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REVIEW

Seeding success: Integrating seed dispersal networks in tropical forest restoration

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Abstract

While the reassembly of fruit-frugivore interactions remains at the forefront of tropical forest restoration, seed dispersal networks emerge as a potential approach to enhance restoration success. This review explores the integration of seed dispersal networks in tropical forest restoration, with the aims of (1) synthesizing important findings in the literature, (2) detailing potential biases in utilizing network theory, and (3) addressing current knowledge gaps and future directions for the field. We first highlight the importance of combining phytocentric and zoocentric approaches when sampling for seed dispersal interactions, as different methodologies have varying effects on network measures, and combining approaches can foster a more comprehensive understanding of dispersal interactions. Furthermore, when integrating seed dispersal networks into restoration goals, we suggest a highly connected and species-rich network is desirable for earlier stages of forest succession where community turnover and transient interactions are pivotal. Nested patterns may emerge throughout varying stages of forest succession, and identifying generalist species that make up nested patterns may be useful for restoration practitioners in both early and later stages of forest regeneration. Modularity should be highest at later stages of succession to maintain community structure and stability, and connector species may play important roles in facilitating seed dispersal across temporal scales. Finally, we emphasize the importance of site-specific long-term datasets, chronosequences, and studies at large spatial scales to continue to understand network reassembly as a function of tropical forest succession and to develop effective strategies that enhance the recovery of tropical forest ecosystems.

KEYWORDS
ecological networks, frugivory, functional traits, mutualism, restoration, seed dispersal

1 | INTRODUCTION

Tropical forest restoration is essential for achieving biodiversity and conservation goals, mitigating climate change, enhancing ecosystem services, and improving overall health and well-being for ecosystems and humans alike (Jørgensen, 2015; Nabhan et al., 2020; Simonson et al., 2021). To assess the success of restoration, it is crucial to understand the functional recovery of an ecosystem in the context of how species interactions reassemble after a disturbance (Brockerhoff et al., 2017; Likens & Lindenmayer, 2012; Moreno-Mateos et al., 2020). Interactions between species, such as animal-mediated seed dispersal, serve as the foundation for many critical ecosystem functions and are integral to forest continuity and the resilience of tropical ecosystems (Akçakaya et al., 2020; Brockerhoff et al., 2017). Ecological networks (Montoya et al., 2006) have proven to be a valuable framework for evaluating the role of species, their interactions, and the importance of emerging community structure on the stability of biological communities and ecosystem functions (Bascompte & Jordano, 2007; Escribano-Avila et al., 2018; Howe, 2016; Jordano, 1987, 2016; Timoteo et al., 2016; Timoteo et al., 2018). In recent years, there has been a push to integrate interaction networks into restoration ecology due to their unique insight into the ecological complexity between species, which could help ensure the recovery of functional ecosystems after environmental change (Howe, 2016; Moreno-Mateos et al., 2020). Without this critical lens, the restoration of tropical forest ecosystems could be jeopardized (Aerts & Honnay, 2011; Timoteo et al., 2016).

Animal-mediated seed dispersal is a well-studied example of a mutualistic interaction that not only provides a fundamental ecosystem function and is instrumental in the conservation and restoration of ecosystems (Bakker et al., 1996; Howe, 2016; Howe & Smallwood, 1982; Wunderle, 1997) but also has been conveyed in an ecological network framework. The dispersal of seeds away from parent plants is vital for the survival of plant species and promotes local regeneration and colonization of vacant habitats (Howe & Smallwood, 1982). Animal-mediated seed dispersal also contributes to the genetic diversity of plants at both local and regional scales and is a driver of evolutionary dynamics in fruiting plants (Bascompte & Jordano, 2007; Galetti et al., 2013). Animals that consume fruits (frugivores) and disperse those seeds are integral to this process, as the seeds of almost 85% of plant species in tropical zones are dispersed by animals (Howe & Smallwood, 1982). Yet despite its importance, seed dispersal is the most threatened process of plant regeneration as seed-dispersing animals face numerous threats such as habitat loss and fragmentation through practices like illegal logging and unsustainable deforestation (Neuschulz et al., 2016). Fragmentation, deforestation, habitat loss, and hunting pressures can all lead to decreased fruit availability and plant diversity loss as more seed dispersers become compromised (Lambert, 2011).

Interactions between plants and their seed-dispersing animal counterparts can be depicted as bipartite networks, whose vertices are divided into two distinct groups (Jordano, 1987, 2016). Individual species within a network are defined as nodes and interactions between partners, such as those between plants and animals, are known as links (Blüthgen et al., 2006). Quantitatively, we can describe patterns of interactions between nodes and links using several different network-level measures or metrics, such as nestedness, specialization, connectance, and modularity. These metrics are inextricably connected to conservation and biodiversity goals (Howe, 2016) (Table 1). Furthermore, we can utilize species-level metrics, such as closeness centrality, to identify critical interactions or keystone species of plants and animals within a system (Table 1).

Mutualistic networks have helped advance forest management goals such as biodiversity maintenance and conservation by identifying critical species and vital interactions that support the structure and function of an ecosystem (Hagen et al., 2012; Messeder et al., 2020). For example, a recent meta-analysis found three keystone plant families across the Neotropics whose removal from seed dispersal networks led to significant changes in network stability, thus if these critical food sources are removed it could have drastic negative effects within an ecosystem (Messeder et al., 2020). Characterizing the functional traits of important species within ecological networks has also emerged as a pivotal step for illuminating significant species characteristics across plant and animal communities (see: Escribano-Avila et al., 2018; Mello et al., 2015; Messeder et al., 2020). Yet, there is a lack of synthesis on what the most beneficial or influential functional traits are in terms of contributing to community turnover and connectivity across recovering landscapes. There is also a lack of consensus on how identifying key species and their functional traits could directly inform conservation and restoration strategies that enhance ecosystem recovery in fragmented areas (Howe, 2016; Ribeiro da Silva et al., 2015).

There are surprisingly few instances in the literature where seed dispersal networks have been examined across successional gradients or within the context of restoration, which limits our understanding of how network dynamics change throughout the successional process (Escribano-Avila et al., 2018; Ribeiro da Silva et al., 2015). Furthermore, there are numerous different field sampling and statistical approaches employed when utilizing seed dispersal networks, which may introduce unwanted potential biases (Jordano, 2016; Jordano et al., 2002). For example, interpretations of the statistical significance of network metrics from null models varies greatly among studies, making it difficult to draw comparisons across geographic or temporal scales. The absence of a unified consensus underscores the need for a comprehensive examination of the varied approaches employed in characterizing seed dispersal networks, as well as a clearer understanding of the potential for network measure to aid in informing tropical forest restoration.

