The reassembly of faunal communities and species interactions in regenerating tropical forests and their potential applications to restoration initiatives

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Dedication

I dedicate this dissertation to mi equipo de sueños and mi familia de FCAT, Rohar, y Sorrell.

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Abstract

As deforestation and biodiversity loss continue to damage tropical forests around the globe, these ecosystems become less capable of maintaining organismal communities and ecological functions essential to their persistence. Ecosystem resilience, or the ability for forests to retain or reestablish their structure, functions, and interactions after a disturbance, depends on remnant biodiversity and species functional roles within the ecosystem. Therefore, restoring functional communities and strengthening ecological interactions is essential for promoting tropical forest regeneration and ensuring the long-term persistence of tropical ecosystems. In this dissertation, we explore the dynamics of assessing faunal community assembly and interaction recovery in regenerating tropical forests and their implications for forest restoration. First, we conducted a systematic review of studies utilizing seed dispersal networks in conservation and restoration, identifying major findings, methodological biases, and suggestions for future research directions. In this review, we highlight the importance of targeting species-rich, generalist interactions in early stages of forest regeneration while promoting stable and resilient interaction networks as forests mature. Second, we used functional diversity measures to test their applicability in assessing understory bird community responses to forest regeneration in the Chocó Rainforest of Northwest Ecuador. We found that not all functional diversity indices are indicative of community responses to forest regeneration, as only functional dispersion, functional divergence, and Rao's quadratic entropy were associated with closed-canopy habitats and later stages of regeneration. Furthermore, we found that sampling for functional diversity requires less effort than traditional taxonomic surveys, which could be useful when utilizing these tools in restoration assessments. Lastly, we used ecological network analysis to investigate the reassembly of seed dispersal interactions across regenerating forests. Seed dispersal networks transitioned from loosely connected, generalist systems in early successional habitats to more specialized, modular, and nested networks in later stages of forest succession. Early stages of regeneration that promote a high number of diverse interactions may be pivotal in shaping successional trajectories for stable ecosystems. Together, our findings have implications for tropical forest restoration by emphasizing elucidating the importance of select functional measures and assessing species interaction recovery to achieve long-term ecological resilience for regenerating tropical forests.

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Introduction

Tropical forests are among the most biodiverse and ecologically significant ecosystems on Earth, serving as critical carbon sinks (Soepadmo, 1993) and supporting two-thirds of all known species (Olson & Dinerstein, 2002). Despite their global importance, these forests are increasingly threatened by deforestation, fragmentation, and biodiversity loss. Over two-thirds of all tropical rainforests have experienced some level of human disturbance (Edwards et al., 2019) leading to disruptions in communities, species interactions, and ecological functions essential for ecosystem resilience and forest regeneration. A defining characteristic of tropical forests are the faunal communities that sustain complex species interactions that contribute to ecological functions, such as pollination and seed dispersal (Brockerhoff et al., 2017). When these mutualistic interactions are disturbed, it can alter an ecosystems resiliency or ability to recover and reestablish functions after a disturbance (Lundberg & Moberg, 2003; Neuschulz et al., 2016). Ecological restoration offers a potential solution to overcome tropical forest loss, where efforts that focus on prioritizing the preservation of key faunal groups that sustain critical species interactions can enhance forest regeneration, resiliency, and the functional recovery of these ecosystems.

Studies assessing the recovery of faunal communities within regenerating tropical forests often rely on taxonomic diversity measures, such as species richness. However, these measures do not account for the recovery of certain functional roles within a community or give any insight into the recovery of species interactions within regenerating forests (Acevedo-Charry & Aide, 2019). Instead, functional diversity measures, which consider species functional traits relative to their ecological roles, provide a more comprehensive framework for evaluating both floral and faunal community recovery (Cadotte et al., 2011). In addition to functional diversity indices, understanding how interactions amongst species reassemble in regenerating forests may also be a more informative way to understand the recovery of ecosystem functions (Derhé et al., 2018; Genes & Dirzo, 2022; Howe, 2016). Understanding how to apply these measures in assessing community responses to tropical forest regeneration will be essential for developing effective restoration strategies that promote long-term ecosystem stability and resilience. Therefore, this dissertation aims to elucidate the recovery of faunal communities and species interactions across regenerating tropical forests and highlight the potential applications for

utilizing functional diversity and species interaction measures to inform more effective and efficient assessments for tropical forest restoration initiatives.

In this dissertation, I investigate: 1) Broader trends in network-based strategies to inform restoration, 2) The relationship between varying diversity measures in assessing faunal community recovery, and 3) Examine the structural dynamics of seed dispersal networks across regenerating tropical forests. Chapter one of this research synthesizes existing literature on seed dispersal networks in relation to tropical forest conservation and restoration, identifying key trends, challenges, and opportunities for applying network theory to conservation and restoration efforts. Chapter two examines the extent to which functional and taxonomic diversity measures elucidate avian community responses to regenerating tropical forests. Finally, chapter three explores how seed dispersal networks reassemble across a regenerating tropical forest gradient. By integrating taxonomic and functional diversity assessments with ecological network analyses, this study provides critical insights into optimizing efficient and reliable methodologies to inform restoration patterns and strategies to facilitate the functional recovery of tropical forest ecosystems.

Patterns in Tropical Forest Succession

Today's tropical forests represent a mosaic of complex life history reflecting cycles of exploitation, abandonment, colonization, and regeneration (Chazdon, 2013). Prior land use vastly shapes successional pathways within tropical forests, where variations in the intensity, frequency, and type of disturbance can drastically alter successional trajectories. For thousands of years, the development and spread of agriculture from early human settlements impacted the structure and composition of tropical forests across the world (Woods et al., 2009) where now, varying successional trajectories can be observed within a single tropical ecosystem (Mesquita et al., 2001). Throughout the tropics, many abandoned agricultural sites and previously disturbed forests are now in late stages of secondary succession, sometimes referred to as primary forests, yet still undergo gradual changes in composition and structure (Bush & Colinvaux, 1994). Even in these late stages of tropical forest succession, disturbances still occur and cause changes to plant communities, animal communities, and structural components of the forest (Chazdon, 2013). This lack of predictability and compounding factors in determining rates and patterns of succession often makes it difficult to characterize varying stages of tropical forest succession.

Relay and initial floristics models are sometimes used to explain patterns of vegetation assembly across forest succession. Temperate forests typically follow a relay floristics model of succession, which begins with an initial stage of the establishment of fast-growing, shade-intolerant pioneer species, and the emergence of shade-tolerant seedlings (Egler, 1954). As vegetation continues to grow and canopies begin to develop and close, shade intolerant trees, shrubs, and lianas are replaced by shade-tolerant species within the understory and subcanopy. These long-lived pioneer species become dominant until there is a shift in community composition as these species begin to die and new cohorts of trees utilize the increased light availability to establish. After the last remaining pioneer species die out, the forest begins to transition to mature forest stages characterized by high structural complexity, increased diversity, and high species richness and abundance (Chazdon, 2013). Succession in tropical forests can follow a similar structure, but sometimes also exhibits characteristics of an initial floristics model, where both pioneer and late-successional species establish simultaneously, but their dominance shifts over time (Egler, 1954). Successional processes are not uniform across landscapes, as factors such as soil conditions, seed disperser presence, and canopy structure can influence successional pathways (Poorter et al., 2023). In some cases, degraded areas may remain trapped in an arrested successional state due to seed dispersal limitations, highlighting the importance of reestablishing animal-plant interactions to facilitate forest recovery (Reyer et al., 2015). Furthermore, forest dynamics are ever changing and do not halt when reaching later stages of forest succession, but rather shift towards localized disturbances that do not alter entire assemblages, unlike early stages of forest succession (Wright, 2005).

Another conceptual framework explores the dynamics between deterministic and stochastic factors influencing community assembly. If deterministic forces shape successional trajectories, successional communities within the same climate should ultimately converge toward a similar species composition over time, regardless of their initial differences (Clements, 1979). This framework also suggests that mature forests should exhibit stable and consistent species compositions (Clements, 1936). However, environmental variation and stochasticity can cause divergence in communities during succession rather than convergence towards similar species composition (Arroyo-Rodríguez et al., 2017; Chazdon, 2013).

Lastly, another conceptual framework of tropical forest succession focuses more on species life-history strategies including arrival time, growth rate, and longevity couples with

species interactions that facilitate dispersal and recruitment (Connell & Slatyer, 1977). Dispersal plays a key role in enabling species to colonize new habitats and establish populations in previously unoccupied areas. Both the rate and mode of dispersal can shape the pace and trajectory of ecological succession, as species vary in their timing and abundance of arrival (Dent & Estrada-Villegas, 2021). Dispersal is often the limiting factor shaping plant community assembly in early stages of forest succession, where filtering becomes the dominate factor shaping community assembly in later stages of succession (Dent & Estrada-Villegas, 2021). Filtering refers to the processes that determine which species can survive and reproduce within a particular environment. This can be shaped by a species niche or life history strategies which determine its establishment within early and late stages of forest succession (Connell & Slatyer, 1977; Howe & Smallwood, 1982). Filtering can lead to the establishment of species while preventing others from persisting, shaping community assembly across stages of forest succession. Environmental filtering operates through multiple mechanisms: tolerance, facilitation, and inhibition (Conell & Slayter 1977). Tolerance is where species with high tolerance to environmental conditions are more likely to establish. Facilitation refers to early colonizer's ability modify the environment to aid other species that eventually replace early colonizers. Finally, inhibition is where some species prevent others from establishing through competition (Conell & Slayter 1977). The interplay between filtering and dispersal can cause variations in successional trajectories and outcomes and greatly shapes community assembly dynamics.

In the Chocó Rainforest ecosystem, some regenerating forests can be described as having a relay floristics model. In abandoned agricultural lands, seedlings and sprouts of secondary and old-growth forests are absent in initial stages of regeneration and introduced to the area through dispersal agents at later stages of regrowth (Connell & Slatyer, 1977; Egler, 1954). However, some disturbed tropical forests systems consist of patches of forests in different stages of succession, including open gap phases, regrowth, and closed canopy phases (Brokaw & Scheiner, 1989). For example, one region of the Chocó Rainforest in Northwest Ecuador, forest structure (tree height, basal area, light availability, and vegetation heterogeneity) reached similar stages to old growth forests after 30-116 years of natural regeneration (Escobar et al., 2024). However, above ground biomass and tree species richness took longer to recover (100-200 years) (Escobar et al., 2024). In some areas, disturbed patches can also harbor high levels of remnant

forest vegetation and would therefore follow an initial floristics pattern where both fast-growing pioneer species and slow-growing species are present in early stages of succession, and the composition of these communities changes as the slow-growing species eventually outcompete the fast-growing species (Arroyo-Rodríguez et al., 2017). Therefore, categorizing succession within the Chocó remains difficult as regenerating areas within this system tend to contain patches of different floristic compositions and varying successional trajectories. These variations in successional trajectories highlight the complexity of forest recovery in the Chocó Rainforest, emphasizing the need to consider both structural and compositional changes over time when assessing ecosystem resilience and restoration potential.

Faunal community recovery during tropical forest succession

Faunal communities play a crucial role in the successional dynamics of tropical forests, influencing seed dispersal, pollination, herbivory, and nutrient cycling (Bello et al., 2024; Mendes et al., 2022; Wunderle, 1997). As forests regenerate, the recovery of animal communities is often non-linear and influenced by habitat complexity, resource availability, and the dispersal capabilities of different species (Acevedo-Charry & Aide, 2019). Ecological succession theory would predict that since patterns in vegetation communities change along a successional gradient, so too would patterns in resource utilization and feeding strategies (Odum, 1969). In the early stages of succession, generalist and disturbance-tolerant species often dominate due to their ability to exploit open habitats with abundant pioneer vegetation and high-light environments (Da Silva et al., 1996; Finegan, 1996). Many of these species are adapted to degraded landscapes and can rapidly colonize regenerating areas (Helms et al., 2018; Mehlhop & Lynch, 1986). However, early successional forests often lack structural complexity and key microhabitats required by specialist species, limiting the recovery of fauna that depend on mature forest conditions.

As succession progresses, increasing canopy cover, tree height, and habitat heterogeneity support more functionally diverse faunal communities (Acevedo-Charry & Aide, 2019; Chazdon et al., 2009; Edwards et al., 2017). The composition of faunal communities also shifts with succession, as pioneer-associated species gradually decline and are replaced by more specialized taxa associated with mature forest conditions. Secondary forests begin to harbor a greater diversity of frugivores, insectivores, and canopy-dwelling species as food resources, such as fleshy fruits, become more abundant. However, even in later successional stages, faunal recovery

can be incomplete if key species, such as large-bodied frugivores or insectivores sensitive to fragmentation, fail to recolonize areas due to lasting anthropogenic pressures (Chanthorn et al., 2019).

As faunal communities shift with succession, the growing presence of functionally diverse species becomes increasingly influential in shaping ecosystem processes and facilitating forest recovery. Birds in particular are an incredibly important taxa for tropical forest regeneration as they perform several ecological roles such as pollination (Ramsey, 1988), insect control (Cooper, 2005), and seed dispersal (Lee, 2018). These contributions enhance ecosystem resilience, enabling forests to recover and sustain essential functions after disturbances. Changes in bird community composition and functional roles across forest succession have been extensively studied, with early research highlighting shifts in dietary guilds and trophic niches across successional stages (May, 1982). The recovery of bird communities is likely to vary between ecosystems due to differences in natural history, physiology, behavior, landscape, and biogeographic variables (Stratford & Stouffer, 2015)

In the early stages of forest regeneration, generalist species dominate, taking advantage of the open habitat and the abundance of pioneer plant species. These species often include granivores and insectivores that exploit the high availability of seeds from herbaceous vegetation and the increased insect populations associated with early-successional growth (Da Silva et al., 1996; Gonçalves Da Silva et al., 2020; Robinson & Terborgh, 1997). As succession progresses and structural complexity increases in older forest systems, avian communities develop a higher proportion of frugivores and omnivores, which play a critical role in seed dispersal and facilitating the recruitment of late-successional plant species (Acevedo-Charry & Aide, 2019; Carlo & Morales, 2016; May, 1982). Increased canopy cover, stratification, and microhabitat diversity in mid-to-late successional forests allow for the recolonization of specialized species that depend on complex vertical forest structures, such as canopy frugivores and insectivorous understory specialists (Bregman et al., 2014; Coddington et al., 2023; Cook et al., 2020). The arrival and persistence of these functionally important species contribute to long-term forest stability by enhancing plant diversity and promoting natural regeneration.

Mammals also play a crucial role in tropical forest regeneration, influencing ecological processes such as seed dispersal, herbivory, and predation. Many medium-bodied and large-bodied mammals often act as keystone species, shaping forest structure through their foraging

and movement patterns (Stoner et al., 2007). Smaller mammals, such as frugivorous bats, also play an important role in shaping forest succession (De La Peña-Domene et al., 2014; Muscarella & Fleming, 2007). Like birds, mammal communities undergo significant shifts during forest succession, with changes in species composition, functional roles, and abundance occurring as forests regenerate. One study found that tropical rainforests have the capacity to recover functionally diverse mammal communities in a relatively short successional timeframe (10-17 years after disturbance) (Derhé et al., 2018). They also found that mean body mass of mammalian species increased with forest age, suggesting that regenerating sites can act as buffers of population decline to large-bodied mammals, which are the most at risk to extinction from anthropogenic disturbances (Cardillo et al., 2005; Derhé et al., 2018; Hoffmann et al., 2011). However, mammalian recovery is often more complex due to larger home ranges, slower reproductive rates, and increased sensitivity to habitat fragmentation and hunting pressure (Acevedo-Charry & Aide, 2019).

Understanding how faunal communities recover in regenerating tropical forests is crucial for conservation and restoration efforts. The presence of key functional groups, particularly large-bodied frugivores, should be a priority in restoration planning, as their absence may limit the dispersal of late-successional tree species. By examining shifts in faunal community composition and functional diversity across forest regeneration stages, we can gain insights into how to optimize conservation strategies and ensure the functional recovery of tropical ecosystems.

Animal-mediated Seed Dispersal is a Critical Ecosystem Function for Regeneration

Ecosystem functions encompass the physicochemical and biological processes that sustain terrestrial life, including biomass production, carbon sequestration, pollination, and seed dispersal (Brockerhoff et al., 2017). Among these, seed dispersal is a fundamental process essential for maintaining plant species diversity and forest regeneration (Howe & Smallwood, 1982; Janzen, 1970). Seeds rely almost entirely on external factors for transport, thus their successful dispersal depends on overcoming three key limitations: (1) seed limitation, where plants produce too few fruits to attract frugivores; (2) dispersal limitation, where animals fail to transport seeds to suitable recruitment sites; and (3) recruitment limitation, where seeds arrive at potential sites but fail to germinate and establish (Howe & Smallwood, 1982). Seed dispersal is facilitated by various biotic and abiotic vectors, including wind, water, gravity, and animals.

Among these, animals that consume fruits (frugivores) and disperse seeds play a particularly vital role in tropical forest ecosystems (Howe & Smallwood, 1982). Zoochory, or animal-mediated seed dispersal, represents a coevolved mutualistic relationship in which plants produce fleshy, nutritious fruits to attract animals that, in turn, disperse seeds away from the parent plant (Howe & Smallwood, 1982). By transporting seeds over long distances, frugivores help overcome dispersal limitations and enhance seed dispersal effectiveness (Schupp et al., 2010). In some tropical forests, over 85% of plant species depend on zoochory for regeneration (Howe & Smallwood, 1982), underscoring the critical role of animal-mediated seed dispersal in maintaining ecosystem resilience, regeneration, and recovery (Wunderle, 1997).

In tropical systems, birds and mammals are often referred to as the most important seed dispersers, where their movements influence plant recruitment, genetic diversity, and community composition. Given the increasing pressures of habitat loss and climate change, seed dispersal is a crucial life-history stage for plants, shaping their future ranges and population persistence (Wang & Smith, 2002). By dispersing seeds across landscapes, frugivorous animals increase the probability that seeds reach favorable sites where they can germinate and establish (Howe & Smallwood, 1982). The locations where animals deposit seeds have both ecological and evolutionary consequences, influencing plant dispersal patterns, recruitment success, and population stability. Seed-dispersing animals, therefore, play a fundamental role in shaping plant communities and promoting forest resilience, particularly in disturbed or regenerating ecosystems (Bascompte et al., 2003; Bascompte & Jordano, 2007; De La Peña-Domene et al., 2014; Garcia et al., 2018; Muscarella & Fleming, 2007).

Disperser feeding behavior and traits can directly impact their seed dispersal effectiveness. Effectiveness is described as the quantity (how many seeds are dispersed) and the quality (probability of recruitment of dispersed seeds) (Schupp et al., 2010). Body size is often referred to as a driving factor in seed dispersal effectiveness, as larger species often consume more fruit and move across greater distances. A recent meta-analysis found that the relationship between the quality and quantity of seed dispersal was mediated by body size, where larger birds were found to disperse more seeds, however had somewhat lower quality of dispersed seeds (Nevo et al., 2023). In terms of quality, animals may deposit seeds in favorable microhabitats like canopy gaps or nutrient-rich dung piles, increasing germination success. Additionally, some animals enhance seed viability through gut passage, where certain primates and birds can scarify

seed coats, improving germination rates (Milotić & Hoffmann, 2016). Alternately, poor dispersal quality can occur if seeds are deposited in unsuitable sites or destroyed during handling or digestion.

Tropical frugivores exhibit a range of behaviors that influence where and how seeds are dispersed. Some species consume fruit in a single tree before moving to a new location, while others transport fruit to nesting, roosting, or mating sites where seeds are later deposited (Schupp et al., 2010). Certain behaviors drive directed dispersal, ensuring that seeds are deposited in favorable environments for germination. For example, male Long-wattled Umbrella Birds (Karubian et al., 2012) and Bellbirds (Wenny & Levey, 1998) perform mating displays in specific locations, such as forest edges or canopy gaps, leading to a higher likelihood of seeds being deposited in sites with increased light availability. Similarly, primates play a crucial role in dispersing large seeds across long distances (Lambert, 2011; McConkey, 2000; Robinson & Terborgh, 1997). They often engage in prolonged feeding sessions, dropping partially consumed fruits to the ground. After seeds are dropped, secondary dispersers, such as agoutis, retrieve and cache the seeds for later consumption. Forgotten cached seeds have an increased probability of germinating in suitable microsites, contributing to forest regeneration (Mittelman et al., 2021).

Despite its importance, seed dispersal is one of the most threatened processes of plant regeneration, as seed-dispersing animals face increasing risks from habitat loss, fragmentation, and overhunting (Neuschulz et al., 2016). The decline of frugivorous species has cascading effects on ecosystems, reducing seed dispersal distances, increasing seed predation, and ultimately limiting plant recruitment and species diversity (Markl et al., 2012). Anthropogenic disturbances such as illegal logging and unsustainable deforestation negatively impact zoochory by disrupting animal communities, decreasing visitation rates to fruiting trees, and reducing seed removal rates (Bregman et al., 2014; Caves et al., 2013; Markl et al., 2012). In the absence of frugivorous dispersers, plant communities experience lower species richness and reduced genetic diversity, leading to altered successional trajectories (Browne et al., 2018; Muller-Landau, 2007). Furthermore, disturbances influence frugivore movement patterns, altering the dispersal potential of seeds across habitats. For instance, in the Afrotropics, areas with higher bird species richness (15 species vs. 6 species) exhibited a drastic increase in seed dispersal rates (71% vs. 8%), a greater median dispersal distance, and a more evenly distributed seed deposition pattern (Bleher & Böhning-Gaese, 2001).

