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Temporal Dynamics and Seed Dispersal in Plant-Frugivore Communities of the Dominican Republic

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TEMPORAL DYNAMICS AND SEED DISPERSAL IN PLANT-FRUGIVORE

COMMUNITIES OF THE DOMINICAN REPUBLIC

by

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ABSTRACT

TEMPORAL DYNAMICS AND SEED DISPERSAL IN PLANT-FRUGIVORE
COMMUNITIES OF THE DOMINICAN REPUBLIC

Spencer Christian Schubert
Old Dominion University, 2022
Director: Dr. Eric L. Walters

Plant-animal mutualisms are a foundational component of biodiversity in terrestrial ecosystems. Most tropical forest plants have adapted to produce fleshy fruits to attract frugivorous animals to disperse seeds. Interaction patterns among plant taxa and their seed dispersers are driven by a complex suite of factors involving their evolutionary history and environmental context, and the structure of these mutualistic networks are theoretically tied to their ecological function. I carried out a series of field studies to investigate the temporal dynamics of mutualistic interactions of plant and avian frugivore communities in the central Dominican Republic and how their characteristics affect seed dispersal in agricultural landscapes. I first investigated the effects of reproductive phenology of a tropical tree (*Guarea guidonia*) on the temporal variation of avian foraging behavior and seed dispersal patterns. I found that temporal variation in seed dispersal was driven most by landscape-level dynamics in the availability of alternative resources rather than tree– or neighborhood–level fruit production. I proceeded to expand my focus on the processes of frugivory and seed dispersal by monitoring the phenology of six local communities and characterizing the temporal dynamics of plant-frugivore networks across a full annual period. By applying multilayer network analyses, I identified a tendency of birds to shift between temporally defined modules in nonrandom patterns that suggest a prevailing influence of resource partitioning on consumer preferences

across seasonal time periods. By systematically sampling seed dispersal at a subset of these monitoring sites, I demonstrated how frugivory measures from network data predict their dispersal potential and ability to colonize new patches in heterogenous landscapes. Finally, I applied network data from frugivorous bird species to design an experiment to test the effect sounds of frugivore taxa with varying degrees of fruit consumption on the movement behavior and use of artificial perches in abandoned pastures by potential seed dispersers, finding that frugivorous bird sounds stimulate an increase in the frequency of avian visitors to degraded habitat. Collectively, my investigations provide insight into the processes of frugivory and seed dispersal in a previously undocumented region and reveal how interaction patterns can translate to ecological outcomes.

Dedicated to my grandfather, Dan Wuthrich, whose artwork captured my imagination and inspired me to work to preserve the natural beauty he saw in the world.
1935 – 2020

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 ECOLOGICAL NETWORKS

Observing, classifying, and quantifying interactions among organisms in complex, ever-changing communities of organisms is a central challenge in ecology. Understanding interaction patterns is key to elucidating how communities assemble and evolve (Diamond 1975, Chase 2003, Kraft et al. 2007). In response to this challenge, the emergence and development of ecological networks tools have increased the potential to analyze interaction structure among species at the community level to relate these to the underlying mechanisms of community organization, population dynamics, biodiversity, and ecosystem processes (Jordano et al. 2003, Montoya et al. 2006, Ings et al. 2009, Thébault and Fontaine 2010, Schleuning et al. 2015). While the earliest formulations of the network concept to explain the relationships among organisms in the natural world date back at least to Darwin's work in the mid-1800s (Egerton 2007), the use of networks in ecology traces its roots to food web theory in the 20th century. In their earliest applications, food webs provided conceptual and quantitative frameworks for understanding energy flow through pools of biomass from the perspective of consumer-resource trophic interactions (Elton 1927, Lindeman 1942). Recent decades have been marked with a resurgence of interdisciplinary scientific interest and theoretical advances fueled by improving computational tools and expanding applications of complex networks in such diverse systems as the internet, public transportation hubs, electrical grids, and cellular networks in an organism (Albert and Barabási 2002, Barabási 2016). In addition to food webs, network analyses are frequently applied to a variety of systems and interaction types, most notably mutualistic and host-parasite networks (Vázquez et al. 2005b, 2009, Tylianakis et al. 2007, Ings et al. 2009).

An ecological network, regardless of the type of interaction it is applied to, is a matrix or graphical representations of species connected by links to represent pairwise relationships between species in a community. Pairwise interactions have traditionally been classified based on either inferred or measurable positive and negative outcomes on either of the two actors involved. Interspecific relationships may take the form of antagonisms (+/-), mutualisms (+/+), competition (-/-), amensalism (-/0), or commensalism (+/0) (Abrams 1987). Binary networks use simple invariant classifications of relationships among interactors, whereas quantitative networks further characterize these relationships by weighted links (Gilarranz et al. 2012).

Measures of interaction strength in the literature are highly variable in ecological networks (Berlow et al. 2004, Wootton and Emmerson 2005), but they can generally be grouped into three categories. (1) Population effects measure the change in abundance of a given species with respect to the change in abundance (or addition/removal) of another species (May 1973, Levine 1976, Paine 1980, Yodzis 1988). Such measures do not explicitly consider the mechanisms underlying the net effect on populations, but rather the composite effect of one species – or individual of a species – on the population of another can be represented as a constant or a function (Laska and Wootton 1998, Wootton and Emmerson 2005). This approach is particularly useful in food webs in which high levels of omnivory and the context dependency of interactions across the life history stages may confound a precise mechanistic understanding of interspecific interaction (Emmerson and Yearsley 2004). (2) Per-capita effects measure the short-term consequences (e.g.,survivorship, assimilation/growth rates, reproduction, or other interpretable fitness components) of encounters between individuals of different species, thus specifying the mechanistic effect of encounters (Paine 1992). One important advantage to per capita interaction strength measurements is that it does not require the assumption of a

community at equilibrium, which is likely to be rare in natural systems (Laska and Wootton 1998). Obtaining information at this level, however, requires information on species interactions to be obtained either through exhaustive empirical observations in the field or inferred from a compilation of existing natural history data from species in the system. Nevertheless, discerning per capita effects can be problematic in systems with cryptic species or when the precise effects of species' encounters are otherwise unclear. (3) Surrogate measures of interaction strength are often used when population effects cannot be experimentally determined and quantifying per capita effects is not feasible (Emmerson and Raffaelli 2004). The use of surrogates for interaction strength is particularly common in mutualistic networks, given that these interactions often involve delayed effects on fitness that are challenging to quantify (however, see Schupp et al. 2017). Interaction frequency, for example, is often rationalized as an effective surrogate measure for plant-animal mutualisms for which the variance in the quality of services provided by mutualist partners is low (Vázquez et al. 2005a).

1.2 NETWORK TOPOLOGY

Resolving the architecture of ecological interaction networks is a primary goal of network analysis. Network topology can be generally subdivided into components of macroscopic and microscopic properties (Trøjelsgaard and Olesen 2016). Macroscopic properties are derived from the network topology at the scale of the entire network, while microscopic network properties represent particular network elements such as the characteristics of nodes and links that represent species and their interactions, respectively.