The goal of this work is to synthesize how seed dispersal networks have been used in tropical forest systems and to emphasize their potential to advance conservation and restoration ecology. Specifically, we focus on three aims: (1) Synthesize findings that have been made utilizing seed dispersal networks in the tropics that are relevant to the fields of conservation and restoration ecology; (2) Highlight potential biases and cautions of utilizing network theory, and; (3) Identify current knowledge gaps in utilizing seed dispersal networks to aid in conservation and restoration of tropical forests, and how these can be addressed in future research. To this end, we conducted a systematic literature review to document research on seed dispersal networks in tropical regions with a specific focus on how studies could relate to conservation and restoration. By systematically reviewing and summarizing a wide range of studies, this review will provide a comprehensive overview of the current state of research in this field and its potential trajectory for future research.

TABLE 1 Glossary of metrics commonly used to describe seed dispersal networks with the name of the metric and its acronym, the type of metric (species-level or SL, network-level or NL), the scale of which the metric is measured, a description of the metric, its ecological significance to restoration and conservation, and citations of definitions of the metric.

Metrics	Level	Scale	Descriptions	Conservation significance	References
Nestedness (NODF)	NL	0–100	Describes the interactions between species, where networks with fewer interactions have a subset of species that have distinct and specialized interactions. More nested networks will typically organize the community cohesively around a central core of generalist interactions.	Nested bipartite networks have been theorized to be more stable than non-nested networks. This is because nestedness implies that generalist seed dispersers interact with a subset of the seeds dispersed by specialists, creating redundancy and ensuring that multiple species can contribute to the dispersal of the same seeds. In the face of environmental changes or the loss of specific species, the presence of generalists in nested networks provides a level of robustness, helping to maintain seed dispersal functionality even if some specialized interactions are disrupted.	Blüthgen et al., 2008; Bascompte et al., 2003
Connectance (C)	NL	0–1	The proportion of realized interactions is divided by the total number of interactions.	The level of connectedness in seed dispersal networks is pivotal for achieving successful conservation and restoration goals, as a higher degree of connectivity ensures the efficient movement of seeds across the landscape, promoting genetic diversity, supporting ecosystem resilience, and facilitating the natural regeneration of plant communities. Connectedness tends to decrease with network size as interactions become more specialized.	Costa et al., 2022; Blüthgen et al., 2006, 2008
Modularity (*M* or Q)	NL	0–1	A measure of the number of subgroups in a network and how exclusively they interact with one another.	Modular networks have been linked to ecosystem stability, as modularity can act as a buffer against the spread of disturbances, allowing for more localized responses to environmental changes or species loss. In the context of seed dispersal, modular networks can enhance the resilience of ecosystems by isolating potential disruptions within specific modules, preventing cascading effects that could jeopardize the overall functionality of the network, and contributing to the stability of plant communities in conservation and restoration contexts. Plant and disperser species that are found within multiple modules are called connectors and may be of high conservation importance. Likewise, hubs, or species with many connections, found within modules may also be important targets for restoration efforts.	Grilli et al., 2016
Network Richness	NL	Cont.	A measure of the amount of both plant and animal species in a network.	A higher network richness promotes greater biodiversity and ecosystem resilience. This diversity ensures that a variety of species contribute to seed dispersal, enhancing the adaptive capacity of ecosystems and increasing the likelihood of successful natural regeneration.	Pocock et al., 2012

(Continues)

TABLE 1 (Continued)

Metrics	Level	Scale	Descriptions	Conservation significance	References
Specialization (H^2)	NL	0–1	The measure of connectance quantifies how specialized interactions between species are within a network and can give information on niche partitioning within a system.	Specialized interactions can foster coevolutionary relationships, where plants and dispersers become finely tuned to each other's needs. This can enhance the precision and efficiency of seed dispersal, optimizing reproductive success for the plants involved. Specialization in seed dispersal networks is vital for maintaining the resilience of plant populations, particularly for those with specific ecological requirements.	Blüthgen et al., 2006
Interaction Frequency	NL	Cont	The number of connections or links between nodes.	A perfectly connected network will have a high interaction frequency, where every disperser interacts with every plant species evenly. A lower interaction frequency indicates there are fewer interactions within a system.	Chacoff et al., 2012
Degree	SL	Cont.	Number of interacting partners a particular species has.	A high species degree for a particular species indicates that it has diverse ecological connections, playing a potentially influential role in the network's structure and functioning. Analyzing species degree is valuable for understanding the importance of individual species in the network and identifying key contributors to seed dispersal dynamics.	Burin et al., 2021; Oldham et al., 2019
Closeness Centrality	SL	Cont.	The sum of the number of shortest distances between the particular species and all other species in the network.	A species with high closeness centrality is more central in the network, meaning it can quickly reach other species or be reached by them. In the context of seed dispersal, a species with high closeness centrality may play a crucial role in facilitating the flow of seeds through the network, influencing the connectivity and efficiency of seed dispersal pathways.	Burin et al., 2021; Oldham et al., 2019
Specialization (d)	SL	0–1	The deviation of observed interactions from opportunistic, abundance-based interaction.	High species-level specialization indicates that a species has a narrow set of preferred interaction partners, while low specialization suggests a more generalist or flexible strategy in engaging with a variety of partners. This information could be crucial in decisions involving species reintroductions and target species for conservation and restoration.	Blüthgen et al., 2006; Olesen & Jordano, 2002

2 | METHODS

2.1 | Literature survey and database

A comprehensive literature survey was conducted to gather relevant studies aimed at seed dispersal networks in tropical forests using Web of Science, PubMed, and Google Scholar. The search terms included "seed dispersal network" or "frugivore* dispersal network" or "plant-frugivore* network" or "mutualistic interaction network" and dispersal in the title, keywords, or abstract. In addition, we checked the Interaction Web Database and the Web of Life Ecological Network Database and searched references listed in studies to build an extensive list of seed dispersal network papers in the tropics. Initial search results returned 2916 articles. The search was then refined by including specific terms related to seed dispersal networks, fruit-frugivore interactions, and tropical regions. After these initial screenings, the abstracts of 428 papers indicated that the research centered around seed dispersal networks in the tropics, and each was then fully analyzed. Studies that met the following criteria were considered for inclusion: (1) overall focus on seed dispersal networks specifically, with results including descriptions of or utilization of network analysis, (2) study focused on or took place in tropical regions, (3) published in peer-reviewed journals or dissertation manuscripts, (4) published between 1990 and 2023, and (5) employed empirical or theoretical approaches to collect data on seed dispersal interactions. To ensure no datasets were overlapping with data from empirical studies, we removed any duplicate studies or studies that used individual networks that were reported in multiple papers, as many of the reviews and meta-analyses gathered used publicly available datasets. We retained the original paper that described a seed dispersal network and did not utilize any papers published after the original article using the same data set. Full-text articles were obtained for the selected studies and thoroughly reviewed to assess their suitability for inclusion in this review. After the second screening, a total of 77 papers were included in our analysis (Table S1).

