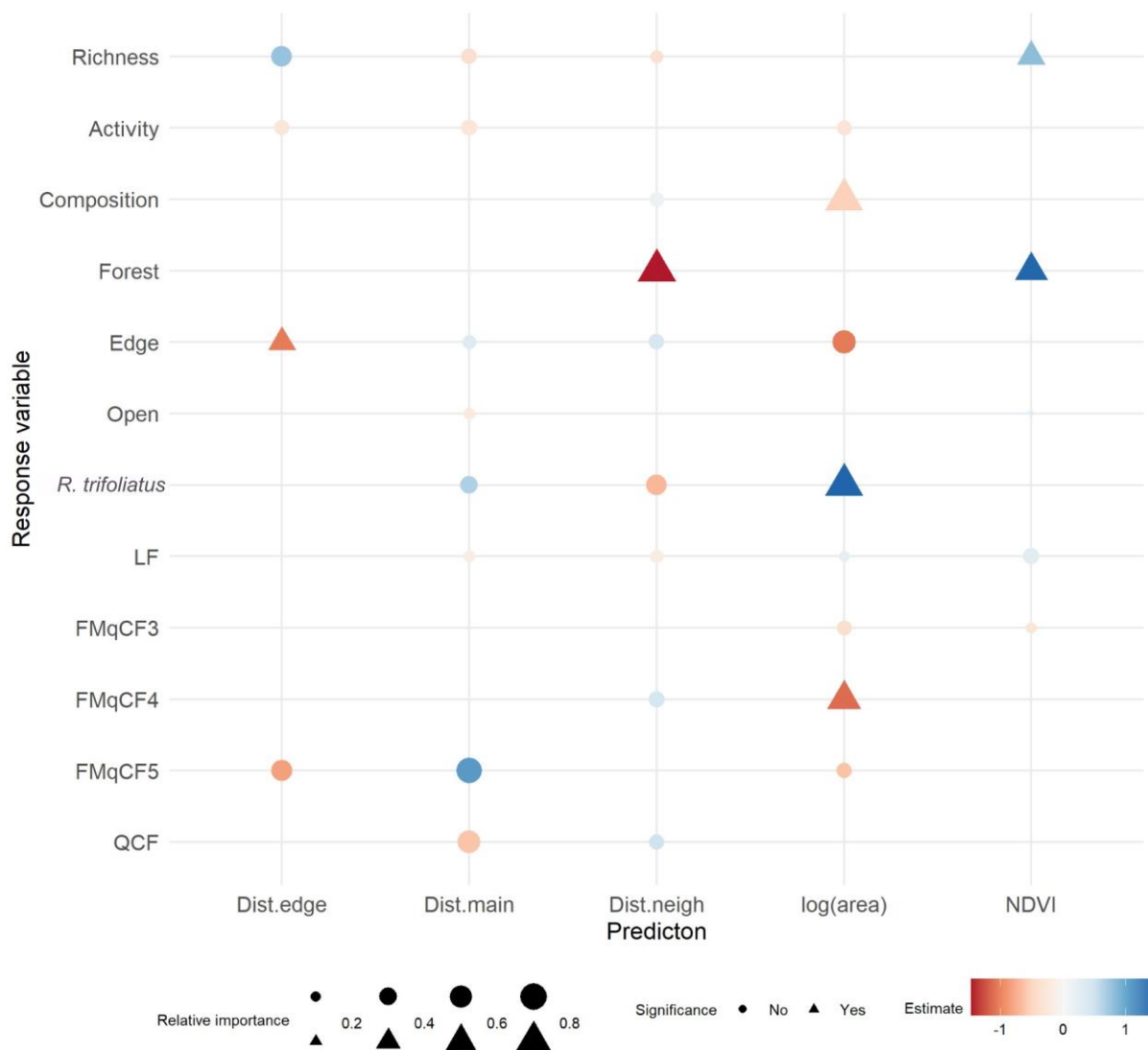
945 **Figure 1.** Map of the Kenyir Lake (A) Location of the study area and sampling sites  
946 in the Kenyir lake, peninsular Malaysia. The solid dots depict each of the 28  
947 sampling sites. (B) Distribution of island sizes in Kenyir lake. (C) Photo of the Kenyir  
948 Lake. *Two columns fitting image*