Frugivorous birds and mammals are vital for seed dispersal in regenerating forests, as they facilitate the establishment of late-successional plant species that might otherwise be disperal-limited (Wunderle, 1997). Specifically, the contributions of birds and bats to seed dispersal are particularly important in early-successional forests (Muscarella & Fleming, 2007). As many of these species can cover large distances relatively quickly, they better facilitate the movement of both pioneer and primary forest seeds into disturbed areas, enhancing connectivity and promoting plant diversity in fragmented tropical forests (Galindo-González et al., 2000). As tropical forest succession progresses, dispersal roles shift, with birds primarily dispersing understory shrubs and treelets early on, while larger-bodied mammals, such as primates, become dominant dispersers for canopy tree species in later stages (Naniwadekar et al., 2019; Ong et al., 2022; Walter et al., 2017). However, the processes governing the reassembly of interactions between frugivores and fruiting plants during restoration remain poorly understood. A deeper understanding of these dynamics is critical for designing effective restoration strategies and mitigating the long-term consequences of defaunation on tropical forest regeneration.

Measuring Seed Dispersal Interactions via Ecological Networks

Ecological networks provide a valuable framework for evaluating species interactions, their roles within communities, and the influence of emerging network structures on the stability and maintenance of ecosystem functions (Bascompte & Jordano, 2007; Escribano-Avila et al., 2018; Jordano, 2016). Specifically, seed-dispersal networks highlight the complexity of plant-animal interactions and their critical role in sustaining ecosystem functions. Studying species interactions can offer more insightful indicators of ecosystem recovery than traditional measures of diversity that use solely species abundance data (Valiente-Banuet et al., 2015). Interaction networks have become essential for advancing forest management and conservation where measures such as nestedness (interactions of species with fewer partners form a subset of the interactions of species with more partners) and specialization (where species develop specific roles or dependencies on a limited number of other species) are patterns strongly linked to biodiversity maintenance and conservation priorities (Howe, 2016). Ecological networks can also identify keystone species, or those that play critical roles through their interactions, by utilizing species-level network indices (Hagen et al., 2012). Given increasing levels of environmental degradation in tropical forest ecosystems, integrating interaction networks into restoration

ecology is urgent, as these networks provide insights into how ecological complexity is restored to ensure long-term ecosystem functionality (Moreno-Mateos et al., 2020).

Typically, species interactions within seed dispersal networks are depicted through bipartite networks, which use adjacency matrices to visualize relationships between two distinct groups, such as plant and disperser species. In these matrices, disperser species are represented in rows, plant species in columns, and seed dispersal events as data entries (Bascompte et al., 2003). These interactions can be recorded as binary presence-absence data (0-1) or as quantitative weightings, where interaction intensity reflects the frequency or strength of dispersal relationships (Jordano, 2016). Most ecological networks rely on frequency-based data, such as the number of seeds consumed by a disperser species through focal observations. Weighted interaction networks provide a more nuanced understanding of interaction strength, allowing researchers to estimate not just whether species interact, but how frequently these interactions occur (Jordano, 2016).

Network analysis can also highlight keystone species within seed dispersal communities, which are mostly described as those responsible for the dispersal of multiple plant species or those that maintain specialized interactions (Escribano-Avila et al., 2018). Many studies have found that abundant generalist dispersers act as keystone species in seed dispersal networks due to their high ability to disperse large quantities of diverse seed species across landscapes (Bastazini et al., 2019; Carlo & Morales, 2016; Palacio et al., 2016). Animal functional traits significantly influence their roles within these networks, with traits such as body size, feeding behavior, and habitat use shaping seed dispersal dynamics. For example, in avian dispersers, beak width and beak length directly determine the types and sizes of fruits a bird can consume and disperse. Larger-bodied birds typically have access to a wider range of fruit sizes, allowing them to disperse diverse plant species across large distances and to diverse microhabitats (Bueno et al., 2013; Dehling et al., 2020; Li et al., 2018). These morphological traits, combined with behavior (e.g. movement patterns, habitat selection, and foraging strategies), influence the overall effectiveness of seed dispersal in an ecosystem.

Species interaction networks and the measures derived from them are subject to methodological biases and limitations, particularly under-sampling (Bueno et al., 2013; Dehling et al., 2020; Li et al., 2018). Many interaction networks are incomplete due to limited sampling effort, leading to biased parameters and misrepresentations of network structure (Chacoff et al.,

2012). For instance, disperser and plant species may be present within an ecosystem but remain undocumented due to unobserved interactions, known as "missing links", which are interactions that theoretically exist but were not detected during field studies (Jordano, 1987). Some links may remain undetected due to sampling constraints, while others may be biologically constrained and are referred to as "forbidden links". Forbidden links are when a plant and animal species co-occur yet do not interact due to mismatches in foraging behavior, morphology, or ecological preferences (Jordano, 2016). To mitigate these biases, incorporating natural history data on plant and disperser species can help infer biological constraints and refine network models (Jordano, 2016). While some studies have attempted to construct meta-networks that integrate broader ecological datasets to account for missing interactions (Pocock et al., 2012), most networks still capture only the most prominent interaction patterns.

Despite these challenges, species interaction networks provide a powerful tool for understanding ecological complexity, informing conservation strategies, and guiding restoration efforts. By identifying key dispersers and their functional contributions, these networks help prioritize species for restoration and highlight potential vulnerabilities in ecosystem stability. As tropical forests continue to experience fragmentation and biodiversity loss, integrating network-based approaches with traditional ecological monitoring will be essential for preserving species interactions, maintaining seed dispersal processes, and ensuring the long-term resilience of these ecosystems.

Tropical Forest Restoration Strategies

In response to accelerating threats to tropical forests, the United Nations put forward a call to action from 2021–2030 called the "Decade on Ecosystem Restoration", prioritizing large-scale efforts to halt disturbances, protect and restore forests, and mitigate biodiversity loss worldwide (UNEP & FAO, 2020). Tropical regions are disproportionately affected by deforestation due to demands for timber, cattle pasture expansion, and monocultural agriculture products such as palm oil, cacao, and grains (Malhi et al., 2014). Therefore, tropical regions are a key priority for global restoration initiatives. While billions of dollars have been invested in tropical forest restoration, project outcomes vary where the type of ecological restoration can have strong influences on restoration outcomes (Brokaw & Scheiner, 1989). Other factors can also contribute to restoration success, including past land-use history, disturbance severity,

restoration strategy (natural regeneration vs. active intervention), biogeographic region, and the ecological metrics used to assess biodiversity recovery (Crouzeilles et al., 2016).

Designing effective restoration strategies requires an understanding of natural successional processes, which provide key principles for guiding ecosystem recovery and ensuring long-term restoration success (Hobbs et al., 2007). Given the complexity and variability of succession in tropical forests, understanding the factors that influence regeneration is critical for effective restoration. Natural regeneration, which is also referred to as passive restoration, occurs when human-induced stressors (e.g., logging, grazing, fire) are removed from an area, allowing secondary succession to proceed without the need for direct intervention (Chazdon et al., 2021). This approach is often cost-effective and can be highly successful in areas with low levels of degradation, where seed banks, dispersal agents, and soil conditions are sufficient to facilitate natural recovery (Chazdon & Guariguata, 2016).

While natural succession can gradually lead to the recovery of ecosystem functions and biodiversity, human intervention is sometimes necessary to accelerate or direct the process, particularly in areas where seed dispersal limitation, soil degradation, or persistent disturbances hinder regeneration (Holl, 1999). Active restoration involves direct human intervention to accelerate succession and reestablish ecological functions (Chazdon et al., 2021). Active restoration techniques often include tree planting, invasive species removal, soil amendment, and faunal reintroductions (Atkinson & Bonser, 2020; Chazdon et al., 2021). Active restoration is particularly necessary in areas where seed dispersal is limited, soil degradation is severe, or competition from invasive species impedes natural succession. However, the effectiveness of active restoration varies, and in some cases, it may be unnecessary or too costly to implement compared to natural regeneration.

Since restoring exact species assemblages is often unrealistic, many restoration efforts prioritize the recovery of functional groups (species that contribute to ecosystem functions such as seed dispersal, pollination, and nutrient cycling) rather than attempting to recreate pre-disturbance species composition (Hobbs et al., 2007). Specifically, frugivorous animals have been a target for many tropical forest restoration initiatives with the goal of enhancing seed dispersal across degraded landscapes (Camargo et al., 2020; Estrada-Villegas et al., 2023; Rehm et al., 2018). This is done through a myriad of techniques, including establishing perches for frugivorous bird species (De Almeida et al., 2016), utilizing bat roosts in degraded pasture sites

(Reid et al., 2013), and planting fast-growing, fleshy fruited pioneer species in active restoration projects (Holl et al., 2020). Though many are still evaluating the effectiveness of these techniques, planting fast-growing fleshy-fruiting early pioneer species has been the most effective in facilitating the return of seed dispersal interactions (Corbin & Holl, 2012; Holl et al., 2020).

Knowledge Gaps and Aims

As biodiversity recovery, community assembly, and strengthening ecological interactions remain a critical goals of restoration ecology, understanding how these processes respond to forest regeneration will help ensure the long-term persistence of tropical ecosystems. Therefore, in this dissertation we explore the reassembly of faunal communities and species interactions in regenerating tropical forests and how this applies to tropical restoration strategies. The first chapter of this dissertation is a systematic literature review on studies pertaining to seed dispersal interactions in relation to conservation and restoration. Specifically, in this chapter we aim to: (1) Synthesize findings on seed dispersal networks in the tropics relevant to the fields of conservation and restoration ecology, (2) Highlight potential biases and caveats of applying network theory to restoration, and (3) Identify current knowledge gaps the applications of seed dispersal networks for conservation and restoration of tropical forests, and how these can be addressed in future research. This review has provided a comprehensive overview of the current state of research in this field and incorporated the potential trajectory for future research in incorporating seed dispersal interactions in restoration goals.

Chapter two of this dissertation examines the extent to which functional diversity indices accurately predict avian community responses to tropical forest regeneration. To this end, I utilized a regenerating forest gradient and light detection and ranging (LiDAR)-derived vegetation indices to investigate their relationships between the composition, taxonomic diversity, and functional diversity of understory avian communities in the Chocó rainforest of northwest Ecuador. Specifically, this chapter aims to: (1) Investigate the composition, taxonomic diversity, and functional diversity of bird communities in relation to changes in forest regeneration, (2) Test for associations between bird diversity indices and regenerating vegetation structure, and (3) Determine how avian functional traits shift across stages of regeneration, and which traits contribute most to changes in functional diversity. This study provides a deeper

understanding of how functional diversity indices can be utilized to assess avian community responses to forest regeneration.

Finally, Chapter three examines how seed dispersal networks reassemble in regenerating tropical forests. This chapter aims to: (1) Examine how seed dispersal interactions change as a function of forest regeneration, (2) Evaluate the extent to which seed dispersal networks retain or change their structure through stages of forest regeneration, and (3) Determine how forest regeneration influences the complexity and stability of seed dispersal networks. I sampled for seed dispersal interactions using both phytocentric (plant-focused) and zoocentric (animal focused) field methods and pooled these interactions to create weighted seed dispersal networks representing four stages of forest regeneration: highly impacted pastures, early successional vegetation, secondary forests, and old-growth Chocó rainforest. Understanding how seed dispersal interactions shift across stages of regeneration is critical, as seed dispersal influences plant recruitment, species composition, and long-term ecosystem stability. Examining the extent to which these networks retain or rewire through forest regeneration can provide key insights into the recovery of ecological processes that shape forest regeneration.

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Chapter 1: 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 to 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 successional 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.

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 (Escribano-Avila et al., 2018; Timoteo et al., 2018, 2016; Howe, 2016; Jordano, 2016; Bascompte & Jordano, 2007; Jordano, 1987). 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; Messeder et al., 2020; Ribeiro Mello et al., 2015). 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, 2002). For example,

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.

Level/Scale		Descriptions	Conservation Significance
Nestedness (NODF) Blüthgen et al. 2008; Bascompte et al. 2003	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.
Connectance (C) Costa et al., 2019; Blüthgen et al. 2008	NL, 0-1	The proportion of realized interactions between plants and dispersers divided by the total number of possible interactions between plants and dispersers.	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.
Modularity (*M* or *Q*)	NL, 0-1	A measure of the number of subgroups of tightly interacting plants and dispersers in	Modular networks have been linked to ecosystem stability, as modularity can act as a buffer against the spread of disturbances, allowing for more localized

Table 1 Continued.

Grilli et al. 2016		a network and how exclusively they interact with one another.	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.
Network Richness Pocock et al. 2012	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.
Specialization (H^2) Blüthgen et al. 2006	NL, 0-1	The measure of connectance quantifies how specialized interactions between plant and disperser 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

Table 1 Continued.

			with specific ecological requirements.
Interaction Frequency Chacoff et al., 2012	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.
Degree Burin et al., 2021; Oldham et al., 2019	SL, Cont	Number of interactin partners a particular plant or disperser 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.
Closeness Centrality Burin et al., 2021; Oldham et al., 2019	SL, Cont	The sum of the number of shortest distances between a particular plant or disperser 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.
Specialization (d) Blüthgen et al. 2006; Olesen & Jordano, 2002	SL, Cont	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.

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.

Methods

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 **(Supplementary Figure 1).**

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 and future research suggestions.

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).

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.

Results

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 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

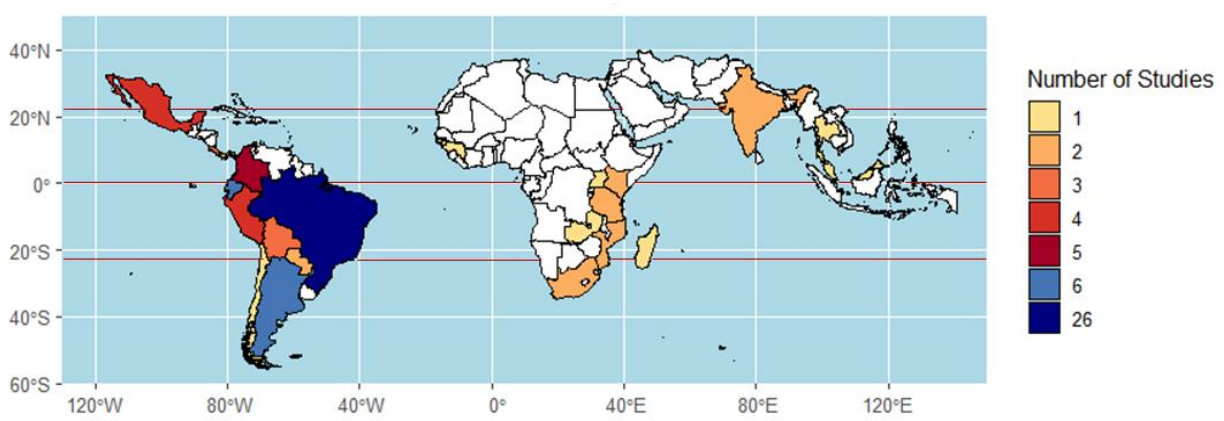

Figure 1: Geographic distribution of studies included in our review, with delineations for the Equator and Tropics of Cancer and Capricorn. Color represents the number of studies conducted in each country. Most studies were conducted in Brazil (n=26).

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 five 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).

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 (i.e., 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 method significantly influenced network metrics (**Figure 2**; **Table 3**). Sampling had a significant effect on WNODF (chi-squared = 7.59, df = 2, p-value = 0.023) and H^2 (chi-squared = 9.44, df = 2, p-value = 0.009) (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

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)

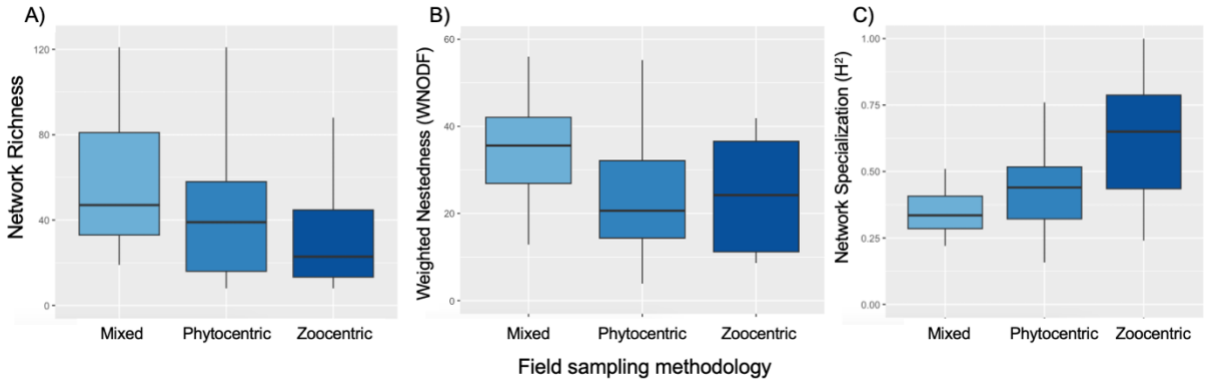

Figure 2: The effects of sampling methods (mixed, phytocentric approaches, or zoocentric approaches) on seed dispersal network metrics including A) network richness or size, B) network-level specialization (H^2), and C) weighted nestedness (WNODF).

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), zoocentric (animal-centric), or a combination of the two types.

Equations	**Chi-squared**	**df**	**P-value**
Method Type ~ Network Richness	18.78	2	0.0001
Method Type ~ Specialization (H2)	9.44	2	0.009
Method Type ~ Weighted Nestedness (WNODF)	7.59	2	0.023
Method Type ~ Modularity (*Q*)	1.42	2	> 0.05
Network Richness ~ Specialization (H2)	107.15	99	> 0.05
Network Richness ~ Weighted Nestedness (WNODF)	139.95	139	> 0.05
Network Richness ~ Modularity (*Q*)	94.47	94	> 0.05

used was also a significant predictor of network richness (chi-squared =18.78, df= 2, $p < 0.0001$), 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, $p > 0.05$). Network richness did not significantly predict network measures (WNODF: chi-squared = 139.59, df = 139, $p > 0.05$; H^2: chi-squared = 107.15, df = 99, > 0.05; Modularity: chi-squared = 94.47, df = 94, $p > 0.05$) **(Table 3**).

Discussion

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 capture the complexities of tropical environments, as diverse seed dispersal networks have been found to correlate to greater ecosystem resilience (Tylianakis et al., 2010; Thebault & Fontaine 2010; Bastolla et al. 2009). 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 ($p < 0.001$) 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 (Vitorino et al., 2022; Ramos-Robles et al., 2018; Howe 2016).

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 itself 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 (Chacoff et al. 2011; 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 toward 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., 2020). 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., 2020; 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-Vero 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 (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 (e.g., 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.

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) and 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 early stages of regeneration encourage the ecological dynamics of early succession to take place, facilitating 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 (Sebastian-Gonzalez et al., 2015; Bascompte et al., 2003) 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 (Thebault & Fontaine 2010; 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 sub-communities 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 (da Silva et al., 2015; Newman, 2006; 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. (2015) 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: Mittelman et al., 2021; Karubian et al., 2012; Fleming and Williams 1990; Wenny & Levey, 1998; Terborgh 1986). 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 for 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.

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; Messeder et al., 2020; Ong et al., 2022; Ribeiro Mello et al., 2015). 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 (Error! Reference source not found.) to assess species contributions to network structure (Mello et al., 2015; González et al., 2010). Others have acknowledged species' contributions to modularity and connectivity among modules to draw conclusions about species' importance (Howe 2016; da Silva et al., 2015; Donatti et al., 2011; Olesen et al., 2007).

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., 2020, 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., 2003). 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 (Raoelinjanakolona et al., 2023; Silva et al., 2020; Bastazini et al., 2019). 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 (Dehling et al., 2021; Silva et al., 2020; Carlo & Morales, 2016; Howe, 2016; Schupp et al., 2010; 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 (Moulatlet et al., 2023; Muñoz et al., 2019; Dehling et al., 2016).

Regardless of body size, frugivorous birds are vital contributors to vegetation regeneration during early stages of forest succession as their dispersal effectiveness aids in promoting the establishment of diverse plant species in degraded landscapes (Quitian et al., 2018; Howe, 2016; Wunderle, 1997). However, some studies have found that larger-bodied birds correlate to higher species-level centrality measures (Moulatlet et al., 2023; Jordano, 2017). The dietary specialization of frugivorous birds greatly determines their roles within seed dispersal networks (Escribano-Avila et al., 2018; Sebastián-González, 2017). 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., 2011). Furthermore, the morphology of frugivorous birds also plays an important role in predicting species roles (Beltrán and 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 level) 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, or the entire range of environmental conditions and resources a plant or animal species may utilize (Vizentin-Bugoni et al., 2019). 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 disperser and plant 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).

