Tropical forest dung beetle-mammal dung interaction networks remain similar across an environmental disturbance gradient

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ABSTRACT

Conservation outcomes could be greatly enhanced if strategies addressing anthropogenic land-use change considered the impacts of these changes on entire communities as well as on individual species. Examining how species interactions change across gradients of habitat disturbance allows us to predict the cascading consequences of species extinctions and the response of ecological networks to environmental change. We conducted the first detailed study of changes in a commensalist network of mammals and dung beetles across an environmental disturbance gradient, from primary tropical forest to plantations, which varied in above-ground carbon density (ACD) and mammal communities. Mammal diversity changed only slightly across the gradient, remaining high even in oil palm plantations and fragmented forest. Dung beetle species richness, however, declined in response to lower ACD and was particularly low in plantations and the most disturbed forest sites. Three of the five network metrics (nestedness, network specialization, and functionality) were significantly affected by changes in dung beetle species richness and ACD, but mammal diversity was not an important predictor of network structure. Overall, the interaction networks remained structurally and functionally similar across the gradient, only becoming simplified (i.e., with fewer dung beetle species and fewer interactions) in the most disturbed sites. We suggest that the high diversity of mammals, even in disturbed forests, combined with the generalist feeding patterns of dung beetles, confer resilience to the commensalist dung beetle-mammal networks. This study highlights the importance of protecting logged and fragmented forests to maintain interaction networks and potentially prevent extinction cascades in human-modified systems.

Keywords: Borneo, land-use gradient, Scarabaeidae, ecological network, species interactions, habitat modification, above-ground carbon, logging, oil palm, commensalist networks

INTRODUCTION

Tropical forests play a significant role in regulating climate and the carbon cycle (Malhi et al., 2014), and protection of pristine tropical forest has long been a focus for conservation (Gibson et al., 2011; Gaveau et al., 2014). However, anthropogenic habitat modification, such as logging and conversion to agriculture, results in forest fragmentation (Betts et al., 2019) and generates novel landscapes (Haddad et al., 2015; Malhi et al., 2014). In turn, this can lead to widespread species extinctions, reshaped community structure, and altered ecosystem functions.

Loss of large-bodied mammals through hunting, habitat degradation, and fragmentation is one of the most ubiquitous anthropogenic impacts on biodiversity globally (Lino et al., 2019; Brodie et al., 2021). These losses also impact tree populations through altered mutualistic and antagonistic interactions (e.g., Chanthorn et al., 2019; Granados et al., 2017). But how defaunation indirectly affects other animals, particularly commensal species, is relatively understudied (Malhi et al., 2016; but see Nichols et al., 2013b). In particular, the effects of mammal defaunation on dung beetle (Scarabaeidae) communities is an important, yet largely neglected, area (Fuzessy et al., 2021; Raine & Slade, 2019)

Dung beetles primarily utilize mammal dung for feeding and breeding; in the process they perform critical ecosystem functions in tropical forests including nutrient recycling, soil bioturbation, and seed dispersal (Nichols et al., 2008). Dung beetle community responses to forest disturbance have been well-documented (Nichols et al., 2007; Nichols et al., 2013). They tend to be minimally affected by selective, low-intensity logging (Slade et al., 2011; Franca et al., 2017), but to undergo altered community composition and the loss of certain functional groups in monocultural plantations (Gray et al., 2014; Beiroz et al., 2019). Indeed, land-use changes and defaunation have strong effects on dung beetle communities globally, reducing overall abundance, richness, diversity, and mean body size (Fuzessy et al., 2021). While dung beetles are often considered to be broadly generalist, most actually exhibit preferences for particular types of dung (Frank et al., 2018; Raine & Slade, 2019; Raine et al., 2019b), suggesting that the loss of particular mammals could alter the composition of dung beetle communities. However, interactions between dung beetles and mammals, and how these interactions are modulated by abiotic conditions and environmental change, remain little studied. Without quantitative data on dung beetle-mammal networks, the specificity of the interactions, and species' plasticity in their associations, it is difficult to understand the cascading effects of mammal defaunation on dung beetle communities (Raine et al., 2018; Raine & Slade, 2019).

