




## RESEARCH ARTICLE

# Seed dispersal networks become more structured and stable with forest regeneration

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## Abstract

**Introduction:** Restoring interactions between frugivorous animals and fruiting plant species is pivotal for reestablishing community structure and ecosystem functions in recovering tropical forests. However, the reassembly of seed dispersal interactions within regenerating tropical forests remains poorly understood.

**Objectives:** In this study, we examined changes in the structure and complexity of seed dispersal interactions and network-level measures across varying stages of tropical forest regeneration in the Chocó Rainforest of northwestern Ecuador.

**Methods:** Using a combination of mist-netting and camera trap surveys, we sampled seed dispersal interactions across four regenerating forest habitats. We then used an ecological network framework to assess how network-level metrics and interaction patterns shift across stages of forest recovery.

**Results:** Early successional vegetation fostered high frequency and diversity of seed dispersal interactions, which decreased in more mature forests. As forests transitioned into mid-successional stages (secondary forests), seed dispersal networks underwent major restructuring, driven by species turnover across habitats. Due to this restructuring, networks shifted from loosely connected, generalist-dominated systems in early stages of forest succession to more specialized and modular interactions in mature forests.

**Conclusions:** Our results demonstrate that interaction loss and replacement across regenerating forests led to the emergence of more complex and structured seed dispersal networks as forests aged, highlighting how the complexity of mutualistic interactions increases during forest regeneration.

**Implications for Practice:** Network analysis can complement traditional vegetation and biodiversity surveys by revealing how species interactions and ecosystem functions recover during tropical forest restoration. Managers can thus use network-level metrics as tools, for example to identify poorly dispersed plant species that may need intervention or to implement actions to attract keystone seed dispersers to restoration sites. Furthermore, early successional habitats can serve as critical transitional zones that support animal movement and plant recruitment in early stages of forest recovery, but long-term recovery requires ensuring that these systems shift toward the structured, stable networks found in mature forests. By monitoring not only the presence of interactions but also how network structures change over time, practitioners can better design strategies that foster resilient seed dispersal systems aligned with reference forest conditions.

**Key words:** birds, Chocó Rainforest bioregion, frugivory, interactions, mammals, mutualisms, natural regeneration

## Introduction

Species interactions are critical to ecosystem stability and resilience, driving key ecosystem functions such as seed dispersal, carbon sequestration, and energy flows (Brocknerhoff et al. 2017; Chanthorn et al. 2019; Akçakaya et al. 2020). These interactions are especially important in tropical forests, which serve as significant carbon pools (Soepadmo 1993) and habitat to two-thirds of all species on the planet (Olson & Dinerstein 2002). Increasing levels of deforestation and land conversion are disrupting species interactions in tropical forests, negatively impacting ecosystem functions and delaying forest recovery (Markl et al. 2012). Ecosystem resilience, or the ability of systems to reestablish functions after a disturbance, depends on the diversity and functional capabilities of mutualistically interacting species (Neuschulz et al. 2016). Therefore, the reassembly of species interactions is critical for regaining

Author contributions: NML conceived, planned the study; NML, JCW, CBA, EO, GP, GL, MQ collected data, analyzed data; NML wrote the manuscript; JK, JLR, CK were involved in planning, supervised the work, aided in interpreting results and editing the manuscript; all authors discussed results and commented on the manuscript.

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doi: 10.1111/rec.70311

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70311/supinfo>

community structure and ecosystem functions in regenerating tropical forests. However, while community composition has been widely studied in the context of regeneration, the role of interaction reassembly in driving tropical forest recovery remains largely unexplored (McAlpine et al. 2016). Studies examining tropical forest regeneration and restoration often do not consider the complex web of interactions between plants and animals which could jeopardize the regeneration of functional ecosystems (Aerts & Honnay 2011; Timóteo et al. 2016). Thus, in this study we ask: how do species interactions reassemble with tropical forest regeneration?

Interactions between fruiting plant species and frugivorous animals play a crucial role in tropical forest regeneration as almost 85% of tropical plant species are dispersed by animals (Howe & Smallwood 1982). Such interactions are vital for the persistence and movement of plant species away from parent plants to new and favorable habitats (Howe & Smallwood 1982). The assembly of plant–animal interactions is intrinsically linked to the first stages of forest regeneration (Wunderle 1997; Wandrag et al. 2017). The ability of early-stage forests to attract and sustain frugivores can directly influence plant recruitment, species composition, and the trajectory of successional processes in tropical forest systems (De La Peña-Domene et al. 2014; Martínez-Ramos et al. 2016; Arroyo-Rodríguez et al. 2017). Yet despite a recent push to integrate plant–animal perspectives into restoration ecology (Howe 2016; Lussier et al. 2024), a recent review found that only 3% of restoration initiatives have monitored seed dispersal by animals (Mazón et al. 2019). Without a clear understanding of how seed dispersal interactions reassemble within these dynamic landscapes, restoration efforts may overlook essential ecological mechanisms that drive forest regeneration.