Various aspects of each included study were extracted to provide a comprehensive understanding of seed dispersal networks in the context of tropical forest conservation and restoration. This included qualitative information such as the goals and hypotheses of each study, site locations, species involved, field methods employed such as focal observations or camera traps, and the statistical approaches utilized in each study. Different types of null models, such as randomized or simulated models, may have been used to compare the observed network structure against randomized or null expectations. If the study included multiple sites or habitats, information on how comparisons were made across these sites was extracted. Finally, we examined the claims made by each study, including key findings related to network dynamics across different habitats, the role of specific species within networks, and if there were suggested implications of the findings for conservation and restoration.

2.2 | Building database of seed dispersal networks

We gathered reported network measures from each paper including network richness, plant richness, disperser richness, as well as the frequency or number of total interactions. This was done to gain a better understanding of the patterns and variations in seed dispersal networks and highlight potential correlations between these parameters and methodologies used to sample for seed dispersal interactions. We carefully screened each review and meta-analysis to ensure no datasets were overlapping with data from empirical studies, and if they were then the duplicate networks were removed.

In addition to network richness, we extracted other network-level metrics such as modularity, specialization, nestedness and weighted nestedness, connectance, robustness, interaction evenness, sampling completeness, and any other network-level metrics reported. We again carefully screened each paper and ensured that measures were calculated and represented in the same way, and if they were not, we manually changed them (for example, changing 75% sampling completeness to 0.75).

2.3 | Statistical analysis

From extracted network-level metrics, we used a Kruskal-Wallis test to test significant relationships between network size and network-level metrics such as weighted nestedness (WNODF), specialization (H^2), and modularity (Q). This analysis helps to discern whether network structures vary significantly with changes in network size, providing insights into how the size of seed dispersal networks may influence key ecological metrics. Furthermore, we used generalized linear models and Pearson correlations tests to determine if sampling type (phytocentric, zoocentric, or a mix of both), sampling effort measures, and taxa (plant and animal) influenced network-level metrics. Different sampling approaches (phytocentric, zoocentric, or mixed) may yield varying network structures (Vitorino et al., 2022). A phytocentric approach emphasizes the perspective of plants, for example by observing frugivory on a particular tree (Schlautmann et al., 2021). A zoocentric approach highlights the perspective of animals, for example through mist-netting bats to collect seeds from fecal samples (Hernandez-Montero et al., 2015). By analyzing their impact on network-level metrics, one can assess the methodological implications of sampling strategies, aiding in the standardization of methodologies for future seed dispersal network studies.

3 | RESULTS

3.1 | Literature survey

Of the 77 papers analyzed in this study, 44 were from the Neotropics, 14 were in the Afrotropics, six were in tropical Asia, and the remainder had multiple regions within their analysis (Figure 1). Numerous

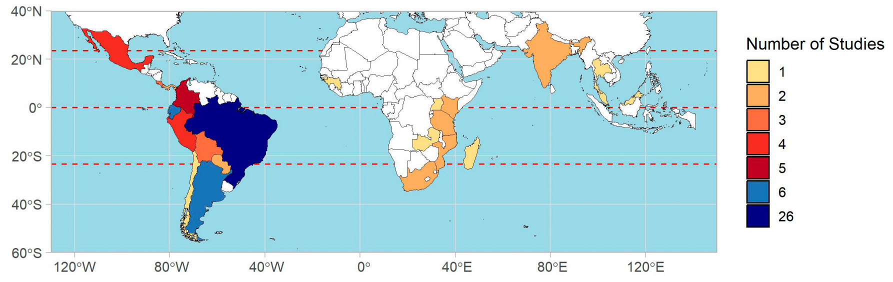

FIGURE 1 Geographic distribution of studies included in our review, with delineations for the Equator and Tropics of Cancer and Capricorn. Color represents the number of studies conducted in each country. Most studies were conducted in Brazil (*n* = 26).

studies took place in Brazil (*n* = 26), and many of those were from Brazilian Cerrado or Atlantic Forest (*n* = 16) biodiversity hotspots, leaving studies in other tropical regions such as Southeast Asia and Central Africa severely limited. Fifty-two papers conducted field sampling for species interactions, while the remaining 28 papers were reviews, meta-analyses, or simulation models. Birds represented the most studied taxa, appearing in 57 papers, and were the only animal taxa included in networks in 31 papers. Excluding review papers, direct observation was the most used field methodology to gather information on seed dispersal interactions (*n* = 34), followed by mist-netting (*n* = 14), camera traps (*n* = 10), and scat surveys (*n* = 10). Only 18 papers used a combination of field methodology to assess seed dispersal interactions, which most often included a combination of direct observations, mist-netting, and camera traps.

Twenty papers focused on utilizing functional traits of both plants and animals to identify their roles in seed dispersal networks and the surrounding ecosystem, 15 of which were within the last 5 years. Other major topics included comparing networks across a landscape gradient (*n* = 19), identifying the role of invasive or non-native species within a network (*n* = 5), and highlighting the roles of specific taxa or field methodology in skewing network measures (*n* = 4). Only one paper to date has examined how seed dispersal networks reassemble over a restoration gradient (Ribeiro da Silva et al., 2015).

3.2 | Network measures

In total, 306 individual networks and their reported metrics were extracted from the 77 papers synthesized for this review. The most reported network-level metrics were modularity (*Q* or *M*), nestedness (WNODF or NODF), and specialization (H^2) (Table 2). Only 91 of 306 networks included a measure of sampling completeness that is, the sample's coverage, or the ratio of the number of individuals of a species in the sample to the number of individuals in an overall assemblage of that species (Chao et al., 2020). Less than 30 networks reported other network measures, including interaction evenness, which evaluates the homogeneity of relative interaction frequencies across all links in the network (Blüthgen et al., 2008), interaction diversity or the richness and relative abundance of species interactions in a community (Dyer et al., 2010), and network robustness, which is the ability of a network to maintain its interactions after a perturbation (Fortuna & Bascompte, 2006). Sampling

TABLE 2 Network metrics used to describe seed dispersal networks in the literature with the range and mean of measures reported from networks gathered for review.