An overlooked consequence of biodiversity loss is the collapse of ecological interactions, which often accompany or even precede species loss (Tylianakis & Morris, 2017). However, the extent to which biodiversity loss affects the interactions among species remains poorly understood (Heleno et al., 2020; Poisot et al., 2021). The effects of habitat modification on biodiversity, particularly in tropical ecosystems, are often assessed by measuring species richness and diversity – metrics that do not adequately account for the ecological roles of, and interactions among, the species in the community (Van Der Putten et al., 2004). Moreover, the focus on individual species or trophic groups has meant that important community-level information on interaction diversity, identity, and resilience is often missed (Pillai et al., 2011).

Ecological networks describe the structure of a community based on the distribution and strength of interactions. Extracted metrics and models can calculate differences at the network level (Tylianakis & Morris, 2017), determine important species both within habitats and at the landscape-scale (Hackett et al., 2019), and help predict how a community will respond to perturbation (Bartley et al., 2019). For example: *Weighted nestedness* quantifies the amount by which the interactions of specialist species are a subset of those of generalists. If specialist species are lost from a highly nested network, the generalist core of the network can be retained, potentially increasing the probability of species coexistence (Rohr et al., 2014). However, it is less clear how this equates to network stability over time (Mariani et al., 2019; Landi et al., 2018). *Network specialization* measures how specialized the interactions are across the network (Blüthgen et al., 2006) based on the degree of resource partitioning across all interacting species. *Interaction evenness* calculates the degree of homogeneity in interaction frequencies across the network and can indicate dominance by particular species. *Generality* gives the weighted ratio of lower trophic levels (e.g., mammal dung) to upper trophic levels (e.g., dung beetle species), and *vulnerability* gives the weighted ratio of higher trophic levels (e.g., dung beetle species) to lower trophic levels (e.g., mammal dung). (Schoener, 1989; Tylianakis et al., 2007).

The majority of networks studied are antagonistic networks, where one species benefits at the cost of another (e.g. host-parasitoid networks (Morris et al., 2014)), or mutualistic networks where both organisms benefit (e.g. pollinator-plant interactions (Dalsgaard et al., 2011)). Commensalist networks, involving interactions where one species benefits without causing affecting the fitness of the other (e.g. dung beetle-mammal dung (Raine et al., 2018), remoras attached to sharks (Mougi, 2016), and epiphytes with their host trees (Sayago et al., 2013)), have been far less studied. Moreover, unlike antagonistic or mutualistic interactions, studies on commensalist networks have tended to focus on single study sites or habitats, resulting in a limited understanding of how commensalist networks change across disturbance gradients.

This is a critical knowledge gap, given the myriad of interactions in nature that are commensal (Poisot et al., 2021).

Here we investigated how a commensalist network responded to changes across a broad disturbance gradient in the tropical forests of Sabah, Malaysia, providing the first quantitative dung beetle-mammal dung interaction networks for Asian forests. We assessed how changes in mammal diversity and above-ground carbon density (ACD) from primary forest to logged and fragmented forest to rubber and oil palm plantations affected the structure of dung beetle-mammal interaction networks. As dung beetles are known to be affected by logging, hunting of mammals, and conversion of forest to agriculture (Fuzessy et al., 2021; Nichols et al., 2007), we predicted that dung beetle diversity would decrease with increasing disturbance, leading to changes in network structure. We predicted that specialist interactions would be most prone to loss, resulting in the networks becoming more nested and less even, with higher generality and lower functionality (see Methods for detailed predictions on each network metric). However, as the abundance and diversity of mammals and dung beetles often remains high in selectively logged forest (Deere et al., 2017; Granados et al., 2016; Slade et al., 2011), we expected changes in the network metrics to be strongest in the most disturbed (fragmented forest and plantation) habitats. We therefore predicted that the dung beetle-mammal dung networks would remain relatively similar in their metrics in primary and logged forests but that they would become simplified (i.e., fewer dung beetle species and interactions) in the most disturbed sites and where mammal diversity was low. In other words, we predicted a threshold after which the network structure would change considerably in response to forest disturbance.

