


UN DECADE ON ECOSYSTEM RESTORATION

RESEARCH ARTICLE

Assessing mangrove restoration practices using species-interaction networks

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Mangroves are uniquely important ecosystems, for preserving biodiversity, sustaining livelihoods, and mitigating against climate change. However, they are degraded globally and are therefore a priority for ecosystem restoration. To date, the assessment of mangrove restoration outcomes is generally poor, and the limited studies that do exist are focused largely on forest area. Thus, more holistic ways of assessing the outcomes of mangrove restoration projects on biodiversity and associated ecological processes are urgently needed. Ecological networks are a useful tool for simultaneously examining both. Here, we assessed the utility of using species-interaction networks for evaluating mangrove restoration outcomes for the first time. We compared the structure and complexity of mangrove ecological networks in replicated “monoculture reforestation,” “mixed species regeneration” and “reference forest” plots in two study areas in Sulawesi, Indonesia, an estuarine, and a coastal fringe mangrove system. We also combined and evaluated sampling methods, utilizing traditional plant–animal sampling while also integrating video recording data in a novel way. We found significant differences in the structure and complexity of mangrove networks between restored and natural plots, with contrasting effects between the two sites. Our results show differences in the complex ways in which taxa interact in mangrove restoration projects, which would be overlooked if common biodiversity metrics, such as species richness, were used alone, with consequences for the restoration of ecosystem functioning. We also highlight the utility of video recording data collection for constructing species-interaction networks, overcoming the detrimental impacts of observer presence for some key species.

Key words: camera traps, ecological networks, forest, marine, plant–animal interactions, Wallacea

Implications for Practice

- Analyses of networks of plant–animal interactions illustrate differences between reference mangrove forests and restored mangrove forest treatments that are not obvious from the assessment of the richness of faunal taxa.
- Video recordings of the sediment stratum are a time and cost effective addition to capturing interaction data for ecological networks, particularly for shy species, providing interaction data on an entirely different group of species than traditional vegetation searches.
- “Monoculture reforestations” are more different in the pattern of plant–animal interactions from “reference forest,” than “mixed species regenerations.”

Introduction

Mangrove forests are uniquely valuable coastal wetlands in the transition zone between land and sea, moderating freshwater flows from inland while coping with tidal inundation. These intertidal forests are highly productive and harbor distinctive assemblages of both terrestrial and aquatic biodiversity (Cannicci et al. 2008; Brander et al. 2012; Malik et al. 2015).

They sustain millions of people globally, contributing to their survival and welfare through protection against coastal erosion and tsunamis, provision of food and material for construction

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and firewood, and through filtering of water-borne pollutants, which improves the water quality (Lee et al. 2014; Huxham et al. 2017; Zu Ermgassen et al. 2021). Mangrove forests are also globally important carbon sinks with carbon densities exceeding eight times those typical for terrestrial tropical forests (Donato et al. 2011). Thus, they are considered high priority habitats in climate change mitigation and adaptation strategies (Locatelli et al. 2014; Duncan et al. 2016).

In response to wide-spread mangrove degradation and increasing perception of the resulting negative environmental and societal consequences, mangrove restoration and rehabilitation (R/R) are now high on the agenda of conservation NGOs and, increasingly, governments (Duncan et al. 2016; Ilman et al. 2016). Numerous R/R projects have therefore been established in the last few decades, generally aiming to re-establish biodiversity and ecosystem services on degraded areas (Bosire et al. 2008; Barnuevo et al. 2017). While the increased focus on restoration has improved their conservation outlook (Friess et al. 2020), many R/R projects to date could ultimately be considered to have failed (Hai et al. 2020). Reasons for this include failure to achieve hydrological restoration before plantation, the use of inappropriate foundation species for the area, selecting an inappropriate life stage for transplant, not accounting for high mortality of planted propagules, and neglecting key social factors, such as ensuring locally agreed goals for the initiative (Trí et al. 1998; López-Portillo et al. 2017; Oh et al. 2017). Even in those cases where some successes were achieved, restoration efforts were seldom fully assessed, and if so, rarely beyond the initial few years (López-Portillo et al. 2017). Hence, after several decades of mangrove R/R projects, our understanding of whether and to what extent biodiversity, ecosystem functions and services, and resilience of re-established forests correspond to those of reference forests is still very limited (Barnuevo et al. 2017; Lee & Khim 2017).

To date, the limited number of mangrove restoration evaluations have mostly considered structural components only; a full evaluation of ecological restoration implies assessing internal self-sustaining processes, to give an overview of functionality, and a consideration of the multiple pathways and mechanisms by which ecological services are delivered (López-Portillo et al. 2017). The success of mangrove restoration has traditionally been measured in terms of the total area of new forest, but this has often relied on the planting of monocultures of robust pioneer species (Ellison 2000). Single species reforestation is often the most cost-effective method to increase forest area, particularly where natural regeneration seeded from nearby sources is unlikely, but typically do not produce forests that are as biodiverse as natural successions, mixed species reforestations, or more natural forests (Crouzeilles et al. 2017; Wang et al. 2019). A focus on area planted as a measure of mangrove restoration success may contribute to the long-term failure of these projects (Lee et al. 2019), as it ignores how habitat complexity and species diversity underpin mangrove functionality and sustainability (Lee et al. 2014). While an improvement on solely measuring total forest area, simple biodiversity measures alone fail to assess the restoration of ecological interactions,

which underpin ecological processes necessary for managed sites to recover (Moreno-Mateos et al. 2020). It is clear that there is a need for the further development of methods for the assessment of long-term success in R/R projects. A promising avenue to do this is by constructing ecological networks to assess plant–animal interactions in restored systems (Raimundo et al. 2018). Ecological networks are the description of an ecological system as a set of nodes depicting units (e.g. individuals, resources, or species) connected by links depicting ecological interactions (Guimarães 2020).

Ecological networks provide insight into ecosystem function via the calculation of various network indices which describe an aspect of the network structure (Guimarães 2020). A particular advantage of an ecological network approach is that it allows for an evaluation of both biodiversity and ecosystem function (Montoya et al. 2006; Forup et al. 2008; Raimundo et al. 2018). For example, plants and pollinating animals may be present in a restored habitat, but may not be interacting sufficiently (or at all), preventing pollination of the plants. Different classes of network indices tell us about different aspects of the ecosystem. Interaction diversity indices, such as weighted connectance, quantify the number of interactions within a network, relative to the number of species present. Greater interaction diversity may increase the rate of ecosystem processes, e.g. higher predator diversity leading to greater herbivore suppression (Snyder et al. 2006). Measures of nestedness, such as weighted NODF, assess whether an interaction network is highly nested, that is, species interacting with specialists are a subset of the species interacting with generalists. Specialist species are often at greater risk of extinction (Henle et al. 2004), but in a nested network the remaining species will have others to interact with (Tylianakis et al. 2010). Calculations of robustness assess a network's fragility to extinction cascades (Memmott et al. 2004; Burgos et al. 2007). A network may be highly dependent on certain key species which, if lost, would lead to secondary extinctions. Therefore analyzing these network indices and others can provide insight into the ecosystems assessed for both scientific study and conservation planning (Tylianakis et al. 2010).