Metrics	Scale	Overall reported values
Weighted nestedness (WNODF)	1–100	26.96 (low: 3.91, high: 58.4)
Connectance (*C*)	0–1	0.22 (low: 0.04, high: 0.39)
Modularity (*M* or *Q*)	0–1	0.379 (low: 0.097, high: 0.67)
Network richness	Cont.	62.4 (low: 8, high: 463)
Specialization (H^2)	0–1	0.416 (low: 0.066, high: 1)
Interaction frequency	Cont.	340 (low: 10, high: 8004)

method significantly influenced network metrics (Figure 2; Table 3). Sampling had a significant effect on WNODF (chi-squared = 7.59, $df = 2$, $p = .023$) and H^2 (chi-squared = 9.44, $df = 2$, $p = .009$) (Figure 2). Mean WNODF measures were similar for both phytocentric and zoocentric approaches (23.5 +/− 1.8 and 23.9 +/− 1.8) and was highest in networks that used mixed phytocentric and zoocentric sampling methods (34.7 +/− 1.8). Specialization was almost 60% lower in mixed sampling methods when compared to zoocentric methods (mix: 0.35 +/− 0.2; zoo: 0.60 +/− 0.2), and 22% lower when compared to phytocentric approaches (phyto: 0.43 +/− 0.2). The sampling method was also a significant predictor of network richness (chi-squared = 18.78, $df = 2$, $p < .0001$), where networks with the highest richness had an average of 71 +/− 4.6 species and were found to use mixed sampling methods. Zoocentric networks yielded the lowest species richness, averaging just 29.5 +/− 4.6 species per network. Sampling type did not significantly impact modularity (chi-squared = 1.42, $df = 2$, $p > .05$). Network richness did not significantly predict network measures (WNODF: chi-squared = 139.59, $df = 139$, $p > .05$; H^2: chi-squared = 107.15, $s = 99$, > 0.05; Modularity: chi-squared = 94.47, $df = 94$, $p > .05$) (Table 3).

4 | DISCUSSION

4.1 | Sampling for seed dispersal interactions

Sampling methods may influence seed dispersal network measures and patterns, especially in highly diverse communities such as those in tropical regions (Vitorino et al., 2022). Sampling methods must

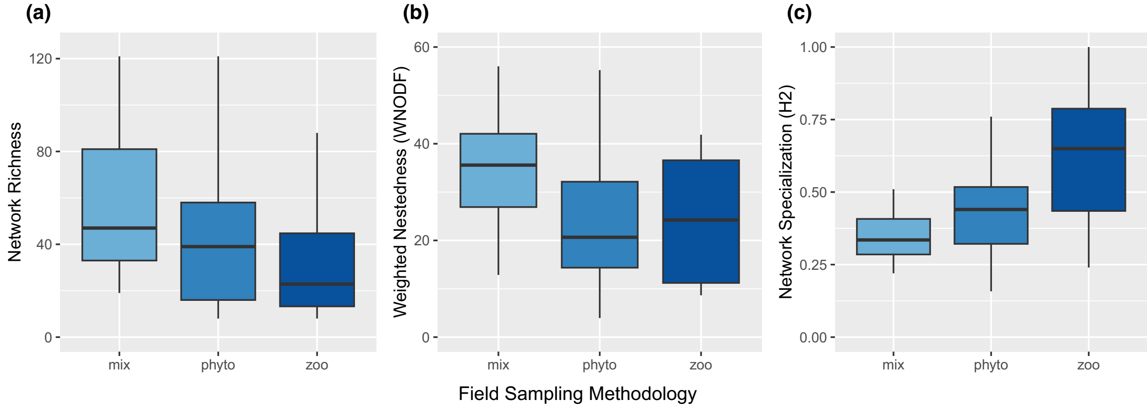

FIGURE 2 The effects of sampling methods (phytocentric approaches, zoocentric approaches, and a mix of both) on seed dispersal network metrics including (a) network richness or size, (b) network-level specialization (H^2), and (c) weighted nestedness (WNODF).

TABLE 3 Summary of results from comparisons of Kruskal-Wallis tests among network parameters including equation used, Kruskal-Wallis chi-squared, degrees of freedom (*df*), and *p*-values. Method type represents the type of sampling methods used when sampling for interactions and is either phytocentric (plant-centric), zoo-centric (animal-centric), or a combination of the two types.

Equations	Chi-squared	*df*	*p*-value
Method type ~ network richness	18.78	2	.0001***
Method type ~ specialization (H^2)	9.44	2	.009**
Method type ~ weighted nestedness (WNODF)	7.59	2	.023*
Method type ~ modularity (Q)	1.42	2	>.05
Network richness ~ specialization (H^2)	107.15	99	>.05
Network richness ~ weighted nestedness (WNODF)	139.95	139	>.05
Network richness ~ modularity (Q)	94.47	94	>.05

Note: Asterix (*) in the *p*-value column represent significance, where $* = p < .05$, $** = p < .001$, and $*** = p < .0001$.

capture the complexities of tropical environments, as diverse seed dispersal networks have been found to correlate to greater ecosystem resilience (Bastolla et al., 2009; Thébault & Fontaine, 2010; Tylianakis et al., 2010). Identifying too few interacting partners within a network was highlighted as a main caution when applying seed dispersal networks to restoration practices, as a lower number of interactions can greatly affect network measures (Howe, 2016). Our findings revealed a significant relationship between sampling methods and network size ($p < .001$) and combining both zoocentric and phytocentric methods yielded the largest overall networks. Therefore, utilizing both phytocentric (plant-centric) and zoocentric (animal-centric) methods when sampling for seed dispersal interactions may provide a more comprehensive approach to building seed dispersal networks (Howe, 2016; Ramos-Robles et al., 2018; Vitorino et al., 2022).

Despite the potential drawbacks, most papers in the reviewed literature tended to adopt a phytocentric approach, emphasizing plant-centric perspectives. Phytocentric approaches typically consist of using direct observation of feeding events on fruiting plants within spatially delimited sampling transects or plots (Ramos-Robles et al., 2018; Ribeiro da Silva et al., 2015; Vitorino et al., 2022). This also includes the use of camera traps on focal fruiting species to document fruit-frugivore interactions. This approach allows for interactions to be identified regardless of disperser size, behavior, or preferred forest strata, and allows for the observation of less frequent dispersers that may be important for consuming substantial amounts of fruit with larger seeds (Naniwadekar et al., 2019; Vidal et al., 2013). However, frugivory may not be a good proxy for seed dispersal effectiveness as it overlooks factors such as seed handling and deposition, which significantly influence the fate and success of dispersed seeds (Schupp et al., 2010). Additionally, the mobility of dispersers isn't always accounted for in a phytocentric approach. Given the varied spatial scales at which seed dispersal networks operate, relying solely on a phytocentric approach may conflate the effects of small-scale community dynamics, such as habitat selection, with landscape-level processes (Freitas et al., 2014; Souza et al., 2021; Vitorino et al., 2022). Effective restoration requires an understanding of how seeds move across the landscape and into degraded lands, therefore an exclusive focus on plant perspectives without accounting for underlying spatial heterogeneity might miss these broader ecological patterns (Carlo & Yang, 2011; Souza et al., 2021).