MATERIAL AND METHODS

Study Site

The study was carried out in a 261,000 ha landscape in the Tawau Region of Sabah, Malaysian Borneo (4° 28’ N to 5° 06’ N; 116° 49’ E to 1et17°30’ E) (Figure 1). Annual rainfall averages ~3,000 mm and mean temperatures vary between 24ºC and 31ºC with a relatively aseasonal climate (UNDP, 2012). The primary forest in this area consists of Virgin Jungle Reserves (mostly on steep slopes) and some areas within Class I (Protected) Forest Reserves. While parts of these primary forests may have undergone limited human disturbance and localised timber felling, they remain largely intact (Milne et al., 2021; UNDP, 2012). The rest of the forest has been logged and degraded to various degrees, demonstrating widespread spatial variation in residual ACD (Asner et al., 2018). There are fragments of forest in the north that are in areas of natural forest management or are in the process of being converted to mosaic plantations. The landscape as a whole forms an important linkage between three flagship protected areas in Sabah: Maliau Basin Conservation Area (58,840 ha) to the West, Danum Valley Conservation Area (43,800 ha) to the East, and Imbak Canyon Conservation Area (30,000 ha) to the North (UNDP, 2012) (Figure 1).

We sampled 12 sites (mean distance: 28.32 ± 1.69 km; median: 27.35 km, range 4-60km) across the disturbance gradient between February and April 2018 (Figure 1; Table S1). Sampling sites captured landscape-scale variability in ACD (range = 9-209 Mg ha^{-1}; derived from Asner et al., (2018), which was adopted as a proxy for habitat condition (Milne et al., 2021; Osuri et al., 2020) (Table S1). At each site, eight trapping points were established along a 1.6 km transect, with 200 m between points, giving 96 trapping locations in total. The authors declare no ethics approval was needed in this study.

Dung collection

Dung from a representative selection of mammals that occur in the study area was collected from local zoos and rehabilitation centres. We aimed to collect dung across all trophic guilds of mammals (herbivores, omnivores, carnivores). There were, however, few carnivores available to sample from zoos, so we collected domestic cat (*Felis catus*) dung from a pet shop, assuming that this would be similar to native leopard cat (*Prionailurus bengalensis*) dung. Using dung from captive rather than wild animals was necessary as it is impossible to find large quantities of fresh dung in the wild. Dung from captive animals has been used in previous studies (e.g. Raine et al., 2018; Wurmitzer et al., 2017), and it is assumed that small differences in dung odour and quality are unlikely to have consequential effects on the attractiveness of the dung for the beetles, although further investigation is required to confirm this.

Twelve dung samples each from eight species were collected: elephant *(Elephas maximus)*, sambar deer (*Rusa unicolor*), Bali cattle (*Bos javanicus* × *B. taurus* hybrid), and common palm civet (*Paradoxurus hermaphroditus*) were obtained from Lokawi Wildlife Park; sun bear *(Helarctos malayanus)* and orangutan *(Pongo pygmaeus)* dung were collected from the Bornean Sun Bear Conservation Centre and Sepilok Orangutan Rehabilitation Centre, respectively; and domestic pig (*Sus scrofa domesticus*) dung was collected from a local farm near Kota Kinabalu, Sabah. All dung samples were collected fresh, immediately after defecation, from multiple animals, to prevent the arrival of coprophagous animals. The natural mass of each dung sample was recorded and the mean mass per species calculated to standardize the mass used for each dung type in the pitfall traps described below (Table S2). All samples from each type of dung were then mixed thoroughly and homogenized to minimize the possible differences among individual dung samples in terms of physical or chemical composition (Raine et al., 2018; Raine et al., 2019). The homogenized dung samples were divided into 12 samples each with a weight equal to the mean mass of dung for each species (Table S2) before freezing to kill pathogens.

Dung beetle collection

Because systematic sampling of dung beetles in naturally occurring dung was not possible, we constructed dung-baited pitfall traps as a proxy for direct dung beetle-mammal dung interactions (see Raine et al., 2018; Raine & Slade, 2019; Raine et al., 2019). We used pitfall traps baited with realistic sizes of native mammal dung sources to give similar odour cues to droppings found in the wild (see Table S2).