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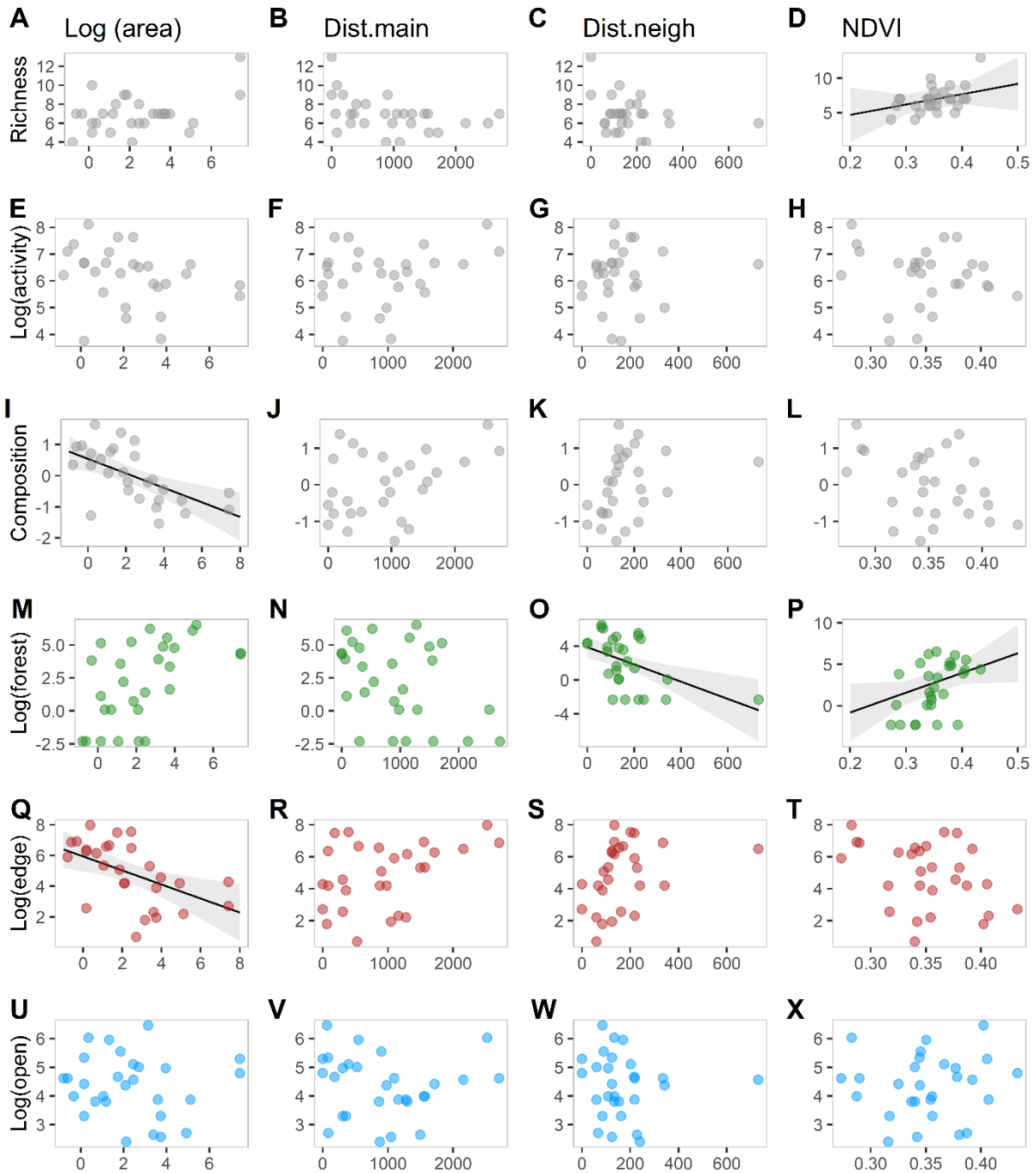
950 **Figure 2.** Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot denoting  
 951 both sampling sites and sonotypes. Sampling sites are represented by circles,  
 952 matching the islands which are sized proportionally to their size ( $\log_{10} x$ ), and  
 953 triangles correspond to the mainland continuous forest sites. Sonotypes are  
 954 represented by their name and colour-coded according to the corresponding foraging  
 955 guild: forest (in green), edge (red) and open-space (blue) (for further details  
 956 regarding each sonotype, see Table 1). Given that the sonotypes *H. kunzi*, *H.*  
 957 *cervinus* and *H. bicolor* are overlapping, for the sake of clarity, the position of these  
 958 sonotypes is replaced by a green line and the sonotypes labels are separated.  
 959 *Single column fitting image*





**Figure 3.** Results of the model averaging procedure. Response variables are shown on the y axis, and predictor variables are shown on the x axis. The variables that were retained in the model selection and averaging appear at the intersection between response and predictor variables. The value of each estimate is depicted with a colour gradient, negative estimates being increasingly red, and positive estimates being increasingly blue. The significance of each selected variable is shown with point shape: significant variables are represented with a triangle, and non-significant variables are shown with a circle. The relative importance of each selected variable within the averaged model is shown with point size, smaller points having a lower relative importance than larger points.