Species interactions and emerging community structures can be evaluated using ecological networks (Bascompte & Jordano 2007). Specifically, a network approach can be used to link interactions to broader ecosystem functions and can depict the complexity, stability, and resilience of plant–animal mutualisms. Network measures, such as nestedness and specialization, are intrinsically linked to conservation and biodiversity goals (Howe 2016). For example, nested patterns in mutualistic networks are predicted to support species coexistence through the emergence of redundant interactions, which can enhance the network's resilience to species removal (Bascompte et al. 2006; Bastolla et al. 2009; Thébault & Fontaine 2010). Examining the extent to which networks retain or transform their structure through forest regeneration can provide key insights into the ecological processes shaping forest succession and inform restoration strategies aimed at restoring both biodiversity and ecosystem functions (Howe 2016; Estrada-Villegas et al. 2023; Dansereau et al. 2025).

While previous studies have shown that restoration improves ecosystem services (Benayas et al. 2009) and that management strategies promoting species interactions can support restoration efforts (Lindell et al. 2013), little is known about how seed dispersal network structures and the interactions themselves change with forest regeneration. Only one study to date has examined seed dispersal interactions across secondary stages

of forest succession (Ribeiro da Silva et al. 2015) and none have looked at interaction assembly across early successional habitats. Additionally, the extent to which network attributes that contribute to stability, such as nestedness, persist across multiple stages of forest regeneration is not well understood. If seed dispersal networks fail to recover their structural complexity and stability, regenerating forests may exhibit altered community assembly and reduced functional resilience (Bomfim et al. 2018; Bastazini et al. 2019; Bello Carvalho et al. 2023).

In this study, we utilized ecological networks to understand seed dispersal interactions along a forest regeneration gradient in the Chocó Rainforest of Northwest Ecuador. Specifically, we aimed to (1) examine the effects of forest regeneration on seed dispersal interactions, and (2) evaluate the extent to which seed dispersal networks change their structure through stages of forest regeneration. We hypothesized that seed dispersal interactions change as a function of forest regeneration, where network stability increases as forest succession progresses. Therefore, we predicted that seed dispersal networks become more nested, modular, specialized, and less connected as forest stages increase in age and structural complexity (Bascompte et al. 2006; Olesen et al. 2007; Ribeiro da Silva et al. 2015). This work provides key insights into the role of seed dispersal interactions in forest succession and contributes to a broader understanding of how mutualistic networks reassemble in regenerating tropical forests.

## Methods

### Study Site

This study was conducted at the Fundación para la Conservación de Los Andes Tropicales (FCAT), a reserve situated within the broader Mache-Chindul Ecological Reserve (REMACH), a significant remnant of the Chocó Rainforest in northwestern Ecuador. The Chocó Rainforest is internationally recognized as a biodiversity hotspot, boasting exceptionally high levels of endemism (Aguilar Mugica et al. 2009). REMACH spans 165,000 ha of humid Chocó Rainforest, wetlands, and waterways within the Rio Esmeraldas drainage basin, though it faces significant deforestation pressures (Durães et al. 2013; Van Der Hoek 2017; Kleemann et al. 2022). At the time of data collection, the FCAT reserve covered 656 ha, with elevations ranging from 350 to 550 m above sea level (asl). It experiences a wet season from January to June and a dry season from July to December. FCAT promotes a community-engaged model of research (Karubian et al. 2025) and this project was designed and implemented with strong involvement by local resident researchers.

The study's research design incorporated plots representing three different stages of forest regeneration in comparison to a reference condition: (1) highly disturbed, recently abandoned agricultural land previously used for cattle grazing and cocoa plantations (PA), (2) early successional vegetation that had been recently abandoned agricultural land but retained substantial amounts of remnant vegetation including herb and understory layers, as well as scattered remnant palms (ES), (3) young

secondary forests formerly used for cocoa cultivation or cattle pasture, which have now been without disturbance for approximately 20–25 years (SEC), and (4) old-growth Chocó Rainforest (OG), which served as a reference condition and experienced minimal recent human activity (e.g. low-intensity selective logging) and surrounds all other plot types.

To determine differences in vegetation characteristics between each plot, we calculated several indices from drone-based LiDAR surveys conducted at FCAT on March 2, 2023. Point cloud data were processed in QGIS to generate digital elevation, surface, and terrain models (DEM, DSM, DTM), from which elevation and canopy height were extracted. Canopy openness was estimated by classifying pixels above/below 15 m to identify gaps, and canopy cover was quantified as the proportion of vegetation points relative to total area, assessed at 2, 10, and 20 m above ground. The habitat types differed primarily in canopy structure. PA and ES sites were characterized by low canopy height (<7 m) with relatively sparse cover and greater openness, reflecting early successional vegetation (Table S1). In contrast, SEC and OG forests exhibited much taller canopies (~27 m) with denser cover and reduced openness, consistent with later successional stages.

### Surveying for Fruit Frugivore Interactions

We sampled for seed dispersal interactions May to August in 2022 and 2023 to coincide with the dry season. A combination of phytocentric and zoocentric sampling approaches is thought to be the best mechanism for sampling seed dispersal interactions (Jordano 2016; Vitorino et al. 2022; Lussier et al. 2024). Therefore, we established a series of multi-strata camera traps (phytocentric) on focal fruiting species to observe frugivorous mammals, while also conducting mist-netting surveys for frugivorous birds (zoocentric). Mist-net sampling was conducted in four replicates across each of the four regenerating forest categories, and plots were randomly distributed within each treatment across the FCAT reserve, with a minimum spacing of 100 m between each. Camera traps were opportunistically placed throughout the entirety of each plot.