Pitfalls and challenges

The effects that anthropogenic disturbances have on seed dispersal processes are highly variable and dependent on the ecological system in question (Jakovac et al., 2021; Markl et al., 2012; Chazdon 2003; Connell & Slatyer, 1977). 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 (Suding et al., 2016; Ruiz and Aide, 2005). 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 (Dattilo et al., 2023; Costa et al., 2022; da Silva & Pizo, 2020; Heleno 2020; Heleno et al., 2013). 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, 1987, 2016; Jordano et al., 2003; Vitorino et al., 2022). Overall, only 6 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 (Olensen 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 (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.

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 attraction of frugivores to 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 and de 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. 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).

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 (Ribeiro da Silva et al., 2015). Ribeiro da Silva (2015) found that through succession, modularity and degree of specialization increased with forest age. 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, where 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 (Mittelman et al., 2020; Genes et al., 2019). 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.

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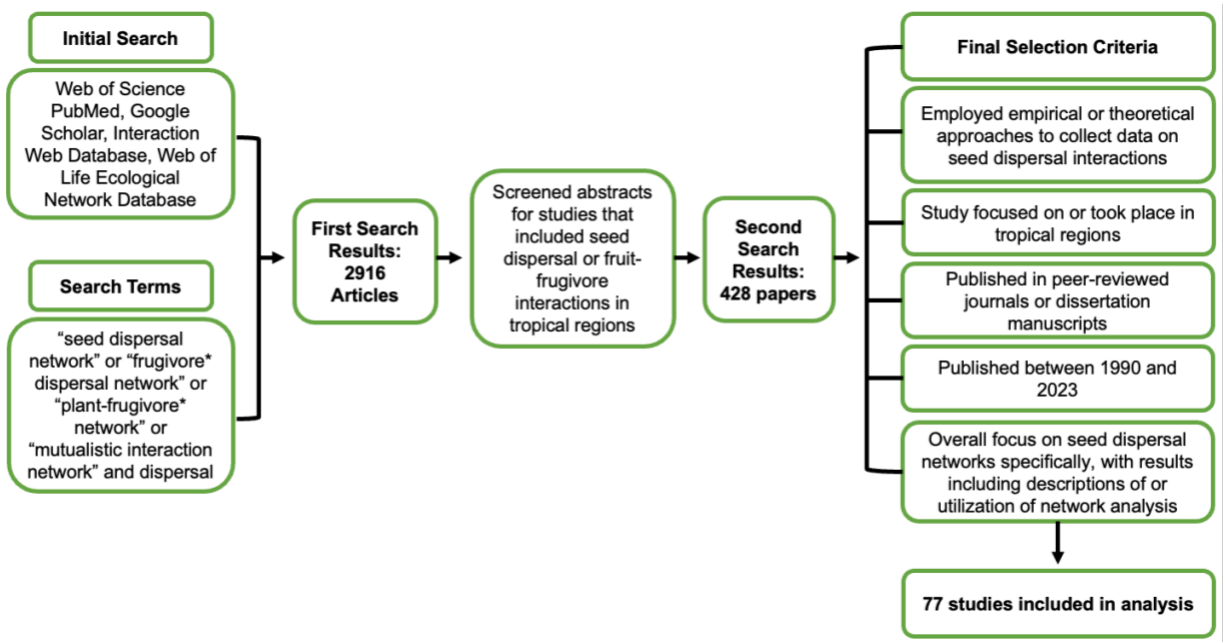
Appendix



Supplementary Figure 1: Selection process used to identify studies on seed dispersal networks in tropical ecosystems. Articles were compiled from multiple databases and sources, then screened based on relevance to seed dispersal networks, geographic focus on the tropics, and methodological criteria. From an initial pool of 2,916 studies, 77 met all inclusion criteria and were retained for full analysis.

Chapter 2: Evaluating functional diversity indices as indicators of bird community responses to tropical forest regeneration in northwest Ecuador

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Abstract

As biodiversity recovery remains a key component of conservation and restoration goals worldwide, conducting accurate community recovery assessments remains a significant challenge for restoration ecology. Community assessments have traditionally relied on taxonomic diversity, such as species richness or Shannon's diversity indices. More recently, functional diversity indices such as functional richness, dispersion, divergence, and Rao's Quadratic Entropy have been utilized as a potentially more informative measure of community recovery. However, the extent to which these metrics reliably predict community responses during forest regeneration remains uncertain. In this study, we test the relationship between taxonomic and functional diversity indices of understory bird communities along a naturally regenerating forest gradient in the Chocó rainforest of northwest Ecuador. We sampled avian communities within highly impacted and lightly impacted early successional vegetation, secondary forests, and old growth Chocó rainforest, and we utilized LiDAR-derived canopy-level vegetation indices to examine relationships between diversity indices and developing forest structure. Unexpectedly, we observed an inverse relationship between most taxonomic and functional diversity measures as a function of forest regeneration class. High species richness, diversity, and functional richness were associated with open-canopy habitats within the early stages of forest regeneration due to a high presence of generalist, disturbance-tolerant species. In contrast, high functional dispersion, functional divergence, and Rao's quadratic entropy were all associated with closed-canopy habitats and later stages of forest regeneration and were mainly driven by differences in beak and wing length. Therefore, not all functional diversity indices indicate the recovery of late-successional understory bird communities. Unlike functional richness, measures such as functional dispersion, functional divergence, and Rao's quadratic entropy are weighted by species abundances and dominant traits within each community and better explain the shifts in composition between habitats and thus could be more useful in assessing faunal communities within regenerating tropical forests. However, functional diversity measures were only indicative of changes between open and closed canopy habitats and did not differentiate between secondary and old-growth forest systems. Lastly, observed low levels of species richness in older forests were likely due to lower detection rates from mist-netting; higher levels of functional diversity within these habitats suggest that functional diversity can be

assessed with less sampling, offering a more efficient approach to evaluating community responses to forest regeneration.

Introduction

Recognizing the regenerative capacity of tropical forests is crucial for addressing climate change and biodiversity loss (Williams et al., 2024). Natural regeneration offers a large-scale, cost-effective solution to forest loss, particularly in areas where forests can recover with minimal human intervention (Bodin et al., 2022; Chazdon & Guariguata, 2016; Williams et al., 2024). Biodiversity measurements of faunal communities within stages of natural regeneration are typically used as indicators of restoration trajectories, as community dynamics can provide insights into the recovery of tropical forests (Crouzeilles et al., 2016; Derhé et al., 2018). This is typically done using taxonomic diversity indices (species richness and abundance), which may fail to capture the full range of functional contributions within a community (Acevedo-Charry & Aide, 2019; Crouzeilles et al., 2016; Moreno-Mateos et al., 2020). Thus, functional diversity indices are becoming increasingly popular to evaluate community responses to topical forest regeneration, as they consider both species richness and abundance in combination with traits relative to species ecological roles (Derhé et al., 2018; O'Brien et al., 2022). However, the extent to which functional diversity indices reliably predict community patterns across stages of succession is not well understood. Therefore, this study aims to understand the drivers of functional diversity across forest regeneration and identify which diversity measures might be useful indicators for ecological restoration.

Tropical forest regeneration depends on the reassembly of functionally significant species, such as tropical birds (Bello et al., 2024; Carlo & Morales, 2016; Lee, 2018). Many studies have utilized bird communities as a tool to compare stages of forest regeneration and restoration success (Barros et al., 2022; Helms et al., 2018; Latja et al., 2016). Birds play a critical role in forest regeneration by dispersing seeds for the majority of tropical woody plants (>85%), especially in degraded areas where seed availability limits recovery (Holl, 1999; Howe & Smallwood, 1982; Wunderle, 1997b). In addition, nectivorous and insectivorous birds influence energy pathways critical to forest regrowth; studies show that they consume up to 2.5 times more resources in open forests compared to old-growth systems (Malhi et al., 2022). Insectivorous birds are important predators of insect herbivores, reducing leaf damage on regenerating trees (Morrison & Lindell, 2012). Avian pollinators also facilitate gene flow of

plants, which is important for the long-term viability of plant populations (Kormann et al., 2016). Furthermore, bird communities can rapidly recolonize disturbed areas depending on local environmental conditions such as vegetation structure, resource availability, and remnant vegetation (Helms et al., 2018; Latja et al., 2016; Reid et al., 2012).

Typically, bird communities transition over stages of forest regeneration to become more similar to mature forest communities over time (Owen et al., 2020). However, the functional recovery of bird communities is inconsistent. Some studies report an increase in functional diversity in bird communities in areas with greater vegetation density and canopy structure in early forest regeneration types (Coddington et al., 2023; Remeš et al., 2021), while others have found no variation across varying stages and types of tropical forest restoration (Barros et al., 2022). Furthermore, a recent study found that both functional diversity and taxonomic diversity decreased as forest recovery progressed (Kortmann et al., 2025). These discrepancies highlight the need to understand what functional diversity indices are useful indicators of forest regeneration, and which might be less helpful in understanding community shifts related to forest succession.

Regenerating vegetation plays a key role in shaping bird distribution and abundance (Cano-Barbacil et al., 2023; Gregory & Gaston, 2000). Regenerating vegetation structure can be assessed using LiDAR (Light Detection and Ranging) imagery. LiDAR imagery is emerging as a transformative tool in restoration ecology, as its ability to capture three-dimensional data makes it particularly valuable for assessing habitat structure and biodiversity within regenerating ecosystems (Viana-Soto et al., 2022). LiDAR is growing particularly important for monitoring structural components of forest regeneration such as vegetation density, complexity, and health (Coops et al., 2021). Functional diversity measures have been shown to strongly associate with vegetation indices (e.g., canopy height, vegetation density, leaf-area density) in tropical secondary and old-growth forests (Coddington et al., 2023; Zahawi et al., 2015). In the initial stages of forest succession, younger forests will have lower basal area, open canopies, and a lack of tall trees (Finegan 1996; Aide et al., 2000). In later stages of succession, mature forests typically consist of larger trees and denser canopies, with a range of vegetation heights and features such as tree cavities, fostering higher plant species complexity (Remeš et al., 2021; Vesk et al., 2008). The use of LiDAR technology to analyze forest regeneration could enhance our

ability to predict which elements of vegetation recovery are crucial for facilitating the recovery of functionally diverse animal communities.

In this study, we utilized a regenerating forest gradient and light detection and ranging (LiDAR)-derived vegetation indices to investigate their relationships between the composition, taxonomic diversity, and functional diversity of understory avian communities in the Chocó rainforest of northwest Ecuador. Specifically, we aimed to: (1) Investigate the composition, taxonomic diversity, and functional diversity of bird communities in relation to changes in forest regeneration, (2) Test for associations between diversity indices and vegetation structure, and (3) Determine how functional traits shift across stages of regeneration, and which traits and environmental variables contribute most to changes in functional diversity. We hypothesize that avian community composition will vary with forest regeneration, where differences in forest structure will act as a filter on avian species composition. Furthermore, we hypothesize that both the taxonomic and functional diversity of avian communities will increase with forest regeneration and canopy-level attributes, as older, structurally complex habitats provide a wider range of resources and niches. The increase in avian functional diversity is expected to reflect a more specialized array of foraging behaviors and habitat use in older regenerating forests. Through this research, we aim to achieve a more comprehensive understanding of what diversity indices might be most effective, efficient, and applicable to conservation and restoration strategies as they relate to assessing community responses to tropical forest regeneration.

Methods

Study site

This study was conducted at the Fundación para la Conservación de Los Andes Tropicales reserve (FCAT) within the greater Mache-Chindul Ecological Reserve (REMACH), a key remnant patch of the Chocó rainforest in northwest Ecuador. The Chocó rainforest is a globally recognized biodiversity hotspot with high levels of endemism (Aguilar Mugica et al., 2009). REMACH encompasses 165,000 hectares (ha) of humid Chocó rainforest, wetlands, and streams within the Rio Esmeraldas drainage, though it is affected by severe rates of deforestation (Durães et al., 2013; Kleemann et al., 2022; Van Der Hoek, 2017).

The FCAT reserve covered 656 ha during the data collection period and ranged from 350 – 550 meters (m) above sea level (asl), with a wet season extending from January to June and a dry season from July to December. The research design included 20 plots evenly distributed

across four habitat categories: highly impacted early successional habitat (HIE), low impact early successional habitat (LIE), mid-successional secondary forest (SEC), and old growth Chocó Rainforest (OG) (**Supplementary Figure 2**). HIE plots were cleared and used as cattle pastures for >20 years until they were abandoned in 2021 when they were purchased by FCAT. LIE plots had lower levels of disturbance, where selective logging and ≤1 year of grazing cattle from 2020-2021 without fire or use of herbicides resulted in less soil compaction and more remnant trees and fruiting vegetation (M Sanchez-Julia, *unpublished data*). SEC areas were predominantly abandoned cocoa plantations that have been naturally regenerating for approximately 25 years. OG represents old growth (undisturbed primary forest) Chocó Rainforest with limited recent human intervention (i.e., low intensity selective logging) that surrounds all other habitat categories. Sampling took place in five replicates across each of the four habitat categories for a total of 20 plots spaced a minimum of 100 meters (m) apart throughout the FCAT reserve (**Figure 3**).

Sampling for bird communities and functional traits

We conducted bird surveys from May-August in 2022 and 2023 to coincide with the dry season and to include resident species rather than migratory species. In each plot, we used mist-netting to account for abundances of understory bird species. This took place in fair weather from sunrise (~6:30) to 12:30 for two consecutive days at each plot, and then we rotated to a randomized plot in a different regeneration type. In total, we completed 120 mist-netting hours for each plot (10 nets [120 m per net line] × 6 hours × 2 days), for a total of 2,400 netting hours across all sites. We checked nets every 20 minutes, and each time a bird was netted, it was placed in a holding bag and brought to a banding station. We kept individuals in bags for no more than 15 minutes. Each bird we captured received a uniquely numbered aluminum band and was identified using *Birds of Ecuador* field guide (Freile & Restall, 2018) before being released at the point of capture. Fieldwork was conducted with MAATE permission (*Ministerio del Ambiente, Agua y Transición Ecológica*) under permit number: MAATE-ARSFC-2022-2589.

Calculating Functional Diversity Indices

To obtain functional traits for each species, we used an open-access dataset that contained morphological, geographical, and behavioral traits for over 12,000 individual species (Tobias et al., 2022). From this data set, we extracted both morphological (beak length, beak width, wing

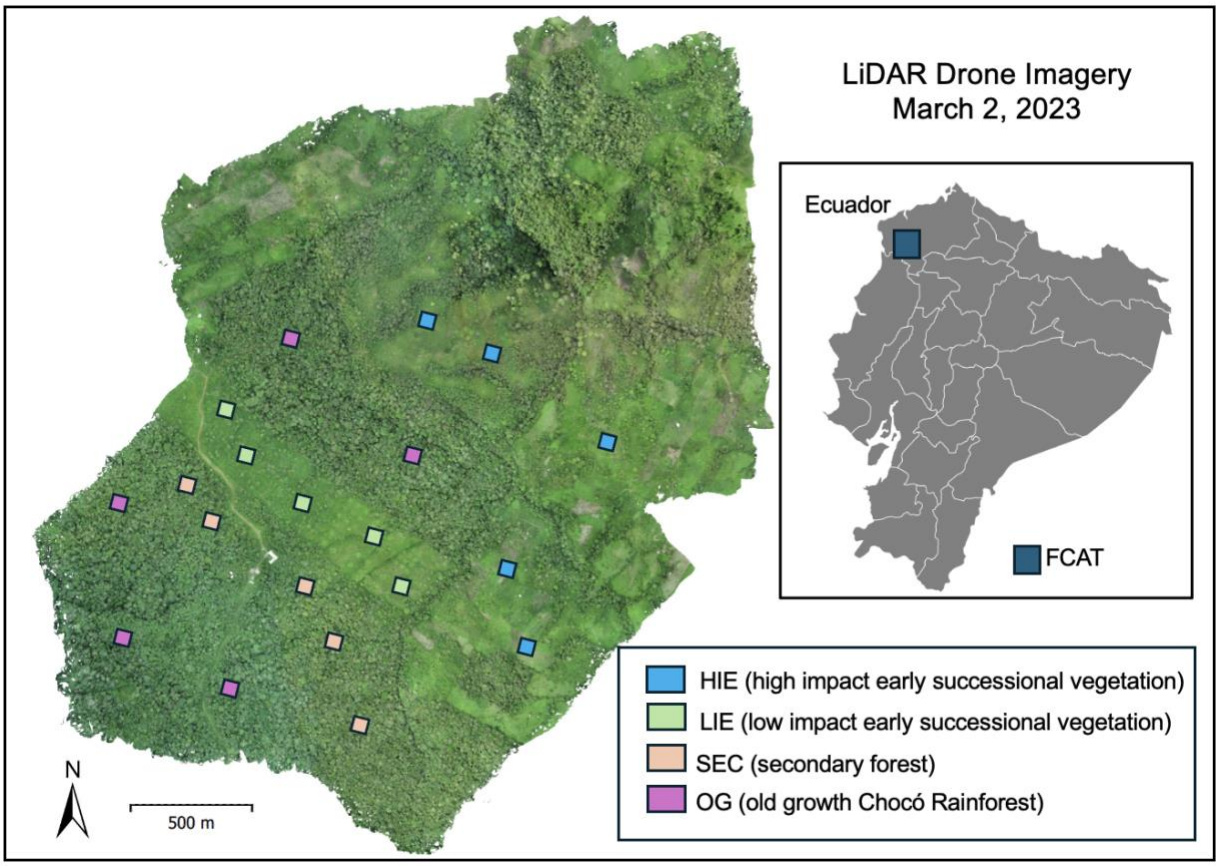

Figure 3: Sampling localities for avian communities within the FCAT reserve. Sampling took place in 20 plots among four habitat categories: highly impacted early successional habitat (HIE, red squares), low impact early successional habitat (LIE, yellow squares), mid-successional secondary forest (SEC, blue squares), and old growth Chocó Rainforest (OG, purple squares).

length, and mass) and behavioral (primary habitat, trophic niche) functional traits for each observed species (**Supplementary Table 1**). These traits are relevant to forest regeneration as they influence species foraging strategies, habitat usage, and dispersal abilities. For example, changes in beak morphology may reflect adaptations to specific food resources such as fruit species, and changes in wing morphology may reflect species abilities to maneuver within complex forest vegetation. We numerically coded categorial traits (e.g., frugivore = 0, granivore = 1). To calculate functional diversity, we took the log transformation of each continuous trait (beak length, wing length, tail length, mass) to normalize the data. We excluded categorical traits (trophic niche, vertical habitat preference, disturbance-tolerance) from functional diversity indices because their inclusion has been shown to reduce the quality of the functional space (Maire et al., 2015).

The resultant trait matrix was paired with weighted abundance data for each regeneration type, where each mist-netting plot was classified as a community. Then, we used the "*dbFD*" function in the *FD* package in R to calculate functional diversity indices (Laliberté et al., 2014). The FD index approach was used, which is the total branch lengths of a functional dendrogram calculated with the Gower distance measure (Podani, 1999). This approach uses a species-trait matrix, which is converted to a distance matrix (Gower distance), and then converted to a dendrogram via the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering method. We calculated functional evenness (FEve) and divergence (FDiv) using the convex hull methodology (Villéger et al., 2008), which uses the Gower distance matrix with PCoA analysis to calculate a matrix of transformed coordinates, and then uses the PCoA matrices to calculate the functional metrics. High FDiv means species abundances are concentrated towards the extremes of the functional trait space, indicating a high degree of niche differentiation (Sayer et al., 2017). This can occur in communities where a few species have very distinct functional traits that are well-separated from each other. Finally, we calculated functional richness (FRic), Rao's Quadratic Entropy (Rao's Q) and functional dispersion (FDis) using the methodology of Villéger et al. (2008). FRic is the total range or variety of functional traits present among species within a given area or habitat. Rao's Q is a measure of functional diversity that considers both species abundances and their pairwise functional dissimilarities. High Rao's Q indicates high dissimilarity among species, even if the number of species and the total range of functional traits (FRic) are low. FDis quantifies the variability or spread of species trait values within a

community where higher FDis indicates greater variability in traits among species, suggesting a community with a wider range of ecological strategies.

Calculating LiDAR-derived Vegetation Indices

We calculated vegetation indices from LiDAR data captured by drone (EP800, 8.8mm, resolution: 5472 x 3648 pixels) within the FCAT Reserve on March 2nd, 2023. The process involved initial data preprocessing to generate a high-resolution digital elevation model (DEM) from the LiDAR point cloud data (Segurado & Silman, 2023). We utilized QGIS for segmentation and classification techniques to delineate canopy features and estimate height and elevation. Elevation for each point was calculated using the DEM model. Elevation among our sites ranged from 416-656 m-asl. To calculate canopy height, the LiDAR data were processed to generate a Digital Surface Model (DSM) and Digital Terrain Model (DTM), and the canopy height was calculated by subtracting the DTM from the DSM using the raster calculator in QGIS. Canopy openness, indicative of light penetration through the canopy, was derived by evaluating gaps in vegetation cover. We calculated canopy openness by setting a threshold value (15 m from ground) to classify pixels based on their height allowing for the determination of open areas within the canopy. The resulting raster layer displayed the percentage of openness across the landscape. Canopy cover, representing the extent of foliage within an area, is quantified by assessing the area occupied by the canopy in relation to the total area. For the canopy cover assessment, we manually classified LiDAR points corresponding to vegetation at a minimum of 15 m from ground level, and the ratio of classified vegetation points to the total area. Finally, we used the density tool to assess distances between canopy points and compute canopy gaps, which allowed us to obtain measures of canopy cover for each plot. We then tested multicollinearity between environmental variables using Spearman's correlation from the *stats* package (Dormann et al., 2013). We found evidence of collinearity between canopy height and canopy openness ($S = 1932$, $p = 0.047$), thus we removed canopy openness from models. Therefore, environmental variables included canopy height, canopy cover, and elevation.