Plant-centric sampling approaches may also inadvertently bias restoration efforts towards a limited set of plant species, such as those only within the visual range of the observer, which can result in monoculture-like outcomes where the diversity of a system is not represented (Freitas et al., 2014; Vitorino et al., 2022). This approach may also limit observations to species with longer fruiting stages, or those fruiting species falling within designated plots. This could lead to over-yield network specialization and produce a significantly lower nestedness value than zoocentric networks (Vitorino et al., 2022). In addition to potentially missing key plant species, critical disperser species may be overlooked leading to a failure to recognize key partnerships that could contribute significantly to restoration success

(Muscarella & Fleming, 2007; Vitorino et al., 2022). For example, Phyllostomid bats are incredibly important seed dispersers in disturbed areas, such as pastures, as they disperse seeds of pioneer and primary species and consequently contribute to the recovery of woody vegetation in disturbed areas (Galindo-González et al., 2000). Taking a solely phytocentric approach in sampling, such as establishing seed traps in disturbed areas to capture seed rain, could disregard the importance of specific bat species. By combining seed traps with a zoocentric approach, like mist-netting for bats to collect fecal samples with intact seeds, researchers can account for these potential missing interactions (Galindo-González et al., 2000; Laurindo et al., 2020; Muscarella & Fleming, 2007).

Zoocentric networks consist of interactions determined by recovering droppings, scat depositions, or regurgitations from frugivorous animals through mist nets, mammal traps, or scat surveys where recovered seeds are either identified from comparisons with reference collections or through DNA barcoding (Ramos-Robles et al., 2018; Ribeiro da Silva et al., 2015; Vitorino et al., 2022; Vizentin-Bugoni et al., 2022). A zoocentric approach incorporates the “effectiveness” aspect of seed dispersal by potentially allowing condition and germination studies to take place after a seed has passed through an animal's digestive tract (Gomes et al., 2022; Schupp et al., 2010). Zoocentric approaches tend to allow for interactions with a higher number of plant species than phytocentric approaches because they do not rely on the visual limitations of the observer (Vitorino et al., 2022). Zoocentric methods also inherently account for the movement of animals across landscapes, providing insights into the spatial variation in seed dispersal based on disperser mobility (Souza et al., 2021). This broader perspective is essential for understanding how seeds are dispersed across various habitats, facilitating the development of restoration strategies that consider landscape-scale processes. By understanding and promoting species that aid in landscape connectivity and community turnover, restoration efforts can better support fostering biodiversity in systems undergoing restoration.

However, there are potential downsides to using a zoocentric approach, as field sampling can be data-intensive and complex. Identifying and tracking many different animal species, especially in highly diverse ecosystems, may present logistical challenges and require extensive field and laboratory (e.g., barcoding) efforts from experienced technicians (González-Varo et al., 2014). Moreover, focusing primarily on animal contributions might lead to an incomplete understanding of the roles that different plant species play in seed dispersal networks. Popular zoocentric sampling methods, such as terrestrial mist netting, may overlook the roles of important disperser species such canopy-dwellers or larger birds, because these individuals are less likely to be captured and thus are excluded (Vitorino et al., 2022).

To reduce these biases, we suggest studies prioritize utilizing both a zoocentric and phytocentric approach to sampling for seed dispersal interactions, which could foster a more complete description of interaction networks (Quintero et al., 2022; Ramos-Robles et al., 2018; Schlautmann et al., 2021; Vitorino et al., 2022). Combined methodology yields higher overall network richness, which could improve the legitimacy and consistency of other network measures like specialization and nestedness. Furthermore, combined methods may further enable the identification of keystone species and critical ecological pathways that may not be identified through one method alone. Recent work has found that extrinsic factors, or indirect factors, are the biggest influences on restoration success (Selwyn et al., 2023). Seed dispersal into degraded lands or restoration sites is considered a crucial extrinsic factor for the recovery of tropical ecosystems. Thus, to fully understand what species are driving these connections among landscapes and aiding in forest recovery, we must first be able to identify as many interacting species within the system as possible.

Combining sampling methods has shown some limitations, such as calculating interaction frequency from different interaction currencies and calculating sampling completeness (Quintero et al., 2022; Vitorino et al., 2022). A recent paper suggests ways in which networks constructed from various sampling methodologies and datasets can be combined, describing five possible ways to help account for these limitations (see: Quintero et al., 2022). Any combination of sampling methods yielded better results in relation to sampling completeness and representability (Quintero et al., 2022). Therefore, despite unavoidable geographic and habitat-based sampling biases for example, camera trapping may yield more success in tropical zones while DNA-barcoding may be more challenging in these areas due to processing and preservation needs (Quintero et al., 2022), integrating phytocentric and zoocentric methods in seed dispersal network studies facilitates a more comprehensive understanding of ecological interactions.

4.2 | Network-level metrics and their potential applications for forest restoration

By capturing a broader spectrum of interactions through diverse sampling approaches, we can yield more accurate assessments of community structure, functional relationships, and the modular organization of ecological networks. In the context of restoration, these refined metrics can better inform targeted interventions that align with the intricacies of seed dispersal dynamics, facilitating the preservation of critical interactions within ecosystems undergoing restoration. Earlier stages of forest succession are characterized by dynamic species turnover (Connell & Slatyer, 1977) thus a species-rich and highly connected seed dispersal network is expected in these stages to capture the transient nature of interactions. Restoration practices that aim to promote highly connected and species-rich networks during this phase encourage the ecological dynamics of early succession to take place, facilitating the diverse species turnover for plants and disperser species. As successional stages progress, restoration practitioner's focus should shift towards observing the emergence of specialized interactions and the formation of modules, reflecting the maturation of ecological relationships essential for sustained ecosystem stability. However, due to the lack of studies on seed dispersal interactions through successional stages, it is unknown exactly when the formation of nested and modular patterns emerges.

Generally, seed dispersal networks tend to show a nested pattern (Bascompte et al., 2003; Sebastian-Gonzalez et al., 2015) where there are a set of generalist species that interact with other generalist species, and then a subset of specialized species whose interactions are nested within the generalist interactions (Bascompte & Jordano, 2007). This characteristic leads to the robustness of seed dispersal networks to extinctions and promotes the persistence of species within an environment (Tylianakis et al., 2010). In earlier stages of succession, a nested pattern in seed dispersal networks could indicate that there are a few key plant species providing resources to a broad number of disperser species, or similarly that a few key disperser species are contributing to the dispersal of several different plant species. Identifying which generalist species are contributing to nested patterns in early stages of succession could be useful for conservation practitioners as they could target these species to promote high interaction frequency, while also preserving key specialized interactions.

Restoration efforts could also use nestedness as a measure of success in later stages of succession when fruit-frugivore communities should be more established and resilient to environmental change. Nestedness is associated with greater resilience to environmental changes, and nested patterns foster interactions that buffer against disturbances (Bastolla et al., 2009; Okuyama & Holland, 2008). Identifying nested patterns in later successional stages may also result in ecosystems that are more efficient in resource use, nutrient cycling, and ecosystem functioning, contributing to the long-term sustainability and health of the restored ecosystem.