To select camera trap localities, we first surveyed fruiting plants to identify areas with high diversity and abundance of ripe fruits (Selwyn et al. 2020). We then deployed 25 Meidase P70 Trail Cameras (64 MP, 1296p HD video) opportunistically across a single habitat in areas of high fruit availability. Cameras were placed at different forest strata, including ground level (fallen fruits/seeds), understory (shrubs and low-hanging fruits), mid-story (medium–large fruiting trees), and canopy (overstory fruiting species). Each camera was programmed for continuous 24-h video recording at medium sensitivity to capture actual frugivory and seed dispersal events. To minimize false triggers, vegetation was cleared within ~1 m around ground-level cameras and obstructing branches were removed near higher placements (Campos et al. 2018). All 25 cameras were deployed throughout a single habitat type for a total of 10 days and were then rotated to another habitat. This accumulated 19,200 hours of camera trap sampling in total, or 200 days within each habitat.

From manually analyzing videos, we extracted the date and time of each interaction, identified the plant and frugivorous animal species present, and documented whether the fruit-frugivore interaction was seed predation, seed dispersal, or no interaction. An active dispersal event was defined as an animal swallowing or carrying away fruit (Saavedra et al. 2014). Seed predation events were excluded from the analysis. Animal species were identified by plumage, tail and body length, and other species-specific physical traits. To avoid oversampling bias in camera traps, we counted interactions between a plant and a specific disperser species within a single camera frame once within a 24-hour period.

Mist-netting for birds coincided with an ongoing bird banding monitoring project at FCAT. Mist-netting took place within five plots across each habitat for 2 days at a time. Ten 10-m nets were placed within each plot and opened between 7:00 am and 12:00 pm, during which netted birds were banded, processed, and held in a bag for ~15 minutes to produce a scat deposition. Scat samples were collected to determine intact seed composition, photographed, and stored in ethanol. When possible, seeds were identified to species using a small reference collection at the FCAT field station; however, due to a lack of data on seed species within this region of the Chocó, most seeds (~75%) were identified only to genus or morphotype. Fieldwork was conducted with MAATE permission (*Ministerio del Ambiente, Agua y Transición Ecológica*) under permit number: MAATE-ARSFC-2022-2589. To examine seed dispersal interactions across habitats, frugivorous birds and mammals were first matched with the respective fruiting plant species-based camera videos and scat depositions. Interactions were separated into distinct matrices based on habitat and sampling method.

### Statistical Analyses

All statistical analyses and models were fitted in R (Version 2023.09.1 + 494) (R Core Team 2021). To accurately merge interaction data across our different sampling methods, we used the grand total standardization method (Quintero et al. 2022). This approach helps standardize merging data sets across vastly different sampling types, but in doing so loses the ability to gather information on sample size or effort. For each interaction matrix, we weighted each value within a given matrix by the total number of interactions within that particular matrix. This standardized value indicates the probability that a randomly chosen interaction in that community corresponds to that specific pair of partners (Quintero et al. 2022). Then, the final matrix is obtained by calculating the mean of each value. Using the transformed matrices, we then combined matrices of different methodologies for each plot, resulting in four standardized matrices representing each of the four habitat types.

To quantify the extent to which seed dispersal networks retain or change their structure through stages of forest regeneration, we calculated the edge overlap between networks. Edge overlap indicates the proportion of shared links across habitats, and is a standardized measure of interaction similarity, ranging from 0 (no shared interactions) to 1 (identical networks) (Timoteo et al. 2018). To determine the relative contributions of species

turnover and interaction rewiring to overall network differentiation, we used the ‘betalinkr\_multi’ function which partitions total network dissimilarity into components reflecting differences in species composition and interaction structure (Novotny 2009). We then calculated: (a) species dissimilarity or the proportion of difference in species composition between the two networks, (b) interaction rewiring, or the proportion of network dissimilarity due to changes in interactions among species shared between networks, (c) interaction dissimilarity due to species turnover explained by differences in which species are present in each network, and (d) the overall network dissimilarity, combining both species turnover and rewiring effects. All network analysis and plotting was completed using the *bipartite* package in R (Dormann et al. 2008).

To assess how forest regeneration influences the complexity and stability of seed dispersal networks, we calculated and compared network-level indices across each habitat using the ‘network\_level’ function from the *bipartite* package, including connectance, specialization ( $H2'$ ), nestedness, weighted nestedness metric based on overlap and decreasing fill (WNODF), modularity, and interaction evenness. Connectance represents the proportion of realized interactions out of all possible interactions, ranging from 0 (no interactions) to 1 (all possible interactions realized) and typically decreases with increasing network size (Jordano 1987). Specialization ( $H2'$ ) measures complementary specialization and reflects the degree of niche partitioning among dispersers and plants. Values range from 0 (random associations) to 1 (complete exclusivity of interactions), with higher values indicating stronger partitioning (Blüthgen & Klein 2011).

Nestedness temperature describes the extent to which specialist species interact mainly with subsets of the partners of generalists, creating a core–periphery structure (Bascompte et al. 2003; Ribeiro da Silva et al. 2015). WNODF quantifies nestedness in weighted interaction matrices, capturing both presence–absence patterns and interaction frequencies. WNODF values range from 0 to 100, with higher scores indicating stronger nestedness (Almeida-Neto & Ulrich 2011). Modularity ( $Q'$ ) reflects the tendency for interactions to be organized into cohesive subgroups (modules). Higher values indicate greater compartmentalization, with species interacting more within modules than between them (Dormann & Strauss 2014). Finally, interaction evenness measures the uniformity of interaction frequencies across the network, where higher values indicate more balanced distributions and lower values suggest dominance by a few species (Tylianakis et al. 2007).