Statistical analyses

All statistical analyses and models were fitted in R (R Core Team, 2022). Abundance data from mist-netting were compiled together into a weighted matrix, where rows represented mist-netting plots (five individual communities per regeneration type), and columns represented individual bird species. Birds observed within mist-netting trials were weighted by their

abundance due to our ability to identify individuals from aluminum bands, which allowed us to avoid counting the same individual twice. The resultant weighted adjacency matrix was then used to assess differences in bird communities and taxonomic and functional diversity metrics across each regeneration type. We used these data to calculate Hill numbers using the *iNEXT* package in R (Chao et al., 2014): q=0 (species richness), Hill q=1 (exponential of Shannon's diversity index), and Hill q=2 (inverse of Simpson's index) (Ellison, 2010). Rarefaction and extrapolated curves were generated to determine how taxonomic diversity increases with increasing sampling effort and completeness. Rarefaction and extrapolation of richness, Shannon diversity, and Simpson diversity were calculated for each mist-netting plot (Chao et al., 2014). Sample-based curves evaluated the number of individuals in a sample by plotting diversity estimates in relation to the number of sampling units, while coverage-based curves were plotted against rarefied completeness in relation to sample coverage. Curves were plotted using doubling of sampling size, and 999 bootstrap replicates were used to estimate 95% confidence intervals.

To test for differences in the composition of understory bird communities across the regeneration gradient, we used abundance data from the adjacency matrix to calculate dissimilarity between plots using the Bray-Curtis dissimilarity index and the "*vegdist*" function in the *vegan* package in R (Oksanen et al., 2022). The Bray-Curtis index accounts for differences in species composition and abundance between plots, providing a measure of dissimilarity that ranges from 0 (identical communities) to 1 (completely different communities with no overlapping species). To evaluate statistical support for differences in avian communities across regenerating stages, we performed a Permutational Multivariate Analysis of Variance (permanova) using the "*adonis*" function in the *vegan* package. Then, to assess the relationship between bird community composition and environmental variables, we used a Redundancy Analysis (RDA). First, the abundance matrix was normalized using the Hellinger transformation (Legendre & Gallagher, 2001). We plotted the RDA using the "*rda"* function in the *vegan* package in R and fitted relative environmental variables to the model using the "*anova.cca*" function with 1000 null model iterations. To determine if specific trophic niches (e.g., frugivores) within communities differed across regeneration types, we used categorical data to perform a chi-squared test using the "*chisq.test*" function in the *stats* package in R.

When considering differences in taxonomic and functional diversity indices, we first tested for spatial autocorrelation using the *spdep* package in R. We created a distance matrix

from the UTM Northing and Easting coordinates of each sampling location. Next, we used the *spdep* package to construct a neighborhood structure based on this distance matrix, converting the neighbor list into spatial weights. This allowed us to assess spatial autocorrelation through Moran's I test. We found evidence of spatial autocorrelation for several of our response variables. Therefore, we performed Generalized Least Squares (GLS) analyses incorporating a Gaussian correlation structure. We chose Gaussian correlations because they allow for a continuous decay of spatial autocorrelation over distance, which is more appropriate for modeling the gradual environmental gradients and the spatial structure in our dataset compared to alternative correlation structures that may assume more abrupt changes. The Gaussian correlation structure was defined using plot coordinates (easting and northing).

For diversity metrics that exhibited significant spatial autocorrelation, we applied GLS regression to account for spatial dependence in model residuals. To evaluate differences in taxonomic and functional diversity across sites, we then modeled taxonomic and functional diversity metrics first as functions of regeneration type, then as functions of environmental variables. Both sets of models retained the Gaussian spatial correlation structure to account for spatial dependence. We used Type II Wald chi-square tests for response variables as a function of regeneration type. We used Type III tests for response variables as a function of environmental variables due to the interaction between canopy cover and canopy height, which was included in models. We then plotted all relationships using the *ggplot2* package (Wickham et al., 2016).

Finally, to determine how functional traits shift across stages of regeneration, and which traits contribute most to changes in functional diversity, we ran a redundancy analysis (RDA) between species abundances across regeneration types, with functional traits as explanatory variables. We tested the significance of each exploratory variable using ANOVA-like permutation tests under the "*anova.cca"* function with 1,000 permutations applied to evaluate individual variable contributions. The "*envfit"* function was again used to fit explanatory variables onto the RDA ordination, and p-values were extracted to determine which variables significantly influenced community structure. Variables with $p < 0.05$ were classified as significant. To examine correlations among explanatory variables, a Pearson correlation matrix was computed using the "*cor*" function in the vegan package for each diversity measure and functional trait.

Results

We recorded a total of 940 individual birds representing 111 different species across all study sites (**Supplementary Table 2**). Among these, the most frequently observed species were *Phaethornis yaruqui* (White-whiskered Hermit, n = 98), *Asemospiza obscura* (Dull-colored Grassquit, n = 64), and *Sporophila funerea* (Thick-billed Seed Finch, n = 48). Rarefaction analysis showed that our sampling effort captured 83–90% of total species richness, 89% of species diversity, and 95% of community evenness (**Supplementary Figure 3**). Understory bird communities differed as a function of regeneration type ($r^2 = 0.47$, $F = 4.68$, $p \leq 0.01$) (**Figure 4**). Richness also varied among habitats ($r^2 = 0.64$, $F = 12.40$, $p \leq 0.01$), where low-impacted early successional vegetation (LIE) had the highest species richness observed (mean = 27.6, variance = 7.8), followed by high-impact early successional (HIE) plots (mean = 25.4, variance = 41.3). Furthermore, bird abundances varied significantly across habitats ($r^2 = 0.43$, $F = 5.70$, $p \leq 0.01$), where the highest bird abundances were recorded in HIE (mean = 56.8, variance = 796) and LIE plots (mean = 66.6, variance = 134.3), while SEC and OG plots had comparatively lower bird numbers (SEC: mean = 37.8, variance = 123.7; OG: mean = 26.8, variance = 83.7).

Both canopy cover and canopy height were higher in older forests (SEC and OG) than in younger sites (HIE and LIE) (cover: $r^2 = 0.83$, $p \leq 0.01$, height: $r^2 = 0.83$, $p \leq 0.01$, height) (Table 4). Elevation was also different across habitats, where younger sites (HIE and LIE) were lower in elevation than older sites (SEC and OG) ($r^2 = 0.63$, $p \leq 0.01$). Considering communities of understory birds across habitats, canopy height was the biggest predictor of community differences in terms of environmental variables (variance = 0.16, $F = 5.82$, $p \leq 0.01$). Canopy height demonstrated strong associations with RDA 1 (0.98), whereas canopy cover exhibited a weaker and non-significant positive relationship with RDA 1 (0.98) and RDA 2 (0.05) (variance = 0.02, $F = 0.92$, $p = 0.47$). Elevation also had a non-significant relationship (variance = 0.03, $F = 0.98$, $p = 0.36$) with RDA 1 (0.53) and RDA 2 (-0.85) suggesting a lesser influence on the observed variation in the dataset. Constrained variables explained about 35.4% of the total variance in our RDA.

Both taxonomic and functional diversity of understory bird communities differed as a function of regeneration stage (**Supplementary Table 3**). Expected species richness (Q_0) and species diversity (Q_1) were highest in HIE and LIE sites and declined in SEC and OG forests (**Figure 5**). In contract, when minimizing the influence of rarer species using Inverse Simpson

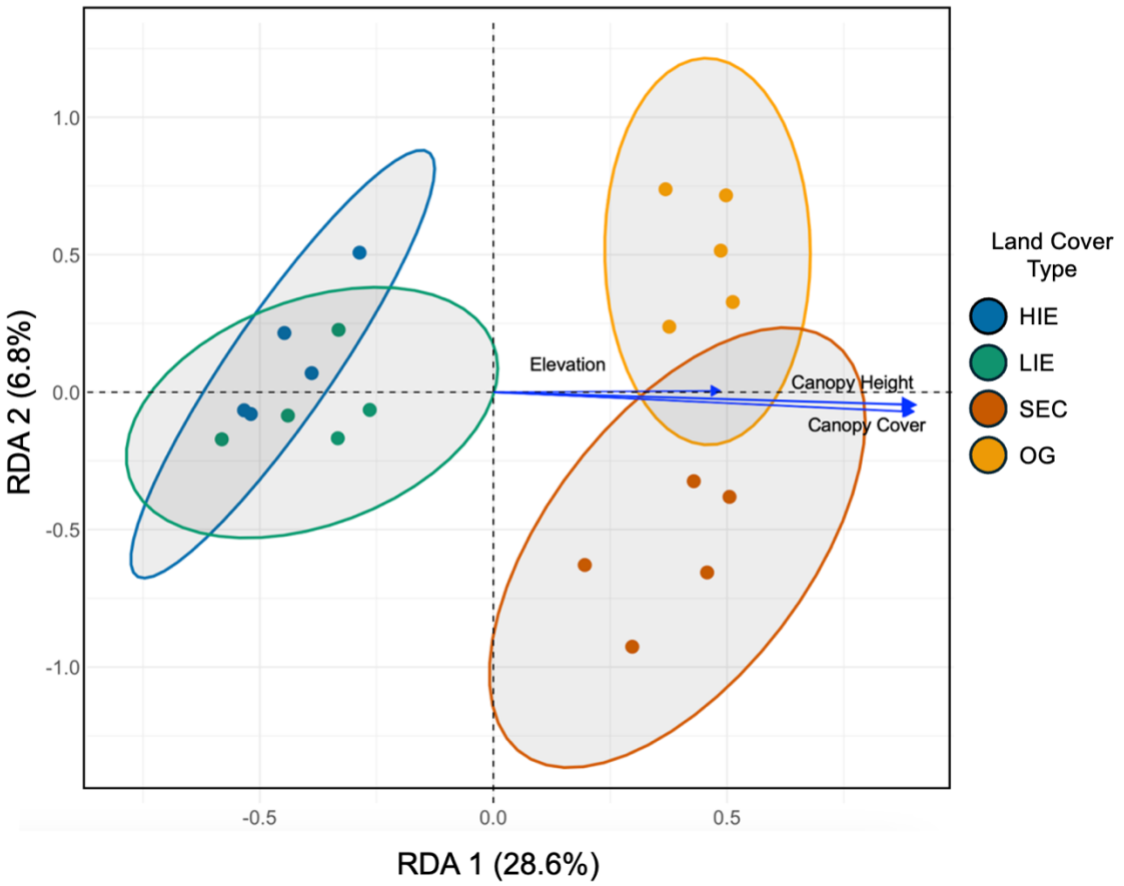

Figure 4: Redundancy Analysis (RDA) biplot of bird community composition constrained by selected environmental variables (canopy cover, canopy height, and elevation), and grouped by regeneration stage (highly impacted early successional habitat (HIE, blue), low impact early successional habitat (LIE, green), mid-successional secondary forest (SEC, orange), and old growth Chocó Rainforest (OG, purple). Points in the plot represent communities or individual plots and blue arrows represent environmental variables. The x-axis (RDA1) explains 28.6% of the variation in bird community composition. The y-axis (RDA2) explains 6.8% of the variation. The direction and length of the arrows indicate the strength and direction of the relationship between each environmental variable and the ordination axes. Samples located in the same direction as an arrow are positively associated with that environmental variable.

Table 4: Vegetation indices calculated from LiDAR data captured by drone within the FCAT Reserve. This included canopy height (m), canopy cover (%), canopy openness (%), and elevation (m-asl). "Stage" represents the four habiats: highly impacted early successional habitat (HIE), low impact early successional habitat (LIE), mid-successional secondary forest (SEC), and old growth Chocó Rainforest (OG).

Stage	Value	Canopy Height (m)	Canopy Cover (%)	Canopy Openness (%)	Elevation (m-asl)
HIE	Mean	6.84	7.59	12.22	466.76
	Variance	3.11	4.56	1.04	1876.79
LIE	Mean	4.93	11.31	14.12	539.94
	Variance	0.33	18.87	0.11	157.50
SEC	Mean	27.22	26.42	12.86	533.54
	Variance	13.76	14.41	0.23	432.5
OG	Mean	26.76	25.53	12.89	533.76
	Variance	94.98	33.07	0.11	140.65

Index (Q_2), we observed that older forests (SEC and OG) had higher diversity than younger successional sites. While changes in species richness (Q_0) and the Inverse Simpson Index (Q_2) were not associated with any environmental predictor, Shannon entropy (Q_1) was driven by changes in canopy height and decreased with increasing canopy (chi-squared = 4.92, p = 0.03) (**Table 5**). Functional diversity indices exhibited a similar trend as Q_2; functional dispersion, functional divergence, and RaoQ were all greater in mature forests (SEC and OG) than in early successional ones (HIE and LIE) (**Figure 5**). Pairwise tests showed that functional divergence of bird communities differed between HIE and secondary forests (p = 0.05), high impact sites and old growth forests (p = 0.02), and low-impact sites and old growth forests (p = 0.03).

Functional divergence was strongly influenced by both canopy height (chi-squared = 11.46, $p < 0.001$) and the interaction between canopy cover and height (chi-squared = 12.53, $p < 0.001$) (**Table 5**). Functional dispersion followed similar patterns and was higher in later successional forests, with differences between HIE sites and both LIE and OG forests (SEC, p = 0.008; OG, p = 0.002), and between LIE and later stages (SEC, p = 0.007; OG, p = 0.002). Functional dispersion was also associated with both canopy height (chi-squared = 5.63, p = 0.02,) and the interaction between canopy cover and height (chi-squared = 5.64, p = 0.02). Rao's Quadratic Entropy also varied between HIE and OG forests (p = 0.02) and LIE with both SEC forests (p = 0.04) and OG (p = 0.01). Like dispersion and divergence, Rao's Quadratic Entropy was also associated with both canopy height (chi-squared = 6.19, p = 0.01) and the interaction between canopy cover and height (chi-squared = 6.87, p = 0.01). In contrast, the functional richness of understory bird communities was lowest in the more mature forests and highest in early successional areas (p = 0.03), and pairwise comparisons revealed that functional richness only differed between HIE and OG (p = 0.03). Both functional richness and functional evenness were not correlated with any environmental predictor variables.

Both younger sites (HIE and LIE) clustered together on the RDA, indicating greater functional similarity compared to mature forest plots (SEC and OG) (**Figure 6**). The RDA model explained 64.73% of total variation in functional diversity (constrained inertia = 0.4122). Functional richness was associated with open-canopy habitats (HIE and LIE), mainly driven by variations in beak width and tarsus length. Both beak width and tarsus length were positively associated with functional richness, yet were negatively associated with functional dispersion, functional divergence, and Rao's Q (**Figure 7**). Functional dispersion, functional divergence,

Table 5: Type III Wald chi-square tests assessing the effects of canopy cover, canopy height, elevation, and their interaction on taxonomic and functional diversity metrics. Generalized least squares (GLS) regression was used to account for spatial dependence in model residuals, with a Gaussian spatial correlation structure applied. Significant relationships ($p < 0.05$) are highlighted in bold with an asterisk (*).

Response Variable	Predictor	Chi Squared	P-value
Species Richness (Q0)	Canopy Cover	0.20	0.66
	Canopy Height	1.48	0.22
	Elevation	1.33	0.25
	Canopy Cover * Canopy Height	0.25	0.62
Shannon Entropy (Q1)	Canopy Cover	0.06	0.81
	Canopy Height	**4.92**	**0.03***
	Elevation	0.76	0.38
	Canopy Cover * Canopy Height	1.96	0.16
Inverse Simpson Index (Q2)	Canopy Cover	0.07	0.79
	Canopy Height	4.36	0.04
	Elevation	0.38	0.54
	Canopy Cover * Canopy Height	2.41	0.12
Functional Richness (FRic)	Canopy Cover	0.00	0.98
	Canopy Height	0.05	0.82
	Elevation	1.72	0.19
	Canopy Cover * Canopy Height	0.01	0.93
Functional Divergence (FDiv)	Canopy Cover	1.18	0.28
	Canopy Height	**11.46**	**< 0.001 ***
	Elevation	3.28	0.07
	Canopy Cover * Canopy Height	**12.53**	**< 0.001 ***
Functional Evenness (FEve)	Canopy Cover	0.56	0.45
	Canopy Height	2.22	0.14
	Elevation	1.07	0.30
	Canopy Cover * Canopy Height	2.64	0.10

Table 5 Continued.

Functional Dispersion (FDis)	Canopy Cover	2.06	0.15
	Canopy Height	**5.63**	**0.02 ***
	Elevation	0.50	0.48
	Canopy Cover * Canopy Height	**5.64**	**0.02 ***
Rao's Quadratic Entropy (RaoQ)	Canopy Cover	2.67	0.10
	Canopy Height	**6.19**	**0.01 ***
	Elevation	0.47	0.49
	Canopy Cover * Canopy Height	**6.87**	**0.01 ***

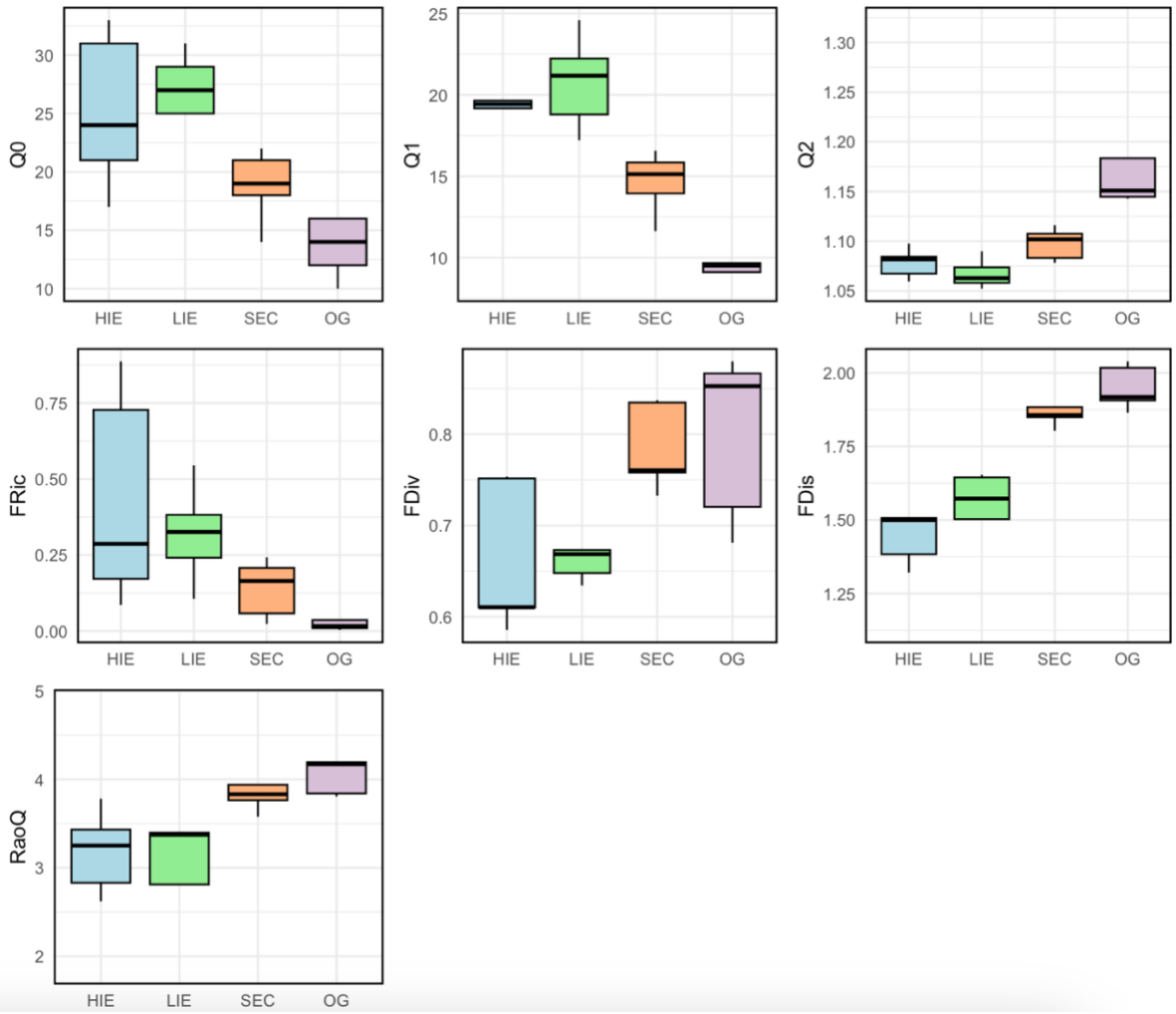

Figure 5: Differences in Hill numbers (Q0 = species richness, Q1 = exponential of Shannon Entropy, Q2 = Inverse Simpson Index) and functional diversity metrics (FRic = functional richness, FDiv = functional divergence, FDis = functional dispersion, and RaoQ = Rao's Quadratic Entropy) across a regenerating forest gradient. Plots include highly impacted early successional habitat (HIE, blue), low impact early successional habitat (LIE, green), mid-successional secondary forest (SEC, orange), and old growth Chocó Rainforest (OG, purple).

