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Altered structure of bat–prey interaction networks in logged tropical forests revealed by metabarcoding

David R. Hemprich-Bennett[1,2] | Victoria A. Kemp[1] | Joshua Blackman[1] | Matthew J. Struebig[3] | Owen T. Lewis[2] | Stephen J. Rossiter[1] | Elizabeth L. Clare[1,4]

[1]School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

[2]Department of Zoology, University of Oxford, Oxford, UK

[3]Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent, UK

[4]Department of Biology, York University, Toronto, Ontario, Canada

Correspondence
David Hemprich-Bennett, Department of Zoology, University of Oxford, 11a Mansfield Road, Oxford, OX1 3SZ, UK.
Email: hemprich.bennett@gmail.com

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Abstract

Habitat degradation is pervasive across the tropics and is particularly acute in Southeast Asia, with major implications for biodiversity. Much research has addressed the impact of degradation on species diversity; however, little is known about how ecological interactions are altered, including those that constitute important ecosystem functions such as consumption of herbivores. To examine how rainforest degradation alters trophic interaction networks, we applied DNA metabarcoding to construct interaction networks linking forest-dwelling insectivorous bat species and their prey, comparing old-growth forest and forest degraded by logging in Sabah, Borneo. Individual bats in logged rainforest consumed a lower richness of prey than those in old-growth forest. As a result, interaction networks in logged forests had a less nested structure. These network structures were associated with reduced network redundancy and thus increased vulnerability to perturbations in logged forests. Our results show how ecological interactions change between old-growth and logged forests, with potentially negative implications for ecosystem function and network stability.

KEYWORDS
Borneo, conservation, ecological interactions, network ecology, rainforest degradation, tropical ecology

1 | INTRODUCTION

Many tropical forests have been degraded by human activity, leading to biodiversity loss (Barlow et al., 2016) as well as the modification of key ecological processes such as the regeneration of plant communities (Ghazoul et al., 2015). Land-use activities are the main driver of vegetation change in Asia (Song et al., 2018), with degraded forests being of particular conservation interest; these habitats may retain high biodiversity yet have minimal protection and are vulnerable to clearance for agriculture and development (Meijaard et al., 2018).

The island of Borneo hosts high biodiversity but has lost much of its old-growth forest, with 46% of its remaining forest classified as degraded by selective logging (Gaveau et al., 2014). Through this process many of the largest and most commercially important trees are removed, leaving a residual forest stand. While logged forests still provide potential wildlife habitat, they typically have a depleted tree community and altered vegetation and soil structure, although not to the same extent as secondary forests recovering from complete deforestation (Gibson et al., 2011). Given the large extent of logged forest in Borneo and other tropical regions, there is considerable interest in understanding the conservation value and viability of these disturbed habitats for biodiversity (Meijaard & Sheil, 2007; Melo et al., 2013), especially given their minimal conservation protection under current policies (Struebig et al., 2015). Mounting evidence suggests that selectively logged forests can support a substantial proportion of the original biota, and are generally more biodiverse than secondary forests (Gibson et al., 2011). Indeed, despite their degradation, Borneo's logged forests retain potentially important communities of ground-dwelling mammals (Deere et al., 2017), bats (Struebig et al., 2013), birds (Edwards et al., 2010) and invertebrates (Slade et al., 2011). Much less is understood, however, about how such habitat degradation impacts the ecological interactions among co-occurring species, such as between predators and prey, hosts and parasites, and plants and their pollinators (Andresen et al., 2018).

A powerful approach for understanding ecological interactions is through network analyses, in which interactions ("edges") are represented by links among biological "nodes" (usually species) (Cirtwill et al., 2018). These networks most commonly depict mutualisms such as pollination and seed dispersal (Bascompte, 2009) or antagonisms such as parasitism and predation (Lafferty et al., 2006). Measuring and comparing aspects of network structure can be informative about a system's resilience to perturbations (Memmott et al., 2004), the importance of component species to a given network function (Freeman, 1978), and the potential for competition between species (Bastolla et al., 2009). Ecological networks have revealed that even when habitat degradation results in increased species richness the community can be more vulnerable to secondary extinctions, showing an "extinction debt" (Magrach et al., 2016). Altered network structure may thus reveal functionally important shifts within ecological communities.

Highly mobile predators such as many birds and bats may be important for stabilizing numbers of prey throughout their habitat (McCann et al., 2005; McCracken et al., 2012), by dampening boom and bust cycles of their prey (Kunz et al., 2011). Forest degradation has been linked to lower bird abundances and reduced top-down control of herbivorous insects, thus increasing herbivory (Peter et al., 2015) and potentially affecting forest restoration (Böhm et al., 2011). Similarly, since bats may suppress herbivorous insects in rainforests (Kalka & Kalko, 2008), the loss of bats might be expected to alter ecosystem functioning via trophic cascades.

Research in palaeotropical forests suggests logging affects bat community composition and abundance by altering roost availability (Struebig et al., 2013), reflecting patterns seen in the neotropics (Peters et al., 2006). While altered bat communities might be predicted to show altered network structures, studies from mutualistic neotropical systems of bats dispersing seeds have shown little difference in network structure in fragmented forest, despite a reduction in the number of food species consumed (Laurindo et al., 2019), possibly as a result of highly resilient bat species which are core to their networks. Bat–seed dispersal networks can be robust to secondary extinctions (Mello et al., 2011), but parallels between mutualistic and antagonistic networks may be limited due to known differences in their structure (Lewinsohn et al., 2006; Thébault & Fontaine, 2010). Therefore, given the key roles of insectivorous bats as predators of arthropods in rainforests, an improved understanding of their feeding ecology and the relationship between forest type and network structure is a priority for the conservation research of bats in forest ecosystems (Meyer et al., 2016).

Genetic tools, particularly high throughput sequencing (HTS), are increasingly used for dietary analyses (Aizpurua et al., 2018; Clare et al., 2009; Czenze et al., 2018; Razgour et al., 2011). The application of DNA metabarcoding to bat and bird faeces makes it possible to obtain detailed information on previously unknown species interactions (Clare, 2014; Creer et al., 2016; Evans et al., 2016; Roslin & Majaneva, 2016). Traditional techniques for studying bat diet typically relied on morphological identification of prey remains, giving researchers a poor taxonomic resolution of the prey taxa consumed, whereas metabarcoding allows much greater levels of precision in dietary analysis (Clare, 2014).