One basic example of a microscopic parameter is the degree value of a node, which is simply the number of other nodes in the network with which it is linked. Furthermore, nodes may

be described by centrality measures based on their relative connectivity within in the network (González et al. 2010). This level of information on particular species may offer insight into their functional role in the community (Jordán et al. 2006, Estrada 2007, Coux et al. 2016). Information about the position of individual species in the network can also be used to predict the cascading consequences on network integrity and function if it goes extinct (Blüthgen 2010, Caughlin et al. 2015); however, testing these predictions has primarily been limited to theoretical studies and simulation rather than empirical tests (Silva et al. 2007, Tylianakis et al. 2010, Fricke et al. 2017).

Macroscopic parameters provide overviews of how communities are organized through their interactions, which are hypothesized to relate to the mechanisms of community assembly and stability (De Angelis 1975, Bascompte et al. 2003, Bastolla et al. 2009, Thébault and Fontaine 2010, Rooney and McCann 2012). Connectance, synonymous with connectedness, describes the proportion of observed links formed between nodes with respect to the total possible number of links between all nodes. As the number of species in the network—network size—increases, connectance decreases exponentially (Jordano 1987b). Nestedness measures the asymmetry of network links with highly nested systems being characterized by specialists tending to interact with a core of generalists and generalists tending to interact more with specialists. Modularity is the measure of a networks tendency to form multiple clusters or compartments of nodes that disproportionately link with one another compared to other nodes in the network.

Beyond the assembly of networks, the use of ecological network analysis in community ecology is broadly defined by two approaches: niche-based interpretation and effect-based interpretation (Blüthgen 2010). The niche-based interpretation adopts a more intrinsic view of

network actors and how the trait-matching synergistically determine relative specialization and network structure. By disentangling the relative roles of traits and phylogeny from neutrality (e.g., the influence of abundance on encounters) with null models, evolutionary ecologists can theoretically explore the evolutionary causes of observed network topology along with their implications for community stability and assembly processes (Bascompte and Jordano 2007, Bastolla et al. 2009, Blüthgen 2010). For example, a trait-based perspective of community organization allows one to understand how network topology affects biodiversity by minimizing competition for mutualistic services and extinction cascades (Bastolla et al. 2009). Nevertheless, the empirical data necessary to test many of these assumptions, such as field experiments, are largely lacking (Dormann et al. 2017).

The effect-based view is defined by its focus on the realized frequencies of interactions among species and how these contribute to an overall ecological effect (Blüthgen 2010). Examples of such ecological effects might include measuring the infectiousness of one or more pathogens among multiple host populations or the propensity for dispersal and recruitment of trees in systems with animal-plant dispersal mutualisms (Pedersen and Fenton 2007, Carlo and Yang 2011).

Despite the appeal of ecological networks for their parsimonious, yet holistic treatment of interspecific relationships among organisms, these networks are still limited in their ability to represent highly heterogeneous and continuously changing natural communities.

1.3 MUTUALISTIC SYSTEMS

While ecologists have long been aware of the interdependencies between organisms with mutualistic relationships such as ant-acacia symbioses (Brown 1960), plant-pollinator

interactions (Galil and Eisikowitch 1968), or plant-disperser interactions (Ridley et al. 1930), early theoretical development of mutualisms in ecology was mostly overshadowed by a broader focus in competitive and trophic interactions during most of the foundational period of ecology (Boucher et al. 1982, Bronstein 1994, Bruno et al. 2003). Unlike predator-prey dynamics, for which the predator directly controls the prey population and has a delayed functional response to the resource, both species involved in a mutualism typically experience delayed and/or indirect positive effects (Donoso et al. 2017, Schupp et al. 2017). When mutualisms are examined using mathematical models similar to those from Lotka-Volterra competition theory, reciprocal positive interactions predict unstable growth of both populations in an "orgy of mutual benefaction" (May 1973, p. 95) and their potential destabilizing influence on communities initially led some to conclude that mutualisms should be more rare than other types of interactions (Boucher et al. 1982). Others argue that mutualistic dynamics cannot be modeled mathematically in isolation of other community interactions and that mutualisms can be stabilized by negative density-dependence and other predator-prey interactions within the community (Ringel et al. 1996).

Mutualistic interactions, nevertheless, are credited with playing a large role in shaping biodiversity in communities over evolutionary time (Bronstein 2015). Given the relative rarity of truly specialized obligate mutualisms compared to other relationships that involve diffuse interactions among many partners (Herrera 1982, Howe 1984, Bronstein 1994), networks have become the preferred tool to study coevolution and ecological dynamics. Mutualistic networks are typically represented as bipartite graphs that consider links between two sets of nodes that represent interactions between mutualist partners corresponding to two assemblages or guilds (e.g., plants and frugivorous animals) (Bascompte 2007).

The concept of coevolution, while relevant to all ecological interactions, has been a

central focus in the study of mutualisms. In the case of specialized, obligate mutualisms, coevolutionary models predict selective pressure resulting in the complementarity of traits, where the phenotypes of interacting species should converge on an efficient morphological match (Nuismer et al. 1999, Guimarães et al. 2011). Yet, beyond the exquisite and frequently invoked morphological matches observed by in nature that apparently reflect the outcome of coevolution, the importance of mutualistic interactions to shape evolution is perhaps best demonstrated by the highly diversified assemblages of plant and animal taxa dependent on mutualistic interactions (Herrera 1989, van der Niet and Johnson 2012). Nevertheless, many have argued that coevolution is unlikely to be important in systems where species interact with many partners with potentially conflicting selection pressures (Hougen-Eitzman and Rausher 1994, Iwao and Rausher 1997, Stinchcombe and Rausher 2001). This paradox has been the subject of much debate among evolutionary ecologists in determining whether and to what extent coevolution between species pairs occurs in large, complex communities of mutualists (Nuismer et al. 2013). The use of networks in theoretical and empirical studies have shed light on these questions by elucidating how the organization of such communities through the complexity of their interactions shape and are shaped by coevolutionary processes.