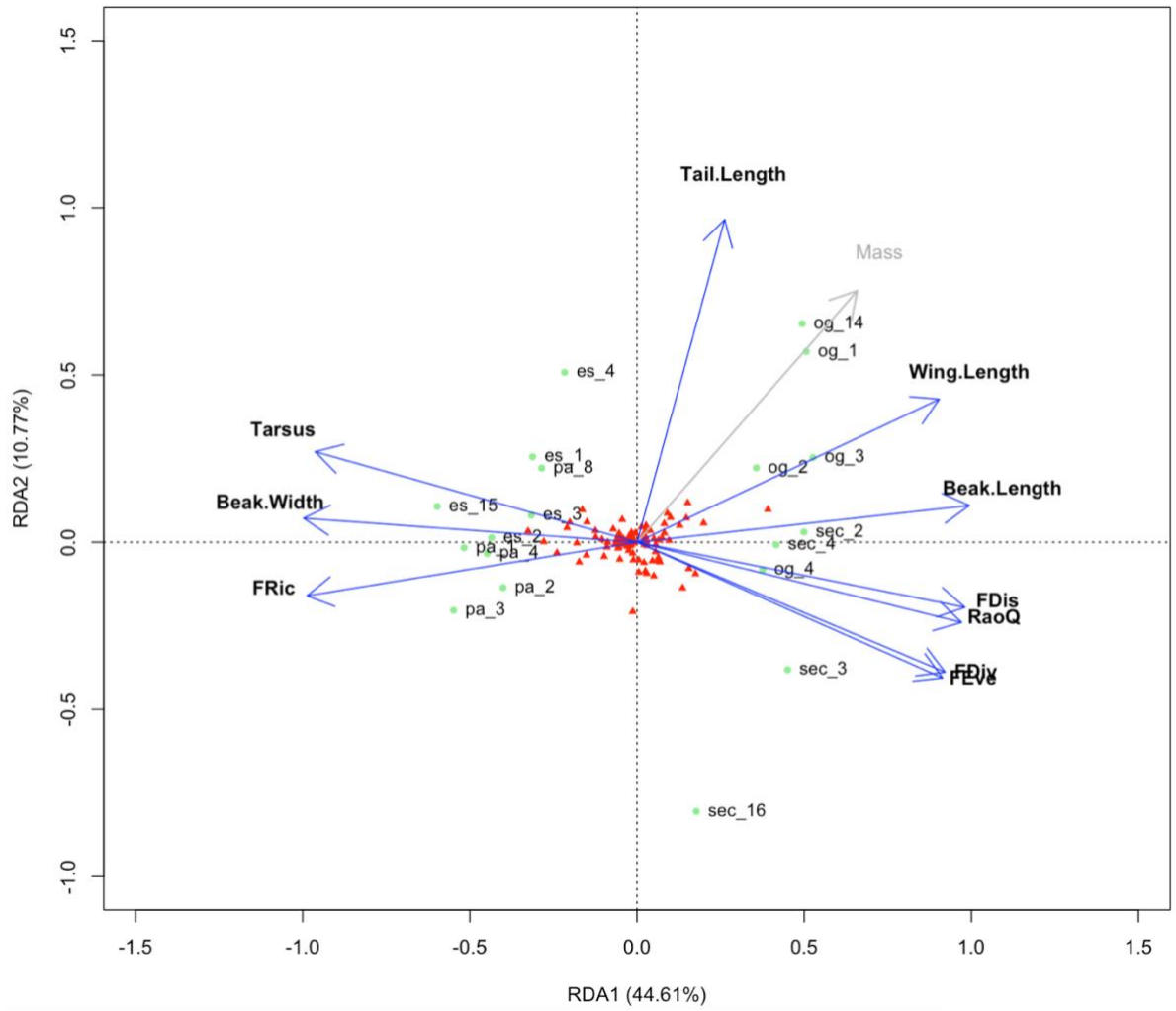

Figure 6: Redundancy Analysis (RDA) biplot illustrating the relationships between functional diversity indices, morphological traits, and community composition. Regeneration plots are represented by green circles, while individual bird species are represented by red triangles. Arrows represent exploratory vectors, with blue arrows indicating variables that significantly ($p < 0.05$) explain variation in community composition, and gray arrows representing non-significant predictors. The x-axis (RDA1) explains 44.61% of the constrained variation, while the y-axis (RDA2) explains 10.77%. Functional diversity indices (FDis: Functional Dispersion, FDiv: Functional Divergence, FRic: Functional Richness, RaoQ: Rao's Quadratic Entropy) and morphological traits were used as explanatory variables. Sites and species positioned closer together share more similar trait compositions. The direction and length of arrows indicate the strength and influence of each predictor on community structure.

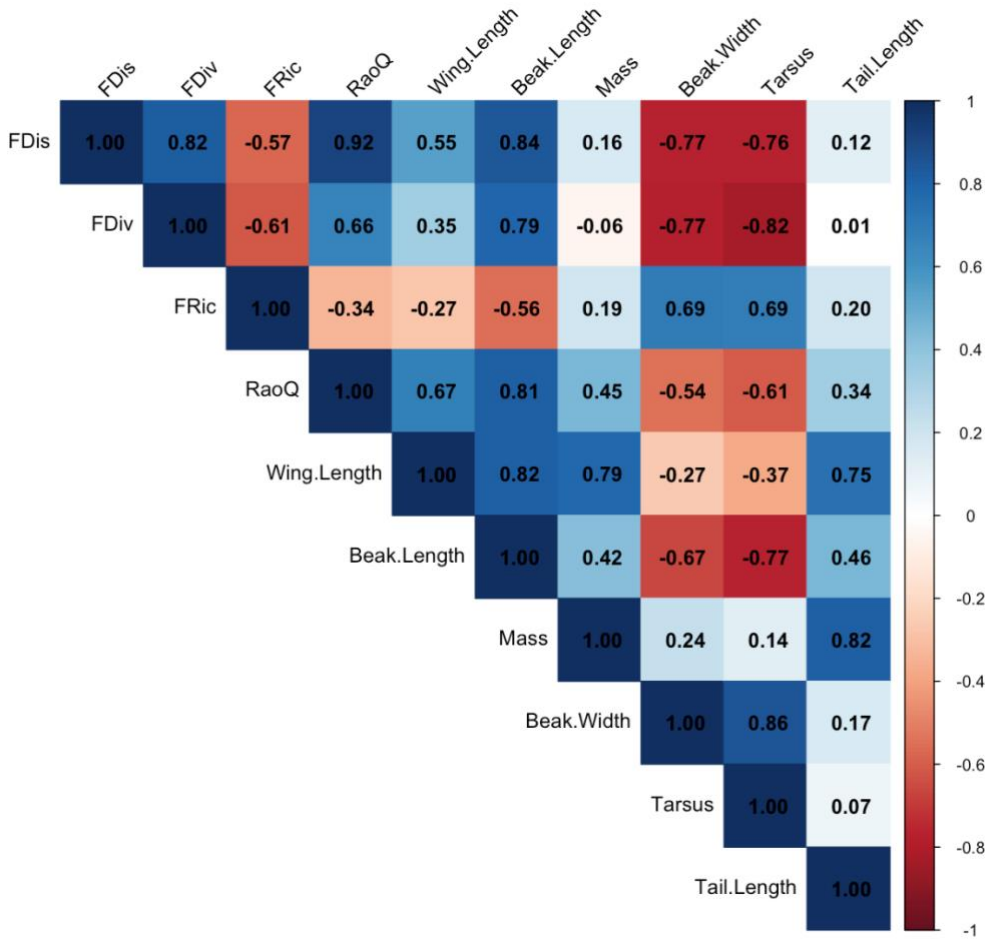

Figure 7: Pearson correlation matrix illustrating the relationships between functional diversity indices (FDis: Functional Dispersion, FDiv: Functional Divergence, FRic: Functional Richness, RaoQ: Rao's Quadratic Entropy) and morphological traits (Wing Length, Beak Length, Mass, Beak Width, Tarsus, Tail Length). The color intensity and shading represent the strength and direction of the correlations, with warmer colors (red) indicating strong positive correlations and cooler colors (blue) representing strong negative correlations. Correlation coefficients are displayed within the matrix, with significant relationships highlighted.

Rao's Quadratic Entropy, and functional evenness were all indicators of closed canopy habitats and associated with both SEC and OG. OG and SEC forests clustered together on the RDA but exhibited distinct trait shifts. Specifically, changes in tail length, mass, and wing length were associated with old growth forests, whereas changes in beak length were more strongly associated to both OG and SEC habitats. Beak length was strongly correlated with differences in functional dispersion (0.85), functional divergence (0.79), and Rao Q (0.81), whereas wing length was positively correlated functional dispersion (0.55), and Rao's Q (0.67).

Discussion

The degree to which natural regeneration promotes functional and resilient communities is a key question for the ecological and conservation research communities. To address this question, expanding diversity assessments, which have traditionally been taxonomically based, to incorporate functional diversity indices will be an important step forward for understanding forest regeneration and restoration ecology (Chazdon, 2008, 2013a; Lamb, 2018; Nabhan et al., 2020). We found that different functional or taxonomic diversity indices provided drastically different results, and that not all measures were equally good indicators of forest regeneration. The strongest differences in bird functional and taxonomic composition were between open and closed canopy environments, where most taxonomic indices were highest in open canopy environments, while three functional diversity measures were highest in closed canopy environments. Functional richness was associated with open-canopy habitats in early stages of regeneration, and functional evenness showed no changes between regeneration stages. Inversely, functional divergence, functional dispersion, and Rao's quadratic entropy increased as a function of canopy cover and height and were indicative of mature forest communities. Therefore, functional divergence, functional dispersion, and Rao's quadratic entropy might be more valuable to consider when assessing community responses to regeneration in tropical forest restoration than taxonomic measures.

The strongest differences in bird functional and taxonomic composition were associated with vegetation changes between open and closed canopy environments. Functional dispersion, functional divergence, and Rao's Q increased with canopy height and density independently of bird species richness, indicating as forests grow taller and more structurally complex, the species that persist have more distinct ecological roles (Remeš et al., 2021). This result is not surprising, as functional diversity measures reflect deeper ecological processes that take longer to recover

compared to simpler metrics like species richness and abundance (Acevedo-Charry & Aide, 2019). Resources provided by taller vegetation might allow the coexistence of species with diverse ecological strategies by providing more niche space (Aguirre-Gutiérrez et al., 2017; Oliveira & Scheffers, 2019). Other work has found similar trends, where increased tree cover positively correlated with increased guild richness and a greater distribution of functional traits (Ikin et al., 2019). However, canopy attributes only explained 35% of the variance in bird communities. Thus, other variables are important to consider, as factors such as food availability can also influence functional diversity by filtering trait assemblages (Flynn et al., 2011; Pena et al., 2023; Quitian et al., 2019). For instance, in a Peruvian cloud forest, early regeneration habitats with dense understories supported more bird species with plant-based diets (flowers, fruits, and seeds), broader elevational ranges, and wider habitat breadths compared to old-growth forests (Ausprey et al., 2022). Furthermore, dispersal ability and historical contingency also contribute to changes in community assembly (Gao et al., 2024), therefore could also contribute to changes in functional diversity.

In this study, species richness and Shannon's entropy were highest in early stages of forest regeneration, likely due to the high abundance of generalist disturbance-tolerant species. Other studies have suggested that generalist species adapt to fast population growth in resource-rich environments dominate earlier successional stages, while species with higher competitive ability in resource-limited environments, or those that depend on resources such as higher structural vegetation complexity, dominate older-growth forests (Pinotti et al., 2012). However, functional richness was also associated with open-canopy habitats (in contrast to functional dispersion, functional divergence, and Rao's quadratic entropy). Functional richness is simply defined as the proportion of the total number of traits available that are occupied by at least one individual and may correlate with species richness (Villéger et al., 2008). Therefore, functional richness is independent of species abundances (Karadimou et al., 2016), and similar to species richness, will increase as the number of species present increases regardless of species rarity. T Thus, high species richness in early successional plots could result in a wider range of functional traits present within a community, but not necessarily equate to a more functionally diverse community overall. Differences in functional richness across regeneration stages were explained by changes in beak width and tarsus length. In this system, open canopy habitats were dominated by a high diversity of small, wide beaked granivorous species including *Oryzoborus funereus*,

Sporophila corvina, and *Sporophila nigricollis.* Therefore, early successional habitats likely maintain a mix of open-area specialists (e.g., ground-foraging species) and habitat-edge opportunists, but lack the ecological specialization seen in forests (Ausprey et al., 2022). Functional richness, like species richness, may not be a good indicator of forest regeneration as it may not reflect community's indicative of late stages of forest recovery if the dominant species present are not functionally diverse.

Functional dispersion, functional divergence, and Rao's quadratic entropy were all associated with closed canopy habitats and thus may serve as more accurate indicators of forest recovery. The observed increase in functional dispersion in mature forests could indicate higher degrees of niche differentiation, where lower rates of competition in older sites may enhance species co-occurrences and complementarity (O'Brien et al., 2022). Studies have suggested that communities with higher functional dispersion may be better able to respond to environmental changes (Flynn et al., 2011; Kuebbing et al., 2018). Similarly, the increase in functional divergence in mature forests could suggest that the distribution of traits becomes more varied and specialized in later stages of regeneration, allowing for greater resource partitioning and reduced competition among species (Sayer et al., 2017).

Functional dispersion was driven by changes in both beak and wing length, whereas changes in functional divergence were more strongly associated with in beak length. Longer beaks may facilitate access to a wider range of food resources, including specialized foraging niches such as probing into tree bark or nectar. Increased wing length in closed-canopy environments could provide enhanced flight efficiency, enabling birds to navigate more complex environments. Landscapes with higher tree cover facilitate the movement of species, where birds with larger wings might have higher mobility across patches of degraded landscapes if the surrounding forest has higher levels of canopy cover (Remeš et al., 2021). Furthermore, high Rao's quadratic entropy values in mature forests signify greater functional diversity overall, meaning the species within a community have more distinct functional traits and are less functionally redundant (Sayer et al., 2017). Changes in Rao's quadratic entropy were also driven by beak and wing length, and also included mass. Mass was associated with few functional diversity indices, indicating that body size influences resource use and habitat specialization independently of other morphological traits. In structurally complex environments, larger-bodied

species may exploit different foraging strata or require larger territories, whereas smaller species may have increased maneuverability in dense vegetation.

Other studies have also found contrasting patterns of taxonomic and functional diversity indices in relation to forest regeneration. Ikin et al. (2019) and Remeš et al. (2022) found that regeneration stage increases both functional diversity and species diversity of bird communities; however, both studies only utilized one measure of functional or taxonomic diversity. Ikin et al. (2019) found that species richness correlated with functional richness and, contrasting with our findings, increased with forest cover. Another study reported an increase in functional diversity measures as a function of forest regeneration in mammalian communities but no differences in taxonomic diversity across regeneration stages (Derhé et al., 2018). In contrast, some have found that regeneration stage did not significantly increase either functional or taxonomic diversity (Barros et al., 2022). When focusing on individual functional diversity measures, one study found that functional divergence, functional richness, and functional evenness of plant communities changed independently of one another, similar to what we observed in avian communities (Pakeman, 2011). These contrasting findings highlight the complexity of biodiversity recovery, suggesting that taxonomic and functional diversity may respond differently to forest regeneration depending on the taxa studied, the metrics used, and the specific environmental conditions of the system.

The observed low rates of taxonomic diversity in closed-canopy forests could be due to low detection rates from mist-net sampling. Substantial effort would be needed to satisfy a species accumulation curve and accurately account for a high proportion of the species residing in these habitats. In contrast, functional diversity indices were indicative of closed-canopy habitat; these measures require less sampling effort and could potentially be a faster and more efficient way of assessing community responses to forest regeneration. However, not all functional diversity indices were characteristic of regeneration, and some functional diversity indices are sensitive to under sampling (Kortmann et al., 2025; Van Der Plas et al., 2017). Specifically, it's been found that functional evenness is highly sensitive to under sampling, and functional richness is moderately sensitive to under sampling, making them potentially less useful in biodiversity surveys (Van Der Plas et al., 2017). Therefore, functional divergence, function dispersion, and Rao's quadratic entropy, which were all less sensitive to under-sampling (Van Der Plas et al.,

2017), and were strongly associated with closed-canopy habitats might be more useful when seeking to understand the functional recovery of communities across forest regeneration.

Within our system, differences in functional diversity only elucidated a split between open and closed canopy habitats; no diversity indices explained the difference between secondary and old-growth communities. This could be because that we did not capture the full set of functional traits or environmental gradients associated with changes in bird communities across stages of regenerating forests. For example, Schuldt et al. (2022) found that bird functional divergence increased with increasing variability in tree diameter, a variable that we did not measure. Thus, consideration of foraging behaviors such as cavity nesting, bark gleaning, and sit-and-wait foraging might have explained the variation between secondary and old growth habitats. In contrast, Sayer et al. (2017) found that avian functional dispersion and functional divergence was comparable among secondary and old growth tropical forests, indicating that high functional diversity could pattern could be a feature of closed-canopy forests. Future research should include a broader scope of potential drivers of functional diversity in bird community recovery that include more environmental parameters and behavioral traits.

Overall, our study contributes to the growing use of functional diversity indices as a means of assess biodiversity responses to forest regeneration. Our findings underscore the importance of selecting robust functional diversity indices that are both ecologically meaningful and resilient to sampling limitations when evaluating community responses to forest regeneration. By prioritizing indices like functional divergence, functional dispersion, and Rao's quadratic entropy, restoration practitioners can more reliably assess community functional recovery, ultimately improving the effectiveness of biodiversity monitoring in regenerating forests.

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Appendix

Supplementary Table 1: Description of each functional trait obtained for each bird species, including its variable type, measurement metric, and functional importance.

Trait	Variable	Description	Functional Importance
Beak Length (mm)	Continuous	Length from the tip of the beak to the base of the skull	Refers to different feeding strategies relating to functional role of species (e.g., seed-dispersers, pollinators).
Beak Width (mm)	Continuous	Width of the beak at the anterior edge of the nostrils	Refers to different feeding strategies relating to functional role of species (e.g., seed-dispersers, pollinators).
Wing Length (mm)	Continuous	Length from the carpal joint (bend of the wing) to the tip of the longest primary feather on the flattened wing	Flight performance, migration, feeding ability. Birds with shorter wings are typically suited for denser vegetation, while birds with larger wings can cover more range and aid in habitat connectivity.
Mass (g)	Continuous	Body mass given as species average (incorporating both male and female body mass)	Energy requirements, activity levels, environmental conditions. Larger-bodied birds require more food to maintain energy and, thus, may play important environmental roles such as dispersing large seeds across landscapes.
Primary Habitat	Categorical	Primary habitat species are found in, including human-modified, shrubland, and forests	Refers to species' ability to perform functional roles across multiple landscapes. Species adapted to human-modified landscapes may be important in connecting disturbed areas to non-disturbed areas.
Trophic Niche/Diet Type	Categorical	Species are put into certain categories if over 60% of their diet is made up of one food source (e.g., frugivore, nectarivore)	Refers to different feeding strategies relating to the functional role of species (e.g., seed-dispersers, pollinators).

Supplementary Table 2: Bird community data for species surveyed across the entire FCAT reserve. Species codes represent 4-digit codes based of each species common name. Trait data, including trophic niches, habitat associations, and morphological traits for each species were collected using an open access data set provided by Tobias et al., 2022. Morphological traits include average mass (g), beak length (mm), beak width (mm), wing length (mm), and tail length (mm). Abundance represents the total number of individuals observed during the study.

Code	Scientific Name	Trophic Niche	Habitat	Abundance	Mass	Beak Length	Beak Width	Wing Length	Tail Length
AMHB	*Amazilia amazilia*	Nectarivore	Shrubland	2	4.3	20.7	2.9	61.8	37.6
BABW	*Campylorhynchus zonatus*	Invertivore	Forest	1	34.6	24	3.9	78.4	82
BANA	*Coereba flaveola*	Nectarivore	Shrubland	24	10	13.2	3.6	54.6	34.1
BAWS	*Pygochelidon cyanoleuca*	Invertivore	Human Modified	1	9.7	8.6	3.6	92.3	48.8
BAYW	*Cantorchilus nigricapillus*	Invertivore	Forest	4	23.9	19.2	4.2	65.8	54.3
BBSC	*Campylorhamphus pusillus*	Invertivore	Forest	1	40.5	55	4.2	95.6	95
BCAS	*Thamnophilus atrinucha*	Invertivore	Forest	5	23.6	19.4	5.4	67.9	56.1
BCHH	*Amazilia amabilis*	Nectarivore	Forest	20	4.3	21.3	2	52.3	29.2
BCOF	*Myiophobus fasciatus*	Invertivore	Shrubland	7	9.9	13.5	5	58.9	54.1
BCRM	*Lepidothrix coronata*	Frugivore	Forest	16	8.3	10.9	3.7	56.8	26.6
BFDA	*Dacnis lineata*	Frugivore	Forest	2	11	13	3.5	58	40.6
BGRA	*Volatinia jacarina*	Granivore	Human Modified	4	9.9	10.4	4.3	47.8	42.8
BGRO	*Cyanoloxia cyanoides*	Granivore	Forest	3	32.5	19.6	10.2	79.6	66.8
BGTA	*Tangara episcopus*	Omnivore	Forest	7	35	14.2	6.4	87.3	64
BHTA	*Tangara gyrola*	Frugivore	Forest	2	21	12.7	4.8	73.5	51.4
BIAN	*Gymnopithys bicolor*	Invertivore	Forest	7	31.1	18.5	5.1	75.3	46.6
BNTA	*Tangara cyanicollis*	Frugivore	Forest	9	17	12.3	4.5	66.1	46.5

Supplementary Table 2 Continued.