Pitfall traps were constructed from plastic containers of various sizes (depending on the size of the dung bait) buried flush to the ground with the dung baits hung above the centre of the trap (Figure S1). All baits were defrosted prior to placement in the field. A polystyrene plate was placed above the container of each pitfall trap as protection from rain and falling debris. The plastic containers were half-filled with a solution of water, detergent, and salt (Gray et al., 2014). The placement of each dung type used in the pitfall traps was randomized between the eight points on each of the 12 sites. The traps were baited and left for 48 hours. Dung beetles were collected into 75% ethanol and stored in a freezer until being identified to species level at Universiti Malaysia Sabah (UMS) using reference collections housed in the Borneensis collection and advice from taxonomists at Oxford University Museum of Natural History (OUMNH). A full reference collection from this study is housed in the Borneensis collection.

Mammal diversity

All mammals whose dung types (or proxy dung types) were represented in the networks were recorded in the study landscape (Table S3). For each dung beetle sampling site, we estimated the species richness and Shannon diversity of mammals in the vicinity using data from motion-triggered camera traps. The 195 cameras were deployed across the study landscape in a nested grid design, with one camera in every other 1 km^2 cell within 8 x 8 km grids. Cameras were unbaited, attached to trees ~30-50 cm above the ground, and active for an average of 90.7 (±3.4 SE) days. As the camera traps were set as part of a different study, the traps did not overlap exactly with the dung beetle sites; however, the distances to the sites were within the range that mammals were known to move across the landscape. The distance between the nearest camera trap and the dung beetle transect ranged from 70 m to 6.8 km (mean distance: 1.9 km ± 0.6; median: 0.7 km). We grouped the data into five-day sampling intervals to reduce the number of zeros (i.e., sampling intervals with no detections) in the dataset (Brodie et al., 2018). We then constructed species-by-sample matrices for each camera station and estimated mammal species richness and Shannon diversity using the *iNEXT* package (Chao et al., 2014; Hsieh et al., 2016) in R (R Core Team, 2020). As beetle sampling was aggregated at the transect level for constructing the networks, for each transect we calculated species richness of mammals (SRM) and Shannon diversity of mammals (SDM) as weighted averages across all camera stations, with the weight being the inverse of the Euclidean distance between the midpoint of the transect and each camera station. The two diversity metrics were calculated based on Hill Numbers that readily account for differences in sampling effort across cameras. As SDM and SRM were correlated (Pearson's $r = 0.79$, $p = 0.002$), we selected the Shannon diversity for use in the analysis as it accounts for both richness and evenness of the species present (Chiarucci et al., 2011; Spellerberg & Fedor, 2003).

Network Metrics

Dung beetle-mammal dung interaction networks were constructed for each site from a weighted matrix of mammal dung and dung beetle species abundances and the frequencies of interactions between them (Blüthgen, 2010). We then calculated five network metrics to explore the specialism and structure of the networks: weighted nestedness (*WN*), network specialization (H_2'), interaction evenness (*IE*), generality (*G*), and functionality (*F*) (a version of vulnerability) using the package *bipartite* (Dormann et al., 2008) in R.

(1) *Weighted nestedness*. We predicted that the most diverse dung beetle communities would contain more specialist species and interactions not nested within the generalist interactions. Therefore, as the diversity of dung beetles declines, the networks would become more nested as specialist interactions were lost and the network became more generalist.

(2) *Network Specialization*. We predicted that the frequency of specialist interactions would be highest where dung beetle and mammal diversity were highest (e.g., in the less disturbed sites) if the optimal dung type was available and dung beetles were exercising choice. Alternatively, if dung beetle and mammal diversity was lower in disturbed sites, fewer dung types might be used, resulting in higher network specialization in the disturbed networks.

(3) *Interaction evenness*. We predicted that interaction evenness would be highest in the less disturbed sites with higher dung beetle and mammal diversity, as interaction

evenness has been shown to decline with increasing habitat modifications (Tylianakis et al., 2007).

(4) *Generality*. High generality indicates that each dung beetle species feeds on multiple mammal dung types. As we predicted that both mammal and dung beetle diversity would decline across the gradient, we correspondingly predicted an increase in network generality in the most disturbed sites as specialist species were lost.