Network architecture has been identified as a key indicator of the influence of coevolution in mutualistic systems. The general nature of different types of mutualistic interactions with respect to their role in organism life history has a broad determination of network patterns. Mutualisms that are relatively intimate and active throughout an organism's life cycle tend to involve relatively few species and, consequently, fewer interacting partners (Guimarães et al. 2011). Protection mutualisms, such as ants-acacia or fish-anemone protection mutualisms, tend to involve fewer species whose interactions are assembled in a modular pattern

(Fonseca and Ganade 1996, Ricciardi et al. 2010). In relatively small mutualistic networks, pairwise interactions are expected to generate strong selective conditions and coevolution (Guimaraes et al. 2007). By contrast, mutualisms that influence only a component of life history occur more often as large, speciose networks (Guimarães et al. 2011). Dietary-reproductive mutualisms between animals and plants, such as pollination and seed dispersal interactions, tend to involve many species with highly generalized interactions assembled in a nested pattern in which more specialized species disproportionately interact with subsets of species connected to the most generalist species at the core of the network (Jordano 1987b, Bascompte et al. 2003). Theoretical studies suggest that coevolution in these large networks must be more heavily influenced by indirect effects (Guimarães et al. 2017). Consequently, such systems tend to promote trait convergence where, within both plant and animal communities, species have broadly similar traits involved in the mutualism, such as plants with scented flowers and pollinator guilds with olfactory acuity (Schiestl and Dötterl 2012). Furthermore, there is a tendency toward trait complementarity, where species that tend interact with the same set of partners have traits that are more similar to each other than to species that are more distant in the network (Guimarães et al. 2011). This perhaps is best reflected by the modular structure of most complex mutualistic networks. Given these patterns modules, rather than species pairs, are hypothesized to form coevolutionary units of mutualistic networks (Bascompte and Jordano 2007).

While it is tempting to attribute consistent patterns in network architecture to coevolutionary processes, many more neutral and ecological mechanisms are demonstrated to have a strong influence in community assembly. On the one hand, networks can be shaped by deterministic coevolutionary dynamics among species over large time scales, predicting that

functional traits and phylogenetic relationships determine linkage rules (Guimarães et al. 2011).

Analyses of mutualistic networks have revealed that interaction patterns are largely explained by

the morphological constraints in functional traits that determine the permissible interactions in

the community between any given species (Olesen et al. 2010). Large fruits and their seeds, for

example, cannot be swallowed and effectively dispersed by birds with small bill width

(Wheelwright 1985a). Nevertheless, trait matching in mutualistic networks does not necessarily

satisfy the predictions laid out by coevolutionary theory. Many network patterns resembling real

networks can be generated from simple null models based on species abundance and encounter

probabilities (Krishna et al. 2008, Vázquez et al. 2009).

The architecture of mutualistic systems is widely hypothesized to relate to community

stability (Okuyama and Holland 2008, Thébault and Fontaine 2010). The convergent structural

properties in mutualistic networks imply that communities are shaped into stable associations of

species through a combination of evolutionary and ecological mechanisms (Jordano 1987b,

Jordano et al. 2003, Thébault and Fontaine 2010). One approach to testing network stability has

been through simulating coextinction cascades (Rezende et al. 2007, Vieira and Almeida-Neto

2015, Fricke et al. 2017). This approach operates under the paradigm that the removal of network

actors (i.e., extinction or extirpation events) can propagate in the system and result in further

losses (Brodie et al. 2014). At the microscopic scale of the network, species with a greater

number of mutualist partners (i.e., higher degree) are expected to be more resilient to extinction

of other members of the community compared to species with fewer partners, since the loss of a

given partner is predicted to be compensated by the ability to interact with other partners

(Memmott et al. 2004, Bastolla et al. 2009, Rohr et al. 2014). At the macroscopic scale, the loss

of species is hypothesized to erode network function; however, not all species are equal in their

structural and functional importance to networks (Dunne and Williams 2009). Intuitively, the loss of poorly connected peripheral species (i.e., specialists) is less likely to affect network function than the loss of generalists at the core (Bascompte and Jordano 2007, Tylianakis et al. 2010, Suweis et al. 2015).

1.4 FRUGIVORY AND SEED DISPERSAL

In ecology, the term "dispersal" is most often used to refer to the unidirectional movement of an organism from its natal area to a new site (Bullock et al. 2002). This life history stage is especially crucial for sessile organisms or others with limited mobility that typically initiate dispersal in a propagule state (Kinlan and Gaines 2003). In contrast to active dispersal associated with many animals, whereby individuals may respond to signals and stimuli from their environment by traveling from one site to another through locomotion, plants are typically dispersed by passive means; that is, adult plants nor their seeds have direct control over the destination of individual seeds. Seed dispersal occurs through various modes of dispersal that can be classified as abiotic or biotic. Examples of abiotic dispersal include transport by wind, water, or gravity, whereas biotic dispersal is accomplished when some other organism is responsible for moving seeds some distance away from the maternal source plant (Fahn and Werker 1972, Howe and Smallwood 1982). Plants from ecosystems around the world display a wide range of apparent adaptations and strategies to facilitate seed dispersal through these different modes, evidencing strong evolutionary pressures selecting for traits that improve the likelihood of favorable dispersal outcomes (Howe and Smallwood 1982). The presence of apparently specialized structures or traits that facilitate seed dispersal through any of these modes are commonly referred to as the dispersal syndrome.

Plant reproduction can be subdivided into three general stages or phases: flowering, fruiting, and germination (Rathcke and Lacey 1985). Dispersal, thus, occurs between the latter two stages as fruits ripen and their seeds are in some way detached from the plant. The simplest form of dispersal occurs when fruits naturally abscise over time and fall to the ground below the parent plant. Here, seeds can conceivably germinate, establish as seedlings, and eventually recruit as new adults in the population. Yet, negligible or short-distance gravity dispersal is inconsequential for many plant populations (Vander Wall et al. 2005). As British paleobotanist Clement Reid noted, it would have taken oak populations nearly one million years to recolonize the space vacated by Pleistocene ice sheets by simple diffusive population growth (Clark et al. 1998). Furthermore, various density dependent factors including shading out by the parent plant, intraspecific competition, and pressures by specialist herbivores and pathogens have been frequently cited as strong barriers to recruitment for propagules that are not effectively dispersed (Janzen 1970, Connell 1971, Augspurger 1984, Caughlin et al. 2015).

Of all the different modes of seed dispersal, zoochory – dispersal by animal vectors – has undoubtedly been the subject of the most intensive study, as my growing understanding of plant-animal relationships has been central to advances in numerous aspects of ecology and evolution including the role of animals in determining the geographic distribution of plants (Nathan 2006), population biology (Jordano et al. 2007), coevolution of traits (Wheelwright 1985a), patterns of organization and evolution in communities of plant and animal mutualists (Bascompte and Jordano 2007), and has far reaching implications for biological conservation.

Plant-animal disperser relationships are typically classified according to the manner in which seeds are transported. Epizoochory is the incidental transport of seeds by the animal on the body's surface and does not confer any benefit to the disperser, with plant's propagules acting as

commensals. Synzoochory is a form of seed transport by which seeds are deliberately carried by the animal to another location, typically for storage or later consumption at a distant site. In these cases, dispersers often function dually as seed predators and seed dispersers depending on the context (Vander Wall 2001). In the case of endozoochory, seeds pass either partially or entirely – regurgitation and defecation, respectively – through the digestive track of animals. Endozoochory typically involves frugivorous animals feeding on the fleshy fruits of plants, and seeds are consumed and dispersed in the process. Consequently, plant-frugivore dispersal relationships are widely considered to represent a clear mutualism between partners whereby the frugivore acquires nutrition in exchange for its dispersal service. Hereafter, all further mention of frugivory and seed dispersal will be in reference to endozoochory unless another mode of seed dispersal is specified. The role of animal seed dispersal is particularly well recognized in tropical forest ecosystems, owing to the prevalence of animal-dispersed plant taxa in in these communities (Howe and Smallwood 1982).