Here we use DNA metabarcoding to assess the impact of rainforest degradation on predator–prey interactions, focusing on insectivorous bats that forage under the forest canopy in Borneo. We captured bats in old-growth and logged rainforest and analysed networks of their interactions with prey using sequence data generated from metabarcoding of their guano. Comparing the taxonomic composition, completeness and structure of these networks, we hypothesized that disturbance causes networks in logged forest to have lower functional complementarity and nestedness than networks in old-growth forest. We also hypothesized that bats in logged forest consume fewer prey taxa than those in old-growth forest.

2 | METHODS

2.1 | Sample collection

We sampled bats using harp traps in three sites within lowland tropical rainforest in Sabah, Malaysian Borneo. Sites were separated by distances of 34–94 km, <500 m above sea level and experiencing similar environmental conditions, with little within-year and between-year climatic variation. In total we sampled at 336 unique trapping locations over 420 trap nights, using up to six traps per night at two old-growth sites (Danum Valley Conservation Area, hereafter "Danum"; Maliau Basin Conservation Area, "Maliau"), and a site heavily disturbed by multiple rounds of logging: the Stability of Altered Forest Ecosystems Project ("SAFE"). For the old growth sites "Danum" and "Maliau," traps were set each night over a 10-night period in both 2016 and 2017. For the logged forest site, traps were set in two 15-night periods each in 2015, 2016 and 2017: the logged site was given a higher sampling effort than the old-growth sites as capture rates were lower, probably due to altered vegetational structure.

Traps were set on access trails and old logging skids, erected by midday each day, and then checked in the evening and following morning, after distinct peaks in bat foraging activity known at the site (8–9 p.m. and 7–8 a.m.) (Struebig et al., 2013). Bats were released immediately at the point of capture if they were pregnant, lactating or juvenile. Otherwise, captured bats were placed into individual cloth bags and processed at a research camp, where any guano was removed and stored at −20°C. Bats were hung in individual bags in a secure humid place during the night/day so that they could rest before release at the following trap check (i.e., all animals were released within 12 hr). For full information on fieldwork see Appendix S1: section 1. This work complied with the ethical and handling guidelines of the American Society of Mammologists, and was approved by Queen Mary University of London, Sabah Biodiversity Centre, Danum Valley Management Committee and Maliau Basin Management Committee (permit numbers in Appendix S1: Section 1).

2.2 | Laboratory work

To build a network of bat–insect interactions for each of the three forest sites studied (Danum, Maliau and SAFE), we sequenced prey DNA from bat guano using metabarcoding. Laboratory work took place following the protocol in Czenze et al. (2018). We extracted DNA from all guano pellets given by each bat using a Qiagen stool mini kit (Qiagen), alongside extraction negative controls, then amplified it using the ZBJ-ArtF1c and ZBJ-ArtR2c arthropod-specific primers (Zeale et al., 2011). Each 10-µl PCR (polymerase chain reaction) contained 5 µl of Qiagen multiplex PCR (Qiagen) master mix, 3 µl of water, 0.5 µl of each 10 µM primer and 1 µl of eluted DNA. The PCR cycling profile was 95°C, 15 min; 50 cycles of 95°C, 30 s; 52°C, 30 s; 72°C, 30 s, and 72°C, 10 min. Quality control (QC) took place on a DNA D1000 TapeStation (Agilent Technologies) and amplicons were quantified on a Qubit dsDNA HS Assay Kit (Invitrogen, Life Technologies). All sample and control amplicons were then sequenced bidirectionally with 10-bp Fluidigm indexes on the MiSeqv2 Chemistry using a 2 × 150-bp run with 300 cycles (Illumina) along with unrelated samples which act as a positive control on sequencing batch effects. PCR, QC and sequencing steps took place at the Genome Centre (Queen Mary University of London).

2.3 | Bioinformatics

The resulting sequences were merged into contiguous reads, the primers were removed, and the reads were length-filtered and collapsed to haplotypes with any singletons excluded from the resulting data set, before clustering sequences into molecular operational taxonomic units (MOTUs) using the Uclust algorithm (Edgar, 2010) in Qiime (Caporaso et al., 2010). To reduce costs and standardize sampling across sites, we restricted sequencing to the 10 bat species for which we were able to obtain at least 10 guano samples from one or more forest sites (see Table 1 for sample sizes). This approach was taken to ensure that, as much as is possible, networks contained the same sets of bat taxa. Many bat species trapped in this study are found across sites but at very low density, with their capture or absence at any given site largely a matter of chance. Including such species in a network would distort the values of network metrics, so we restricted analysis to a common set of species. Metrics analysed here such as "nestedness" (described below) should be seen as representing the core set of most common bat species and their interactions. Removing rare or unevenly distributed species was suggested by Blüthgen (2010) to reduce the confounding impact of observation frequency. We only took this approach for bats and not for insect prey, where diversity was much higher (see Section 3), and most MOTUs were rare.

TABLE 1 Bat species and samples used to construct the ecological networks

	Old-growth forest		Logged forest
	Danum	Maliau	SAFE
Hipposideros cervinus (fawn roundleaf bat)	184	90	110
Hipposideros diadema (diadem roundleaf bat)	2	10	3
Hipposideros dyacorum (Dayak roundleaf bat)	0	13	9
Hipposideros ridleyi (Ridley's roundleaf bat)	2	1	14
Kerivoula hardwickii (Hardwicke's woolly bat)	3	0	23
Kerivoula intermedia (small woolly bat)	29	9	44
Kerivoula papillosa (papillose wooly bat)	21	0	6
Rhinolophus borneensis (Bornean horseshoe bat)	1	26	10
Rhinolophus sedulus (lesser woolly horseshoe bat)	10	4	14
Rhinolophus trifoliatus (trefoil horseshoe bat)	14	19	28

Unless otherwise stated, we generated the three networks by clustering sequences into MOTUs at 0.95 similarity, chosen to balance over- and under-splitting of MOTUs. We then compared representative sequences of each MOTU to one another using Blast+ (Camacho et al., 2009), with the resulting data being filtered in Lulu (Frøslev et al., 2017) to combine suspected duplicate MOTUs. However, as the choice of clustering threshold used to cluster the sequence data into prey MOTUs can have a strong effect on the conclusions drawn (Clare et al., 2016; Hemprich-Bennett et al., 2020), we examine a range of clustering thresholds for a subset of the analyses to ensure that our conclusions are robust to our choice of this key parameter.