In this study, we compare the structure and complexity of mangrove species–interaction networks using two R/R sites in Northern Sulawesi, Indonesia, an estuarine and a coastal fringe mangrove system. We evaluate the utility of ecological networks for restoration assessment by comparing metrics from forest restoration treatments to adjacent reference forests that had not been deforested. At each of the two focal sites, past R/R approaches comprised mono-specific reforestation and mixed species natural or facilitated regeneration, allowing for an analysis of which restoration strategy produces networks more similar to the reference forests. To address these questions we had three central hypotheses; (1) the vegetation structure at each site will affect network metrics; (2) there will be fewer animal species and interactions in restored mangrove treatments (mixed species regeneration and monoculture reforestation) than in the reference forest, leading to significant differences in network structure; and (3) the monoculture reforestation will show greater differences from the reference forest than the mixed species regeneration (Fig. 1).

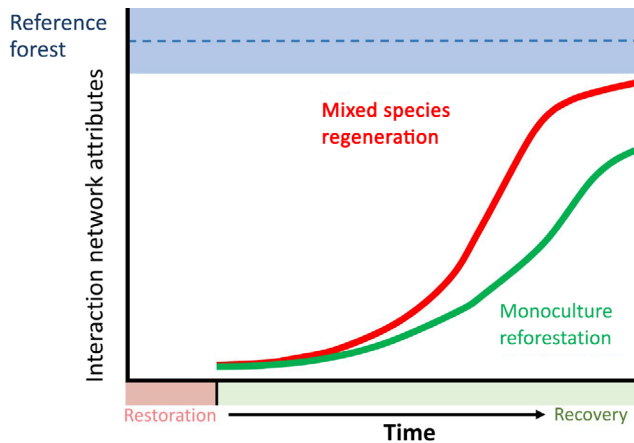


Figure 1. Conceptual figure outlining our hypothesis that, for a given recovery time post restoration, monoculture reforestation will show greater differences from the reference forest baseline than mixed species regeneration in terms of species interaction network attributes. The red line represents the mixed species regeneration, the green line the monoculture reforestation, while the blue dashed line represents the reference forest.

Methods

Study Sites

We used two restoration sites to represent different mangrove geomorphological settings; Tiwoho ($1^{\circ}35'41.57''N$ $124^{\circ}50'41.75''E$) a coastal fringe mangrove and Likupang ($1^{\circ}40'11.40''N$ $125^{\circ}2'13.45''E$) a riverine/estuarine mangrove, respectively, situated on the west and north coasts of the province of North Sulawesi, Indonesia (Fig. 2). Both sites experienced semidiurnal tides during the study period. Tidal inundation was monitored between 18 July, 2019 and 02 August, 2019 at Tiwoho and 03 August, 2019 and 21 August, 2019 at Likupang (Hobo Onset Water Level Loggers 0–4 m). At Tiwoho, the maximum tidal range was 30 and 5 cm at the spring and neap tide days, respectively. At Likupang, the maximum tidal range was 140 and 60 cm at the spring and neap tide days, respectively. At Tiwoho, the forest floor was inundated at 8 out of 15 days monitored (i.e. no tidal inundation at the neap tide period), whereas the forest floor at Likupang was inundated daily, throughout the entire 15-day tidal monitoring period. The two forests have a similar history of exploitation for shrimp farming and forest restoration, which was largely completed in 2004 and 2005 in Tiwoho and in 2003 in Likupang (i.e. 14–16 years prior to the vegetation sampling undertaken here). Both sites had relatively undisturbed forests that have not been logged, serving as our reference forests (Djamaluddin et al. 2019). Detailed site descriptions in Supplement S1.

At both Likupang and Tiwoho, six 10×10 m sampling quadrats were randomly set up in the three comparison forest areas (hereafter termed management “treatments”: (1) reference forest; (2) monoculture reforestation; and (3) mixed species regeneration (i.e. 18 quadrats per site, 36 in total, 15–90 m in between them). Sampling took place in August and September 2019 towards the end of the dry season in Sulawesi (Whitten et al. 2002). In order to sample at times of likely maximum

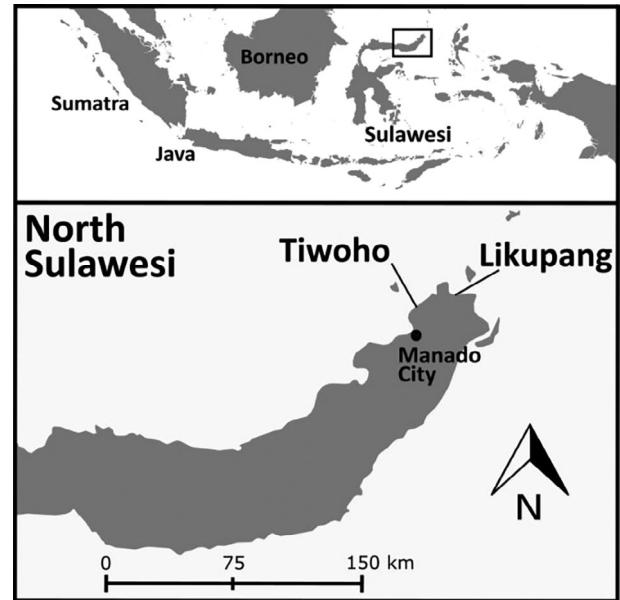


Figure 2. Position of North Sulawesi in Indonesia (top panel), and of the Tiwoho and Likupang mangrove study sites in North Sulawesi (bottom panel).

animal activity (Palmer 1995), sampling took place in the weeks around spring tides. Sampling was carried out within 3 hours on either side of low tide.

Data Collection

Vegetation Surveys

Vegetation structure: The Gap Light Analysis Mobile App (GLAMA) (Tichý 2016), was used in all quadrats to calculate a vegetation structure index, Canopy Cover (CaCo), following Gonsamo et al. (2013). This method provides an index of vegetation structure by rescaling hemispherical projections of photographs taken from a single position to perpendicular projections of light gaps. The 16-megapixel reverse camera of a Vivo Y15 smartphone was used. Standard settings were used on GLAMA, with a 70° hemispherical masking, and only the blue channel of light (Zhang et al. 2005). Photos were taken at shoulder height (1.6 m), ensuring the camera was kept level, with photos taken in each of the four corners of the quadrat and in the center. The CaCo index values produced by the five photos were averaged to give a mean CaCo index value for each quadrat. Periods of intense direct sunlight were avoided as this can bias the CaCo index calculation.