Modularity, which describes the existence of subcommunities within ecological networks (Fortuna et al., 2010; Newman, 2006), was not related to network size. This is possibly due to modularity being strongly influenced by ecological factors such as human impact and the number of competing species within an ecosystem, as more modular networks are species-rich and are found in areas with lower levels of human impact (Sebastian-Gonzalez et al., 2015). Phylogeny and foraging behaviors also affect modular structure and are found to have significant effects on the functional roles of species within a network (Donatti et al., 2011; Galetti et al., 2013; Schleuning et al., 2014). Modular patterns have been found to increase network stability and resilience to species loss while minimizing perturbations after a disturbance (Fortuna et al., 2010). It is thought that a perturbation or disruption to a network can be kept within a single module, and therefore would not influence the entirety of a network thus promoting network stability (Newman, 2006; Ribeiro da Silva et al., 2015; Sebastian-Gonzalez et al., 2015). Identifying modular patterns in later stages of succession could be beneficial for restoration practitioners as it could enhance the resilience and adaptability of ecosystems by creating distinct, functionally specialized ecological communities. Modular structure not only contributes to ecosystem stability but also facilitates precise interventions in case of disturbance, supporting successful forest regeneration. Donatti et al. (2011) exemplify this strategy by identifying specific plant species, termed “connectors” between modules, as crucial for maintaining network structure. Connectors are species found in multiple modules across different landscapes. Identifying connector species could serve as a valuable management strategy, allowing potential targeted efforts in later stages of forest restoration (Howe, 2016).

Specialization was significantly related to network size and sampling type, whereas networks with zoocentric sampling approaches yielded the highest specialization measures. In earlier stages of succession, a lack of specialization allows for greater flexibility and adaptability, enabling a broader array of species to participate in seed dispersal and contribute to the dynamic turnover characteristic of early successional environments. In later stages of succession, specialized interactions become more significant as they signify the establishment of more stable and finely tuned ecological relationships, which could lead to more efficient dispersal of particular plant species. For example, large disperser species may have specialized interactions with larger seeded plants, and may be particularly effective in transporting seeds over longer distances or to suitable germination sites (see: Fleming & Williams, 1990; Karubian et al., 2012; Mittelman et al., 2021; Terborgh, 1986; Wenny & Levey, 1998). This efficiency can enhance the establishment and survival of plant species in the later stages of forest restoration (Rehm et al., 2018; Viani et al., 2015).

In summary, practitioners should aim to promote a highly connected seed dispersal network in earlier stages of restoration to promote species establishment, with particular attention to generalist species that contribute to nested interactions. As forests progress into later stages of succession and become more mature, a specialized and modular seed dispersal network becomes more favorable.

4.3 | Identifying important species-level metrics and functional traits

Utilizing species-level metrics and functional traits to determine species roles within an interaction network can aid in identifying “keystone” species, or a species upon which the network structure and stability depends (Escribano-Avila et al., 2018; Harvey et al., 2017; Mello et al., 2015; Messeder et al., 2020; Ong et al., 2022). For example, species-level measures in pollination networks identified key flowering plants and pollinator species that were used as targets for restoration initiatives (Devoto et al., 2012). Seed dispersal studies have also utilized species-level indices such as centrality and closeness (Table 1) to assess species contributions to network structure (Mello et al., 2015). Others have acknowledged species' contributions to modularity and connectivity among modules to draw conclusions about species' importance (Donatti et al., 2011; Howe, 2016; Ribeiro da Silva et al., 2015).

Species-level measures can be predicted by regional and evolutionary effects. Disperser species that came from stable evolutionary lineages where there were low extinction rates and high levels of specialization were found to have higher centrality measures (Burin et al., 2021). Large disperser species face a high risk of extinction, which causes concern for the sustainability of dispersal services in degraded habitats (Ripple et al., 2017). Targeting these influential yet vulnerable species in restoration efforts could therefore help mediate the threat of extinction while simultaneously promoting forest regeneration through the protection of these seed-dispersing species. The application of these findings may be useful in informing conservation efforts as gaps in ecosystem function could be supported by other, distantly related taxa (e.g., mammals and birds as seed dispersers).

Considering the functional traits of species within a network offers additional insight into the critical ecological roles of specific dispersers and plant species (Schleuning et al., 2015). Interacting partners in seed dispersal networks match according to their functional traits, and traits relating to food choice and foraging behavior can influence partner compatibility in seed dispersal interactions (Dehling et al., 2021; Garibaldi et al., 2015; Jordano, 1987). Over 50% of all papers analyzed used functional traits of plants and animals as a major part of their analyses, and nearly 70% of papers that reported data on functional traits took place within the last 5 years, indicating that this is an area of increasing topicality and relevance in modern-day conservation.

Traits exhibited by fruiting plants play a pivotal role in shaping their interactions within networks, with certain characteristics rendering them key contributors to successional trajectories for degraded ecosystems. Fruit abundance, fruit size, and water content are highly correlated with nested patterns, number of interactions, and species interaction strength (Ramos-Robles et al., 2018). Fruit abundance is an important trait in other systems as well, as the number of available fruits can influence the success of fruit removal and can alter interaction structure where plants with many fruits could be more important in networks (Palacio et al., 2016). Fruit morphology, specifically fruit and seed size, can limit interactions where only certain disperser species may be able to consume fruit. For example, only frugivores with a large gape width may be able to consume and disperse large seeds across habitats (Donoso et al., 2017; Galetti et al., 2013). This is known as the forbidden link hypothesis, where some species interactions are impossible due to a mismatch between traits (Jordano et al., 2002). Overall, woody generalist plants with small fruiting berries in the *Melastomataceae*, *Myrtaceae*, *Moraceae*, and *Urticaceae* families were found to be the most frequent keystone plant species in tropical seed dispersal networks (Escribano-Avila et al., 2018).

Many restoration strategies involve planting generalist, fast-growing fruiting species to attract frugivores to degraded sites to facilitate seed dispersal (Peters et al., 2016). Generalist plant species often play a significant role within seed dispersal networks; they are typically highly connected because they are consumed by many disperser species (Bastazini et al., 2019; Raoelinjanakolona et al., 2023; Silva et al., 2020). For example, in the tropical forest system of Veracruz Mexico, plants contributed the most to the nested structure of a seed dispersal network (Ramos-Robles et al., 2018). If these highly connected generalist species are removed or lost the resilience of the network, particularly in forest edges within fragmented habitats, may decrease (Raoelinjanakolona et al., 2023). Targeting generalist frugivorous and fruiting plant species in reforestation initiatives can help ensure the preservation of essential biotic interactions (Peters et al., 2016).

Seed dispersal into degraded lands is a crucial step for tropical forest succession, however, frugivores vary in how effectively they move seeds across landscapes. Body size has been shown to determine movement patterns in frugivores, where larger frugivores might be able to move longer distances or over larger tracts of degraded landscapes (Ripple et al., 2017; Saavedra et al., 2014; Wheelwright, 1985). Therefore, large generalist frugivores may be better at effectively colonizing disturbed habitats, while others may be more sensitive to disturbed landscapes (Carlo & Morales, 2016; Dehling et al., 2021; Howe, 2016; Schupp et al., 2010; Silva et al., 2020; Wunderle, 1997). However, small obligate frugivores (Pipridae family) and small generalist frugivores (Thraupidae family) have also been identified as keystone species in seed dispersal networks in addition to larger disperser species such as large rodents, monkeys, and other frugivorous megafauna (Escribano-Avila et al., 2018). These contrasting findings could be the result of unique species pools of dispersers and plants within each ecosystem (Dehling et al., 2016; Moulatlet et al., 2023).