For a subset of analyses indicated below, networks were generated for each site at every MOTU clustering level from 0.91 to 0.98 similarity before quality control in Lulu, allowing us to test the robustness of conclusions to changes in clustering level used.

2.4 | Analysis

We imported binary adjacency matrices, showing the presence or absence of interactions between individual bats and the MOTUs that they consumed into R version 3.4.4 (R Core Team, 2017) for analysis. For network-level analyses, these matrices were then summed by bat species (i.e., a_{ij} denotes all instances of bat species *i* consuming MOTU *j*), giving weighting to the network. A weighting of “5” for interaction a_{ij} would show that we detected five instances of bat species *i* consuming MOTU *j* in a site.

To compare networks between logged and old-growth forest, we focused on two components of network structure: nestedness and functional complementarity (Figure 1). Nestedness represents the extent to which the interactions of specialist nodes are nested subsets of the interactions of the generalist nodes (Almeida-Neto et al., 2008), which in this case would correspond to specialist bats feeding on subsets of the prey of generalist bats, and the generalist bats consuming both commonly and rarely consumed prey. Highly nested communities are more resilient to perturbations (Memmott et al., 2004), as the generalists and specialists perform the same role, conferring redundancy. Decreases in the nestedness of plant–pollinator communities following disturbance leads to reduced functional redundancy (Soares et al., 2017). We calculated nestedness as weighted nestedness based on overlap and decreasing fill (WNODF) (Almeida-Neto et al., 2008) and discrepancy (both reviewed in Payrató-Borràs et al., 2020). In the context of trophic interactions, functional complementarity (Blüthgen & Klein, 2011; Devoto et al., 2012; Peralta et al., 2014) measures the extent to which species have complementary, nonoverlapping diets by measuring the branch lengths of a functional dendrogram of their dietary dissimilarity, where bat species are more closely positioned in a dendrogram based on how many prey they share (Petchey & Gaston, 2007). These metrics describe some of the most important elements of network structure and respond relatively consistently to alterations to MOTU clustering level (Hemprich-Bennett et al., 2020), while allowing us to assess how phenomena such as habitat alteration affect ecosystem functioning. We followed the recommendation in Hemprich-Bennett et al. (2020) to check how clustering level influences these conclusions, as outlined below.

To test whether each of these metrics differ significantly between logged and old-growth habitats more than would be expected by chance, we obtained two null distributions for each metric, network and clustering threshold: (i) using the “permatswap” algorithm (Oksanen et al., 2019) to randomize each network for each MOTU clustering level 1,000 times, preserving the row and column sums, and (ii) a more relaxed null-model using the “permatfull” algorithm (Oksanen et al., 2019), where row sums were allowed to vary. Two methods were then used to determine if the observed value was significantly different from the null-distribution. First, the observed value was deemed to be significantly different from chance if it was

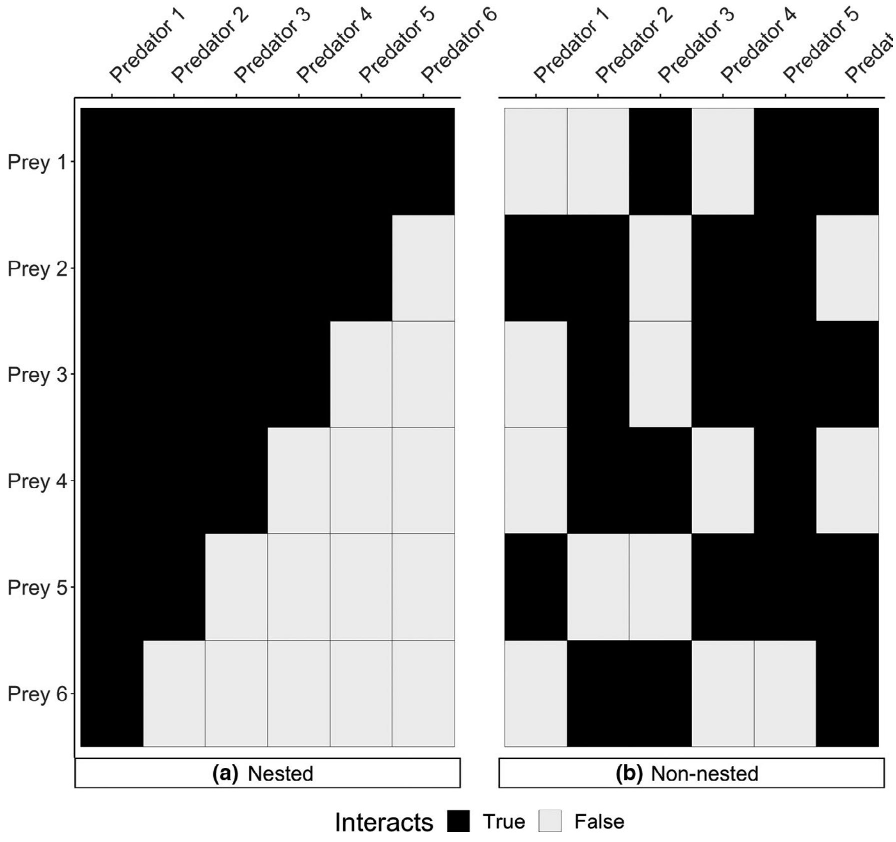

FIGURE 1 Networks characterized by extreme (a) nestedness and (b) non-nestedness in bipartite networks

outside of the "expected" range of 2.5%–97.5% of the randomly generated values. Two networks were also deemed different from one another if their "expected" ranges did not overlap. Second, a *z*-score was calculated for each metric, network, null-model and clustering threshold, using the formula (observed value − mean of the null-values)/*SD* of the null-values. Values close to 0 indicate an observed value which falls within the range expected based on the null model.