BRAT	*Attila spadiceus*	Invertivore	Forest	2	39.1	22.3	7.3	85.6	67.8
BTBA	*Threnetes ruckeri*	Nectarivore	Forest	34	5.2	33.4	3	56.6	36.3
BTFG	*Automolus ochrolaemus*	Invertivore	Forest	2	40.2	22.7	4.8	87.1	74.8
BTSA	*Saltator maximus*	Frugivore	Shrubland	8	47.6	20.7	8.9	96.1	88.9
BURW	*Myiothlypis fulvicauda*	Invertivore	Forest	6	14.9	14.3	4.5	63.3	49.7
CBAN	*Poliocrania exsul*	Invertivore	Forest	4	26.5	21.1	5	66.6	47.3
CHTY	*Zimmerius albigularis*	Invertivore	Forest	16	10.4	9	3.2	49.6	44.5
CHWA	*Myiothlypis chlorophrys*	Invertivore	Forest	3	16.2	12.9	4.6	61	48.1
CIMB	*Pachyramphus cinnamomeus*	Invertivore	Forest	3	20.3	16.8	7.6	77	59.4
CIVI	*Vireo chivi*	Invertivore	Forest	14	16.1	14	4.4	68	52.1
COAR	*Pteroglossus torquatus*	Frugivore	Forest	2	219.1	104	22.9	146.9	150.5
COTF	*Todirostrum cinereum*	Invertivore	Shrubland	10	6.3	14.8	4.8	42.5	33.8
CRWO	*Thalurania colombica*	Nectarivore	Forest	12	4.5	20.4	2.3	52.3	33.1
CTST	*Epinecrophylla fulviventris*	Invertivore	Forest	6	10.4	15	4.1	50.9	33.2
DCGQ	*Asemospiza obscura*	Granivore	Shrubland	64	11.2	10.4	4.8	52.4	42.3
DUAN	*Cercomacroides tyrannina*	Invertivore	Forest	1	16.3	18.2	4.9	62.7	60.4
DUPI	*Patagioenas goodsoni*	Frugivore	Forest	1	176	17	4	148.7	99.6
DWAN	*Microrhopias quixensis*	Invertivore	Forest	2	7.9	15.6	4.1	53	52.7
ECTR	*Turdus maculirostris*	Omnivore	Forest	4	69.6	22.5	4.9	112.6	97.7
FRTA	*Ramphocelus flammigerus*	Frugivore	Forest	15	33	18.4	8.2	88.6	74.8
GAGW	*Myiothlypis fraseri*	Invertivore	Woodland	1	11.6	13.5	5	65	55.7
GANT	*Taraba major*	Invertivore	Forest	1	59.2	26.3	7	90.6	81
GBAN	*Crotophaga sulcirostris*	Invertivore	Human Modified	1	82	26.9	9.5	129.3	162.7
GCBR	*Heliodoxa jacula*	Nectarivore	Forest	5	8.1	26.4	2.5	70.3	44.2
GMAK	*Cryptopipo litae*	Frugivore	Forest	8	14.9	13.3	4.3	69.2	46.8

Supplementary Table 2 Continued.

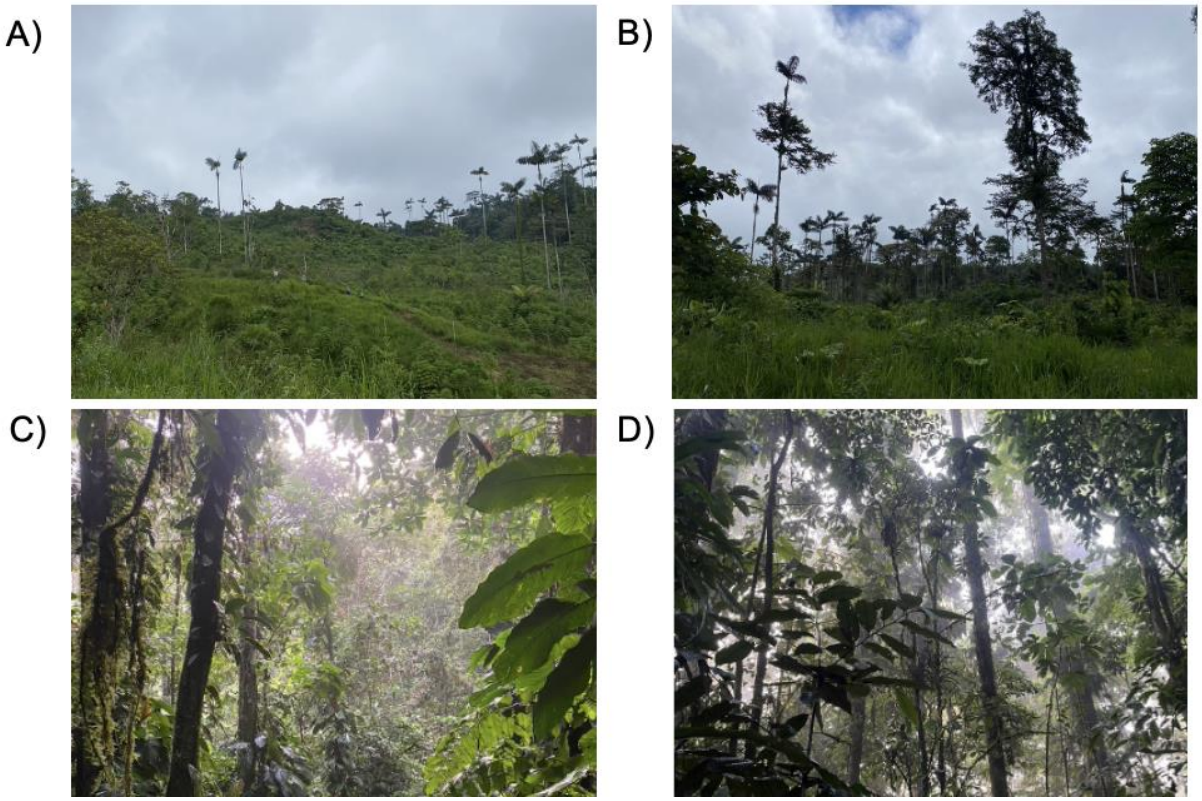
GOWO	*Colaptes rubiginosus*	Invertivore	Forest	1	55.8	27	7.1	123.7	76.3
GRET	*Discosura conversii*	Nectarivore	Forest	3	3	14.4	1.3	42.2	42
GRHO	*Chlorophanes spiza*	Frugivore	Forest	6	19	15.9	4.5	68.3	48.2
GYBM	*Progne chalybea*	Invertivore	Shrubland	1	50	15.3	5.6	130.6	66.4
HOWR	*Troglodytes aedon*	Invertivore	Shrubland	19	10.9	15.9	3	51.4	41.1
LBST	*Heliomaster longirostris*	Nectarivore	Forest	1	6.6	35	2.7	58.4	30.7
MUTO	*Ciccaba virgata*	Omnivore	Forest	1	284	33	9	240.6	149.1
NOSC	*Schiffornis veraepacis*	Omnivore	Forest	6	31.1	21.2	5.3	87.3	70.2
OBEE	*Euphonia xanthogaster*	Frugivore	Forest	22	13	10.7	4.8	61.4	36
OBFL	*Mionectes oleagineus*	Frugivore	Forest	21	11.2	11.8	4.2	60.5	48.2
OBSP	*Arremon aurantiirostris*	Omnivore	Forest	4	34.5	16	6.6	72.7	66.4
OCEE	*Euphonia saturata*	Frugivore	Forest	2	13.3	10	3.9	57.7	32.3
OCYE	*Geothlypis semiflava*	Invertivore	Shrubland	4	17.2	14.7	3.3	59.7	52.7
ORFC	*Myiotriccus ornatus*	Invertivore	Forest	2	10.6	10.3	3.6	52.4	26.5
OLPI	*Picumnus olivaceus*	Invertivore	Forest	5	10.6	10.3	3.6	52.4	26.5
OLWO	*Sittasomus griseicapillus*	Invertivore	Forest	4	13.1	16.1	4	76.7	76.5
ORFL	*Myiotriccus ornatus*	Invertivore	Forest	5	9.9	13.2	5.4	59.6	41.2
OSFT	*Mionectes olivaceus*	Frugivore	Forest	26	15.3	13.7	4.1	69	40
PAAN	*Myrmotherula pacifica*	Invertivore	Shrubland	6	10.1	15.3	3.6	50.6	28
PAPA	*Forpus coelestis*	Omnivore	Shrubland	1	26.1	16.6	9.4	76.8	39.4
PATA	*Tangara palmarum*	Omnivore	Forest	1	39	15	5.9	92.5	70.4
PBRW	*Dendrocincla fuliginosa*	Invertivore	Forest	5	38.7	29.9	6.4	104.9	86.7
PCFA	*Heliothryx barroti*	Nectarivore	Forest	3	5.5	21.9	2.2	63.8	57
PCHU	*Amazilia rosenbergi*	Nectarivore	Forest	4	3.7	23.9	2.2	52.8	30
PLXE	*Xenops minutus*	Invertivore	Forest	2	10.6	13.1	2.8	55.7	43.6

Supplementary Table 2 Continued.

PVTH	*Turdus obsoletus*	Omnivore	Forest	2	74.8	22.2	5	116	86.1
RCMA	*Ceratopipra mentalis*	Frugivore	Forest	15	15	12.1	4.4	58.5	28
RFSP	*Cranioleuca erythrops*	Invertivore	Forest	1	16.9	14.6	3.2	64.8	71.4
RMFL	*Myiozetetes cayanensis*	Invertivore	Shrubland	1	25.9	14.4	5.4	84.1	71.4
RTAH	*Amazilia tzacatl*	Nectarivore	Forest	22	4.8	21.9	3.1	56.4	34.2
RUFP	*Lipaugus unirufus*	Frugivore	Forest	1	82.1	24	7.2	132.4	112
SBAN	*Crotophaga ani*	Omnivore	Human Modified	2	110.1	30.6	9.9	144	180.6
SCBW	*Microcerculus marginatus*	Invertivore	Forest	2	18.2	19.2	3.4	58.7	24.2
SCFC	*Myiarchus phaeocephalus*	Invertivore	Woodland	1	26.3	22.5	7.1	93	89.8
SCPT	*Lophotriccus pileatus*	Invertivore	Forest	2	7.5	13.2	3.6	48.9	39.3
SHTY	*Phyllomyias griseiceps*	Invertivore	Forest	1	7.2	9	3.7	51.6	45.2
SHWO	*Lepidocolaptes souleyetii*	Invertivore	Woodland	3	25.7	32.7	4.1	92.3	84.5
SLAN	*Myrmotherula schisticolor*	Invertivore	Forest	3	9.6	15.5	3.3	54.9	36.9
SLSP	*Synallaxis brachyura*	Invertivore	Shrubland	28	18.3	16.3	3.4	57.9	76.7
SOBT	*Camptostoma obsoletum*	Invertivore	Shrubland	5	8.1	9.8	3.2	52.3	40.9
SPWO	*Xiphorhynchus erythropygius*	Invertivore	Forest	3	46.8	34.8	5.4	115.6	108.1
SQCU	*Piaya cayana*	Invertivore	Forest	1	102	32	8.8	145.5	278.6
SRFL	*Myiobius sulphureipygius*	Invertivore	Forest	6	11.6	14.6	4.2	66.4	56.2
SRWS	*Stelgidopteryx serripennis*	Invertivore	Shrubland	3	15.7	10.5	3.4	107.5	47.8
STFL	*Mionectes olivaceus*	Frugivore	Forest	2	15.3	13.7	4.1	69	40
STHR	*Phaethornis striigularis*	Nectarivore	Forest	6	3	23.7	2.4	39.1	36.4
STTA	*Tangara icterocephala*	Frugivore	Forest	4	22	12.6	5.1	70.5	45
STXE	*Xenops rutilus*	Invertivore	Forest	1	11.2	13.3	2.9	65.8	49
TBEU	*Euphonia laniirostris*	Frugivore	Forest	28	15	10.1	5.6	61	37.1

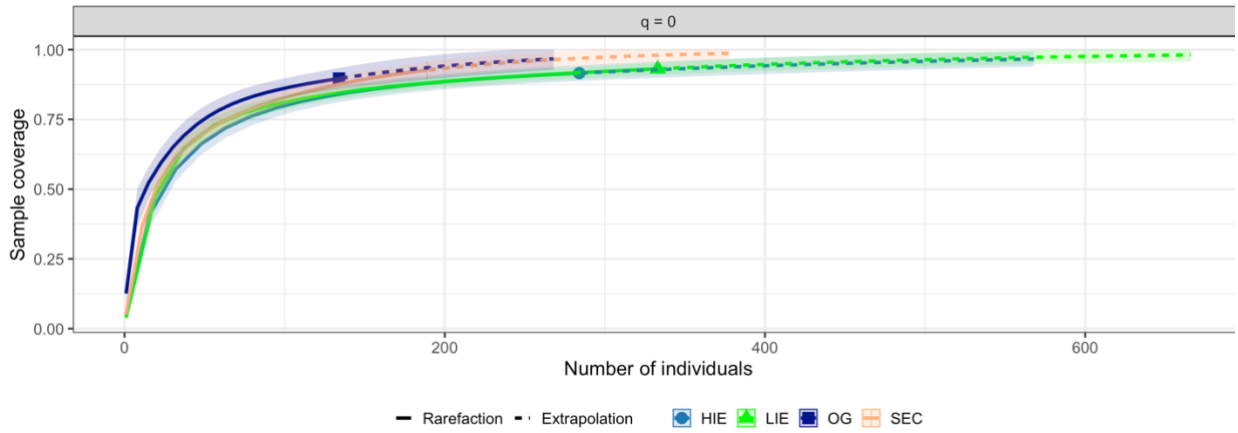
Supplementary Table 2 Continued.

TBSF	*Sporophila funerea*	Granivore	Human Modified	48	13	12.6	6.9	55	48.7
TCTA	*Chrysocorypha delatrii*	Invertivore	Forest	1	18	15.2	4.9	71.4	58.1
VASE	*Sporophila corvina*	Granivore	Human Modified	40	10.6	10.7	5.3	52.9	42.8
VBHU	*Amazilia julie*	Nectarivore	Forest	14	3.3	16	1.2	43.1	26
WBMA	*Manacus manacus*	Frugivore	Forest	26	16.7	11.5	4.4	52.2	32.8
WBWO	*Glyphorynchus spirurus*	Invertivore	Forest	3	14.6	13.7	4.4	68.7	66
WFLA	*Myrmotherula axillaris*	Invertivore	Forest	3	8.1	15	3.4	50.9	36.5
WSTA	*Tachyphonus rufus*	Invertivore	Shrubland	1	34.4	18.7	6.1	83	77.2
WTGS	*Atticora tibialis*	Invertivore	Forest	1	10.6	7.4	3.4	88.2	53
WTRS	*Platyrinchus mystaceus*	Invertivore	Forest	4	9.7	13.1	7.3	55	29.9
WTSI	*Eutoxeres aquila*	Nectarivore	Forest	13	10.6	27.5	3.6	70.5	54
WWHE	*Phaethornis yaruqui*	Nectarivore	Forest	98	5.4	45.6	2.6	59.5	53.8
WWPU	*Malacoptila panamensis*	Invertivore	Forest	6	42.6	29.3	9.5	87.4	71.8
YBEL	*Elaenia flavogaster*	Invertivore	Woodland	3	24.8	12.7	5	77.4	70.6
YBSE	*Sporophila nigricollis*	Granivore	Shrubland	35	9.6	9.1	5	52.4	43
YBSI	*Spinus xanthogastrus*	Granivore	Forest	2	12.7	10.5	4.3	65.2	40.5
YCTY	*Tyrannulus elatus*	Invertivore	Shrubland	3	7	8.3	3.2	48.2	40.7
YOFL	*Tolmomyias sulphurescens*	Invertivore	Forest	1	14.3	13.4	5.4	63	55.5

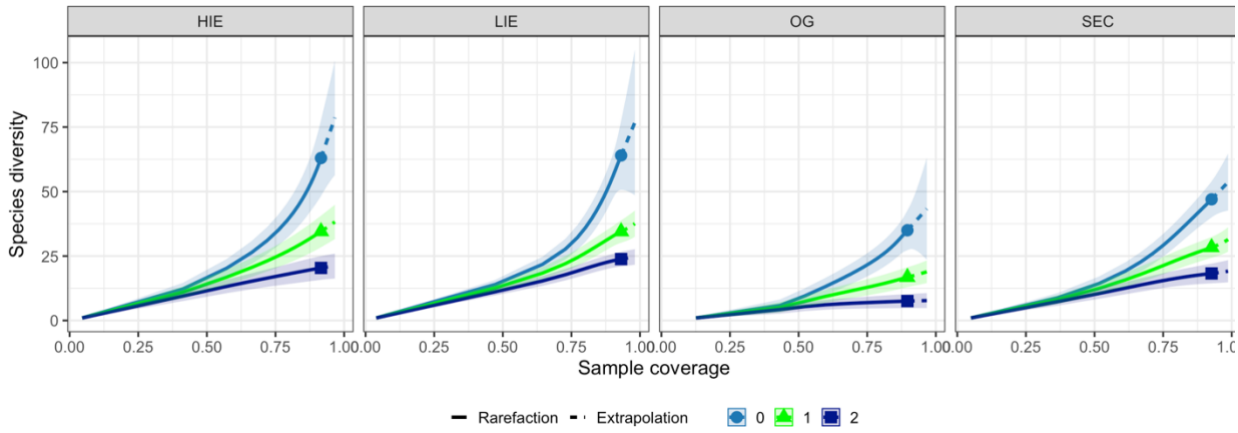


Supplementary Figure 2: Examples of forest structure within each stage of forest regeneration sampled, including A) highly impacted early successional vegetation, B) low impact early successional vegetation, C) secondary forest, D) old growth Chocó Rainforest.

A)



B)



Supplementary Figure 3: Sampling completeness curves across four habitat types, representing different stages of regeneration and old-growth forest. The curves are color-coded: purple for 2 years of regeneration, blue for 10 years, pink for 25 years, and green for old-growth forest. A) Displays the overall sample coverage between sites where all plots within each habitat type are aggregated together, while B) examines the hill numbers/species diversity within each plot, where q = 0 (species richness), q = 1 (Shannon Diversity), and q = 2 (inverse Simpson).

Supplementary Table 3: Type II Wald chi-square tests assessing diversity indices as a function of regeneration stage (HIE, LIE, SEC, OG). Generalized least squares (GLS) regression was used to account for spatial dependence in model residuals, with a Gaussian spatial correlation structure applied. Significant relationships ($p < 0.05$) are highlighted in bold.

Response Variable	Chi Squared	P- Value
Species Richness (Q0)	34.44	**< 0.001**
Shannon Entropy (Q1)	79.32	**< 0.001**
Inverse Simpson Index (Q2)	25.66	**< 0.001**
Functional Richness (FRic)	11.46	**0.001**
Functional Divergence (FDiv)	14.27	**0.002**
Functional Evenness (FEve)	4.42	0.22
Functional Dispersion (FDis)	35.60	**< 0.001**
Rao's Quadratic Entropy (RaoQ)	20.98	**< 0.001**

Chapter 3: Seed dispersal networks restructure to become more specialized across tropical forest regeneration, northwest Ecuador

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Abstract

Restoring interactions between frugivorous animals and fruiting plant species is pivotal for reestablishing community structure and ecosystem functions in regenerating tropical forests. Seed dispersal networks provide a framework for understanding how interactions change during regeneration, where network-level measures such as nestedness and modularity can describe patterns of resilience in interactions against disturbances. However, the reassembly of interactions between frugivorous animals and fruiting plant species as a function of forest regeneration remains poorly understood. In this study, we investigated how seed dispersal networks reassemble across regenerating forests in the Chocó Rainforest of northwestern Ecuador. Using a combination of mist-netting and camera trap surveys, we sampled seed dispersal interactions across four stages of forest regeneration: highly impacted pastures, early successional vegetation, secondary forests, and old-growth Chocó rainforest. We built quantitative networks of observed interactions between fruiting plants and seed dispersing animals and then extracted key network-level metrics including specialization, nestedness, modularity, and interaction frequency. We found that early successional habitats 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, with substantial interaction loss and rewiring between regeneration stages. This shift in interactions led to the emergence of more complex and structured seed dispersal networks in mature forests, as they shifted from loosely connected, generalist dominated systems in early successional habitats to more specialized and modular interactions in mature forests. Our results highlight how the complexity of mutualistic interactions between seed-dispersing animals and plants increases during natural regeneration within secondary forests, potentially enhancing ecosystem functions in these highly threatened systems.