To test whether the observed network measures differed from random, we generated 100 null networks per habitat using the ‘vaznull’ method from the ‘nullmodel’ function within the *bipartite* package, which preserves marginal totals and connectance while randomizing species pairings (Dormann et al. 2008, 2009). However, this method does not allow for comparisons of connectance across networks; therefore, for null models specifically testing the connectance value, we used the ‘r2dtable’ method. We then compared observed indices against null distributions to compute  $z$ -scores and  $p$ -values, identifying

whether observed patterns deviated significantly from random expectations (Olesen et al. 2007; Emer et al. 2020).

To calculate interaction diversity and effective number of interactions, we analyzed individual networks from each sampling locality rather than pooled habitat-level networks. This resulted in separate interaction matrices for each plot type within each habitat, or five overall networks for mist-netting surveys and one for camera trap surveys. This approach allowed us to capture variability at the plot level and then test for differences across habitats. Interaction frequency was calculated as the total abundance of each plant–disperser interaction, corresponding to the raw counts recorded in the interaction matrix (i.e., the value of each cell) (Chacoff et al. 2018). Interaction diversity quantifies the diversity and evenness of interactions between plants and dispersers, indicating how evenly distributed links are across all potential pairings (Dormann et al. 2008). We measured this using Shannon diversity ( $H'$ ) with the ‘networklevel’ function. We then calculated the effective number of interactions by exponentiating Shannon diversity values, providing the average number of partners per species while accounting for uneven interaction distributions (Blüthgen et al. 2008). For each interaction variable, we performed an analysis of variance (ANOVA) with plot type as the predictor and post hoc comparisons between plot types using Tukey’s Honest Significant Difference (HSD) test.

## Results

Over 2 years, we captured 1,240 individual birds in mist nets (Table S2), resulting in 275 fecal samples, of which about 42% (115) had intact seeds and amounted to 303 interactions. Furthermore, we observed 719 individual animals from our camera traps (Table S3), of which approximately 23% (163) included an observed seed dispersal interaction, and only these data were used to form networks. Overall, we documented 466 realized seed dispersal interactions across all four habitats between 68 frugivorous animal species and 104 fruiting plant species (Fig. 1). Highly connected disperser species based on overall species-level degree across all plots included *Ramphocelus flammigerus*, *Euphonia xanthogaster*, and *Vireo chivi*.

We observed a slight decrease in the overall animal ( $r^2 = 0.18$ ,  $p = 0.07$ ) and plant ( $r^2 = 0.21$ ,  $p = 0.06$ ) species richness as sites transitioned from PA to OG, as well as the Shannon diversity of both realized dispersers ( $r^2 = 0.22$ ,  $p = 0.05$ ) and plants observed in interaction matrices ( $r^2 = 0.23$ ,  $p = 0.05$ ) (Table S4). We also observed a strong decreasing trend in the patterns of interactions between species from PA to OG habitats (Fig. 2). Both interaction diversity ( $r^2 = 0.23$ ,  $p = 0.05$ ) and the effective number of interactions ( $r^2 = 0.23$ ,  $p = 0.05$ ) were highest in early stages of forest regeneration (PA and ES) and lowest in old-growth forests. Interaction frequency was, on average, highest in early successional vegetation and decreased with forest regeneration ( $r^2 = 0.33$ ,  $p = 0.01$ ). We did not detect any pairwise differences between early stages of forest regeneration (ES) and secondary forests (SEC) (Table S5); however, we observed that interaction frequency, diversity, and the