Choice of MOTU clustering threshold in ecological metabarcoding studies has been shown to alter measurements of most network metrics (Hemprich-Bennett et al., 2020), and so to assess the impact of node resolution on the networks analysed here, we performed this analysis on data generated at each MOTU clustering threshold between 91% and 98%. A conclusion can be considered to be robust if it is consistently found across all MOTU clustering thresholds used.

As sample size varied greatly across species and sites (Table 1), we checked the impact of sample size and species diversity included in our analysed networks by using random subsamples of the bats captured at each site to generate smaller networks ranging from 40 individuals to the full network dimension, with 1000 iterations per increment. Each focal metric was calculated for the subnetworks, and the Shannon diversity (Shannon, 1948) of nodes used to create the network was recorded. These values were plotted to observe if network size (number of individuals used to make the network) or bat diversity were important determinants of network structure. If the rank order of a measured metric was not shown to be strongly determined by network size or bat diversity, then any conclusions drawn from it can be considered robust to sampling effort. We also calculated each network-level metric using every possible subset of bat species from the pool of bats sequenced for each network, and using only the most abundant bat species sequenced, to estimate how robust our conclusions were to the species selection criteria.

To determine the contribution of a given bat species to the measured networks, we also generated subnetworks by removing each species individually from the original networks and calculating each network metric. The influence of the species was then calculated by subtracting the subnetwork's measured value from the whole-network value. We then ranked these calculated differences to show which species had the greatest and smallest impact on each network metric per site. Species' influence on the networks was also calculated by "species strength" as used by Bascompte et al. (2006).

To obtain information on the taxonomic composition of bat diets, we compared a representative sequence for each MOTU using Blast+ 2.7.1 (Camacho et al., 2009) against a database of arthropod CO1 sequences from the Barcode Of Life Database (BOLD) (Ratnasingham & Hebert, 2007), as accessed on April 27, 2018. Using the program Megan 6.11.7 (Huson et al., 2016) and the quality-control parameters outlined in Salinas-Ramos et al., (2015), we excluded all sequences that could not be assigned to order level, and used the Blast assignments to determine the taxonomic composition of each guano sample. For each bat species at each site, we calculated the proportion of individuals that consumed a given order of prey. We focused on taxonomic order (rather than, e.g., family or genus) due to the greater success in sequence assignment (1921 MOTUs assigned to order, compared to 692 MOTUs assigned to family) at this level as sequence library completeness for Bornean arthropods is low.

To assess whether bats in logged forest consume fewer discrete prey taxa than in old-growth forest, we calculated the degree (number of prey MOTUs consumed) for each individual bat using the R package "bipartite" (Dormann et al., 2008) and analysed these data with a fixed effects model, using species, habitat type (old-growth or logged forest) and site as fixed effects, using backwards model selection with the Akaike information criterion (AIC), to detect whether models using habitat type or site were stronger predictors of bat degree.

To assess the potential presence of prey species in bat diets, we compared our sequence data to publicly available sequences on BOLD (Ratnasingham & Hebert, 2007) on June 1, 2018 using the R package "bold" (Chamberlain, 2019). We assigned sequences to species level using the highest obtained "similarity" score per sequence if it was >0.98. The output data were then compared to a list of Malaysian crop pest species names obtained from Vun Khen (1996).

Beta-diversity of MOTUs detected between each site and year was calculated using Whittaker's beta-diversity (Whittaker, 1960), and Bray–Curtis dissimilarity of the diets of each bat species was calculated, both using the R package "vegan" (Oksanen et al., 2019).

All code used for analyses in this paper can be found at: https://doi.org/10.5281/zenodo.5236561; see Appendix S1: section 2 for additional detail on laboratory work and bioinformatic analyses.

3 | RESULTS

We captured 3292 bats of 41 species, and from the 961 faecal samples collected, sequenced 699 from 10 focal species (Table 1). These 699 faecal samples yielded 18,737,930 contiguous reads, ($\bar{x}$ 19,324 *SD* 11,573 for each guano sample, $\bar{x}$ 3,925 *SD* 222 for negative controls) which were used to assemble the paired-end files. After removing adapters and primers, and any sequence with incomplete adapter or primer, this was reduced to 10,064,815 sequences, which was further reduced to 932,459 unique haplotypes after collapsing to haplotype, removing singletons, and discarding sequences outside of 2 bp of the expected read-length. At 95% clustering this was condensed to 14,623 MOTUs, which LULU then reduced to 3526 MOTUs (see Appendix S1: section 3). For basic network plots see Appendix S1: section 4, for network summary statistics see Appendix S1: section 5, and for degree distributions of nodes within the networks see Appendix S1: section 6.

Null models (Figure 2, Table 2) indicated that the logged site was consistently less nested than the old-growth sites (using the metrics "discrepancy" and "WNODF"). In an old-growth forest site (Danum), values for functional complementarity were almost always within the expected range. No metrics analysed showed alterations in their rank order between the different MOTU clustering thresholds used, and so any conclusions drawn are unaltered