(5) *Functionality* is a version of vulnerability, a metric originally proposed for predator-prey food webs (Schoener, 1989; Tylianakis et al., 2007). Here, we calculated the number of beetle species that interacted with each mammal dung type. This metric therefore describes how the loss of interactions might affect the removal of dung from the ecosystem, and so the of loss of potential ecological functionality in the system. For example, low functionality corresponds to a loss of dung beetles using the dung, and so potentially to reduced ecosystem functioning. Conversely, high functionality indicates that each dung type supports a large number of dung beetle species, thus the system would be considered less sensitive to perturbation. As we predicted that both mammal and dung beetle diversity would decline across the gradient, we correspondingly predicted a decrease in functionality of the system in the most disturbed sites.

Data Analysis

We investigated how changes in ACD and Shannon diversity of mammals (SDM) impacted dung beetle diversity (species abundance, species richness, and Shannon diversity) using regression models with ACD, SDM, and their statistical interaction as predictor variables (ACD and SDM were not correlated; Pearson's $r = 0.068$, $p = 0.83$). We used non-rarefied effective Shannon diversity ($e^{H'}$), by taking the exponential form of Shannon diversity (Jost, 2006), because it accounts for evenness in species abundance and because, for most networks, the number of individuals was below the threshold of 100 needed for rarefaction (Frank et al., 2018). For species diversity, we used linear models with Gaussian errors, while for species abundance and species richness we used generalized linear models with Quasipoisson (species abundance) and Poisson (species richness) error structures. We selected the best-fitting models using likelihood ratio tests. Model residuals were tested for adherence to model assumptions such as homogeneity of variances and normally distributed residuals.

The network metrics chosen were not highly correlated (Pearson's coefficient values ≤ |0.5|; Figure S2). To test the significance of the network metrics, we compared the observed values to those obtained by 1,000 randomized networks generated by Patefield's r2dtable and the swap method (see Dormann et al., 2008). The Patefield method generates relatively unconstrained null models controlling only for the network dimensions and the condition that marginal totals remain identical to the observed network. The swap method additionally constrains the null model to retain the connectance and interaction distribution of the observed network, which reduces Type I error and generates more conservative P-values (Dormann et al., 2009; Dalsgaard et al., 2011). For each metric in each site, the divergence of the observed value from the distribution of randomly derived values from both null models were calculated. The network metric values were considered significant at $p < 0.05$. Pearson correlation coefficients, averaged across all indices, were calculated between the observed values and the two null models to compare the fits of the null models. If the swap model was a better fit to the observed data than the Patefield model, this would suggest that there were properties of the network aside from changes in species abundances and the numbers of links that were important in structuring the network. In addition, as the swap model was a more constrained model, the results generated are more conservative, so if the results are still significant using this model we can be confident in the differences between observed and null network metrics. Graphical representations of the interaction networks were generated using the package *bipartiteD3* (Terry, 2021) in R version 3.5.2 (R Core Team, 2020).

To investigate how the network metrics were associated with changes in ACD and mammal diversity, we fitted individual linear models for each network metric as a function of ACD, SDM, dung beetle species richness (SR), and all possible interactions. Species richness was fitted as a covariate in the models as it showed significant changes across the gradient with ACD but not with SDM (Table 1; Figure 2a). Model selection was carried out using backward selection and likelihood ratio tests; model residuals were tested for adherence to model assumptions. To quantify the overall variance explained by each variable, as well as variance after controlling for the other variables, for each metric we fitted the models with each of SR, SDM, and ACD fitted either first or last in the model (i.e. after removal of variation explained by the other two variables) in the model. Metric scores were standardized using a z-transformation so that the magnitudes of the coefficients would be directly comparable (Schielzeth, 2010).

We examined the roles of each dung beetle as an indicator species for dung of particular mammal species or habitat types using indicator valuation in the R package *labdsv* (Roberts, 2019), with a random reallocation procedure of 999 permutations. This allowed us to assess the degree of specificity (uniqueness to a particular site or dung type) and fidelity (frequency of occurrence) (Sullivan et al., 2018). Species of dung beetles were considered indicator species of a particular mammal dung or habitat type if the *IndVal* value was greater than 0.75 (indicator scores) and were considered to have a preference for a particular dung or habitat if they had a value greater than 0.25 (preference scores) (Legendre, 2013, Sullivan et al., 2018).