1.5 BACKGROUND ON FORESTS OF HISPANIOLA AND STUDY AREA

For my dissertation research, I chose to develop a project in the tropical wet forest ecosystems of Hispaniola. The Caribbean Island of Hispaniola – Haiti and the Dominican Republic – is home to numerous terrestrial biomes, including desert, scrubland, tropical dry and wet forests, cloud forests, and alpine forests. Before major settlements by European colonists, tropical wet forests covered more than half the island's surface, yet this cover has been reduced to less than 15% in modern day (Dinerstein et al. 1995). The most heavily deforested regions have been at low and middle elevations (~0–800 m a.s.l.), where cattle grazing and mixed cultivation are the predominant land practices (International Resources Group 2001). Similar to

other regions of the Neotropics, the overwhelming majority of plants in the tropical wet forests in this region are dispersed by frugivorous animals. Given that 88% of non-volant mammal species have gone extinct from the Caribbean archipelago since the late-Pleistocene (Morgan and Woods 1986), birds are the most prolific frugivores contributing to seed dispersal on these islands. Despite the importance of this unique avian community to forest biodiversity, little is known about the interactions between birds and plants in this region, nor is its ecological significance well understood by the various governmental and nongovernmental organizations responsible for forest management and land development.

My field research was conducted in the watershed of Rio Yaque del Norte within a radius of approximately 15 km of the town of Jarabacoa in La Vega province. Since virgin patches of forest are scare on the island of Hispaniola and almost exclusively restricted to high elevation sites, all of the sites used in my study are embedded within rural agricultural landscapes. Most sites can best be described as agro-pastoral landscapes, with stands of riparian forest, secondary forest fragments, abandoned fields, cultivation, and grazed fields/savanna. Overall, this landscape profile and level of disturbance is well representative of the current state of most remaining wet forest habit in the Dominican Republic.

1.6 OBJECTIVES

In this dissertation, I began with a population-level study of flowering and fruiting phenology of a tropical tree common to the study area known to reproduce in an episodic manner with multiple annual reproductive cycles. I sought to understand the potential adaptive value of this subannual reproduction pattern from the perspective of the consumer-resource relationship mediated by how phenology dictates the temporal aspect of fruit production, ripe fruit

availability, and the response of frugivorous birds. I hypothesized that large pulses in fruit productivity over short periods could have limiting benefits to the quantity of seeds removed by birds, due to satiation, thereby conferring fitness advantages to trees that invest energy and resources into the sporadic or gradual production and maturation of ripe fruits. Furthermore, I aimed to determine the extent to which neighboring fruit resources or landscape-level fruit availability influence the foraging behavior of seed dispersers.

Next, I expanded my focus on phenology to incorporate a community-level view of the temporal dynamics of plant-frugivore networks. In addition to describing and quantifying the full extent of biodiversity of plant and avian assemblages involved in frugivory and seed dispersal in the region, I focused on how the variation in fruit resources across different periods of the year drives the turnover and resorting of mutualistic links as well as addressing whether competition or facilitation were most likely to drive changes in partner preference.

Accompanying my community-level study of phenology and frugivory, I simultaneously and systematically sampled seed deposition in the landscape of a subset of the study sites to link observed patterns in frugivory with the realized effect on seed dispersal in these relatively degraded and heterogenous farmland landscapes. Specifically, I aimed to determine the relative effects of fruit abundance and patterns of frugivory on the propensity of plant taxa to disperse into the landscape and colonize novel patches. I also compared the frequency of seed delivery to different habitat types found across the study sites to understand the process of seed dispersal in a heterogenous landscape.

Finally, I delved further into the subject of indirect effects on the process of seed dispersal by investigating the role that ambient sound and social information play on directing the movements of frugivorous birds in the non-forested matrix. I designed an experiment to test the

effect of bird sounds from different levels of frugivory and functional roles found from my empirical plant-frugivore networks on the frequency of visits to artificial perches in forest restoration plots.

CHAPTER 2

SUBANNUAL PHENOLOGY AND THE EFFECT OF STAGGERED FRUIT RIPENING

ON DISPERSAL COMPETITION

2.1 INTRODUCTION

Seed dispersal plays an essential role in the life history of sexually reproducing plants, with diaspore movement acting as an underlying driver of species distribution and community composition (Hamrick et al. 1993, Cain et al. 2000, Levine and Murrell 2003). Dispersal mutualisms with frugivorous animals are the predominant mode of seed dispersal in many tropical forest ecosystems (Howe and Smallwood 1982). To increase fitness, plants dependent on this process must attract frugivores that provide effective seed dispersal through delivery of propagules to suitable habitats (Schupp 1993, Schupp et al. 2010). Seed dispersal mutualisms, however, rarely occur as obligate pairwise relationships between species but instead are typically networks of interactions among many species within a community (Howe 1984, Jordano 1987b). Consequently, spatial and temporal variation in fruit availability often determines the outcome of seed dispersal, since the process is mediated through selective feeding behaviors by frugivores. The abundance of alternative fruit resources within plant neighborhoods leads to competition among fruiting plant species, particularly when dispersal services are limiting, or facilitation when frugivorous animals are attracted to the area (Carlo 2005, Donoso et al. 2017). Fruiting phenology, therefore, affects both the individual as well as the community of fruiting species because frugivores adjust their feeding behaviors according to preference and fruit availability (Carlo et al. 2003, Naoe et al. 2018). In contrast to temperate ecosystems, where seed dispersal by frugivores is largely a discrete episodic process with annual cycles (Thompson and Willson

1979, Stiles 1980, Herrera 1982, Griz and Machado 2001), many tropical forest trees have fruits available year-round with high intra-annual fluctuation of ripe fruit availability that shapes frugivore resource selection (Carnicer et al. 2009, Gleditsch et al. 2017). Much of this variation is driven by plant taxa that reproduce in multiple episodes per year by flowering / fruiting subannually, or even continuously (Newstrom et al. 1994). While various studies have examined the role of heterospecific neighborhood fruits on frugivore-mediated competition and facilitation of seed dispersal (Gleditsch et al. 2017, Rumeu et al. 2019), few have considered how subannual reproduction influences the temporal dynamics of seed dispersal in tropical plant communities.