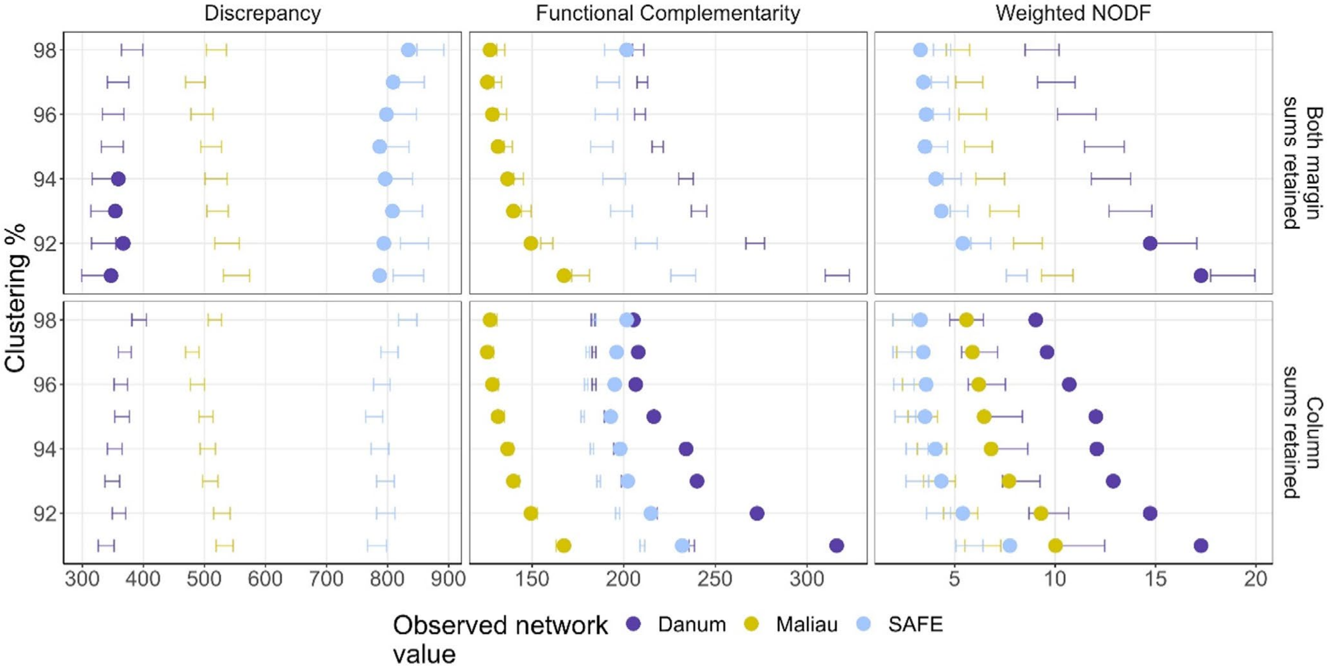

FIGURE 2 Summary plot showing the observed values (circles) and 95% confidence intervals (bars) given by the random values generated for each metric studied at each MOTU clustering level, showing how conclusions drawn are altered by MOTU clustering level. Two null-models are plotted, "both margin sums retained" (the more constrained model) and "column sums retained" (the more relaxed model). Danum and Maliau are the old-growth sites, and SAFE is the logged site. The observed values for each network were only plotted for the networks and metrics where the observed values fell outside of the range of 95% of the random values. For SAFE, the observed network value was plotted at all clustering thresholds because it fell outside the 95% confidence intervals (CIs) of the random values, but many observed values for Danum or Maliau are not shown as they fell within the 95% CI. For most metrics studied, the 95% CIs do not overlap at most clustering levels used, showing that the networks differ regardless of clustering level used

by this bioinformatic parameter. Relatively high values of WNODF would indicate a nested structure, and relatively low values of functional complementarity indicate less complementarity between the predators. Functional complementarity in logged forest was intermediate between the old-growth sites, and was probably not impacted by habitat degradation. While the logged forest site (SAFE) was consistently more less nested than the two old-growth forest sites, at some clustering thresholds for these metrics one of the old-growth sites (Maliau) was closer in value to the logged forest site than it was to the other (Danum), indicating that not all between-site network differences can be attributed to the logging. The common bat species Hipposideros *cervinus* and *Kerivoula intermedia* had the highest species strengths across sites (Appendix S1: section 7), and their removal caused the largest alteration to most metrics (see Appendix S1: section 8). *Rhinolophus borneensis* was shown to be important for the functional complementarity of an old-growth site (Maliau).

Rarefaction revealed little impact of the diversity or richness of bats included in a network on any observed metric, but strong effects of the number of samples used to generate a subnetwork (see Appendix S1: section 9). Functional complementarity and WNODF showed distinctions between logged and old-growth forest sites once sampling effort approached completion. Reducing the number of bat nodes in a network to the possible subsets of bat species sequenced altered the network metrics calculated, but it only consistently altered the rank order of the networks studied for a given metric when a large number of bat species were removed (Appendix S1: section 10) and importantly was robust to removing the rarer species (Appendix S1: section 11), showing that our criteria for deciding which samples to sequence probably had little effect on the conclusions.

The lowest AIC was given for models retaining all three explanatory variables (site, habitat type and species) to explain a bat's degree (number of MOTUs detected). Using this model we found a significant difference in degree for bats in old-growth vs. logged forest (*F*: 84.84 on 11 and 688 *df*, $p < .01$, adjusted $R^2 = .57$; see Table 3). The effect of habitat type on the number of MOTUs consumed by an individual bat (its degree) was greater than the effect of species identity (Table 3, Figure 3), with bats in old-growth forest consuming a greater number of MOTUs than bats in logged forest. There was no significant difference shown between the two old-growth forest sites. The difference was lowest in *Hipposideros* species and greatest in *Rhinolophus* species such as *R. trifoliatus*. This lower degree in logged forest shows that bats in this habitat generally consumed a lower richness of prey items than their conspecifics in old-growth rainforest.

Lepidoptera, Diptera (especially Cecidomyiidae) and Blattodea (especially Ectobiidae) were the most common prey orders consumed

TABLE 2 Observed network values for Danum and Maliau (old-growth) and SAFE (logged), and *Z*-values calculated by the formula observed value − mean of the null-values)/*SD* of the null-values