The relative attractiveness of dung types and habitat types was quantified as N_i/N_{max}, where N_i is the total number of dung beetle individuals captured on dung type on in a particular habitat i and N_{max} is the maximum number of dung beetles found for any dung type or habitat in the network. The relative species attractiveness was recorded as S_i/S_{max}, where S_i is the dung beetle species richness on a dung type or in a habitat i and S_{max} is the maximum dung beetle species richness found for any dung type or habitat in the network (Frank et al., 2018).

An interaction accumulation plot was generated to identify the completeness of feeding interactions of dung beetle species. To test for sampling completeness across dung types and dung beetle communities in each site, we used rarefaction or extrapolation to a given degree of sample completeness using sample coverage (Chao & Jost, 2012; Hsieh et al., 2016) using the package *iNEXT*. A bootstrap method based on 50 replications was used to construct 95% confidence intervals for the expected interpolated and extrapolated curves in any given sample coverage.

RESULTS

In total, 9,236 individuals of 50 species of dung beetles were collected from 96 dung-baited pitfall traps using eight mammal dung types. The interaction accumulation plot plateaued at approximately 500 individuals, and even low sample sizes had several interactions, suggesting that sample size was not limiting in our study (Figure S3). Most mammal dung types recorded a high sample coverage (80-100%) across the gradient, even in plantations and highly disturbed forest sites, suggesting that the data were robust in terms of the numbers of dung beetle species attracted to each mammal dung type (Figure S4). The one exception was sun bear dung, which had low coverage in some logged, fragmented forest sites (33-49% coverage). Sun bear dung (in primary forest: site 1, disturbed, logged-over forest: site 11, plantation: sites 9 & 12) and civet dung (moderate condition logged-over forest: site 3, and plantation: site 9 & 12) did not attract any beetles. A total of 31 mammal species was detected in 17,680 sampling days across all camera stations. Mammal diversity and abundance changed little across the habitat gradient, with similar diversity in primary forest and plantation, and the highest values in heavily logged and fragmented forests (Table S1 and S3).

Correlations between observed and null model means increased slightly from Patefield (|r|=0.8949±0.37; Pearson correlation coefficient of null model vs. observed, averaged across all indices ± 1 SE) to swap (|r|=0.8981±0.33), indicating that connectance and interaction distribution were important in structuring in the networks. The majority of the network metrics differed significantly from the null expectation under random association ($P < 0.05$) for both null models (Figure S5), indicating that the results were robust. Overall, networks were significantly more specialized, less general, more even, had less functionality, and, in some sites, had lower nestedness than expected by chance (i.e., by a random assembly of interactions across the majority of forest sites). In the most disturbed plantation sites, however, only the Patefield model was significantly different for several of the metrics (network specialization, interaction evenness, generality, and functionality). This suggests that the networks in the most disturbed sites were defined by the abundance and number of species, rather than the network properties (e.g. connectance, interaction distribution) themselves. Indeed, the loss of both dung beetle species, and the numbers of interactions in the most disturbed sites can be seen in Figure 3 (e.g. Site 11 & 12) where some dung types have no interactions at all.

Dung beetle abundance and diversity were not predicted by either ACD or SDM. However, dung beetle species richness significantly increased with increasing

ACD (Figure 2a; Table 1 & S1). Overall, the dung beetle-mammal dung networks did not vary greatly across the disturbance gradient, and only decreased in complexity (i.e. lower numbers of species and fewer links) and more simplified in the plantation sites (Sites 11 and 12) (Figure 3). ACD and SR significantly explained the changes in only three of the five network metrics (nestedness, network specialization, and functionality). Networks generally had a low network specialization and high interaction evenness and generality. Interaction evenness and generality did not significantly vary with ACD, mammal diversity or dung beetle species richness (Table 2). Generality was highly variable across the network (Table 2, Figure 4). Network specialization decreased significantly with ACD. However, it showed the opposite pattern with dung beetle species richness, where network specialization was highest (and dung beetle richness lowest) in oil palm plantations (Table 2, Figure 4). Decreasing ACD was associated with significant decreases in functionality and nestedness (Table 2, Figure 4). The decrease in functionality across the carbon gradient appeared to be driven by changes in species richness (which were highly significant), with the lowest functionality and the lowest richness of beetles being found in oil palm plantations. ACD was only associated with increases in nestedness when the former was placed first in the models, suggesting that it was not a strong predictor of changes in nestedness. Mammal diversity (SDM) did not explain any of the network metrics (Table 2).