Regardless of body size, frugivorous birds are vital contributors to vegetation regeneration during the early stages of forest succession as their dispersal effectiveness aids in promoting the establishment of diverse plant species in degraded landscapes (Howe, 2016; Quitian et al., 2018; Wunderle, 1997). However, some studies have found that larger-bodied birds correlate to higher species-level centrality measures (Jordano, 2017; Moulatlet et al., 2023). The dietary specialization of frugivorous birds greatly determines their roles within seed dispersal networks (Escribano-Avila et al., 2018; Sebastián-González, 2015). Birds that consume daily fruit and interact with a wider range of plant species were found to occupy more central roles in seed dispersal networks when compared to opportunistic frugivores, yet opportunistic frugivores are most likely to persist in low-quality habitats (Mello et al., 2015; Schleuning et al., 2012). Furthermore, the morphology of frugivorous birds also plays an important role in predicting species roles (Beltrán & Howe, 2020; Dehling et al., 2016). Body mass, gape width, and wing-tip length were all found to be positively associated with interaction strength within a forest interior in the Bolivian Andes (Saavedra et al., 2014). Pointed wings have been associated with forest canopy species that might have the ability to move seeds long distances, which could be important in facilitating seed dispersal to degraded lands (Quitian et al., 2018).

Functional traits are just one component of seed dispersal networks; foraging strategies, behaviors, accessibility, risk assessment, and competition also play a significant role in determining a species' involvement within a network (Howe, 2016). Spatial scales (e.g., fundamental niches across large spatial scales versus realized niches at smaller spatial scales or population levels) may also contribute to the structure of interactions, regardless of species identities and environmental factors, and must be considered when prioritizing restoration actions. For example, we may see higher nestedness at the regional scale than at the local level due to the wider availability of interacting partners utilizing the fundamental niche (Vizentin-Bugoni et al., 2022). Temporal scales and seasonality also play significant roles in resource availability throughout the year. Therefore, to ensure frugivore's presence and permanence in restored sites, restoration practitioners should consider targeting and planting species that fruit regularly throughout the year to support frugivore populations and long-term ecosystem health.

In summary, restoration practitioners can enhance seed dispersal effectiveness by identifying and prioritizing species within seed dispersal networks based on species-level metrics such as closeness or nestedness, as well as functional traits such as gape-width or fruiting phenology. Understanding frugivore dynamics, including movement patterns, dietary specialization, and foraging behaviors could help in targeting species that effectively disperse seeds across landscapes. Targeting generalist plant species, especially those from stable evolutionary lineages, is crucial as they attract a diverse range of frugivores to degraded sites, facilitating natural regeneration processes. However, practitioners should consider fruit size and abundance into restoration plans to ensure that different functional groups are accounted for (Raoelinjanakolona et al., 2023). Finally, it is important to acknowledge dispersal effectiveness, as frugivory and movement of seeds do not always guarantee effective seed dispersal (Howe, 2016; Schupp et al., 2010).

4.4 | Pitfalls and challenges

The effects that anthropogenic disturbances have on seed dispersal processes are highly variable and dependent on the ecological system in question (Chazdon, 2003; Connell & Slatyer, 1977; Jakovac et al., 2021; Markl et al., 2012). Thus, determining a numerical "goal" of a particular network measure in a restoration context proves especially challenging due to the inherent variability and context-dependency of communities following a disturbance event. In a theoretical example, selective logging can directly impact vegetation structure and composition, affecting the availability of resources for both plant species and their dispersers (Howe, 2016). Network measures in this context are expected to differ from, for example, a recovering pasture as pastures often result in a drastic simplification and loss of diversity of plant and animal communities (Menezes Pinto et al., 2021). Pastures can impact the diversity of seed dispersers and result in networks with few generalist species that are adapted to open environments. Restoration goals may also vary based on the type of disturbance. For example, in logging-affected areas, the emphasis might be on restoring large-seeded plant species that were impacted, while in fragmented landscapes, the focus could be on reconnecting habitat patches to facilitate dispersal. As each community presents unique ecological circumstances, the identification of all-encompassing metrics becomes difficult, emphasizing the need for context-specific understanding of measures in seed dispersal networks.

Species pools also influence the composition, dynamics, and success of ecological restoration efforts (Ruiz-Jaén & Aide, 2005; Suding et al., 2016). The presence of invasive species within a species pool can have significant implications for restoration success. Invasive species may outcompete native species for resources, disrupt existing ecological interactions, and alter seed dispersal dynamics (Costa et al., 2022; Dattilo et al., 2023; Da Silva & Pizo, 2020; Heleno et al., 2013, 2022). For example, non-native plants could cause increased competition for frugivores' attention between alluring invasive fruits and the fruits of native plants, which can reduce the dispersal of native seeds (Costa et al., 2022). Additionally, the introduction of non-native seed dispersers could hold negative implications for network reassembly as well (Emer & Timoteo, 2020). For instance, the introduction of large-gaped terrestrial mammals to the island of São Tomé positively influenced the dispersal of large-seeded plant species, contributing to an "upsizing" of the seed dispersal network (Heleno et al., 2022). This likely holds negative implications for the native plants of São Tomé and other heavily invaded oceanic islands across the globe, which generally rely on small, native animals to disperse their seeds (Heleno et al., 2022).

Finally, species interaction networks, as well as measures describing them, are subject to methodological biases and shortcomings as well, specifically under-sampling (Fernando Acevedo-Quintero et al., 2020; Jordano, 1987, 2016; Jordano et al., 2002; Vitorino et al., 2022). Overall, only six papers included measures of sampling completeness for their networks. Under-sampling results in a variety of biased parameters and network patterns (Chacoff et al., 2012). For example, there may be unobserved interactions between a disperser species and a plant species that are present in an ecosystem (Olesen et al., 2011; Jordano, 1987). Due to human limitations and biases, a large fraction of these missed interactions cannot be sampled due to biological constraints and sampling limitations (Jordano, 2016). One way to account for this bias is to include natural history information on disperser and plant species within the ecosystem, which allows for the inference of biological constraints (Jordano, 2016). Though some studies have attempted to create "meta-networks" to account for all missing links and sampling bias (see: Pocock et al., 2012) most networks will only be able to highlight major components of interaction occurrences (Jordano, 2016). Thus, a measure of sampling completeness is important to report when utilizing seed dispersal networks in restoration and conservation.