Species biomass: A thorough vegetation survey was carried out in all Likupang quadrats, along with 16 out of 18 Tiwoho quadrats (all 6 monoculture reforestation quadrats, five out of six of mixed species regeneration, and five out of six of the reference forest). All trees within the quadrats were identified to species level and diameter at breast height (DBH) was measured on adult trees at 1.3 m above the sediment (Comley & McGuinness 2005), calculated as dividing the circumference of the trunk of a tree by π . Adult trees were defined as trees of

>1 m height and >2 cm DBH. A biomass index was calculated for each plant species by multiplying the number of adult trees in each quadrat by the average DBH for that quadrat.

Species-Interaction Recording

Interaction data were collected in three ways, as networks constructed by combining multiple sources of evidence have been shown to reveal a much greater variety of interaction types (Wirta et al. 2014). Data were collected for all interactions between animals and plants, as well as between animals and the mangrove sediment. Both plant–animal (i.e. herbivory, pollination, and detritivory) and sediment–animal interactions (i.e. bioturbation and macrofauna feeding on microfauna) are important aspects of mangrove ecosystem processes (Marinelli & Waldbusser 2005; Cannicci et al. 2008; Kristensen 2008). There was no discrimination by interaction type, all plant/sediment–animal interactions were recorded (including both passive “habitat use,” and more active interactions such as herbivory).

Active vegetation search: An active search was carried out for animals on the vegetation in each 10 × 10 m quadrat for 45 minutes, to a height of 2.5 m, modified from Gibson et al. (2011). This timed search focused on examining the vegetation to find animals interacting with the target plants; however, animals found on the sediment were also collected, with each collected animal placed in an individually labeled tube. The plant species from which the animal was collected was recorded for each sampled animal. Searches were carried out by a single observer (DOC). Details of taxonomic identification in Supplement S1.

Leaf basket collection: To record cryptic plant–animal interactions, 10 leaf baskets were collected in each quadrat during the active vegetation search. Leaf baskets were considered the cluster of leaves at the tip of a branch, and each leaf basket was collected at “breast height,” 1.3 m above the sediment (Feldpausch et al. 2011). Each leaf basket was collected from a different tree, and the sampled 10 trees were selected to represent the tree species cover in the quadrat, that is, if *Rhizophora apiculata* was judged to cover 70% of the quadrat seven of the leaf baskets were taken from that species. All leaf baskets were then placed in individual labeled transparent plastic bags and examined over the following week for any animals which emerged.

Video data collection: A GoPro Hero4 was placed at shoulder height (1.6 m) in each quadrat, facing downwards so that the camera was recording the vegetation and sediment beneath it, fastened with cable ties to overhanging branches. In this position, the camera was recording a horizontal area of approximately 5 m² at ground level (covering an area of approximately 1.6 × 3.1 m). Cameras were placed as close to the most south-westerly corner of each quadrat as possible, to standardize placement. The camera recording was commenced at 11:30 hours. For extraction of animal interaction records, the first 30 minutes of the video was discarded to allow a “settling down” period for animals to re-emerge. The 45 minutes from 12:00 hours were then used for data extraction of plant/sediment–animal interactions. If an animal left the field of view of the camera during this period, this was noted and any similar animal that entered the

field of view was not counted to prevent double-counting. All video data extraction was carried out by a single observer (MF).

Cameras were placed at all quadrats, but one camera failed to record in the Likupang reference forest; therefore, for comparisons involving merged interaction data or just video camera data, the Likupang reference forest had a sample size of five quadrats, as opposed to six quadrats for all other treatments.

Combining Interaction Data at the Quadrat Level

It is necessary to ensure that different methods utilized for collecting interaction data are comparable (Wirta et al. 2014). A correction factor was therefore applied to account for the difference in the area surveyed between data collection methods. The leaf basket collection and active vegetation search collected samples from throughout the 100 m² quadrats, while the video data collection only surveyed a 5 m² section of each quadrat. It was assumed that this 5 m² section could be considered representative for any 5 m² section of the quadrat. Therefore, each record from the video data collection was multiplied by 20 to represent the inferred number of records for a full 100 m² quadrat. For evaluation purposes, we analyzed interaction data both combined and separately (see below).

Data Analysis

All analyses were carried out in R Software v.3.6.3 (R Core Team 2020). Likupang and Tiwoho were analyzed separately due to their different geomorphological setting and that a different species was used for their monoculture plantings (*R. apiculata* and *Ceriops tagal*, respectively). Interaction turnover between these sites was examined as it does not require formal statistical testing. The R code and data for these analyses is available at https://github.com/oconned5/Mangrove_restoration_networks.

Betadiversity and Interaction Turnover

Interaction β -diversity represents differences in the set of observed interactions between sites (Poisot et al. 2012; Graham & Weinstein 2018). To assess interaction turnover or whole network dissimilarity (β_{WN}) between sites (Likupang–Tiwoho), and between treatments within sites (monoculture reforestation–mixed species regeneration–natural), we used the *betalink* package (Poisot 2016). This method quantifies the total interaction turnover as $\beta_{WN} = \beta_{ST} + \beta_{OS}$ and partitions it into species turnover (i.e. β_{ST} , the interaction diversity in the pool of species that are not shared between two networks) and interactions rewiring (i.e. β_{OS} , interactions only occurring at one location despite both species being present at both locations) (Biella et al. 2020). In addition, we calculated species composition dissimilarity (β_S) between locations. Each of these metrics was calculated using the Jaccard similarity metric (Novotny 2009).

Network Indices

Sampling completeness of interactions was estimated for each individual quadrat sampled, following the approach of Macgregor et al. (2017), taking the mean sampling completeness per species, weighted by the estimated interaction richness.

Plants were taken as the focal level in sampling completeness calculations and animals were considered the interacting level. Sampling completeness was calculated using both the Chao1 (Chao 1984) and ACE (Chao et al. 1993) estimators using the R package *vegan* (Oksanen et al. 2019). This was performed for the combined interaction data, as well as for the vegetation search and video recordings separately.

Interaction networks were constructed for each quadrat using combined interaction data. The species-level indices *normalized degree* (the sum of links per species, scaled by the number of possible partners [Martín González et al. 2010]) and *proportional generality* (a quantitative version of *normalized degree*) were calculated for common mangrove species in the lower level of the network (*Bruguiera gymnorrhiza*, *C. tagal*, *Rhizophora apiculata*, and *R. mucronata*) and for sediment using the *bipartite* R package (Dormann et al. 2009). Species-level analyses were carried out on key identified tree species and sediment as management in these restored mangrove systems was focused on restoring tree species and the sediment layer.

In order to compare the structural properties of networks between treatments, a number of standard quantitative network indices were computed using the *bipartite* R package (Dormann et al. 2009): *weighted connectance*—the weighted diversity of interactions per species divided by number of species in the network, *wNODF*—a weighted nestedness measure (Almeida-Neto & Ulrich 2011), *generality*—the weighted mean number of lower-level species (plants) connected to higher-level (HL) species (animals) and *vulnerability*—the weighted mean number of HL species connected to lower-level species (Bersier et al. 2002; Tylianakis et al. 2007), *robustness HL*—the robustness of animal species to plant extinctions (Memmott et al. 2004; Burgos et al. 2007), *interaction evenness*—a measure of the distribution of interactions in the network (Tylianakis et al. 2007), *H2*—a quantitative measure of the level of network specialization (Blüthgen et al. 2006) and *number of species HL*—total number of animal species in each quadrat. In addition, the QuanBiMo algorithm (Dormann & Strauss 2014) was used to calculate *weighted modularity*—a metric that assesses the extent to which the network is divided into discrete compartments. This was carried out with the *computeModules* function set to 10^8 steps, which first calculates modularity *Q*. As modularity *Q* is dependent on network size, *weighted modularity* was calculated by computing *z*-scores from null model expectations (Dormann & Strauss 2014).