As a general principle, plants that produce greater quantities of flowers and seeds increase fitness by maximizing the number of propagules dispersed away from the source plant (Murray 1987, Blendinger and Villegas 2011, Palacio and Ordano 2018). Higher quantities of ripe fruits are expected to increase the probability of detection and frequency of dispersal by frugivores (i.e., "the crop size hypothesis"; Snow, 1971). Plants, therefore, trade off costs of growth with the frequency and intensity of reproduction that allows for effective interactions with seed dispersers (Obeso 2002, Ordano et al. 2017). Two alternative fruit production strategies by bird-dispersed plants have consistently been recognized in tropical forests (Janzen 1970, Snow 1971, McKey 1975, Howe and Estabrook 1977, Howe and Smallwood 1982). On the one hand, trees that attract primarily obligate frugivores tend to have larger seeds, energy-rich fruit pulp with high lipid and protein content, lower overall fecundity, and extended periods of ripe fruit availability. On the other hand, trees that attract generalist or facultative frugivores, generally have smaller seeds, high water-content sugary fruits, and relatively high-quantity fruit yields that ripen over a short period (Howe 1993).

The scale at which frugivorous animals perceive and travel across the landscape are key

determinants of fruit selection and seed dispersal for species that fruit simultaneously (Carlo and Morales 2008, Morales et al. 2013). Resource tracking, an increase in consumer feeding rate with increasing resource abundance, can be driven by either (i) a numerical response where more consumers are drawn to a resource, or (ii) a behavioral response where individual animals increase foraging effort relative to a particular resource (Yang et al. 2008). As predicted by optimal foraging theory, frugivores recruit to patches of high resource density and avoid areas where feeding opportunities are scarce (Root 1973, Reynolds 2012, Blendinger et al. 2015). At finer spatial scales, increasing fruit quantity can lead to increased visits from seed dispersers from surrounding areas (Blendinger and Villegas 2011).

In this study, I investigated temporal variation in seed dispersal interactions between a subannually reproducing tropical tree, *Guarea guidonia* (*Meliaceae*) and an assemblage of resident frugivorous birds. I monitored the reproductive phenology of a marked population of fruiting trees and conducted focal observations of frugivorous bird foraging activity to test the extent to which seed dispersal depends on fruit availability at three spatial scales: (a) at the scale of individual trees, I hypothesized that the abundance of ripe fruit of the focal tree would have a positive effect on visitation rate from avian seed dispersers; (b) at the scale of neighborhoods, I hypothesized that the abundance of alternative fruit resources would have a negative effect (i.e., competitive) on visits to focal *Guarea* trees; and (c) at the landscape scale, I predicted a negative effect of alternative fruit availability beyond the neighborhood on visits to *Guarea* trees.

2.2 METHODS

Study Area

The study was conducted from March 2016 to August 2017 on a private farm in the

foothills of the Cordillera Central of the Dominican Republic near the town of Jarabacoa (500–625 m a.s.l.) The study area was restricted to 180 ha of a mosaic landscape containing remnant and secondary broadleaf forest fragments embedded in a matrix of other cover types, including palm (*Roystonea hispaniolana*) savannas, cattle pastures, pine (*Pinus occidentalis*) stands, and other small-scale subsistence agricultural practices. Mean annual precipitation is 1340 mm and while winter (Jan–Feb) and summer months (Jun–Aug) are comparatively drier, there is no distinct wet or dry season and mean monthly rainfall is typically >70 mm (https://en.climate-data.org/north-america/dominican-republic/la-vega/jarabacoa-766532/). Previous surveys of this site and surrounding areas identified 71 woody plant species – including trees, shrubs, and lianas – with nearly all native species producing fleshy fruits (Schubert unpublished). A total of 76 avian species have been documented at the site, with 48 of these known to feed on fruits based on either direct observation or reports from the literature (Table 1).

Focal Tree Species and Phenology

I selected *Guarea guidonia* (*Meliaceae*) as a focal species to investigate temporal patterns in seed dispersal. *Guarea guidonia* (hereafter "*Guarea*") is a large dioecious tree, widespread across the Caribbean and mainland Neotropics (Pennington and Clarkson 2013). Fertilized flowers develop into lignacious, globular capsules that dehisce after 8–10 months to expose 3–4 seeds with a fleshy, red-orange aril. Seeds are an ovaloid shape, averaging 10.6 mm in length and 6.6 mm in diameter (Liogier 1978). The fleshy aril accounts for only ~15% of the total seed dry mass and is rich in lipids (Table 2). Phenology data from other studies indicate that this species varies from annual to subannual (Carlo et al. 2003, Zimmerman et al. 2007). Subannual phenology is also well documented from other members of the genus *Guarea* (Bullock et al.

1983, Bawa et al. 2003).

I used ArcGIS 10.0 (ESRI, Redlands, CA, USA) to generate 50 random sampling points over ~50 ha of riparian forest fragments, manually classified using hand-drawn polygons, based on satellite imagery (ESRI World Imagery 2016). Each point was visited Mar–May 2016 to search for the closest *Guarea* tree within 10 m of each point. Only reproductive trees (>12 cm in diameter at breast height [dbh]) that could be unambiguously identified as female (i.e., fruit-bearing, based on a combination of crown and ground surveys for fruit capsules) were selected for the study. Any trees with an obstructed view from surrounding dense vegetation such that <50% of the crown was visible from within 15 m of the tree were excluded. All individuals selected were marked and measured for dbh. A total of 24 female trees were marked for the study. Each tree was visited every 13–15 days (hereafter "biweekly") over an 18-month period, May 2016 – Oct 2017, to record characteristics of reproductive phenology. Recording the presence and condition of flowers enabled us to track the number of flowering episodes and, hence, anticipate the fruit cohorts that would later mature. Observers used standardized 30-s counts to quantify reproductive characteristics in 2–3 non-overlapping sections of the crown (Koenig et al. 1994). Counts were conducted both for flowers and fruits with counts performed separately for trees where both flowers and fruits were present. I differentiated among inflorescences and enumerated the number of inflorescences with at least one flower blooming, and I differentiated ripe from unripe fruits based on whether capsules had dehisced and bore at least one red, arillated seed. The arillated seeds were probed from the fruits by birds when first dehiscing, but after several days often hung loosely from the fruits, at which point they soon fell naturally to the ground. Thus, freshly ripe fruits were distinguishable from lingering old fruits whose seeds had already been consumed or had fallen.

Foraging Observations

I sampled foraging at focal *Guarea* trees from 18 March to 10 August 2017. Observations began following the first detection of ripe fruits during the biweekly phenology censuses, and observations concluded once all mature fruits had begun to rot and had fallen from the crowns of the trees. The fruiting period was divided into four non-overlapping sub-periods, each spanning approximately 5 weeks, in which each tree with ripe fruit detected in the surveys was observed once, to distribute observer effort evenly across the population during the fruiting period. Before each foraging observation, the observer quantified the number of ripe and unripe fruits to estimate the density of ripe fruits on the focal tree. Focal foraging observations proceeded with the observer seated quietly from a position 10–15 m away from the tree. Visits from all birds were recorded over the course of a 2-hr period. Observations were subdivided into alternating 30-min intervals in which the observer recorded either (a) the duration of stay of each bird (i.e., arrival and leave times) in the crown of the tree, or (b) foraging behavior of individual birds (i.e., failed to remove seed, swallowed, or dropped).