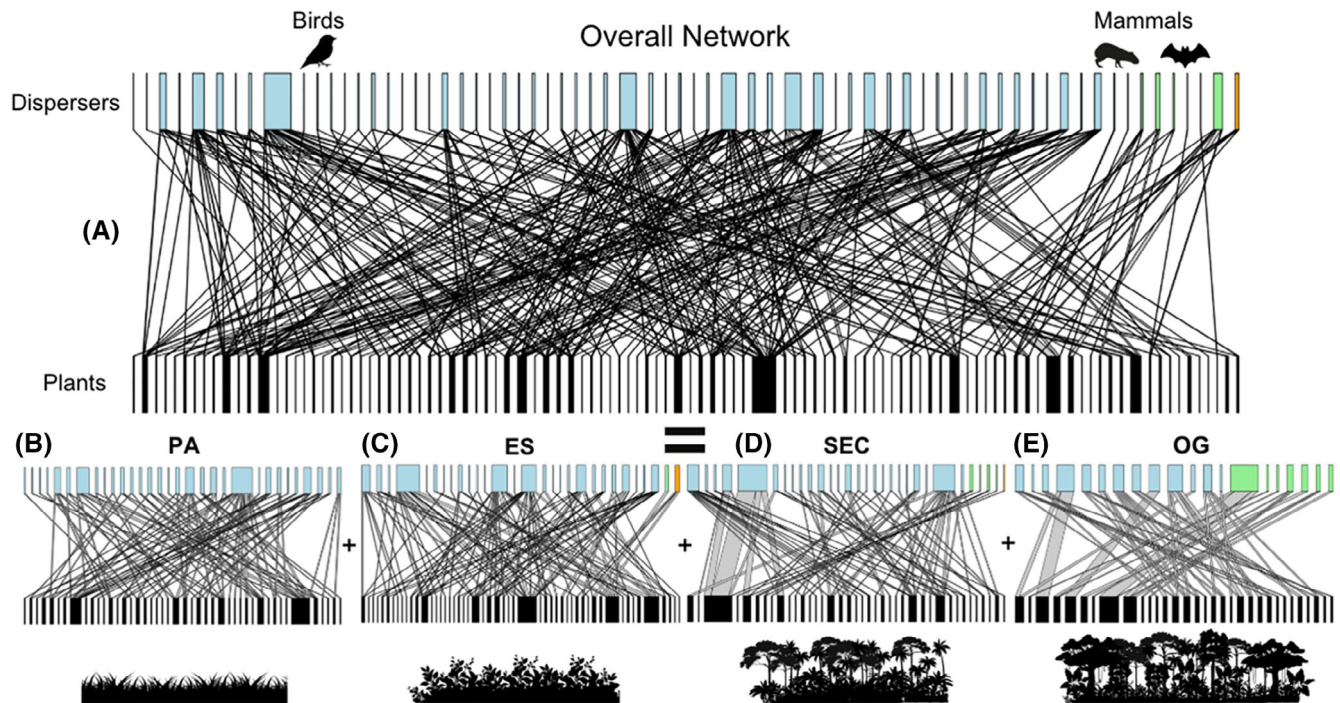


Figure 1. Quantitative seed dispersal network for the FCAT system (A), with four subnetworks (B) representing each of the four sampled stages of forest regeneration. Each node (rectangle) represents a species, and the width of each node represents its relative abundance in that network. Colored nodes represent dispersers: birds = blue, bats = orange, and other mammals = green. Black nodes represent fruiting plant species. Edges (lines connecting each species) represent weighted interactions, where thicker edges indicate stronger dispersal relationships between plants and their dispersers. Overall, we observed 465 realized seed dispersal interactions across all habitats between 68 frugivorous animal species and 104 fruiting plant species.

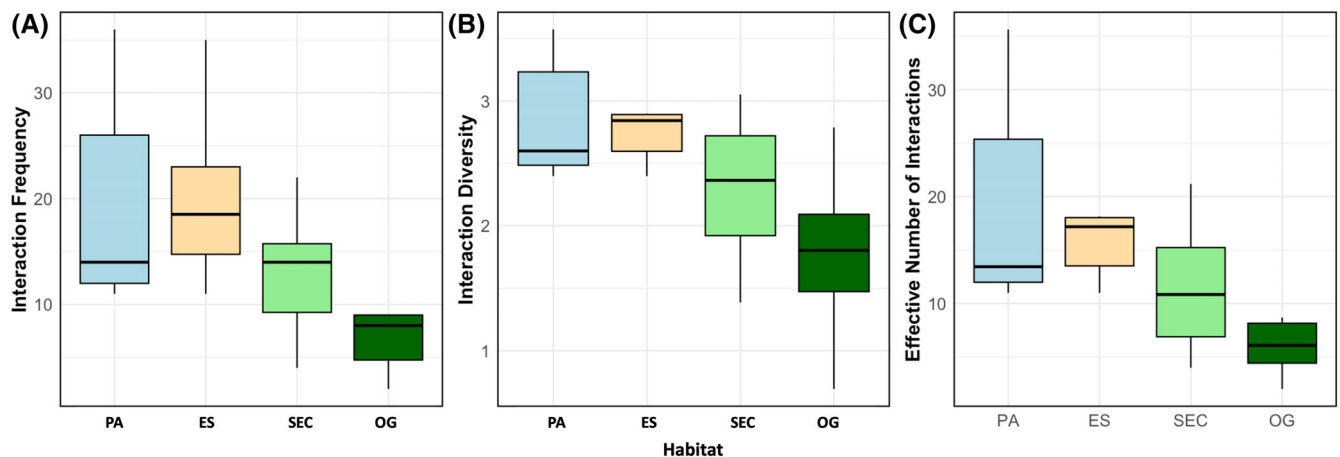


Figure 2. Interaction frequency (A), interaction diversity (B), and the effective number of interactions (C) across four stages of forest regeneration.

effective number of interactions differed between early successional stages (PA and ES) and old-growth forests (OG) (Fig. S1).

Seed dispersal networks restructured across stages of forest regeneration (Fig. 3). We observed similarities in interactions between the two earliest and two latest stages of regeneration, where early stages (PA and ES) shared 46% of interactions, and secondary and old growth (SEC and OG) forests shared

42% of interactions. However, there were fewer shared interactions between early stages of regeneration and late stages of regeneration; less than 10% of interactions were shared between pasture-like habitats and secondary forests. Even fewer (<1%) interactions were shared between the early stages of forest regeneration (PA and ES) and old growth forests. Dissimilarity comparisons of seed dispersal networks across habitats revealed that species turnover was the dominant driver of network