The spatial relationship between quadrats was assessed using distance-based Moran eigenvector map (dbMEM) variables (Borcard & Legendre 2002; Dray et al. 2006). This approach reduces the dimensionality of the spatial relationship between study quadrats into variables which are then used in further analyses to represent these relationships (Miller et al. 2019). Both network level and species-level indices were tested for significant spatial autocorrelation using forward selection (Blanchet et al. 2008) with double-stopping criterion after testing the global model significance, following Bauman et al. (2018).

Analysis of Indices

Any differences in network structure between forest types was assessed by modeling network indices separately as response variables to the explanatory variables treatment (reference forest, monoculture reforestation, and mixed species regeneration) and an index of vegetation structure. The comparison reference level was set to reference forest for the treatment variable. A selection of general and generalized linear models (GLMs) was used, utilizing beta, Gaussian, inverse Gaussian, Poisson, and negative binomial error distributions where appropriate, with the best fitting link family. Model selection was carried out using AIC, informed by standard plots of model fit and r^2 . R package *betareg* was utilized for beta GLMs (Cribari-Neto & Zeileis 2010) and the package *MASS* was utilized for negative binomial GLMs (Venables & Ripley 2002). All model *p*-values were adjusted for multiple comparisons following the false discovery rate method (Benjamini & Hochberg 1995), using the *p.adjust()* function in R with method “fdr.”

The above analyses of network indices were carried out on the merged networks, and, for comparison also for separate networks constructed for the video data and vegetations search data (active vegetation search and leaf baskets collection) (Supplement S2 and S3, Tables S1–S3). Likewise, the *number of interactions* (total number of interactions observed in each quadrat) was modeled for merged networks and for both video and vegetation search data collection separately.

The species-level indices *normalized degree* and *proportional generality* were analyzed in the same way, assessing differences between treatments within both Likupang and Tiwoho. These analyses were carried out for sediment, and the trees *B. gymnorrhiza*, *C. tagal*, *R. apiculata*, and *R. mucronata* in the quadrats they were present, as species-level indices for a focal species can only be calculated for a network where the focal species was present (sample size for each of these comparisons given in Tables S4 & S5). As well as a variable describing overall vegetation structure for a quadrat, for tree species in each of these models the biomass of the focal tree species in each quadrat was included, as this was considered likely to influence the plant species' role in the network.

Quantitative bipartite networks were plotted to show the differences in the network structure by pooling replicate data for each treatment in both sites, using the *plotweb()* function in *bipartite* (Dormann et al. 2009). Boxplots and scatterplots created in R package *ggplot2* (Wickham 2016) were used to plot results from the analyses.

Results

Betadiversity and Interaction Turnover

Species dissimilarity (*S*) between sites (Likupang–Tiwoho), and between treatments within sites (monoculture reforestation–mixed species regeneration–natural), were comparable across the board, with a mean dissimilarity of 0.336 (range 0.276–0.4) (Table 1). Despite moderate species dissimilarity ($\beta_S = 0.316$), interaction turnover between Tiwoho and Likupang was quite low ($\beta_{WN} = 0.0813$). This was due to the fact much of the network dissimilarity could be attributed to species dissimilarity ($\beta_{ST} = -0.139$). The patterns for

interaction turnover were distinctly different between the two study sites. For Likupang interaction, turnover was highest between the monoculture reforestation and the mixed species regeneration ($\beta_{WN} = 0.247$), with relatively little difference between the reference forest and monoculture reforestation ($\beta_{WN} = 0.084$). In contrast in Tiwoho, there was very little interaction turnover between the monoculture reforestation and the mixed species regeneration ($\beta_{WN} = 0.069$) and reference forest ($\beta_{WN} = 0.053$), with the largest interaction turnover seen between the reference forest and the mixed species regeneration ($\beta_{WN} = 0.269$). Overall, interaction rewiring (β_{OS}) was a larger factor in interaction turnover (β_{WN}) in both Likupang (β_{OS} mean = 0.423) and Tiwoho (β_{OS} mean = 0.381), than species turnover (β_{ST}) in Likupang (β_{ST} mean = -0.262) and Tiwoho (β_{ST} mean = -0.251).

Interaction Data Collection Summary and Number of Interactions

Leaf baskets produced 40 records of interactions (mean = 1.11 per quadrat) and active vegetation searches 696 (mean = 19.33 per quadrat). Video recordings produced 859 records of interactions from a 5 m² focal area, and when multiplied up, this resulted in 17,180 interactions (mean = 490.86 per quadrat) to represent the number of inferred interactions for each 100 m² quadrat. More interactions were recorded from Likupang (total = 10,009; monoculture reforestation = 1,464, mixed species regeneration = 4,399, reference forest = 4,146) than in Tiwoho (total = 7,907; monoculture reforestation = 3,430, mixed species regeneration = 2,188, reference forest = 2,289) (Table S6).

There was no significant difference in animal species richness between treatments in either Likupang or Tiwoho (Fig. 3, Tables S7 & S8). However, the number of interactions recorded was significantly lower in the Likupang monoculture reforestation than in the reference forest (negative binomial GLM: adjusted $r^2 = 0.633$, $F_{[3,13]} = 8.854$, estimate \pm SE = -540.794 \pm 136.723, $p < 0.01$), while the reference forest and mixed species regeneration did not differ in number of interactions recorded (Fig. 4, Table S7). Similarly, when only video recorded interactions were considered, significantly fewer records of interactions were collected on video in the Likupang

monoculture reforestation than in the reference forest (negative binomial GLM: adjusted $r^2 = 0.633$, $F_{[3,13]} = 9.035$, estimate \pm SE = -527.395 \pm 155.253, $p < 0.01$), while in the reference forest and mixed species regeneration this did not differ (Fig. S3). In addition, when only active vegetation search and leaf basket interactions were considered, significantly fewer records of interactions were collected in the Likupang monoculture reforestation than in the Likupang reference forest (negative binomial GLM: adjusted $r^2 = 0.455$, $F_{[3,13]} = 1,672$, estimate \pm SE = -0.738 \pm 0.247, $p < 0.05$), while the reference forest and mixed species regeneration did not differ (Fig. S4). In contrast, there were no significant differences between treatments in Tiwoho for number of interactions recorded (Table S8). There were no significant relationships between the number of interactions and CaCo vegetation index in Likupang or Tiwoho (Tables S7 & S8).