*Two columns fitting image*



**Figure 4.** Relationships between bat sonotype richness (A-D), activity ( $\log_{10} x$ ) (E-H), assemblage composition (axis 1 of the NMDS) (I-L), and the activity of forest ( $\log_{10} x$ ) (M-P), edge ( $\log_{10} x$ ) (Q-T), and open-space foraging bats ( $\log_{10} x$ ) (U-X) and Area ( $\log_{10} x$ ) (A, E, I, M, Q, U), distance to the mainland (*Dist.main*) (B, F, J, N, R, V), Distance to neighbour (*Dist.neigh*) (C, G, K, O, S, W) and *NDVI* (D, H, L, P, T, X). In each panel, the solid black line is the prediction given by the averaged model obtained from the dredge, and the shaded area represents the 95% confidence interval. The predictions of the selected model were only shown for significant variables.

*Two columns fitting image*

984 **Table 1.** List of all sonotypes identified during the acoustic bat surveys across the  
985 insular fragmented landscape of the Kenyir Lake, peninsular Malaysia. For each  
986 sonotype, we indicate the potential species matching that sonotype, corresponding  
987 foraging guild, total activity (number of bat passes), and number of sampling sites in  
988 which each of the sonotypes was recorded. Bat passes that could not be identified  
989 were labelled as “unknown”.

Sonotype name	Potential species	Guild	# of bat passes	# of sites occupied (%)
<i>H. diadema</i>	<i>Hipposideros diadema</i>	Forest	392	11 (39.3%)
<i>R. affinis</i>	<i>Rhinolophus affinis</i>	Forest	146	7 (25%)
<i>R. tricoloratus</i>	<i>Rhinolophus tricoloratus</i>	Forest	2268	12 (42.8%)
<i>R. luctus</i>	<i>Rhinolophus luctus</i>	Forest	6	2 (7.1%)
<i>R. refulgens</i>	<i>Rhinolophus refulgens</i>	Forest	2	1 (3.6%)
<i>H. kunzi</i>	<i>Hipposideros kunzi</i>	Forest	1	1 (3.6%)
<i>H. cervinus</i>	<i>Hipposideros cervinus</i>	Forest	1	1 (3.6%)
<i>H. bicolor</i>	<i>Hipposideros bicolor</i>	Forest	2	1 (3.6%)
CF.46	<i>Hipposideros lekaguli</i> <sup>2</sup>	Forest	1	1 (3.6%)
FM	Species from the subfamilies Kerivoulinae and Murinae, <i>Nycteris tragata</i> , <i>Coelops frithii</i> , <i>C. robinsoni</i> , <i>Lyroderma lyra</i> , <i>Megaderma spasma</i>	Forest	35	6 (21.4%)
LF	<i>Arielulus circumdatus</i> , <i>A. cuprosus</i> , <i>Chaerephon johorensis</i> , <i>Chaerephon plicata</i> , <i>Cheiromeles torquatus</i> , <i>Mops mops</i> ,	Open-space	2048	28 (100%)
FMqCF2	<i>Hesperoptenus blanfordi</i> , <i>H. doriae</i> , <i>H. tomesi</i>	Open-space	162	11 (39.3%)
FMqCF3	<i>Pipistrellus stenopterus</i>	Open-space	1441	27 (96.4%)
FMqCF4	<i>Tylonycteris robustula</i> , <i>Glischropus tylopus</i> , <i>Hesperoptenus blanfordi</i> , <i>P. tenuis</i> , <i>P. javanicus</i> , <i>Myotis adversus</i> , <i>M. horsfieldii</i> , <i>M. hasseltii</i> , <i>M. montivagus</i> , <i>Scotophilus kuhli</i> , <i>Miniopterus magnater</i> ,	Edge	13 195	28 (100%)
FMqCF5	<i>Glischropus tylopus</i> , <i>Tylonycteris pachypus</i> , <i>T. robustula</i> ,	Edge	389	15 (53.6%)

<sup>2</sup> This species has not been sampled around our study site to our knowledge

QCF	<i>Myotis ridleyi</i> , <i>M. muricola</i> , <i>M. ater</i> , <i>M. siligronensis</i> , <i>Pipistrellus tenuis</i>	Edge	119	16 (57.1%)
	<i>Emballonura monticola</i> ,			
Unknown	<i>Taphozous melanopogon</i> , <i>T. longimanus</i> ,		988	26 (92.8%)
	<i>Saccolaomius saccolamius</i> ,			

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