Introduction

Species interactions are critical to ecosystem stability and resilience, driving key ecosystem functions such as seed dispersal, carbon sequestration, and energy flows (Akçakaya et al., 2020; Brockerhoff et al., 2017; Chanthorn et al., 2019). 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 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; 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 (Arroyo-Rodríguez et al., 2017; De La Peña-Domene et al., 2014; Martínez-Ramos et al., 2016; Wandrag et al., 2017; Wunderle, 1997). 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, mutualistic networks 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). Furthermore, modular networks are considered stable as modules (subgroups that form within a network) can contain the impacts of species extinctions, minimizing network-level impacts (Krause et al. 2003; Teng & McCann 2004). Modularity is also useful in separating functional groups or diet guilds within a network (Guimerà & Amaral 2005; Mello et al. 2011). Examining the extent to which these networks retain or transform their structure through succession can provide key insights into the ecological processes shaping forest regeneration and inform restoration strategies aimed at restoring both biodiversity and ecosystem functions (Estrada-Villegas et al., 2023; Howe, 2016).

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 and modularity, 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 (Bastazini et al., 2019; Bomfim et al., 2018; 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 how seed dispersal interactions change as a function of forest regeneration, 2) Evaluate the extent to which seed dispersal networks retain or change their structure through stages of forest regeneration, and 3) Determine how forest regeneration influences network-level measures of seed dispersal networks. We hypothesized that seed dispersal interactions change as a function of forest regeneration, where network stability increases as forest succession progresses (Ribeiro da Silva et al., 2015). 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; Fründ et al., 2010; Mello et al., 2011; 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), an ecological reserve situated within the broader Mache-Chindul 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 hectares (ha) of humid Chocó rainforest, wetlands, and waterways within the Rio Esmeraldas drainage basin, though it faces significant deforestation pressures (Durães et al., 2013; Kleemann et al., 2022; Van Der Hoek, 2017). The FCAT reserve currently covers 656 hectares, with elevations ranging from 350 to 550 meters (m) above sea level (asl). It experiences a wet season from January to June and a dry season from July to December.

The study's research design incorporated plots representing four different stages of forest regeneration: (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, which experienced minimal recent human activity (e.g., low-intensity selective logging) and surrounds all other plot types. Sampling was conducted in five replicates across each of the four regenerating forest categories, totaling 20 plots. Plots were randomly distributed within each treatment across the FCAT reserve, with a minimum spacing of 100 meters (m) between each.

Surveying for fruit frugivore interactions

We sampled for seed dispersal interactions May-August in 2022 and 2023 to coincide with the dry season and to include resident bird species rather than migratory species. A combination of phytocentric and zoocentric sampling approaches is thought to be the best

mechanism for sampling seed dispersal interactions (Jordano, 2016; Lussier et al., 2024; Vitorino et al., 2022). Therefore, we established a series of multi-strata camera traps on focal fruiting species to observe frugivorous mammals, while also conducting mist-netting surveys for frugivorous birds. Camera traps (n=25, *Meidase P70 Trail Cameras*, 64MP 1296p HD videos) were opportunistically positioned throughout each plot within each regeneration stage. We conducted fruiting plant surveys to identify areas with a high diversity and abundance of ripe fruits to maximize potential observations of fruit-frugivore interactions (Selwyn et al., 2020). Single camera traps were focused on ripe fruit for ten days each at varying heights, including ground level on fallen fruits and seeds, understory level on fruiting shrubs and low hanging fruit, mid-story on medium-large fruiting tree species, and at higher canopy levels on overstory fruiting species. We programmed the cameras to 24-hour video mode with medium sensitivity to record seed dispersal interactions throughout the day and night. This allowed us to record actual frugivory events, rather than assuming frugivory or seed dispersal from photos. To prevent false triggers, the vegetation was cleared in a 1-square meter area around ground-level cameras, and stray branches or vegetation in reach of mid-level cameras were also removed (Campos et al., 2018). Cameras were placed in one regeneration stage for a total of ten days before being rotated to another. This accumulated 19,200 hours of camera trap sampling in total, or 800 sampling days, with 4800 hours, or 200 days in each plot.

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 twenty-four-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 successional stage for two days at a time. Nets were open 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 were identified only to genus or morphotype, which is representative of an individual plant species. Fieldwork was conducted with MAATE permission (*Ministerio del Ambiente, Agua y Transición Ecológica*) under permit number: MAATE-ARSFC-2022-2589.

Statistical analyses

All statistical analyses and models were fitted in R (Version 2023.09.1 + 494) (R Core Team, 2022). To examine seed dispersal interactions across forest regeneration, frugivorous birds and mammals were first matched with the respective fruiting plant species-based camera videos and scat depositions. We combined interactions from camera traps and mist-netting data across the season to create a weighted interaction matrix for each individual replicate (n=5 per regeneration stage), as well as a pooled interaction matrix representing each overall stage of forest succession. We then converted the weighted interaction matrices into bipartite networks using the bipartite package in R (Dormann et al., 2008).

To examine how seed dispersal interactions change as a function of forest regeneration, we calculated interaction frequency, interaction diversity, and the effective number of interactions for each sampling plot using the bipartite package in R (Dormann et al., 2008). For these measurements, we treated each replicate (n=5) as a bipartite network. Interaction frequency was calculated from the total number of recorded plant-disperser interactions per plot (Chacoff et al., 2018). Interaction diversity is defined as a measure of the diversity of interactions between two different groups, indicating how evenly distributed the connections are across all possible pairings within the network (Dormann et al., 2008). Interaction diversity was calculated using the "Shannon diversity (H')" measure with the network-level function in the bipartite package. The effective number of interactions is a value that represents the average number of interactions each node has, considering the uneven distribution of connections across all nodes, providing a more informative measure than simply counting raw interaction numbers (Blüthgen et al., 2008). This was calculated by exponentiating the Shannon diversity values. For each interaction variable, we performed an analysis of variance (ANOVA) in R with plot type as the predictor variable to test for overall differences among plots. To identify pairwise differences between plot types, we conducted a Tukey's Significant Difference test on the ANOVA results.

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 (Timoteo et al., 2018). To calculate edge overlap, we created an edge list where each row represented an observed interaction between a disperser species and a fruiting plant species, which was then separated by regeneration stage. We then transformed each edge list into a set of unique species interactions by concatenating species pairs into a string format. From this edge list, we calculated overlap density as the ratio of shared interactions to total interactions, which provided a measure of network similarity (Timoteo et al., 2018). We then constructed an overlap matrix, where rows and columns corresponded to the four forest regeneration stages, and calculated the edge overlap between each stage. This was a standardized measure of interaction similarity, ranging from 0 (no shared interactions) to 1 (identical networks).

To determine how forest regeneration influences the complexity and stability of seed dispersal networks, we used the network-level function within the bipartite package to calculate network-level indices including connectance, specialization, nestedness, and modularity for networks of interactions pooled over time representing each stage of forest regeneration. Connectance is a measure of the proportion of realized interactions among all possible interactions within a network and decreases with increasing network size (Jordano, 1987). Connectance ranges from a value between 0-1, where 1 indicates that all possible interactions are realized. We extracted values using the "connectance" measure from the species-level function in the bipartite package in R. Specialization was extracted using the "H2′" measure from the network-level function, which is measure of complementarity specialization and characterizes the degree or partitioning among dispersers and plant species in the entire network (Blüthgen & Klein, 2011). This measure indicates the extent to which observed interactions deviate from those that would be expected given the species marginal totals, where random associations between species would have a lower value (0), and a network with only exclusive interactions would indicate a higher value (1) (Blüthgen & Klein, 2011).

Nested structure is characterized by (i) a "core" group of generalist disperser or plant species that interact extensively with one another and drive most of the interactions, (ii) specialist species with relatively few interactions that predominantly interact with generalists, and (iii) minimal interaction between specialist species (Bascompte et al., 2003; Ribeiro da Silva

et al., 2015). We quantified nestedness using the "nestedness" index from the network-level function within the bipartite package in R. Nestedness measures fall on a scale from 0 to 100, with higher values indicating stronger nestedness (Almeida-Neto & Ulrich, 2011). Modularity measures the extent to which interactions in the network are organized into clusters or tightly interacting cohesive subgroups within the larger network. To assess modularity in our bipartite networks, we utilized the "Q'" modularity measure (Dormann & Strauss, 2014) tailored specifically for bipartite structures. Modularity (Q') reflects the degree to which species interactions are compartmentalized into distinct modules, where interactions within modules are more frequent than expected by chance. Q' values range from 0 (indicating a low number of modules) to 1 (indicating a strong modular structure suggesting a greater degree of functional compartmentalization in the network).

To test whether the networks were significantly more modular, nested, or specialized than expected by random, we generated 100 null networks for each regeneration stage based on our four observed seed dispersal networks (Emer et al., 2020; Olesen et al., 2007). For randomly generated networks, we kept connectance and the number of interacting species constant using the vaznull model in R (Dormann et al., 2008, 2009). This model is conservative because it preserves marginal totals (i.e. takes account of interaction abundance) and keeps network connectance constant. Thus, differences between the null models and real networks represent the role of interactions between specific pairs of species in defining network attributes. To assess whether observed network-level measures differed significantly from random expectations, we computed z-scores and p-values by comparing observed values to null model distributions.

Results

Over two years, we captured 1240 individual birds in mist nets **(Supplementary Table 4**), resulting in 275 fecal samples, of which about 42% (115) had intact seeds. Furthermore, we observed 719 individual animals from our camera traps **(Supplementary Table 5)**, of which approximately 23% (163) included an observed seed dispersal interaction, and only these data were used to form networks. When pooling these data, we documented 465 realized seed dispersal interactions across all regeneration stages between 68 frugivorous animal species and 104 fruiting plant species (**Figure 8**). Birds were responsible for 66% of interactions overall and made up 70% of interactions in earlier stages of forest regeneration (PA and ES). However, in old growth forests, birds were responsible for 56% of the interactions, and the remaining 44% were

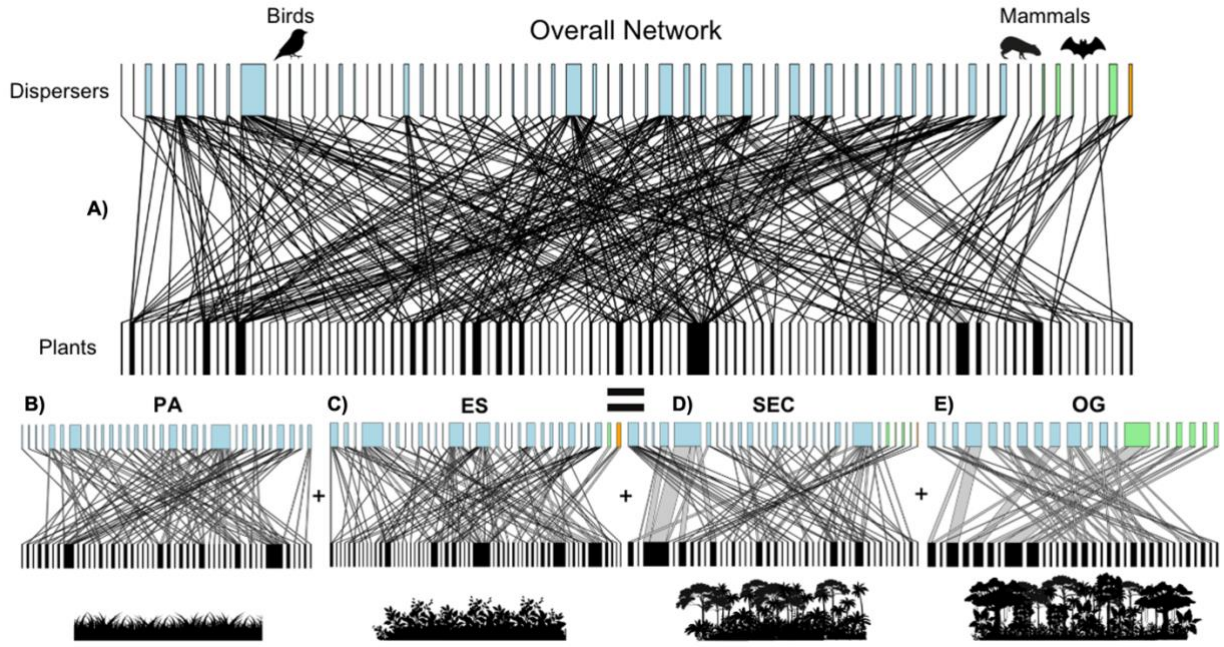

Figure 8: Quantitative seed dispersal network for the FCAT system (A), with four subnetworks (B) representing each of the four sampled stages of forest regeneration (PA = highly impacted pasture, ES = low impact early successional vegetation, SEC = secondary forest, and OG = old growth Chocó Rainforest). 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.

from mammal dispersers. We did not observe differences in animal ($r_s = 0.18$, p=0.07) or plant ($r_s = 0.21$, p=0.06) species richness across the regeneration gradient. However, the Shannon diversity of both realized dispersers ($r_s = 0.22$, p=0.05) and plants observed in interactions ($r_s = 0.23$, p=0.05) did differ, where disperser diversity was highest in ES habitats and plant diversity was highest in PA habitats.

Interaction patterns differed as a function of forest regeneration **(Figure 9**). Both interaction diversity ($r_s = 0.23$, p = 0.05) and the effective number of interactions ($r_s = 0.23$, 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, the highest in early successional vegetation and Interaction patterns differed as a function of forest regeneration (Fig. 2). Interaction frequency was, on average, highest in early successional vegetation and decreased with forest regeneration ($r_s = 0.33$, p = 0.01). We did not detect any pairwise differences between early stages of forest regeneration (ES) and secondary forests (SEC); however, we observed that interaction frequency, diversity and the effective number of interactions differed between early successional stages (PA and ES) and old growth forests (OG) (**Supplementary Figure 4**).

Seed dispersal networks rewired across stages of forest regeneration (**Figure 10**). 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 forests shared 42% of interactions. However, there were fewer shared interactions between early stages of regeneration and late stages of regeneration; less than 17% 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.

The overall structure of seed dispersal networks differed across stages of forest regeneration (**Table 6**). Younger stages of regeneration were not nested, modular, or specialized, and ES habitats were less connected than predicted by null model distributions. Networks in more mature forests also exhibited lower connectance than expected but were more specialized. Secondary forests had modular networks relative to null models, exhibiting stronger structural compartmentalization than other habitats. Old growth forests were the only nested networks comparable to null models, indicating that interactions in mature forests were structured around a core set of generalist plant or disperser species where specialists interacted primarily within this core group of generalists.

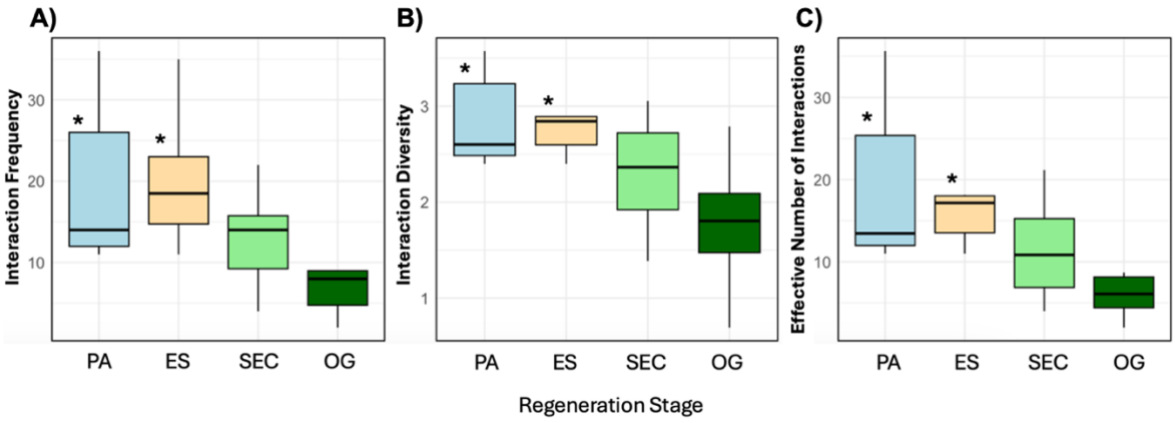

Figure 9: Interaction frequency (A), interaction diversity (B), and the effective number of interactions (C) across four stages of forest regeneration (PA = highly impacted pasture, ES = low impact early successional vegetation, SEC = secondary forest, and OG = old growth Chocó Rainforest). Asterisks (*) represent significant differences ($p < 0.05$) from old growth forests (OG).

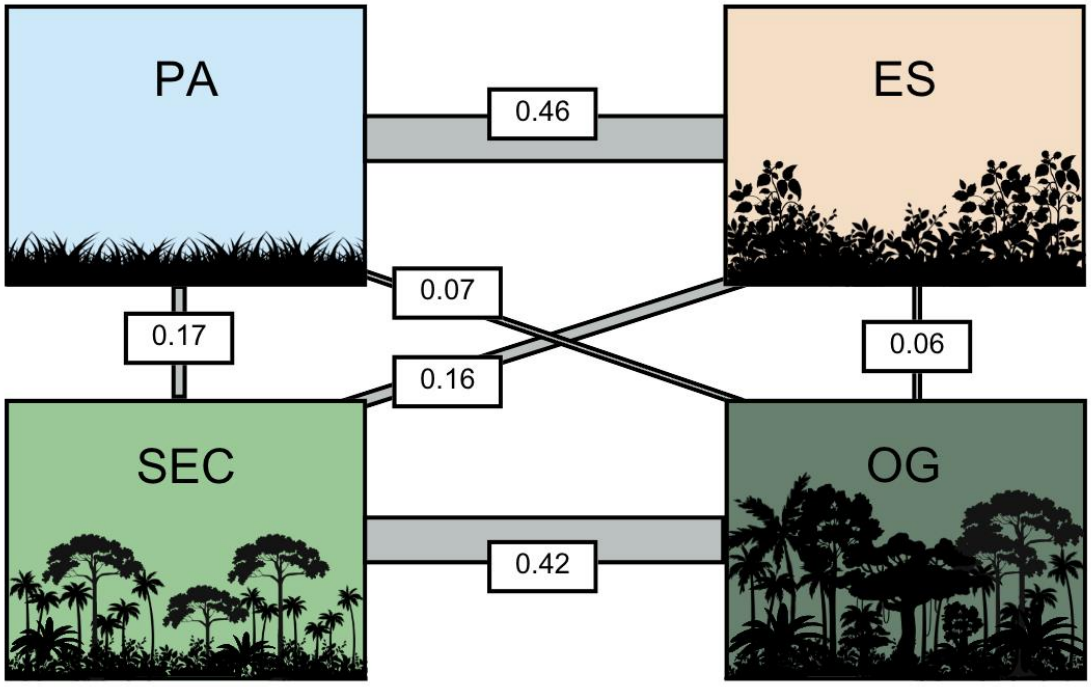

Figure 10: The proportion of shared links across habitats ('edge overlap') between each regeneration stage. The widths of the grey lines between each stage are proportional to the correlation of shared links between each pair. Higher values represent a higher proportion of shared links between networks.

Table 6: Summary of network-level metrics across four forest regeneration stages (PA = highly impacted pasture, ES = low impact early successional vegetation, SEC = secondary forest, and OG = old growth Chocó Rainforest). 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 ($p < 0.05$). Significant results are denoted with an asterisk (*)

Stage	Measure	Nestedness	Specialization	Connectance	Modularity
PA	**Observed**	9.01	0.12	0.07	0.61
	Null Mean	2.00	0.12	0.07	0.59
	Null SD	0.57	0.01	0.001	0.02
	Z Score	0.39	-0.17	-0.63	0.62
	P-Value	0.67	0.86	0.52	0.53
ES	**Observed**	8.04	0.31	**0.07***	0.51
	Null Mean	7.18	0.31	0.09	0.51
	Null SD	1.37	0.03	0.002	0.03
	Z Score	-0.79	0.026	-7.96	0.05
	P-Value	0.42	0.79	< 0.001*	0.96
SEC	**Observed**	6.72	**0.45***	**0.06***	**0.66***
	Null Mean	0.65	0.32	0.08	0.57
	Null SD	1.30	0.04	0.002	0.04
	Z Score	0.15	3.07	-6.40	2.51
	P-Value	0.89	0.002*	< 0.001*	0.01*
OG	**Observed**	**20.67***	**0.64***	**0.08***	0.76
	Null Mean	13.10	0.52	0.12	0.72
	Null SD	2.85	0.03	0.003	0.04
	Z Score	2.66	3.51	-10.27	1.00
	P-Value	0.008*	<0.001*	<0.001*	0.31

Discussion

As global efforts are underway to prioritize tropical forest restoration (UN 2021), understanding how seed dispersal interactions reassemble may elucidate the role of mutualistic interactions in facilitating forest regeneration. Ecosystem resilience is often defined as a system's ability to recover its structure and function following disturbance. In our system, early stages of forest regeneration had both high frequency and diversity of seed dispersal interactions, which decreased as regeneration progressed. As forests transitioned from early successional habitats into mid-successional stages (secondary forests), seed dispersal interactions underwent major restructuring, defined here as the loss, gain, and replacement of interactions that alter overall network organization. From this rewiring of interactions, seed dispersal networks shifted from loosely connected, generalist dominated systems in early successional habitats to more specialized and structured networks in mature forests. However, secondary forests still 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.