Sampling Completeness and Analyses of Merged Network Indices

Analysis of species level and network indices presented here have been carried out on merged networks incorporating video

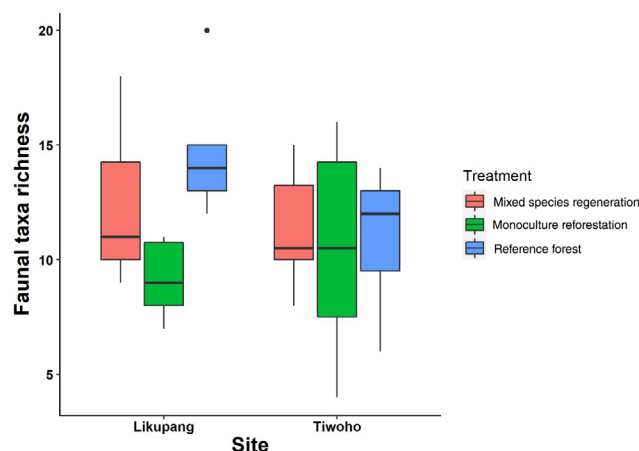


Figure 3. Boxplot of number of species higher level (animals) by treatment for all interaction data collected.

Table 1. Betadiversity and interaction turnover using Jaccard beta diversity index. β_S , species composition dissimilarity between locations; β_{OS} , interaction rewiring, interactions only occurring at one location despite both species being present at both locations; β_{ST} , species turnover, differences in networks due to species not being present at both locations; and β_{WN} , interaction turnover or whole network dissimilarity, $\beta_{WN} = \beta_{OS} + \beta_{ST}$.

Comparison Groups	Species and Interaction Turnover			
	β_S	β_{OS}	β_{ST}	β_{WN}
Between sites				
Tiwoho–Likupang	0.3162393	0.2207792	-0.1394395	0.08133971
Likupang (between treatments)				
Monoculture reforestation–mixed species regeneration	0.3818182	0.6428571	-0.3962818	0.2465753
Mixed species regeneration–natural	0.3513514	0.3404255	-0.1894821	0.1509434
Natural–monoculture reforestation	0.3043478	0.2857143	-0.2015038	0.08421053
Tiwoho (between treatments)				
Monoculture reforestation–mixed species regeneration	0.328125	0.2727273	-0.2037618	0.06896552
Mixed species regeneration–natural	0.4	0.6206897	-0.3520329	0.2686567
Natural–monoculture reforestation	0.2758621	0.25	-0.1973684	0.05263158

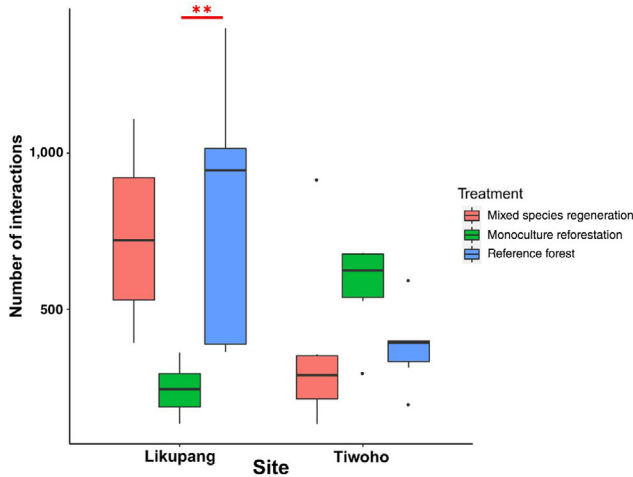


Figure 4. Boxplot of *number of interactions* by treatment for all interaction data collected. Significant differences from the reference forest baseline are highlighted with a red line between the treatments showing a difference and a star indicating significance level.

recordings, leaf baskets, and vegetation searches (full-model outputs in Tables S7 & S8). Assessments of separate video and vegetation network indices are in Tables S1–S3. The different treatments in this study produced networks with distinctly different structures (Figs. 5 & S5–S10). Each quadrat showed high sampling completeness of interactions (Chao1: mean = 96.91, range = 78.95–100; ACE: mean = 96.57, range = 87.06–100); therefore, analyses of network indices calculated at the quadrat level were carried out, testing whether there were (1) differences between treatments and (2) relationships between network indices and CaCo. No significant spatial autocorrelation was detected for any of the network indices (network level or species level), so no dbMEM variables were retained for the final GLMs.

Analyses of Merged Network Species-Level Indices

The plant community was dominated by *Rhizophora* species, particularly in Likupang, with *Rhizophora apiculata* most common and *Rhizophora mucronata* also prevalent (Full_vegetation_survey.csv, available at https://github.com/oconned5/Mangrove_restoration_networks/blob/main/Full_vegetation_survey.csv). *Bruguiera* species (largely *Bruguiera gymnorrhiza*) were also common, particularly in Likupang. *Ceriops tagal* was abundant in the Tiwoho monoculture reforestation and scattered elsewhere. Other identified tree species were rarer and not included in species-level analyses.

Likupang

Bruguiera gymnorrhiza had significantly higher *normalized degree* in the Likupang reference forest than in the mixed species regeneration (beta GLM: pseudo $r^2 = 0.731$, log-likelihood: 9.222 on 5 degrees of freedom [df], estimate \pm SE = -1.317 ± 0.471 , $p < 0.05$) (Fig. 6A), while it was absent in the monoculture reforestation.

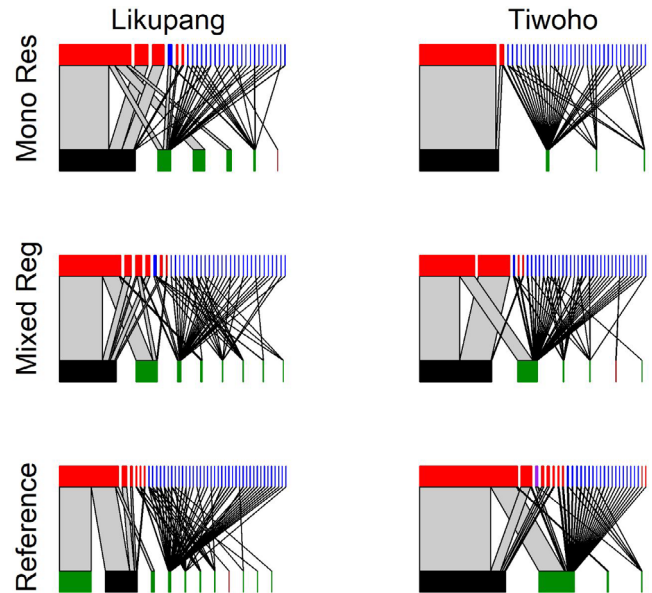


Figure 5. Quantitative bipartite plot showing interactions between animals (top of each plot) and plants and sediment (bottom of each plot). Black rectangles represent sediment, green rectangles plant species, and brown rectangles dead wood. Red rectangles represent animals only recorded via video, blue rectangles represent animals only recorded via direct vegetation search and leaf baskets and purple rectangles indicate animals recorded via both the video and the vegetation search methods. Gray bars indicate interactions, with the thickness of the interactions showing the number of interactions. Reference=reference forest; mixed reg=mixed species regeneration; mono res=monoculture reforestation. For each treatment's individual bipartite plot (see Figs. S5–S10).