Neighborhood Plot Surveys

To evaluate the effect of neighborhood context on *Guarea* frugivory, I conducted two sets of surveys accompanying each focal observation to record bird and fruit abundance within 15-m radial plots around the focal tree. All stems were identified, measured, and marked at the beginning of the study. Before the foraging observation, I conducted point counts of all potential avian consumers of *Guarea*. Upon arrival at the focal tree, the observer – following a 5-min period of silence to account for potential disturbance to the area – recorded visual and auditory

detections of all potentially frugivorous bird species over a 10-min period. Distance of birds

from the focal tree was estimated using a rangefinder (Halo XL450, Halo Optics, New Roads,

LA, USA). Given that birds detected 15–25 m from the focal tree were likely to stray into the 15-

m radius plot after the 10-min count period, I also included those detections in the final analyses

of local frugivorous bird abundance.

Following each observation, I conducted surveys in the 15-m circular plots around the

focal tree to quantify neighborhood fruit availability. During each fruit survey, the observer

surveyed the crown of each plant to quantify fruit abundance. Classification of ripe fruits varied

and was based on taxon-specific criteria, including color change (e.g., from green to

red/blue/black), stage of dehiscence, and presence of beak marks indicating the fruit had softened

enough to be palatable to birds (e.g., *Cecropia schreberiana*). All fruit abundance surveys in

neighborhood plots were conducted immediately after the avian focal observation was complete.

When possible, I enumerated all fruits in view. However, in cases of exceptionally large fruit sets

or plants for which the crown was partially obscured, observers counted fruits in 2–3 non-

overlapping sections of the crown and estimated the fruit abundance using a logarithmic Fruit

Abundance Index (FAI, i.e., 1 = 1–10, 2 = 11–50, 3 = 51–100, 4 = 101–500, 5 = 501–1000, 6 =

1001–5000, 7 = 5001–10000, 8 > 10000) to quantify both immature and ripe fruits held by each

plant (Saracco et al. 2005). To produce a plot-level metric for my analyses, I estimated fruit dry

mass using species-specific measurements of these values of fruits collected from the study area

and data from the literature, when samples could not be collected for certain species (Jordano

2007). For each plot survey, I estimated the quantity of fruits by taking the median value within

the FAI score range and summed these for all plants with ripe fruits, by species. Estimated totals

were then converted to dry species-specific fruit pulp mass (hereafter "neighborhood fruit

biomass") to account for large disparities in fruit size among taxa.

Landscape Seed Dispersal Patterns

To address whether landscape-level patterns of fruit availability influenced seed dispersal of focal trees, I monitored seed deposition in collection traps as a proxy measure of fruit presence and relative quantity. I deployed 20 screen traps from a PVC frame (0.5 m^2, 1 m tall, 1 mm mesh) in four pasture areas within the boundaries of the study area. Traps were placed haphazardly beneath different types of isolated perches that had no other canopy or perching structure within 10 m. Perch types included palms, dead palms, live fence trees (*Gliricidia sepium*), and mango trees (*Mangifera indica*). Traps in each field were spaced 20–60 m, and all fields were separated by at least 200 m. Seed deposition by gravity occurred only in traps set beneath *R. hispaniolana*, and these seeds were distinguished from seeds dispersed by frugivores based on whether the exocarp of the fruit was removed by digestion or was intact. Traps were visited biweekly to collect the contents and enumerate seeds of all species, identifying with the aid of a reference collection from the site. Previous field research from a similar agroforestry study area in Puerto Rico showed that most seeds of most bird-dispersed plants collected from isolated bird perches approximately reflect their abundance in neighboring forest patches, albeit with the most common species slightly underrepresented and some rare species relatively overrepresented (Carlo and Morales 2016).

Data Analysis

I used an information-theoretic approach to evaluate candidate models assembled from potential predictor variables of avian frugivore activity at focal study trees. Because the data

were over-dispersed, I used a hurdle approach to generalized linear mixed models, fitted to a

truncated Poisson distribution to evaluate the effects of predictor variables (Martin et al. 2005,

Zuur et al. 2009). Hurdle models allowed for separating the process of disperser visits into two

parts: (a) whether any visits occurred, and (b) the number of visits for non-zero observations.

This was realized by first estimating the probability of a non-zero count, and then separately

evaluating the non-zero data using a truncated count model. I considered fixed effects: day-of-

year expressed in radians, focal tree ripe fruit count, and neighborhood fruit biomass with

Guarea and heterospecific taxa considered separately. In addition to examining date with respect

to the annual calendar, I considered an additional bimodal effect of date by measuring radians

with an origin at the midpoint of the fruiting period recorded for *Guarea*. All models included

tree / plot ID and observer ID as random effects. I ranked a priori candidate models using

Akaike's Information Criterion (AICc) values for small sample sizes (Burnham and Anderson

2002), and I considered all models with ΔAICc < 7 to show support (Burnham et al. 2011).

Because the landscape measures of seed dispersal in collection traps were collected continuously

and at a sampling frequency independent of the focal foraging observations, I relied on date-

related variables in my primary analysis but interpreted their effects relative to trends in seed trap

data.

I conducted a second analysis of the effects of neighborhood fruit biomass on local avian

abundance. I classified birds as either *Guarea* dispersers or frugivores that do not consume

Guarea, determined *a posteriori* (Table 1). I used generalized linear mixed models to analyze the

effect of *Guarea* and heterospecific neighborhood fruit biomass on each of these two groups of

birds. I considered tree / plot ID and observer ID as random factors and used a Poisson

distribution. All analyses were conducted using R 3.5.1 (R Development Core Team 2021) with

packages "bbmle" (Bolker 2020) and "glmmTMB" (Magnusson et al. 2017) used for analyses

and "ggplot2" (Wickham et al. 2016) used to produce figures.

2.3 RESULTS

Phenology and Seed Dispersers

Flowering occurred in the *Guarea* population in eight distinguishable episodes over the

16-month monitoring period (Fig. 1). In 2016 – the beginning of the reproductive activity that

produced the 2017 fruit crop – two large flowering peaks were observed in June and August with

a smaller subset of individuals flowering again October–December (Fig. 1). Female trees

flowered between 1 and 4 episodes in 2016, with 62.5% of trees flowering twice (N = 24). Fruits

from the 2016 cohort first began maturing in March 2017. Time to fruit maturity from the onset

of first bloom ranged from 250 to 344 days (mean 311 ± 21 [*SD*]). The duration of the ripe fruit

phase ranged from 58 to 147 days (mean 110 ± 21 [*SD*]) and duration of ripe fruits on the tree

was positively predicted by the number of flowering episodes (linear regression: $\beta = 15.395$, *SE*

$= 7.276$, t $= 2.116$, p $= 0.0471$; Fig. 2). The multimodal flowering pattern, however, was not

reflected at the population level. Instead, I observed a single protracted period of ripe fruit

availability (Fig. 1).