In our system, 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. 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 (Gonçalves Da Silva et al., 2020; Pinotti et al., 2012). We observed a high presence of small generalist frugivorous birds in earlier stages of forest regeneration, which could be responsible for facilitating high numbers of interactions (Emer et al., 2018; W. 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 forests fragments (González-Varo et al., 2017). These interaction hubs may also be critical in shaping successional pathways for regenerating tropical forests.

Seed dispersal networks underwent substantial restructuring across forest regeneration stages, 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 (Mortelliti & Lindenmayer, 2015; Chesson 2000). 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.

One possible driver of this reorganization is disperser turnover, 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 additionally 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. 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.*

Though early stages of regeneration exhibited high interaction frequencies, they did not differ from null expectations and lacked patterns of connectivity, specialization, modularity, and nestedness. The lack of realized interaction patterns suggests high interaction redundancy and generalized dispersal dynamics, where dispersers interact broadly with plant species in an

unstructured manner (Emer et al., 2020). In contrast, the restructuring of seed dispersal networks across regeneration stages led to the emergence of specialized and modular networks in secondary forests, suggesting a shift toward more distinct species groups and interaction compartments with species beginning to form more exclusive relationships. Modularity is a key structural feature of ecological networks, promoting stability by buffering disturbances within interaction compartments and reducing the spread of disruptions across the entire network (Newman, 2006; Olesen et al., 2007; Ribeiro Mello et al., 2011).

The emergence of modularity in secondary forests may indicate increasing ecological stability, as functionally cohesive species groups become more established and organize into more resilient structures, potentially supporting long-term ecosystem persistence. This is further supported by the observed nested pattern in old growth forests, indicating that a core group of generalist dispersers interacts with many plant species, while specialists maintain more selective interactions (Almeida-Neto & Ulrich, 2011). A nested structure is characteristic of stable, well-integrated networks, where interaction redundancy enhances resilience to species loss (Bascompte et al., 2003; Sebastian-Gonzalez et al., 2015). 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). As a result, the highest levels of specialization were also observed in mature forests. The co-occurrence of these patterns suggests that dispersal networks in later successional stages have greater functional stability and resilience compared to younger forests.

Overall, our findings demonstrate that while early successional forests may serve as important interaction hubs 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, continuously reorganizing 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. Finally, while regenerating secondary forests within our system were highly specialized and modular, nested patterns of interactions found in old growth reference conditions may take longer to recover. Future research should aim to identify the mechanisms driving the reassembly of seed dispersal networks and pinpoint key species that act as catalysts

for forest regeneration. A deeper understanding of these processes will be essential for developing effective conservation and restoration strategies that promote both biodiversity and ecosystem resilience.

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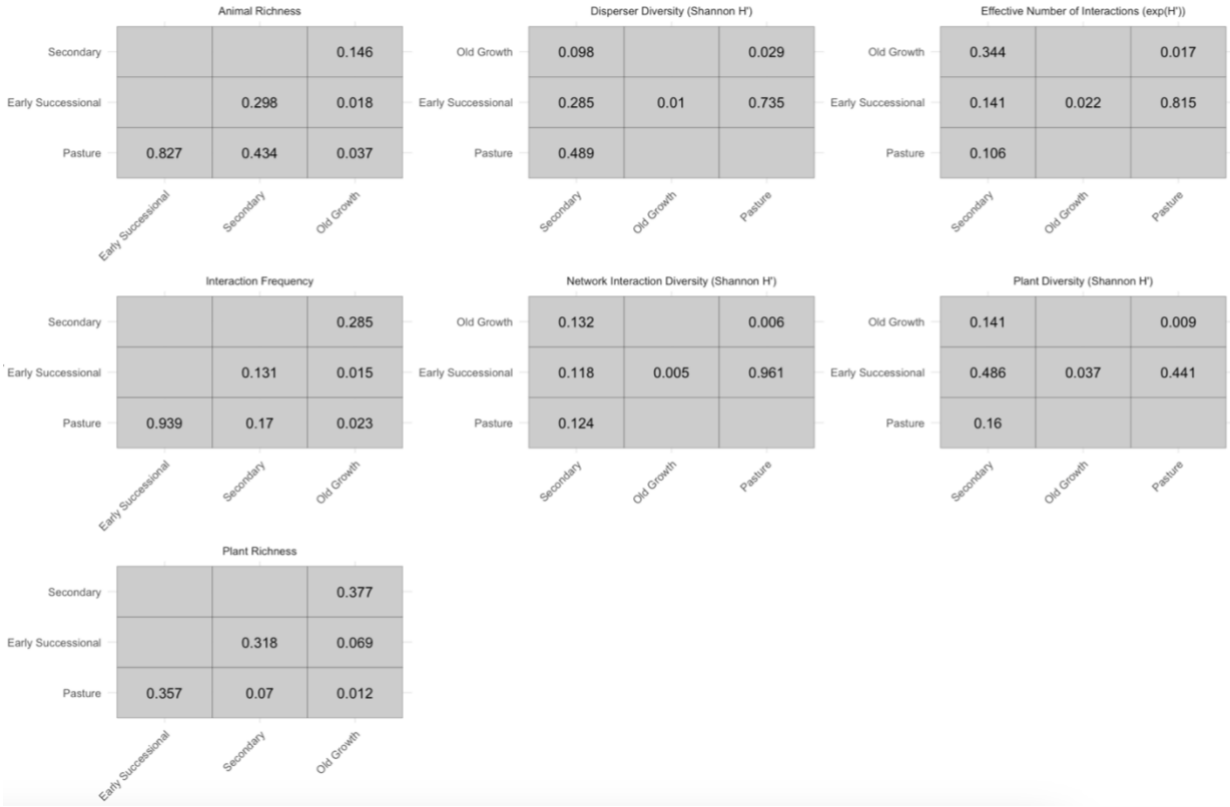
Appendix



Supplementary Figure 4: Results of Tukey pairwise comparisons between stages of forest regeneration for varying network-level measures represented by p-values.

Supplementary Table 4: Disperser species captured within mist-nets with realized interactions included in network analysis.

Common Name	Scientific Name	Interaction Abundance
Bananaquit	*Coereba flaveola*	12
Band-tailed Barbthroat	*Threnetes ruckeri*	2
Bay-headed Tanager	*Tangara gyrola*	6
Black-crowned Antshrike	*Thamnophilus atrinucha*	2
Black-faced Dacnis	*Dacnis lineata*	2
Blue-black Grosbeak	*Cyanoloxia cyanoides*	3
Blue-capped Manakin	*Lepidothrix coronata*	14
Blue-gray Tanager	*Thraupis episcopus*	5
Blue-necked Tanager	*Stilpnia cyanicollis*	6
Bright-rumped Atilla	*Attila spadiceus*	4
Buff-rumped Warbler	*Myiothlypis fulvicauda*	6
Buff-throated Foliage Gleaner	*Automolus ochrolaemus*	1
Buff-throated Saltator	*Saltator maximus*	9
Chivi Vireo	*Vireo chivi*	17
Choco Manakin	*Cryptopipo litae*	4
Choco Tyrannulet	*Zimmerius albigularis*	5
Cinnamon Becard	*Pachyramphus cinnamomeus*	1
Collared Aracari	*Pteroglossus torquatus*	2
Dull-colored Grassquit	*Asemospiza obscura*	6
Ecuadorian Thrush	*Turdus maculirostris*	9
Flame-rumped Tanager	*Ramphocelus flammigerus*	21
Golden-bellied Warbler	*Myiothlypis chrysogaster*	1
Green Honeycreeper	*Chlorophanes spiza*	4
Large-billed Seed Finch	*Sporophila crassirostris*	1
Northern Schiffornis	*Schiffornis veraepacis*	7
Olivaceous Piculet	*Myiotriccus ornatus*	3
Olive-crowned Yellowthroat	*Geothlypis semiflava*	3
Olive-striped Flycatcher	*Mionectes olivaceus*	7
Orange-bellied Euphonia	*Euphonia xanthogaster*	24
Orange-billed Sparrow	*Arremon aurantiirostris*	5
Orange-crowned Euphonia	*Euphonia saturata*	3
Ornate Flycatcher	*Myiotriccus ornatus*	1
Pacific Antwren	*Myrmotherula pacifica*	2
Pacific Parrotlet	*Forpus coelestis*	2
Red-capped Manakin	*Ceratopipra mentalis*	10

Supplementary Table 4 Continued.

Rufous Piha	*Lipaugus unirufus*	3
Rufous-tailed Hummingbird	*Amazilia tzacatl*	1
Scaly-breasted Wren	*Microcerculus marginatus*	2
Slaty Antwren	*Myrmotherula schisticolor*	1
Slaty Spinetail	*Synallaxis brachyura*	2
Smooth-billed Ani	*Crotophaga ani*	2
Southern Beardless Tyrannulet	*Camptostoma obsoletum*	2
Spotted Woodcreeper	*Xiphorhynchus erythropygius*	1
Tawny-crested Tanager	*Tachyphonus delatrii*	1
Thick-billed Euphonia	*Euphonia laniirostris*	37
Thick-billed Seed Finch	*Sporophila funerea*	5
Variable Seedeater	*Sporophila corvina*	7
White-bearded Manakin	*Manacus manacus*	16
White-whiskered Puff Bird	*Malacoptila panamensis*	2
Yellow-bellied Seedeater	*Sporophila nigricollis*	8
Yellow-bellied Seed Finch	*Sporophila nigricollis*	1
Yellow-bellied Siskin	*Spinus xanthogastrus*	1
Yellow-crowned Tyrannulet	*Tyrannulus elatus*	1

Supplementary Table 5: Disperser species observed on camera traps with realized interactions included in network analysis.

Common Name	Scientific Name	Interaction Abundance
Black-winged Saltador	*Saltator atripennis*	4
Blue-gray Tanager	*Thraupis episcopus*	4
Blue-necked Tanager	*Stilpnia cyanicollis*	5
Buff-throated Saltator	*Saltator maximus*	4
Central American agouti	*Dasyprocta punctata*	16
Central American Wooly Possum	*Caluromys derbianus*	1
Choco Toucan	*Ramphastos brevis*	19
Collared Aracari	*Pteroglossus torquatus*	27
Dull-colored Grassquit	*Asemospiza obscura*	3
Ecuadorian Thrush	*Turdus maculirostris*	2
Flame-rumped Tanager	*Ramphocelus flammigerus*	5
Lowland Paca	*Cuniculus paca*	4
Orange-bellied Euphonia	*Euphonia xanthogaster*	6
Orange-Billed Sparrow	*Arremon aurantiirostris*	1
Pacific Antwren	*Myrmotherula pacifica*	3
Pallid Dove	*Leptotila pallida*	1
Purple Quail Dove	*Geotrygon purpurata*	5
Red-tailed Squirrel	*Sciurus granatensis*	1
Roufous Motmot	*Baryphthengus martii*	2
Roufous-fronted Wood Quail	*Odontophorus erythrops*	1
Rufous Mouse Opossum	*Marmosa lepida*	8
Smooth-billed Ani	*Crotophaga ani*	4
South American Coatimundi	*Nasua nasua*	3
South American Raccoon	*Procyon cancrivorus*	1
Tayra	*Eira barbara*	2
Thick-billed Euphonia	*Euphonia laniirostris*	12
Unknown Bat Species	*Chiroptera*	7
Variable Seedeater	*Sporophila corvina*	4
White-Bearded Manakin	*Manacus manacus*	5
Yellow-bellied Seedeater	*Sporophila nigricollis*	3

Conclusion

Major Findings

Tropical forests are among the most biodiverse ecosystems on Earth, yet they are growing increasingly threatened by deforestation and habitat degradation. As efforts to restore these ecosystems remain a global conservation priority, understanding how biodiversity and ecological interactions recover is essential for informing effective conservation and management strategies. To address these challenges, this work examined functional diversity measures and seed dispersal networks across varying stages of tropical forest regeneration, along with their potential applications to advance restoration practices. This research is structured into three chapters, (i) synthesizing current knowledge on seed dispersal networks in tropical forests, (ii) evaluating the effectiveness of functional diversity measures in tracking faunal community recovery, and (iii) analyzing the reassembly of seed dispersal interactions across successional gradients. Together, these studies contribute to a broader understanding of how species interactions and functional traits can inform restoration strategies, ultimately advancing efforts to rebuild resilient and self-sustaining tropical forests.

Restoring ecological interactions is a key priority for effective forest restoration. Frugivore-plant interactions play a central role in shaping community structure and ecosystem functions, making their restoration a crucial component of tropical forest recovery. Therefore, the goal of chapter one was to better understand how seed dispersal interactions could be utilized to advance tropical forest conservation and restoration. Specifically, we examined (i) major patterns and findings in studies utilizing ecological networks to examine seed dispersal in the tropics with implications for conservation and/or restoration, (ii) biases in applying ecological networks to interactions and restoration initiatives, and (iii) current knowledge gaps and future directions for the field. To answer these major components, we conducted a systematic literature review with a specific focus on how studies could relate to conservation and restoration.

Our findings from chapter one emphasizes that, from a restoration perspective, prioritizing highly connected, species-rich seed dispersal networks may be beneficial in early successional stages, while more stable interaction patterns such as nestedness, specialization, and modularity may be important priorities for secondary forest systems. We also found that utilizing a singular sampling approach for measuring seed dispersal interactions (i.e. phytocentric or zoocentric) could lead to potential biases in resultant network measures. For example, zoocentric

(animal-based) sampling approaches yielded the lowest levels of network richness and the highest levels of specialization, whereas a combination of both types of methodologies resulted in the largest networks with a higher presence of generalist interactions. This integrated approach allows for a more comprehensive understanding of how dispersal interactions reassemble throughout succession. We suggest that future work should focus on elucidating the effects of different restoration techniques on seed dispersal network reassembly to develop effective and context-specific restoration strategies.

As restoring biodiversity remains a central goal of ecological restoration, accurately assessing community recovery remains a significant challenge. Functional diversity indices offer promising insights into how functional roles within communities recover with forest regeneration, yet the effectiveness of individual measures for reliably predicting changes in communities is not fully understood. Therefore, our goal for chapter two was to assess functional diversity measures of understory bird communities to determine their applicability to community assessments in regenerating forests. Specifically, we compared the relationship between taxonomic and functional diversity measures of understory bird communities in relation to forest regeneration stage and vegetation structure across regenerating forests in the Chocó Rainforest of Northwest Ecuador. In addition to vegetation structure and regeneration stage, we also examined how morphological traits contributed to the changes in functional diversity indices.

The findings from chapter two revealed an inverse relationship between taxonomic and functional diversity measures across forest regeneration stages. While bird species richness, diversity, and functional richness peaked in early successional, open canopy habitats due to an influx of generalist species, late successional, closed canopy habitats were characterized by increases in functional dispersion, functional divergence, and Rao's quadratic entropy. These changes were primarily driven by shifts in beak and wing length. Furthermore, I showed that not all functional diversity indices are equally indicative of forest regeneration. Functional dispersion, functional divergence, and Rao's quadratic entropy emerged as more reliable indicators of faunal community recovery compared to other measures because they were associated more strongly with closed canopy systems indicative of later stages of forest succession. Therefore, these indices could serve as valuable tools for restoration practitioners seeking to assess forest recovery without relying solely on taxonomic surveys. Future research

should refine these metrics by testing their applicability across different ecosystems and taxa, as well as integrating them with remote sensing technologies for broader-scale monitoring.

Similarly to biodiversity recovery, successful forest restoration is also predicated on the recovery of species interactions and ecosystem functions. Understanding how fruit-frugivore relationships reassemble in the context of seed dispersal can provide an invaluable tool for addressing conservation and ecosystem restoration. Knowledge of seed dispersal processes and interactions post-disturbance can be used to accelerate the recovery of degraded areas by highlighting which species should be targeted for restoration efforts. Therefore, in chapter three I examined the reassembly of seed dispersal interactions across regenerating forest fragments in the Chocó Rainforest of Northwest Ecuador. Here, I utilized avian mist-netting and camera trap observations to survey for seed dispersal interactions across regenerating forests. I then used these observed interactions to build weighted bipartite networks for varying stages of regeneration, and then compared network measures such as nestedness, specialization, connectance, and modularity to assess changes in interactions across regeneration types.

Findings from chapter three highlighted how seed dispersal networks undergo substantial restructuring across successional stages, with interaction loss and replacement occurring as forests mature. Early-successional forests support a high diversity and frequency of dispersal interactions, whereas mid- and late-successional forests exhibit increased network specialization and modularity. These findings suggest that the high interaction diversity in early succession may serve as a foundation for long-term ecosystem resilience by facilitating species establishment and connectivity. Over time, the development of more specialized dispersal networks may contribute to the structural and functional stability of forest communities.

Limitations

Chapter one may be affected by publication and language biases. Studies published in non-English languages or less accessible regional journals may have been underrepresented, potentially excluding valuable case studies from the global South. Additionally, most network studies reviewed were based on short-term datasets and conducted in specific geographic regions, which limited the generalizability of patterns across tropical forest ecosystems. The reliance on published network metrics also introduces bias, as many studies apply different sampling efforts, analytical frameworks, and interaction definitions, which may compromise cross-study comparability.

In chapter two, we used functional diversity indices to evaluate community recovery. However, these indices are sensitive to trait selection and the availability of trait data. We primarily utilized morphological traits of understory birds, which may not fully capture the breadth of ecological functions performed by these species. Behavioral traits, such as cavity nesting or habitat preference, were not included in analyses; therefore, functional diversity metrics were potentially biased. Furthermore, due to discrepancies in field sampling for morphological traits, we relied on a generalized open-access data set to quantify traits for each species observed, which may not account for intraspecific variation or local adaptations. This study also assumes that vegetation structure and regeneration stage are the primary drivers of diversity patterns, but other environmental variables, such as microclimate, disturbance history, landscape connectivity, and specific measures of remnant vegetation structure, were not explicitly included. These unmeasured factors may have contributed to or explained our observed patterns better than those considered.

Additionally, mist-netting and camera trapping methodologies used in chapters two and three may be subject to detection biases, leading to skewed results within closed-canopy habitats. Mist nets are known to under-sample canopy species and highly mobile birds. In contrast, camera traps on focal plant species lead to a bias in species selection, potentially causing incomplete interaction networks and underestimation of network complexity in some forest types. The data collection for chapters two and three also took place across a shortened field season (June-August) and, therefore, did not capture the scope of migratory species that could utilize this ecosystem at varying times of the year. Migratory species could significantly shape avian community dynamics and alter seed dispersal patterns across seasons. Finally, while bipartite network metrics offer valuable indicators of community structure, their ecological interpretation remains debated. Many metrics, such as modularity and nestedness, are sensitive to network size and sampling intensity. There are also many limitations to using null models to test for network-level patterns. They do not allow for direct comparisons of networks across habitats but only highlight if observed network-level patterns differ from randomly associated interactions.

Future work

Ultimately, this work highlights the potential of functional diversity and seed dispersal network measures as powerful tools in understanding community assembly and species

interactions in regenerating tropical forests. Future work should focus on identifying keystone species that play essential roles in shaping forest regeneration. For example, practitioners can ensure the abundance and persistence of species of frugivores that are critical for seed dispersal across degraded landscapes or plant species that act as attractants to frugivorous animal species. Functional traits of frugivorous birds can also have an impact on their role within seed dispersal networks; thus, understanding how these traits influence network structure can inform strategies that aim to maintain and enhance seed dispersal by frugivorous birds. Additionally, incorporating long-term datasets, chronosequences, and large-scale spatial studies will be crucial for understanding how these networks reassemble across greater spatial and temporal scales. By addressing these research gaps, we can move toward a more holistic approach to tropical forest restoration that prioritizes both biodiversity conservation and the restoration of essential ecosystem functions.

Vita

Nicole Lussier was born in Providence, Rhode Island where she spent her childhood and early adulthood. She attended North Providence Highschool and graduated in May of 2016. Shortly after, she enrolled at Wheaton College in Massachusetts as an undergraduate student where she majored in Biology and minored in Animal Behavior. At Wheaton, Nicole developed a love for ecology and ornithology and held several internships including one at Southwick's Zoo in Mendon MA. She also participated in multiple study abroad programs, studying wildlife conservation in Tanzania with the School of International Training, biodiversity and tropical ecology in Costa Rica and Belize, and working under Dr. Jessie Knowlton on a long-term bird banding project in the high Andes Mountains of Southern Ecuador. In the summer of 2019 while working in Ecuador with Dr. Knowlton, she began field work for her honors thesis titled "Mixed species bird flocks in the high Andes Mountains." Nicole graduated Wheaton College an honors student in May of 2020 and was awarded an undergraduate prize in Ecology for her honors thesis work. Upon graduation from Wheaton, Nicole joined the Department of Ecology and Evolutionary Biology as a PhD student in Dr. Charlie Kwit's lab at the University of Tennessee in September of 2020. Her initial projects focused on seed dispersal by *Ursus americanus* and other mammals of in the southern Appalachians, but she quickly realized her true passion was in tropical ecology and transitioned her research to take place in the Chocó Rainforest of Northwest Ecuador. There, she worked alongside colleagues at the Fundacion para la Conservación de los Andes Tropicales to complete her dissertation work.