Normalized degree was significantly higher for *R. apiculata* in both the Likupang monoculture reforestation and mixed species regeneration, than in the reference forest (beta GLM, pseudo $r^2 = 0.64$, log-likelihood = 6.776 on 6 df: reference forest—monoculture reforestation, estimate \pm SE = 3.437 ± 1.045 , $p < 0.01$; reference forest—mixed species regeneration, estimate \pm SE = 2.862 ± 0.865 , $p < 0.01$) (Fig. 6B, Table S4). *Normalized degree* for *R. apiculata* also had a significantly positive relationship with both CaCo vegetation index (estimate \pm SE = 0.179 ± 0.07 , $p < 0.05$) and *R. apiculata* biomass (estimate \pm SE = 0.015 ± 0.005 , $p < 0.05$) (Table S4).

Rhizophora mucronata had significantly lower *normalized degree* in the Likupang reference forest than in the monoculture reforestation (beta GLM: pseudo $r^2 = 0.693$, log-likelihood: 15.19 on 6 df, estimate \pm SE = -1.734 ± 0.64 , $p < 0.05$) (Fig. 6C, Table S4), while there was no difference to the mixed species regeneration. *Rhizophora mucronata normalized degree* also had a significantly positive relationship with *R. mucronata* biomass (estimate \pm SE = 0.014 ± 0.002 , $p < 0.001$), as did *R. mucronata proportional generality* (Gaussian GLM: adjusted $r^2 = 0.439$, $F_{[4,8]} = 3.343$, estimate \pm SE = 0.00918 ± 0.002782 , $p < 0.05$) (Table S4).

Tiwoho

Ceriops tagal had significantly higher *normalized degree* in the monoculture reforestation than in the Tiwoho reference forest

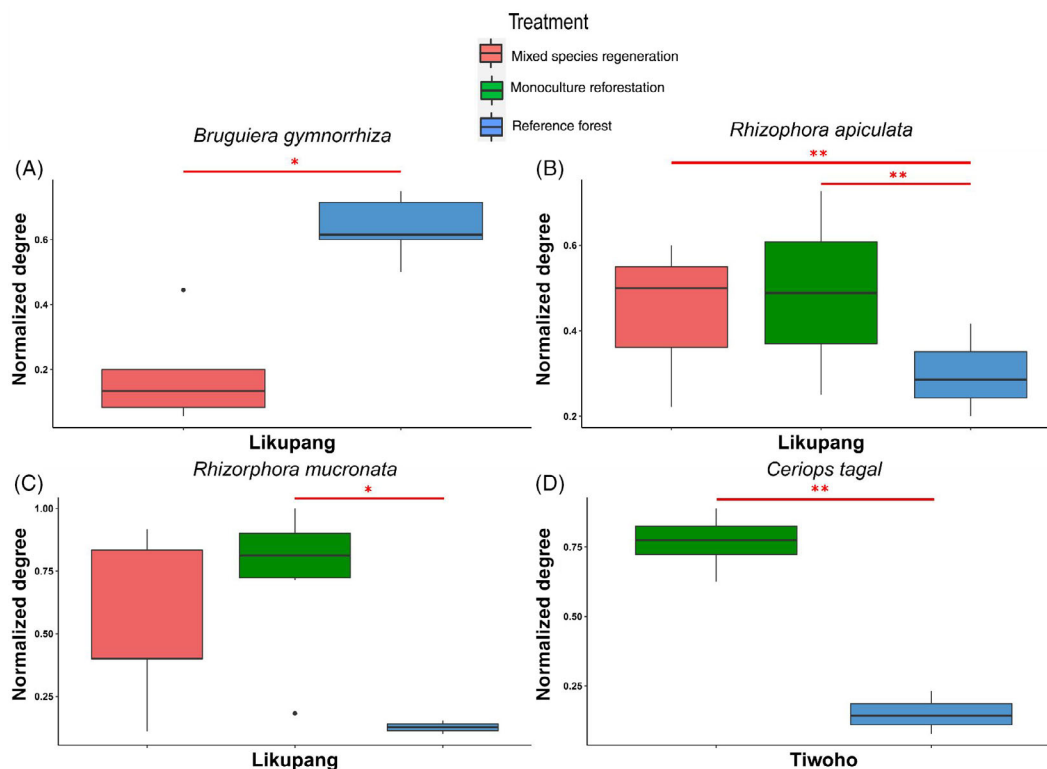


Figure 6. Boxplot of *normalized degree* for (A) *Bruguiera gymnorrhiza* per treatment in Likupang, (B) *Rhizophora apiculata* per treatment in Likupang, (C) *R. mucronata* per treatment in Likupang and (D) *Ceriops tagal* per treatment in Tiwoho. Focal plant species is listed above each box plot and study site is listed below. Significant differences from the reference forest baseline are highlighted with a red line between the treatments showing a difference and a star indicating significance level.

(beta GLM: pseudo $r^2 = 0.908$, log-likelihood: 11.59 on 5 *df*, estimate \pm SE = 1.381 ± 0.371 , $p < 0.005$) (Fig. 6D, Table S5), while it was absent in the mixed species regeneration.

Other species-level metrics did not differ between treatments (Tables S4 & S5).

Analyses of Network-Level Indices

Likupang

The Likupang monoculture reforestation had significantly higher *weighted connectance* than the reference forest (beta GLM, pseudo $r^2 = 0.61$, log-likelihood = 46.94 on 5 *df*: reference forest—monoculture reforestation, estimate \pm SE = 0.511 ± 0.110 , $p < 0.001$), while the mixed species regeneration and reference forest did not differ (Fig. 7, Table S7).

Tiwoho

Weighted connectance was significantly higher in the Tiwoho reference forest treatment than in either the monoculture or mixed species regeneration (beta GLM: pseudo $r^2 = 0.363$, log-likelihood = 17.29 on 5 *df*: reference forest—monoculture reforestation, estimate \pm SE = -0.924 ± 0.307 , $p < 0.05$; reference forest—mixed species regeneration, estimate \pm SE = -0.396 ± 0.143 , $p < 0.05$) (Fig. 7, Table S8). The mixed species regeneration had significantly higher *H2* than the reference forest

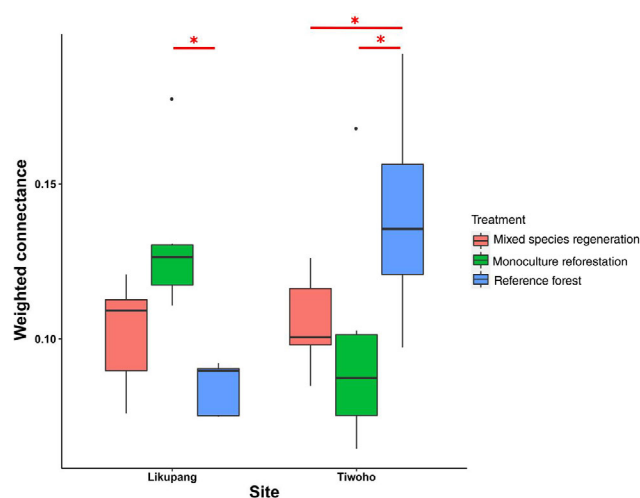


Figure 7. Boxplot of *weighted connectance* for each treatment and site. Significant differences from the reference forest baseline are highlighted with a red line between the treatments showing a difference and a star indicating significance level.

in Tiwoho (Gaussian GLM: adjusted $r^2 = 0.559$, $F_{[3,14]} = 8.167$, estimate \pm SE = -0.379 ± 0.1067 , $p < 0.05$) (Fig. 8, Table S8), while the monoculture reforestation and reference forest did not differ.