Corresponding to the overall low network specialization and high generality, the indicator value analysis demonstrated low indicator scores. No species had *IndVal* scores > 0.75, suggesting that most dung beetle species have wide niches (i.e., are present in a variety of dung and habitat types). We identified 11 dung beetle species with significant preference scores in different habitat types. In particular, several dung beetle species (e.g., *Copris agnus, Onthophagus rorarius, Onthophagus aphodiodes*) were associated with less disturbed sites (Figure 3; Table S4). There were 14 dung beetle species with significant preference scores among dung types (*IndVal* > 0.25; see Table S4 & S5). No species showed strong preferences for any dung type in rubber or oil palm plantation. Attractiveness across animal dung types (N_i/N_{max}: $F_{7,88} = 31.912$, $P < 0.0001$; S_i/S_{max}: $F_{7,88} = 16.66$, $P < 0.0001$) and across habitats (N_i/N_{max}: $F_{11,84} = 4.18$, $P < 0.0001$; S_i/S_{max}: $F_{11,84} = 3.55$, $P = 0.0004$) varied significantly. Pig dung was the most attractive while sun bear dung was the least (Figure 2b).

DISCUSSION

Dung beetle-mammal dung interaction networks in the tropical rainforests of Borneo remained structurally similar in forests that had been moderately disturbed by logging. Beyond a threshold, however, networks became simplified, with decreases in dung beetle species richness and the non-utilization of several dung types in oil palm plantations. This resulted in fewer dung beetle-mammal dung interactions and more specialized networks in the most disturbed habitats (Figure 3). Although most dung beetle species were fairly generalist across dung types, dung beetle species richness changed across the disturbance gradient in response to variation in ACD, driving changes in some of the network metrics. However, dung beetle total abundance did not change significantly across the disturbance gradient, a pattern that has been found globally and appears to be driven by an increase in abundance of generalist species in disturbed habitats (Fuzessy et al., 2021).

Our results are novel relative to prior work in Brazil, where defaunation led to a decrease in dung beetle species richness associated with lower diversity and availability of dung types (Culot et al., 2013; Fuzessy et al., 2021). In our study, mammal diversity varied little across the disturbance gradient. Hunting pressures are low in this region of Sabah and mammal diversity and abundances are generally high (Deere et al., 2017; Granados et al., 2016). We suggest that this high diversity of mammals, even in the most heavily logged sites, and the generalist feeding patterns of dung beetles, resulted in few changes to the overall structure of the networks until they were severely perturbed (e.g., in oil palm plantation). Similarly, simplification of networks in highly disturbed habitats has been found in antagonistic plant-herbivore and mutualistic plant-pollinator networks, where agricultural intensification altered interaction structure and robustness (Morrison et al., 2020; Tylianakis et al., 2007).

Dung beetle richness and ACD together explained changes in several network metrics (Figure 4). Nestedness was lowest at high beetle diversity, corresponding to the highest ACD sites. This indicates undisturbed sites had more specialized, non-nested interactions, with some beetles preferring specific dung types that more generalist species were not utilizing (e.g., civet, sun bear, sambar deer; Figure 3). However, many of the sites with the highest nestedness did not differ from the randomized networks, suggesting that there were few specialist interactions that were not nested within the more generalist network structure. Together, these results reveal that some specialist species and interactions may be lost when forests are disturbed by logging and conversion to plantations but that, overall, the communities and networks will remain relatively stable as long as the diversity and abundances of beetles remains high.