		Danum			Maliau			SAFE		
Metric	**Clustering threshold**	**Observed value**	**Z-score: both margin sums retained**	**Z-score: column sums retained**	**Observed value**	**Z-score: both margin sums retained**	**Z-score: column sums retained**	**Observed value**	**Z-score: both margin sums retained**	**Z-score: column sums retained**
Discrepancy	91	347	2.46	1.189	531	−1.967	−0.232	787	−3.649	0.477
	92	367	2.964	1.147	524	−1.296	−0.671	794	−4.131	−0.388
	93	354	2.26	0.801	511	−1.15	0.24	808	−2.368	1.381
	94	359	2.716	0.922	504	−1.593	−0.39	796	−2.136	1.069
	95	364	1.444	−0.201	502	−1.091	−0.063	787	−2.601	1.248
	96	362	1.255	−0.166	492	−0.389	0.647	798	−2.691	1.061
	97	376	1.94	1.167	482	−0.4	0.24	809	−2.777	0.737
	98	398	1.971	0.923	523	0.398	0.965	834	−3.268	0.108
Functional complementarity	91	316.124	−0.032	101.319	167.424	−3.455	5.377	231.882	−0.017	34.222
	92	272.728	0.467	78.016	149.399	−4.97	−4.616	214.833	1.02	32.661
	93	239.978	−0.441	62.917	139.82	−4.838	−4.606	202.16	1.276	32.19
	94	234.001	0.149	60.275	136.667	−4.217	−4.3	198.062	1.443	32.575
	95	216.422	−1.282	42.508	131.422	−4.48	−6.447	192.914	1.812	33.465
	96	206.548	−1.565	41.19	128.398	−4.291	−6.126	195.107	1.66	32.403
	97	207.916	−1.346	44.778	125.592	−4.822	−7.287	196.14	1.693	31.848
	98	205.265	−1.627	42.67	127.111	−5.009	−8.81	201.62	2.221	35.36
WNODF	91	17.265	−2.722	10.066	10.021	−0.156	7.954	7.745	−1.334	6
	92	14.733	−2.244	9.817	9.299	1.764	9.532	5.401	−3.54	3.878
	93	12.894	−1.577	9.371	7.702	0.595	8.722	4.332	−3.81	4.161
	94	12.075	−1.341	8.742	6.811	0.098	7.627	4.046	−3.435	3.464
	95	12.028	−0.96	9.44	6.463	0.774	8.042	3.518	−3.167	3.69
	96	10.704	−0.815	8.334	6.199	0.968	8.865	3.573	−3.447	4.268
	97	9.596	−1.003	7.24	5.884	0.405	8.777	3.437	−3.632	4.352
	98	9.032	−0.699	7.994	5.586	1.406	8.887	3.295	−4.893	3.568

Notes: Two null-models are shown, “both margin sums retained” (the more constrained model) and “column sums retained” (the more relaxed model). All numbers are given to a maximum of three decimal places.

TABLE 3 Degree model coefficients from fixed effects model, testing for the effects of habitat type (logged or old-growth) and species identity on the degree of the individual bats studied

Term	Estimate	*SE*	Statistic	*p*
Habitat: Logged	9.078	0.874	10.384	<.001
Habitat: Old-growth	14.330	0.630	22.740	<.001
Site: Maliau	−1.903	1.187	−1.603	.109
Site: SAFE	NA	NA	NA	NA
H. diadema	−2.680	2.948	−0.909	.364
H. dyacorum	−5.045	2.458	−2.053	.040
H. ridleyi	2.407	2.820	0.854	.394
K. hardwickii	−0.915	2.336	−0.392	.695
K. intermedia	0.708	1.382	0.512	.609
K. papillosa	−3.681	2.230	−1.651	.099
R. borneensis	4.198	1.928	2.178	.030
R. sedulus	0.617	2.201	0.281	.779
R. trifoliatus	2.491	1.552	1.605	.109

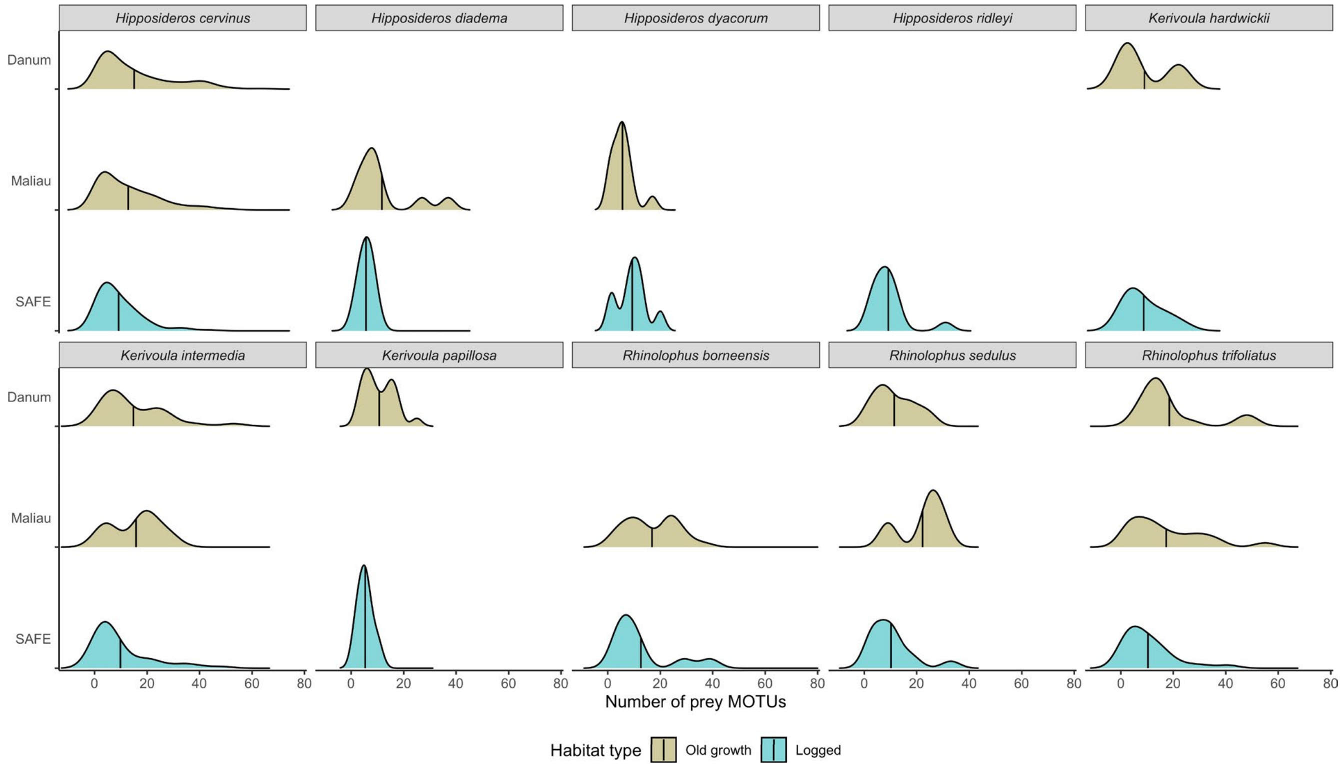

FIGURE 3 Smoothed histograms showing the number of MOTUs consumed by the individual bats for each focal bat species at each site. Species on average consumed a greater number of MOTUs in old-growth forest than in logged forest. The *y*-axis is unique for each species, but is uniform within a species. The vertical line within a plot shows the mean number of prey MOTUs for that bat species at that site

(Figure 4; Appendix S1: section 12). The lepidopteran pest species *Pleuroptya balteata* was detected in the diet of several bat species (Appendix S1: section 13) and at each site sampled, and *Psilogramma menephron* was consumed by *H. cervinus* in the logged forest site. However, relatively few individual bats were recorded as consuming these species.