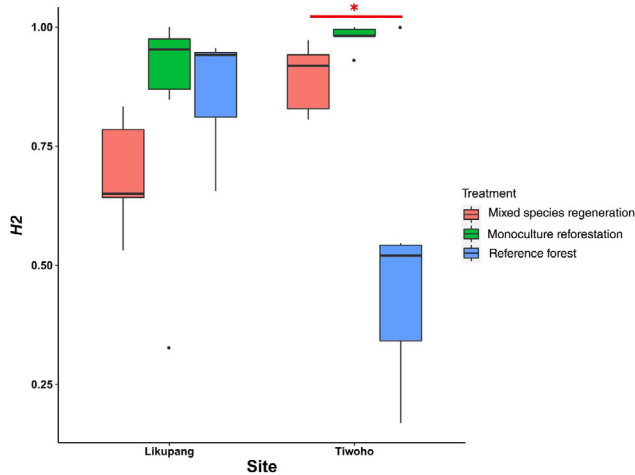


Figure 8. Boxplot of $H2$ by treatment and site. Significant differences from the reference forest baseline are highlighted with a red line between the treatments showing a difference and a star indicating significance level.

Other network-level metrics did not differ between treatments (Tables S7 & S8).

Discussion

We use ecological networks to assess mangrove restoration success for the first time, advancing previous attempts to measure mangrove restoration outcomes based mainly on tree cover or diversity indices. In addition, we integrated video recordings of interaction data to target behaviorally cryptic, but functionally important mangrove faunal species groups. Initial investigations of species diversity did not uncover clear patterns between mangrove treatments. Species dissimilarity between sites (Likupang–Tiwoho), and between treatments within sites, were broadly similar. Despite moderate species dissimilarity, interaction turnover between Tiwoho and Likupang was quite low due to the fact that much of the network dissimilarity could be attributed to species dissimilarity. In addition, there was no significant difference in the number of faunal taxa found between mangrove treatments in either Tiwoho or Likupang. However, by assessing species interactions, some differences between treatments became apparent. The total number of species interactions per quadrat was significantly lower in the Likupang monoculture reforestation than in the reference forest or mixed species regeneration. This was consistently the case across comparisons of merged interaction data, video recording interaction data, and vegetation search data. No such differences for number of interactions were present in Tiwoho, demonstrating the need to treat each of the mangroves systems independently. To further assess this, species-level network metrics were used to assess how animals were interacting with the key plant species in these systems.

Species-level network metric *normalized degree* provided insight into the importance of the key plant species identified in different mangrove treatments. *Bruguiera gymnorrhiza* showed significantly higher *normalized degree* in the Likupang

reference forest than in the mixed species regeneration (links per species scaled by number of possible partner species). In contrast, both *Rhizophora apiculata* and *R. mucronata* had a higher *normalized degree* in the Likupang monoculture reforestation than in the reference forest, while *R. apiculata* also showed higher *normalized degree* in the mixed species regeneration. This difference may reflect the age structure of the forest and ecological role of these trees in the different treatments. The *Rhizophora* species, particularly *R. apiculata*, were dominant and abundant in the younger, dense, restored mangrove stands in Likupang. Therefore, unsurprisingly they had relatively more interaction links in these stands, and *normalized degree* for the *Rhizophora* species was also related to their overall biomass per quadrat. However, in the Likupang reference forest, the mangrove stands were much less dense, with more large, well-spaced out, trees and more old *B. gymnorrhiza* and *Sonneratia alba* (not assessed due to small sample size). In the reference forest, the older *B. gymnorrhiza* therefore presumably contributed disproportionately to leaf matter and root surface area, proving to be of more importance to interacting animals than in the restored treatments where younger *B. gymnorrhiza* faced more competition from abundant *Rhizophora* species (Lutz et al. 2013; Lindenmayer & Laurance 2017). In Tiwoho, *C. tagal*, the dominant tree species in the monoculture reforestation had a significantly higher *normalized degree* than *Ceriops tagal* in the reference forest, an intuitive result given the almost complete absence of other trees from the *C. tagal* monoculture, in comparison to the reference forest where *C. tagal* faced competition from multiple other species. It is clear that *C. tagal* populations in Tiwoho showed a similar pattern to *Rhizophora* species in Likupang, revealing an overall strong signal that the species used in monoculture reforestations unsurprisingly gain greater importance to interacting animals than they usually have in reference forest. The pattern of faunal interaction with the sediment did not differ between treatments in either site in terms of *normalized degree* (links per species), perhaps as it was generally a small number of decapod species that were present throughout both sites that were involved in those interactions. The results from the species-level metrics must be taken in the context of the fact that individual tree species were often not present throughout mangrove treatment areas, so sample sizes were small for some comparisons.

Network-level metrics again provided insight into how species interactions may be operating differently within the mangrove treatments. *Weighted connectance* (diversity of interactions per species) showed a different pattern in the reference forest in comparison to the restored forest treatments in both mangrove systems. Intriguingly, this pattern flips between the two study sites. In Likupang, the monoculture reforestation shows significantly higher *weighted connectance* than the reference forest, while in Tiwoho the reference forest shows significantly higher *weighted connectance* than either the monoculture or mixed species regeneration. Why the two systems show contradictory patterns is not immediately clear, but this is perhaps unsurprising. Likupang is an estuarine mangrove while Tiwoho is a coastal fringing mangrove, these systems would be expected to show ecological differences (Hutchings & Saenger 1987), also there were differences in

mangrove restoration implementation between sites. What does seem apparent is that there are differences in species interactions between the reference forest and restored mangrove forest treatments, even though overall our analyses did not reveal differences in faunal taxa richness between treatments. In addition, $H2$, a network-level measure of specialization which measures how specialized interactions are in the overall network, was significantly lower in the Tiwoho reference forest than in the mixed species regeneration. Interaction specialization was very high across all the other treatments apart from the Tiwoho reference forest. This was not surprising given the lack of plant diversity in the mangrove sites studied (Dunne et al. 2002). Why interactions are less specialized in the Tiwoho reference forest may be due to its relatively demanding environment. Coastal fringe mangroves are much more impacted by salt, receive less sediment input and are more vulnerable to storm damage than estuarine mangroves (Hutchings & Saenger 1987). In addition, while the forest floor was inundated daily in Likupang, in Tiwoho, it was only inundated 8 out of 15 days monitored (see Methods). This more variable inundation schedule may have created a more challenging environment for mangrove fauna. In these harsh and changeable circumstance, animal species may need to be relatively generalist to maintain populations in old-growth coastal fringe mangroves (Foufopoulos & Ives 1999; Henle et al. 2004; Büchi & Vuilleumier 2014).