Overall, the dung beetle-mammal dung networks had low network specialization. The most specialized networks were generally found in sites with high ACD, but also increased with decreasing dung beetle species richness. Increased network specialization in the plantations was likely due to the loss of interactions and lower beetle richness. This results in some dung types not being used and therefore, a more even distribution of interactions (Figure 3). Similarly, the interaction networks showed decreasing functionality across the carbon gradient with the lowest functionality in oil palm plantations, with some dung types being unused. Interestingly, the comparison with the randomized networks showed that all networks across the gradient were more specialized, less even, and less general than expected by chance. Together, these results indicate that while most dung beetle species are capable of consuming many dung types. This is something that should be investigated further with food-choice experiments (e.g. Raine et al., 2019b). Thus, while the overall species richness and composition across the dung types may have varied only minimally until the networks became severely perturbed, the abundances of individual species on the different dung types changed (Figure 2b). Similarly, the indicator species analysis showed few specific indicator species for each habitat or dung type. The species remaining in the oil palm were common taxa that occurred across the gradient (Figure 3). However, the indicator analysis suggested that some of the less disturbed sites did have species that were specifically associated with them; these species may therefore be more vulnerable to forest loss (Figure 3; Table S4). This is consistent with previous work suggesting that dung beetle communities are similar between primary and logged forests, but there is a loss of species once forests are converted to oil palm with a subset of the forest species increasing in abundance and becoming dominant (Edwards et al., 2013; Gray et al., 2014; Slade et al., 2011).

Previous work on insect-parasitoid networks across a disturbance gradient from forest to agriculture, found that there were few changes in food web metrics except in the most severely modified habitats, such as pasture and rice (Tylianakis et al., 2007). Our study therefore adds to the evidence that, although communities may tolerate moderate levels of disturbance, there are likely to be thresholds beyond which they become simplified and no longer resemble those of the original habitat. In our study, the similarity in network structure across the disturbance gradient was most likely driven by many species showing opportunistic feeding preferences, rather than relying on specific dung types. This type of ‘rewiring’ (Ramos-Jiliberto et al., 2012) and plasticity of interactions in perturbed communities can allow for enhanced resilience (Noreika et al., 2019). However, we note that as species richness decreases in the face of multiple perturbations, the system may react strongly, shifting towards a simplified network with fewer interactions (also see Grass et al., 2018). This change from diverse, complex networks to species-poor, simplified networks with disturbance has been demonstrated theoretically (Fortuna and Bascompte, 2006) and supported empirically (Lever et al., 2014; Biella et al., 2020; Baldock et al., 2019) but has rarely been validated in natural communities (Tylianakis et al., 2007).

Building multiple interaction networks over large spatial scales is challenging and time-consuming. While we sampled networks across a wide landscape (~261,000 ha) spanning a substantial gradient in forest carbon and land conversion, we had no temporal replication; understanding how networks respond to disturbances over time would be an important extension of our work. Mammal diversity did not show large changes across most of the study landscape. Repeating this study across a landscape more heavily impacted by defaunation would enable the importance of the loss of large mammals on the networks to be explored in greater depth, potentially allowing us to disentangle the effects of defaunation from forest quality.

Nevertheless, our study provides some of the first evidence of changes in commensalist interaction network structure across a disturbance gradient that is representative of many (if not most) forested landscapes in Southeast Asia. This allows us to begin to predict the effects of habitat disturbance on dung beetle-mammal networks in the face of logging, forest conversion, and defaunation. Our results suggest that with appropriate management and low levels of hunting, logged forests and forest fragments can retain ecological assemblages and interactions that are structurally and functionally similar to those in primary and minimally disturbed forest. However, the complexity and stability of interaction networks show marked changes when habitats are severely modified, and once these thresholds are passed, the system may have a limited capacity to respond to further environmental changes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest in this study.

AUTHOR CONTRIBUTIONS

LYC, EMS, JFB, DFRPB, CSV, and GR conceived the research idea. EMS, JFB, DFRPB, GR and CSV secured funding for the data collection. LYC and EMS designed the study with support from JFB and DFRPB. LYC, SWT, NJD, EMS, JFB collected the data. LYC, EMS, JFB, TDH conducted the data analyses. LYC and EMS led the writing of the first draft, and all authors contributed to writing and editing the final manuscript.

DATA AVAILABILITY STATEMENT

The data used in this study are archived on Zenodo (DOI: https://doi.org/10.5281/zenodo.5787905).

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