I recorded 437 detections of 18 frugivorous bird species across all point counts. From 160

hr of foraging observations at focal trees, I recorded 344 visits from 10 frugivorous species

(Table 1). Only six species were observed feeding on *Guarea* seeds, with two species feeding on

seeds on only a single occasion (Fig. 3). Hispaniolan Woodpeckers (*Melanerpes striatus*) were

the most frequent seed dispersers at focal trees, accounting for more than half (52.1%) of visits.

Black-whiskered Vireos (*Vireo altiloquus*) were the second-most frequent seed dispersers

(35.7%). Seed dispersers also varied in their feeding behavior during visits to the tree. Hispaniolan Woodpeckers, Black-whiskered Vireos, and Gray Kingbirds (*Tyrannus dominicensis*) typically only consumed one seed (Fig. 4). However, these species showed varying capacities as seed dispersers based on foraging behavior. For example, Hispaniolan Woodpeckers ingested as many as eight seeds in a single visit, while the maximum number of seeds consumed for Black-whiskered Vireos and Gray Kingbirds were four and two, respectively. On the other hand, I recorded only one instance of a Black-crowned Palm Tanager (*Phaenicophilus palmarum*) swallowing seed out of four occasions where I observed feeding behavior, with most foraging attempts resulting in seeds falling to the ground.

Drivers of Frugivory at Focal Trees

The abundance of avian frugivores that did not consume *Guarea* exhibited a positive relationship with heterospecific fruits. The best predictor of seed disperser visits, as determined by the best-supported candidate model, was bimodal date (Table 3). Foraging activity of seed dispersers was greatest at the beginning of the *Guarea* fruiting period with a second peak in the final two months (Fig. 5). Seed disperers were less likely to visit trees at the tails of the fruiting period (i.e., closer to beginning and end); however, those trees that did register at least one visit were more likely to have a greater number of visits during these subperiods (Table 4).

Contrary to expectation, I did not detect a positive effect of daily ripe fruit set of focal trees on visits by seed dispersers. The best-supported model did not contain ripe fruit density (Table 3). Similarly, neither heterospecific nor conspecific neighborhood fruit biomass was predictive of seed disperser visits. This lack of influence of neighborhood fruits on seed dispersers was further demonstrated by my findings that showed no relationship between the abundance of these

species and neighborhood fruit biomass (Table 5).

Seed Dispersal and Landscape Fruit Availability

The bimodal pattern of visit frequency by avian seed dispersers to *Guarea* trees corresponded closely with patterns of seed dispersal observed in seed traps (Fig. 6). *Guarea* seed deposition in traps increased beginning in late March and peaked in mid April before a sudden decline. A smaller peak in *Guarea* dispersal was observed in July and early August. The decline in *Guarea* seed dispersal was independent of fruit availability, since the number of trees bearing ripe fruit changed little over this period. This decline in *Guarea* seed dispersal corresponded with large peaks in *Cupania americana* and *Ocotea coreacea*, alternative fruit-bearing species fed upon by *Guarea* dispersers.

2.4 DISCUSSION

Despite flowering subannually, *Guarea* trees produced ripe fruits continuously over a single extended period. The length of a particular tree's ripe fruit phase related positively with the number of prior flowering episodes, demonstrating that trees in late-stage flowering provided fruits to seed dispersers over a larger temporal window. Counter to expectation, the daily ripe fruit set of focal trees was not predictive of interactions with seed dispersers, suggesting a lack of consistent tracking of *Guarea* by seed dispersers. Even at the neighborhood scale, neither conspecific nor heterospecific ripe fruit biomass were predictive of foraging activity of seed dispersers, suggesting that resource composition did not play a large role in seed dispersal at the scales examined. While fruit availability did not show a pronounced temporal modality, disperser visits to focal trees was markedly bimodal over the fruiting period. Visits peaked late March–

early April and again, to a lesser extent, in July. These patterns suggest that bird activity and seed dispersal were controlled by processes at larger spatial scales than the local or neighborhood. By examining the temporal changes in seed deposition across the landscape, my observations indicate that the most likely driver of the mid-season decline in *Guarea* seed dispersal was the emergence of ripe fruits of alternative fruiting species over the landscape. Once *Ocotea coriacea* and *Cupania americana* ripened, seed dispersal of *Guarea*, both at the scale of the individual trees and landscape (i.e., in seed traps), decreased precipitously, despite the continued abundance of ripe *Guarea* fruits.

The finding that focal tree daily ripe fruit set had no effect on seed disperser visits contrasts with most field studies that show a positive relationship between tree crop size and fruit removal (Davidar and Morton 1986, Jordano 1987a, Ortiz-Pulido and Rico-Gray 2000, Palacio et al. 2017). In a meta-analysis of seed dispersal field studies of 50 plants species from 27 families, Palacio and Ordano (2018) found broad support for crop size having a positive effect on both visits and fruit removal by frugivorous birds and evidence for strong selection on crop size, a trait known to be heritable (de Moraes et al. 2005, Manju and Sreelathakumary 2006, Denton and Nwangburuka 2011, Meena and Bahadur 2014). Phenology, however, can potentially mediate selection on crop size, where plant species with shorter fruiting periods experience stronger selection on crop size from interactions with their seed dispersers (Palacio and Ordano 2018). When compared with plants with annual reproduction that present fruits to dispersers in a single episode, species with subannual reproduction are more likely to experience temporally variable interactions with seed dispersers, obscuring any obvious selection on crop size. Moreover, as evidenced from the *Guarea* phenology data, crop size within the same fruiting period can result from the accumulation of multiple flowering events, presumably decoupling selective pressures

on flower and fruit production.

Although my analysis detected no distinguishing effects of neighborhood fruit biomass driving either facilitation of fruit removal or competition among the focal species and other fruiting plants, seed trap data implied interspecific competition among plants at larger spatial scales. There is a general lack of consensus from studies that have considered the indirect effects of plant neighbors on seed dispersal, suggesting that such effects are highly variable and context-dependent by species over space and time (Smith and McWilliams 2014, Gleditsch et al. 2017). Some of the clearest examples of neighbor-induced competition in tropical environments come from situations in which crowded conspecific neighborhoods lead to lower per capita visits to trees (Manasse and Howe 1983, Saracco et al. 2005). While it is possible that intraspecific competition at larger spatial scales – particularly during the middle of the fruiting season when *Guarea* is at peak fruit abundance – could have played a role in depressing foraging activities at focal trees, this dynamic would not lead to a decline of *Guarea* seeds in seed traps. Hence, the most parsimonious explanation for the reduced foraging and dispersal of *Guarea*, despite sustained ripe fruit abundance in the population, is interspecific competition.