This study incorporates general collection of interaction data using video recording. A small number of studies have utilizing targeted video recordings of specific flowering/fruitlet trees to construct hummingbird pollination or vertebrate frugivory networks (Maglianesi et al. 2014; Vizenin-Bugoni et al. 2014; Ramos-Robles et al. 2018). Here, we present one of few examples of the utility of using cameras to record a more general cross-section of the environment to uncover the presence and behavior of shy animals which are otherwise difficult to record (Nordhaus et al. 2009). Video recordings were extremely successful at capturing interaction records not otherwise recorded by traditional vegetation searches and visual survey. The only animal recorded by both main methods of interaction data recording was the wide-spread arboreal ant *Oecophylla smaragdina*, otherwise video recordings and vegetation searches captured the activity of entirely different groups of animals. Ninety-eight percent of the video recordings captured ground-dwelling decapod species, mostly small *Parasesarma* crabs, important omnivores and detritivores in mangrove systems (Cannicci et al. 2008; Diele et al. 2013; Cannicci et al. 2021), which were often recorded feeding on senescent leaves or manipulating and feeding on sediment. Video recordings of the sediment also proved effective in capturing animal-sediment interactions of particularly shy but functionally important species, such as; *Thalassina anomala* whose burrowing activity is a major agent of soil turnover, but is usually difficult to survey (Nickell & Atkinson 1995), and the presence and behavior of the key nutrient cycling species *Neosarmatium smithi* (Giddins et al. 1986; Nakanishi et al. 2020). The behavior and interactions of the functionally important decapod species would have been missed in our bipartite ecological network without the inclusion of video-surveying. While contributing comparatively

few interactions, vegetation searches revealed much more diversity of interacting species, and incorporated mangrove species known to be key herbivores (*Littoraria* snails and Chrysomelidae beetles), predators (*O. smaragdina* and numerous Arachnida species), and pollinators (Apidae) (Cannicci et al. 2008). Overall, video recordings captured a large number of records of mostly shy but mobile animals, while vegetation searches captured a smaller number of records, but a more diverse variety of arboreal species, which were more sedentary but cryptic. Hence, it proved valuable to include different ecosystem components (i.e. vegetation and sediment surface), and employ complementary methods for recording interaction data (Wirta et al. 2014).

These results should be taken in the context of a number of study limitations. Data collection was undertaken at daytime ebb tide only due to the difficulty of accessing the site during flood tide periods, and only around spring tide days to capture periods of maximum faunal activity. If logistically possible, future studies should include data collection during flood tide and different points in the tide cycle, as well as at night. Our data collection was focused on capturing plant-animal interactions, necessitating the placement of cameras so that they faced down towards the tree base and leaf litter. Therefore, the faunal groups which were recorded were largely invertebrates and fish, which encompassed the main herbivores and detritivores in this system. The only terrestrial vertebrate recorded was the invertivore reptile (Reptilia) *Emoia atrocostata*. Future research could include camera traps placed in the canopy to record the presence of important vertebrate herbivores, such as the cuscus family (Phalangeridae), although they are thought to be increasingly uncommon in the region due to hunting pressure (summarized in Martin et al. 2019). In addition, passive acoustic monitoring could be utilized to survey important top predators in this system, particularly the mangrove avifauna (Acevedo & Villanueva-Rivera 2006; Buelow & Sheaves 2015), allowing for the building of multi-level interaction network including predatory interactions, giving even greater insight into the structure and function of these mangrove systems.

In this study, we demonstrate the insight gained by taking species interactions into account when assessing mangrove restoration success. Our results show mixed support for our initial hypotheses, providing valuable insight. Overall, vegetation structure did not show a strong effect, but mangrove forest treatment did. While faunal taxa richness did not differ significantly between restored and reference forest treatments, we illustrate how animal species may interact with their environment differently in important ways. Overall, the monoculture reforestation showed greater differences from the reference forest than the mixed species regeneration, with more consistent differences at a network-level in number of interactions and *weighted connectance* (diversity of interactions per species). Such differences in species interactions could have functionally important impacts on restoration projects, as the rate of herbivory, detritivory, pollination, and other interactions will affect ultimate restoration success, inviting further research into specific aspects of ecosystem function in similar systems. We advocate that going

forward the collection of species interaction data should be incorporated into monitoring plans for habitat restoration, allowing us to build on our understanding of the restoration of species interaction patterns and how that may assist in maintaining self-sustaining restored habitats.

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Supporting Information

The following information may be found in the online version of this article:

- Supplement S1.** Supplementary methods.
Supplement S2. Vegetation search network analyses.
Supplement S3. Video data network analyses.

Table S1. Summary of GLM analyses of **Likupang** vegetation search (active vegetation search and leaf baskets collection) network metrics.

Table S2. Summary of GLM analyses of **Tiwoho** vegetation search (active vegetation search and leaf baskets collection) network metrics.

Table S3. Summary of GLM analyses of **Likupang** video data network metrics.

Table S4. Summary of GLM analyses of **Likupang** network metrics for key plants species and sediment.

Table S5. Summary of GLM analyses of **Tiwoho** network metrics for key plants species.

Table S6. Number of times animals interacted with each specific parts of plants and other materials in the networks produced in this study.

Table S7. Summary of GLM analyses of **Likupang** combined network metrics and number of interactions.

Table S8. Summary of GLM analyses of **Tiwoho** combined network metrics and number of interactions.

Figure S1. Scatterplot of Foliage Projective Cover vs Canopy Cover (CaCo) vegetation structure indices for Likupang.

Figure S2. Scatterplot of Foliage Projective Cover vs Canopy Cover (CaCo) vegetation structure indices for Tiwoho.

Figure S3. Boxplot by treatment of number of interactions for video interactions.

Figure S4. Boxplot for treatment by number of interactions for just vegetation search (active vegetation search and leaf baskets).

Figure S5. Quantitative bipartite plot for Likupang monoculture reforestation treatment.

Figure S6. Quantitative bipartite plot for Likupang mixed species regeneration treatment.

Figure S7. Quantitative bipartite plot for Likupang reference forest treatment.

Figure S8. Quantitative bipartite plot for Tiwoho monoculture reforestation treatment.

Figure S9. Quantitative bipartite plot for Tiwoho mixed species regeneration treatment.

Figure S10. Quantitative bipartite plot for Tiwoho reference forest treatment.

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