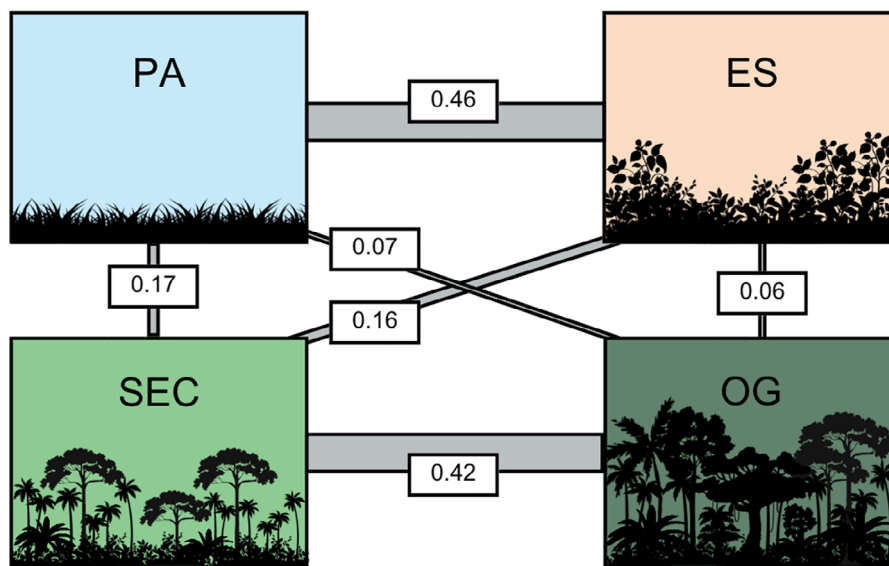


Figure 3. The proportion of shared links across habitats (‘‘edge overlap’’) between each habitat. The widths of the gray lines between each stage are proportional to the correlation of shared links between each pair. Higher values represent a higher proportion of shared links between networks.

dissimilarity in all cases (Table 1). Old growth plots were highly dissimilar from post-disturbance plots, with overall network dissimilarity approaching (PA-OG: 0.99; ES-OG: 0.996; SEC-OG: 0.96). This was largely driven by differences in species composition ( $S$ , 0.77–0.89), while interaction rewiring among shared species was minimal (0.04–0.12). Comparisons among regenerating stages showed slightly higher contributions of rewiring; for example, PA-ES had  $OS = 0.23$ , indicating that differences in interaction structure among shared species were more relevant in early stages of regeneration. Across all pairwise comparisons, species turnover accounted for the majority of network differences ( $ST = 0.72$ – $0.95$ ), whereas rewiring and species loss played a relatively minor role.

The overall structure of seed dispersal networks differed across stages of forest regeneration (Table 2). Interaction evenness was greater than null models in all habitats, suggesting disproportionate contributions of certain species to interaction networks. This was further depicted by high levels of specialization across all habitats, with levels increasing with forest maturity. Nestedness was highest in OG habitats, while values in earlier stages were similar to or below null expectations. ES and SEC habitats had modular networks relative to null models, exhibiting stronger structural compartmentalization than other habitats, though modularity was highest in OG forests but did not deviate from null expectations.

## Discussion

As global efforts are underway to prioritize tropical forest restoration (UN 2019), understanding how seed dispersal interactions reassemble may elucidate the role of mutualistic interactions in facilitating forest regeneration. Many restoration strategies, such as applied nucleation, rely heavily on animal-mediated seed dispersal to enhance natural regeneration processes beyond initial

**Table 1.** Pairwise dissimilarity of seed dispersal networks across habitats. ES, early successional; OG, old growth Chocó Rainforest; PA, pasture; SEC, secondary. Dissimilarity was partitioned into species turnover ( $S$ ), or dissimilarity in species composition; rewiring ( $OS$ ) among shared species; total species dissimilarity ( $WN$ ); overall network dissimilarity ( $ST$ ); fraction of dissimilarity due to species losses ( $ST.l$ ); fraction of dissimilarity due to species gain ( $ST.h$ ); and fraction of dissimilarity due to balances turnover of mutual replacement of species and interactions ( $ST.lh$ ).

Comparison	$S$	$OS$	$WN$	$ST$	$ST.l$	$ST.h$	$ST.lh$
PA-ES	0.66	0.23	0.96	0.72	0.30	0.18	0.24
PA-SEC	0.79	0.11	0.98	0.87	0.25	0.30	0.31
PA-OG	0.84	0.07	0.99	0.93	0.08	0.21	0.63
ES-SEC	0.87	0.06	0.99	0.93	0.40	0.15	0.38
ES-OG	0.89	0.04	0.996	0.95	0.25	0.10	0.60
SEC-OG	0.77	0.12	0.96	0.84	0.46	0.04	0.34

planting sites (Corbin & Holl 2012; Lindell et al. 2013; Holl et al. 2020). These approaches assume that dispersers will redistribute seeds into surrounding degraded areas, thereby accelerating recovery and increasing plant diversity. Thus, seed dispersal networks are critical for determining dispersal potential, recruitment, and regenerating vegetation diversity, which ultimately shapes the trajectory of overall vegetation recovery.

In our system, as forests transitioned from early successional habitats into mid-successional stages (secondary forests), seed dispersal interactions underwent major restructuring, driven by species turnover across habitats. These results highlighted that networks in regenerating forests are non-randomly assembled, with early and mid-successional stages characterized by modularity and reduced connectance, while old-growth forests exhibit stronger nestedness and higher specialization. Therefore, as forests progress toward resembling reference conditions in old-growth forests, networks shifted from loosely connected,

**Table 2.** Summary of network-level metrics across four forest habitats. ES, low impact early successional vegetation; OG, old growth Chocó Rainforest; PA, highly impacted pasture; SEC, secondary forest). The table presents observed values, null model means and standard deviations (SD) for nestedness, specialization, connectance, and modularity. Z-scores and *p*-values indicate whether observed values significantly differ from null expectations ( $p < 0.05$ ).