Beta-diversity of MOTUs detected between sites and sampling events was high (Appendix S1: section 15), and between species (Appendix S1: section 16).

4 | DISCUSSION

We found substantial differences in bat–insect interactions between logged and old-growth forest networks. Bats consumed significantly fewer prey MOTUs in the logged forest site than both old-growth forest sites; indeed, habitat type had a stronger effect on the number of MOTUs consumed by an individual bat than species identity.

Network structure also differed in several key aspects between the logged forest and old-growth sites. Structural differences in

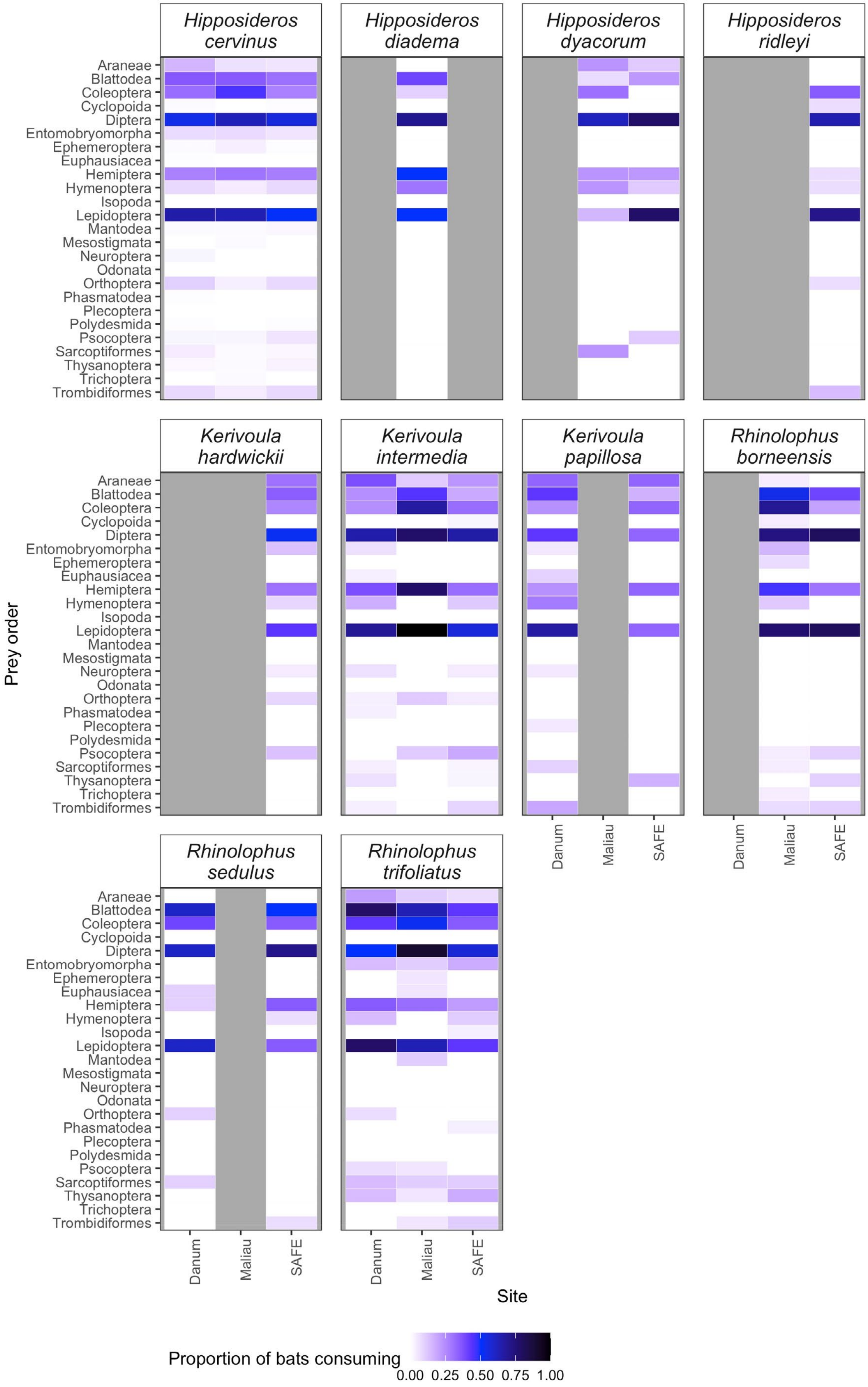

FIGURE 4 The proportion of individual bats of each species found to consume each taxonomic order at each site studied

nestedness indicate that logged forest networks are more specialized than old-growth rainforest networks. Systems that are specialized in this manner may be more vulnerable to extinctions than those with a more generalized structure (Memmott et al., 2004), such as the old-growth rainforest networks analysed. Rainforests in Southeast Asia are facing multiple stressors, including the effects of selective logging, habitat fragmentation and climate change (Deere et al., 2020; Struebig et al., 2015). Our findings of altered network structure in an area which has been selectively logged indicate that such logged forests may be more sensitive to the effects of these future perturbations.