4.5 | How seed dispersal is integrated in restoration practices

Investigating the temporal dynamics of frugivore movements and their response to attractants in degraded sites could provide valuable insights into the effectiveness of restoration strategies over time. In general, forest frugivores have little incentive to move into or between degraded areas due to the higher predation risk and lower resource availability (Da Silva et al., 1996; Duncan & Chapman, 2002). Thus, restoration practices target frugivorous species in many ways to increase seed dispersal to degraded areas, improving restoration outcomes and lowering restoration costs (Wunderle, 1997). These include a variety of planting styles (applied nucleation, mixed-species plantings), establishing artificial bird perches, and creating artificial bat roosts. Mixed-species plantings were found to maximize the attractiveness of frugivores in degraded sites (Lindell et al., 2013). Plants with fast-growing, fleshy-fruited pioneer species have been shown to attract bird species, and utilizing a mix of fruit traits and color variations has been shown to have positive effects on seed dispersal in degraded habitats (Camargo et al., 2020; Viani et al., 2015). Artificial perches in open areas have been found to yield very low levels of seedling recruitment (De Almeida et al., 2016). Similarly, although bat roosts have been found to increase seed rain for early successional species (Ferreira & Melo, 2016), they did not increase plant recruitment (Reid et al., 2013). The effects of differing restoration practices on seed dispersal networks require further study, emphasizing the importance of diverse approaches and understanding their impacts on different ecological parameters.

The strengthening of functional communities within a seed dispersal network during refaunation efforts is also an important aspect of restoration success (Correia et al., 2017). Trophic rewilding (i.e., refaunation), or targeted species reintroduction with the goal of population re-establishment (Mittelman et al., 2022), is a strategy that has shown initial promise in the restoration of ecological networks in some study systems (Genes & Dirzo, 2022). Specifically, rewilding of seed dispersal networks through the reintroduction of generalist species could increase the number of interactions within a system (Raimundo et al., 2018). This can promote network connectance, nestedness, and robustness as the number of interaction pathways is increased and functional homogenization is decreased by the introduction of new species to the network (Mittelman et al., 2022). In areas that have been subjected to defaunation and are vulnerable to secondary extinctions, an intervention that targets these network metrics could prove to be highly impactful. In addition, restoration efforts may be more impactful when ecological redundancy is increased rather than focusing recovery efforts on a single flagship species, especially in highly dynamic systems that benefit from a diverse assemblage of individuals that perform similar ecological functions (Correia et al., 2017).

4.6 | Looking forward: Addressing knowledge gaps and future directions

Using seed dispersal networks as a tool to aid in tropical forest restoration efforts could offer a comprehensive and ecologically significant approach, enabling the evaluation of both biodiversity recovery and the recovery of a crucial ecosystem function. Our review supports the proposed shift away from individual species conservation towards the conservation of entire interaction networks to promote ecosystem processes at the landscape level, as outlined in Harvey et al. (2017). However, while it has long been suggested that seed dispersal has the potential to accelerate restoration efforts within degraded landscapes (Wunderle, 1997), very few studies have taken a network-level approach to understanding the role of seed dispersal at various stages of succession.

Howe (2016) was one of the first to explicitly draw attention to this suggestion, and yet to date, there are still minimal studies that have explored seed dispersal networks through a successional lens. There was only one result generated from our search that focused on seed dispersal networks throughout successional stages (see: Ribeiro da Silva et al., 2015). Ribeiro da Silva et al. (2015) found that through succession, modularity and degree of specialization increased with forest age (Emer et al., 2018). As niches become more defined throughout different phases of succession after initial restoration processes, specialization and modularity increase as resource partitioning decreases and species vary in their functional roles.

Comparing network measures across temporal scales presents challenges due to the reliance on null models for establishing the significance of network metrics. Null models are often used to determine the statistical significance of network metrics; null models assess whether observed network patterns deviate from what would be expected if interactions were formed at random (Jordano, 2016). The significance of certain metrics depends on the specific null model used, however, there was no consistent or standardized approach to selecting appropriate null models and drawing significant conclusions in our literature search. As a result, the temporal dynamics of seed dispersal networks may be difficult to interpret consistently (Howe, 2016). To combat these discrepancies, we emphasize the importance of site-specific long-term datasets, large spatial scales, and the use of chronosequences to continue to uncover deeper nuances of seed dispersal networks through succession (Chang & Turner, 2019).

The use of chronosequences at local levels represents an opportunity to observe seed dispersal networks over temporal scales, which could better inform network reassembly across varying stages of forest succession. Chronosequences are sets of ecological sites that share similar attributes but represent different ages and are commonly used in restoration studies. Mutualistic interactions have the potential to be connected via individual species dispersion and colonization dynamics (Hagen et al., 2012), which can result in networks being connected across timescales leading to the formation of a multi-layer network or a meta-network (Moulatlet et al., 2023). Meta-networks that observe interactions across temporal scales could highlight both disperser and plant species that play important roles in connecting fragmented landscapes (Emer et al., 2018). For example, future studies could have individual networks representing different temporal markers (e.g., successional stage) throughout the same recovering ecosystem, where networks would be connected by nodes or species occurring at multiple markers. This would allow restoration practitioners to better understand species and interaction turnover, as well as identify connector or keystone species across varying successional stages.

Finally, understanding how different restoration techniques influence seed dispersal network reassembly is pivotal for developing effective and context-specific conservation and restoration strategies. Varying restoration practices each introduce distinct ecological dynamics that may shape the interactions between plants and dispersers. Active restoration methods, such as direct planting and habitat modification, might exert immediate effects on seed dispersal patterns by altering landscape structures. For example, island plantings, which are isolated habitat patches of plantings within a landscape, could impact the spatial dynamics of seed dispersal and in turn influence how seeds move between landscapes (Holl et al., 2020). Furthermore, introducing new species into restored ecosystems introduces a layer of complexity, potentially altering the composition of disperser communities and their interactions with native plants (Genes et al., 2019; Mittelman et al., 2022). In contrast, passive restoration, which allows natural processes to drive recovery, may exhibit a more gradual influence on seed dispersal dynamics and produce different measures at different stages of succession.

In conclusion, this systematic review of seed dispersal networks reveals key insights into field methods, network measures, functional traits, and implications for forest restoration efforts, outlining where we are in this field of research today. Our findings not only illuminate the current landscape of tropical forest restoration research as it pertains to seed dispersal networks but also offer opportunities for a shift in the paradigm for the better. Utilizing seed dispersal networks as key tools in restoration practices can provide a comprehensive approach, evaluating enabling work that transcends solely biodiversity recovery to encompass the restoration of crucial ecosystem functions.

AUTHOR CONTRIBUTIONS

NML conceived the idea and designed the methodology. NML and REC collected and analyzed data. NML and REC wrote the manuscript. JLR and CK contributed to reviewing and editing manuscript drafts. CK oversaw the project.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.95x69p8sx.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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