Stage	Measure	Nestedness	WNODF	Specialization	Connectance	Interaction Evenness	Modularity
PA	<b>Observed</b>	9.01	1.23	0.69***	0.06	0.63***	0.60
	Null mean	10.20	2.01	0.12	0.056	0.62	0.59
	Null SD	1.74	0.60	0.011	0.005	0.0008	0.02
	Z-score	-0.68	-1.30	49.12	0.45	4.49	0.73
ES	<b>Observed</b>	8.06	3.85*	0.69***	0.05*	0.58***	0.58**
	Null mean	8.04	7.08	0.31	0.066	0.61	0.50
	Null SD	1.51	1.33	0.03	0.006	0.004	0.03
	Z-score	0.014	-2.43	12.16	-2.48	-8.64	3.02
SEC	<b>Observed</b>	6.72	2.63*	0.71***	0.05*	0.54***	0.64*
	Null mean	6.58	6.28	0.33	0.069	0.58	0.57
	Null SD	1.43	1.43	0.04	0.0066	0.0058	0.031
	Z-score	0.10	-2.55	9.70	-2.55	-8.28	2.47
OG	<b>Observed</b>	23.29***	0.55*	0.89***	0.04*	0.52***	0.74
	Null mean	13.59	2.98	0.53	0.054	0.58	0.72
	Null SD	2.75	1.08	0.03	0.005	0.005	0.03
	Z-score	3.53	-2.25	11.50	-2.41	-11.82	0.44

*P*-value ranges are denoted with an asterisk (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

generalist-dominated systems into more specialized and structured networks in mature forests. Secondary forests of intermediate age (20–30 years) lacked significant nestedness and exhibited lower apparent levels of specialization and modularity compared to old-growth forests, though modularity observed in old-growth forests did not differ from that expected under the null models. These findings suggest that while some aspects of network structure begin to converge toward reference conditions within a few decades of natural regeneration, key features of mutualistic interaction networks such as nestedness and modularity may require longer timescales to fully resemble the structure observed in old-growth forests.

Early stages of regeneration fostered high interaction diversity and interaction frequency compared to secondary and old-growth forests. Intermediate levels of disturbance can foster greater biodiversity by preventing competitive exclusion and allowing a mix of species with different ecological niches to coexist (Connell 1979). High levels of diversity and species coexistence could have facilitated species to interact with one another more frequently, resulting in a high number of interactions within early stages of forest regeneration. This high level of interaction diversity in early-successional stages is likely shaped by the broader landscape context. In our system, this could be due to a high abundance of generalist disperser species within the open canopy habitats that consume large quantities of small generalist and accessible fruiting plant species (Pinotti et al. 2012; da Gonçalves Silva et al. 2020). Furthermore, the surrounding matrix in our study region is relatively forested and structurally complex, which influences the persistence and movement of the frugivore assemblage within our system. In heavily deforested or agricultural landscapes, interaction richness would likely be much lower due to local extinctions and dispersal limitations. We observed a high presence of small generalist frugivorous birds in earlier stages of forest regeneration

such as *Euphonia laniirostris*, *Euphonia xanthogaster*, and *Ramphocelus flammigerus*, which could be responsible for facilitating high numbers of interactions (Emer et al. 2018; Li et al. 2022). As generalist species often play key roles within seed dispersal networks (Carlo & Morales 2016; Palacio et al. 2016), these early stages of regeneration may serve as important interaction hubs and sustain connectivity between regenerating forest fragments (González-Varo et al. 2017). These interaction hubs may enhance seed rain diversity, promote recruitment of late-successional plant species, and maintain functional connectivity across fragmented landscapes. By supporting a high volume of interactions, especially through mobile generalists, regenerating sites could help bridge ecological processes between degraded and more mature forest patches, shaping successional pathways for regenerating tropical forests.

Seed dispersal networks underwent substantial restructuring across habitats, with only ~16% overlap in interactions between pasture and early successional habitats with secondary forests. This sharp decline in interaction overlap suggests that as forests transition into mid-successional stages, major shifts in species composition and interaction dynamics occur, leading to the emergence of distinct dispersal networks. Regenerating forests within this region exist within a fragmented landscape, and the species capable of colonizing them are limited by habitat connectivity, matrix quality, and historical species loss (Chesson 2000; Mortelliti & Lindenmayer 2015). As such, even old-growth fragments may no longer support the full complement of species historically present, and later successional stages are shaped not only by succession but by the subset of species that remain regionally available.