Bats foraging within the logged forest site consumed fewer prey MOTUs than those within old-growth forest. For example, *Rhinolophus trifoliatus* consumed a mean of 10 MOTUs in the logged forest at SAFE, but a mean of 17 at Maliau and 18.5 at Danum (*SD* 9.5 at SAFE, 14.2 at Maliau, 13.4 at Danum). Indeed, the effect of habitat type was greater than that of the bat species in question, showing a strong alteration to foraging activity within logged forest. The most abundant bat species were found to have key roles in the structuring of their networks (Appendix S1: sections 7 and 8). Common predators will encounter a greater richness of prey than rarer species, through the ecological sampling effect (Dormann et al., 2017). While rare nodes are thought to have a stabilizing effect on ecological networks (McCann, 2000) and are of conservation interest, abundant species are probably key to ecosystem functioning (Baker et al., 2018) as they are involved in a high proportion of the trophic energy transfer within a system. A possible strategy for conservation of ecological function could therefore be to prioritize the species most important to a system (Montoya et al., 2012). If, using this framework, we find that the most common bat (*Hipposideros cervinus*) is probably the species most key to the network, while also being the species with the least reduction in the number of prey MOTUs it consumes in the logged forest site (Figure 3).

Diptera and Lepidoptera were commonly consumed across all bat species, with Blattodea also being consumed frequently (Figure 4). Most of the consumed members of Blattodea were within the family Ectobiidae (Appendix S1: section 12), a family of cockroaches which had not previously been documented to be important for rainforest bats. Two species of moths known as crop or forestry pests were found in bat diets: *Pleuroptya balteata* was consumed at all sites and *Psilogramma menephron* was consumed in the logged forest. Although they represented only a small percentage (0.4%) of the MOTUs consumed by the bats overall, the bats were foraging in forest habitat and so these prey species are probably occurring at lower densities than would be expected in managed landscapes. Natural habitats can be important sources of pests to nearby agricultural areas (Tscharntke et al., 2007) and so their consumption by predators is potentially of some economic importance; in this case *Ps. menephron* is an important pest of timber trees and *Pl. balteata* feeds on leaves of mango, tea and rambai (Vun Khen, 1996). These observations represent one of the few examples of bats in the region consuming pests, potentially providing ecosystem services.

Due to the highly labour-intensive nature of capturing forest-interior bats it was only possible to sample three ecological networks. With limited replication (only one logged forest site and two old-growth sites sampled), it is not possible to attribute differences between the sites unambiguously to the effects of logging, rather than other site-specific differences. In particular, while our species-removal analyses show our conclusions are robust to species-inclusion criteria (Appendix S1: sections 10 and 11), we caution that the data sets are a sample of the overall bat community. Beta-diversity of MOTUs detected between the sampling events was high (Appendix S1: section 15), indicating probable sampling incompleteness, although we stress that the most functionally important interactions are typically captured in “incomplete” networks (Hegland et al., 2010). Sampling completeness is a common issue in both tropical entomology (Novotný & Basset, 2000) and network ecology (Chacoff et al., 2012), due to the large number of species and interactions and the frequently prohibitive sample sizes required to fully sample a site. Interaction weighting of our network was generated using the frequency with which an interaction was detected, but this may understate the importance of specialists in a system because while their individual interactions may in fact be stronger than those of generalists (e.g., consuming a greater biomass of the prey nodes which they interact with), an individual's strong interaction in nature could be interpreted as equivalent to any of the more abundant weak interactions belonging to a generalist. However, using weighting in ecological networks remains more informative of network structure than omitting weighting and constraining a network to be binary (Bersier et al., 2002). The networks studied are also composites of multiple sampling events, due to the low proportion of bats and interactions in a site that can be captured per round of sampling. While internetwork differences are assumed to be due to differences in bat feeding between sites, it is impossible to exclude temporal effects. Bats sampled for this study were necessarily restricted to adult males and nonreproductive adult females. As there is some evidence for demographic differences in bat diet (Czenze et al., 2018), it is possible that this affected our data set. However, as this criterion was applied uniformly across all study sites, it is unlikely to have altered our conclusions.

This work documents marked differences in network structure across the landscape that are consistent with variations in forest management, and which are likely to have implications for community stability and dynamics. It also highlights the utility of metabarcoding-based approaches for more comprehensive investigation of between-habitat differences in tropical forest predator–prey networks. The PCR primers used are the most commonly used primer pair for studying insectivorous bat diet, and so their performance is well known. However, they have previously been stated to preferentially amplify Diptera and Lepidoptera (Alberdi et al., 2018), and so the frequent detection of these orders may be due to primer bias. However, insectivorous bats such as the species studied here are broadly expected to feed predominantly on Diptera and Lepidoptera (Arrizabalaga-Escudero et al., 2019; Bell & Fenton, 1984; Clare et al., 2009), and a test of the correlations between occurrences of prey orders in our sequencing data (Appendix S1:

section 14) found few negative correlations between these two orders and any others detected.

5 | CONCLUSIONS

Combining DNA metabarcoding and network analysis allowed us to measure how the ecological interactions which structure ecological communities differ between logged and old-growth forest. We show that in a logged forest bats and their prey exhibit altered network structures, which make them more at risk of local extinctions, adding to the previous findings that logged forest bat communities have altered composition and abundance (Struebig et al., 2013). Logged forests, although often heavily degraded, comprise a large proportion of the remaining rainforest extent and support considerable biodiversity, and so are highly important for conservation. However, our data also indicate that such forests are potentially more fragile than their old-growth counterparts, and so efforts should be made to reduce future environmental perturbations where possible.

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AUTHOR CONTRIBUTION

S.R., E.C., D.H.B., M.S. and O.T.L. conceived the project, D.H.B., V.K. and J.B. undertook field collections and laboratory work, D.H.B. analysed the data with input from E.C., and D.H.B. wrote the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT

Field and sequencing data are archived at https://doi.org/10.5281/zenodo.3247465. Analysis scripts are available at https://doi.org/10.5281/zenodo.5236561.

ORCID

David R. Hemprich-Bennett https://orcid.org/0000-0002-3555-4295
Joshua Blackman https://orcid.org/0000-0002-5260-3677
Matthew J. Struebig https://orcid.org/0000-0003-2058-8502
Owen T. Lewis https://orcid.org/0000-0001-7935-6111
Stephen J. Rossiter https://orcid.org/0000-0002-3881-4515
Elizabeth L. Clare https://orcid.org/0000-0002-6563-3365

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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