We found that disperser turnover was the main driver in the reorganization of networks across our habitats, where open-habitat and edge-adapted disperser species dominate early

succession but are later replaced by forest specialists as canopy cover increases and habitat complexity grows (González-Varo et al. 2023). Shifts in plant species composition likely contribute to this restructuring, as successional changes in the plant community introduce new fruiting species that attract different dispersers (Tuomisto et al. 2003). The replacement of fast-growing generalist plant species with late-successional species with specialized interactions may promote the recruitment of new disperser species, while the arrival of new dispersers may, in turn, facilitate the establishment of these plant species. Rewiring among shared species was only slightly higher between regenerating stages, suggesting that network differences are mostly explained by changes in which species are present rather than by changes in the interaction patterns among species that are shared across plots. For example, early stages of forest regeneration were dominated by interactions from small generalist frugivores, including *Vireo chivi*, *Euphonia laniirostris*, and *Euphonia xanthogaster*. The dominant dispersers then shifted between early and late stages of forest regeneration, where most of the interactions in later stages of regeneration were from large-bodied frugivores including *Pteroglossus torquatus*, *Cuniculus paca*, and *Dasyprocta punctata*. The arrival of these dispersers in later stages likely facilitates the establishment of late-successional plant species, reinforcing the turnover-driven differences observed in the networks. Fruit characteristics are also known to change across forest regeneration, shifting from highly abundant, relatively small generalist fruiting plant species to more specialized, larger seeded plant species in mature forests (Pinotti et al. 2012).

Though pasture habitats exhibited high interaction frequencies and evenness, they lacked patterns of connectivity, nestedness, and modularity. They did, however, exhibit levels of specialization, though lower than more mature habitats. These patterns suggest high interaction redundancy and generalized dispersal dynamics, where dispersers interact broadly with plant species in an unstructured manner (Emer et al. 2020). In contrast, restructuring of networks as they shifted to early successional and secondary forests resulted in networks that were specialized and modular, suggesting a shift toward more distinct species groups and interaction compartments with species beginning to form more exclusive relationships. For mutualisms, theory predicts that persistence is linked to nestedness rather than modularity, with modularity potentially reducing stability (Thébaud & Fontaine 2010). A nested structure is characteristic of stable, well-integrated networks, where interaction redundancy enhances resilience to species loss (Atmar & Patterson 1993; Bascompte et al. 2003; Sebastian-Gonzalez et al. 2015). Consistent with this, old-growth showed high nestedness without being significantly modular, whereas mid-successional stages exhibited greater modularity that likely reflects habitat and morphological filtering during regeneration rather than enhanced stability.

High nestedness often indicates a greater degree of specialization among species within a network, while modularity can facilitate specialization by allowing species to evolve specific interactions within their modules (Fortuna et al. 2010; Payrató-Borràs et al. 2020). As a result, the highest levels of

specialization were also observed in mature forests. This is consistent with niche partitioning in Neotropical forests across vertical strata and fruit–disperser traits (Dugger et al. 2019), suggesting that as structure and resource heterogeneity recover, interactions become more specialized and nested rather than more modular. The co-occurrence of these patterns suggests that dispersal networks in later successional stages have greater functional stability and resilience compared to younger forests. This structure may lead to more reliable and targeted seed dispersal, promoting the recruitment of late-successional plant species with specific dispersal requirements and reinforcing community assembly processes. In contrast, early successional forests, which lack this structure, may experience more stochastic or limited dispersal, potentially constraining the regeneration of late-successional species.

Overall, our findings demonstrate that while early successional forests may serve as important facilitators of interaction assembly in fragmented landscapes, the long-term recovery of dispersal networks depends on how early-state disturbance-driven systems transition into more specialized and structured networks as forests mature. The low interaction overlap across successional stages indicates that seed dispersal networks are highly dynamic, driven by species turnover as they continuously reorganize in response to environmental and community-level changes. This restructuring has critical implications for the trajectory of forest recovery, influencing which species and interactions persist with successional changes. Shifts in network structure can determine the dispersal success of plant species with different traits, potentially filtering which species recruit and establish at each stage, shaping long-term plant community composition. Finally, while regenerating secondary forests within our system were highly specialized and modular, nested patterns of stable interactions found in old growth reference conditions may take longer to recover. Our findings highlight the importance of incorporating studies of fauna and their interactions into restoration monitoring, as seed dispersal interactions play a central role in ecosystem recovery in tropical forests. Future work should aim at identifying statistical methodology for comparisons between network-level measures across spatial and temporal scales. A deeper understanding of these processes will be essential for developing effective conservation and restoration strategies that promote both biodiversity and ecosystem resilience.

### Acknowledgments

We would like to thank the staff and researchers at the Fundación para la Conservación de Los Andes Tropicales for their continued support and collaboration. We would like to thank the group of undergraduate researchers who aided in the data collection of this work, including Maggie Millar, John Huston, Lily Benson, Charlie Darmstadt, Taylor Mathes, and Courtney Velasquez, in addition to our field technicians and collaborators Rachel Crafford and Judith Santano. NML's data collection for this work was supported by the British Ecological Society (SR23\1280), the American Philanthropical Society, the American Ornithological Society, the Wilson Ornithological

Society (Stewart23\_NL), the Association for Tropical Biology, and the University of Tennessee. JLR was supported by the National Science Foundation (DEB 23-39839).

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## Supporting Information

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

**Figure S1** Tukey comparisons between forest stages.

**Table S1.** Environmental variables for sites in FCAT reserve.

**Table S2.** Disperser species captured in mist-nets.

**Table S3.** Disperser species observed on camera traps.

**Table S4** ANOVA results for community metrics.

**Table S5** Tukey-HSD results for community measures across habitats.

*Coordinating Editor: Jeronimo Sansevero*

*Received: 19 June, 2025; Revised: 15 December, 2025; Accepted: 15 December, 2025*