Fruits of the genera *Guarea*, *Cupania*, and *Ocotea* all contain lipid-rich pulp (i.e., >50% nutritional content, Galetti et al. 2000, Stevenson et al. 2017). Preference for energy-rich lipid nutrients in fruit pulp by frugivorous birds is associated with metabolic demands of migratory birds (Smith and McWilliams 2010), but it is also a preferred dietary strategy of many tropical birds to meet the high metabolic demands associated with caring for offspring at the nest (Lamperti et al. 2014, Carleton and Smith 2016). All avian dispersers of *Guarea* at my study site were breeding residents known to feed on *Cupania americana, Ocotea coriacea and O. leucoxylon* (Chapter 3). While fruits of these genera have similar lipid content and propagule

size, the per-seed pulp dry mass of *Ocotea* was 6.72 and *Cupania* 3.10 times greater than *Guarea*, respectively (Table 2). Based on seed trap data, these relative values matched the hierarchical fruit preference of these taxa at times when all three fruits were available (Fig. 6). Periods of relatively high *Guarea* dispersal corresponded closely with the absence, or low abundance, of these lipid-rich taxa, suggesting that interspecific competition was mediated through resource preference. Ripe *Ocotea* and *Cupania* fruits were relatively abundant and frequent in the neighborhood plots during their respective fruiting phases, recorded at 61% and 52% of plots, respectively. However, I found no evidence that this local-scale availability affected foraging activity at focal *Guarea* trees.

The lack of facilitative or competitive effects at the scales of focal trees or plant neighborhoods is likely manifested by the comparatively stronger temporal variation in fruiting at the landscape scale for *Guarea* seed dispersers. Because *Guarea* dispersers are resident year-round, their breeding phenology implies that fruits are generally fed upon by birds that are either in the process of acquiring a breeding territory, already nesting, or provisioning food to recently fledged offspring. Consequently, frugivorous birds in my study were interacting with fruit resources over relatively confined home ranges as opposed to migratory or nomadic movements that might take place at other times of the year. Hispaniolan Woodpeckers, the most numerous seed disperser at the study site, radio-tagged for a separate study at the site spent most of their time within 800 m of their nest tree during the breeding season but occasionally moved ≥ 2 km (Schubert unpublished). While little information is available for Black-whiskered Vireos, the next most numerically important seed disperser, movement studies in other vireos have shown that resident vireos in forested environments can readily foray up to 2 km daily (Morton et al. 2010). This range of movement for such avian taxa are consistent with the scale of my study area

and point to a generally larger scale of movement and tracking of fruits at a scale much larger than the neighborhood scale used in the present study. Curiously, the bimodal effect of date was manifested by trees with ripe fruits that were less likely to be discovered by seed dispersers early and late in the fruiting period. Trees that were attended were disproportionately more likely to recruit many frugivore visitors. Such a dynamic may suggest a positive feedback response driven by social cues among birds to locate *Guarea* fruits during times when other preferred resources are relatively scarce (Gu et al. 2017, MacDonald et al. 2019).

Previous studies have highlighted the critical role of some tropical plant taxa with protracted phenologies in sustaining frugivore populations in times of low or unpredictable fruit availability in the community (Terborgh 1986, Van Schaik et al. 1993, Carlo et al. 2003). Extended fruit production as a reproductive strategy is hypothesized to have evolved, in part, as a result of predictable and reliable dispersal by frugivores that specialize on such fruit resources (Howe and Estabrook 1977, Carlo et al. 2003). My study, however, highlights apparent resource switching of frugivores from *Guarea* to other more preferred resources. I offer an alternative hypothesis for the adaptive value of extended fruit production. Rather than evolving in the context of reliable frugivore presence and fruit removal, extended fruiting could potentially serve as a form of bet hedging in landscapes where the response of frugivores is highly context-dependent in the phenology and availability of other more preferred fruit resources. By displaying few ripe fruits at any given point in time but extended over a period when other ripe fruits are available, plants with relatively inferior fruit quality may capitalize on spatio-temporally unpredictable fruit availability. While this bet-hedging strategy of fruit production likely has prevalent effects on tropical forest communities, interpreting a direct evolutionary link between frugivory and phenology should be done cautiously, since other environmental

conditions such as the presence of pollinators, solar irradiance, and precipitation likely play a large role in fruiting phenology (Van Schaik et al. 1993, Zimmerman et al. 2007). Future work, integrating both community phenology and animal seed dispersal data, especially including the applications of network analyses and long-term data sets, promises to provide a venue for more effectively integrating the various drivers of fruiting phenology.

TABLE 1. A list of avian taxa detected in the study area, with subsequent classification as known frugivores and *Guarea guidonia* dispersers.

Family	Species	Common Name	Frugivory	*Guarea* consumer
Odontophoridae	Northern Bobwhite	*Colinus virginianus*		
Columbidae	Rock Pigeon	*Columba livia*	X	
	Common Ground Dove	*Columbina passerina*	X	
	Ruddy Quail-Dove	*Geotrygon montana*		
	Scaly-naped Pigeon	*Patagioenas squamosa*	X	
	White-winged Dove	*Zenaida asiatica*	X	
	Zenaida Dove	*Zenaida aurita*	X	
	Mourning Dove	*Zenaida macroura*	X	
Cuculidae	Hispaniolan Lizard-Cuckoo	*Coccyzus longirostris*	X	
	Mangrove Cuckoo	*Coccyzus minor*	X	
	Smooth-billed Ani	*Crotophaga ani*	X	
Caprimulgidae	Greater Antillean Nightjar	*Antrostomus cubanensis*		
	Antillean nighthawk	*Chordeiles gundlachii*		
Apodidae	Black Swift	*Cypseloides niger*		
	White-collared Swift	*Streptoprocne zonaris*		
	Antillean Palm-Swift	*Tachornis phoenicobia*		
Trochilidae	Antillean Mango	*Anthracothorax dominicus*		
	Hispaniolan Emerald	*Chlorostilbon swainsonii*		
	Vervain Hummingbird	*Mellisuga minima*		
Scolopacidae	Spotted Sandpiper	*Actitis macularius*		
	Wilson's Snipe	*Gallinago delicata*		
Ardeidae	Cattle Egret	*Bubulcus ibis*		
	Green Heron	*Butorides virescens*		
	Little Blue Heron	*Egretta caerulea*		
	Snowy Egret	*Egretta thula*		
	Yellow-crowned Night-Heron	*Nyctanassa violacea*		
Cathartidae	Turkey Vulture	*Cathartes aura*		
Accipitridae	Sharp-shinned Hawk	*Accipiter striatus*		
	Red-tailed Hawk	*Buteo jamaicensis*		
Tytonidae	Ashy-faced Owl	*Tyto glaucops*		
Todidae	Narrow-billed Tody	*Todus angustirostris*	X	
	Broad-billed Tody	*Todus subulatus*	X	I
Picidae	Hispaniolan Woodpecker	*Melanerpes striatus*	X	O
	Antillean Piculet	*Nesoctites micromegas*	X	I
Falconidae	Peregrine Falcon	*Falco peregrinus*		
	American Kestrel	*Falco sparverius*		
Psittacidae	Hispaniolan Parrot	*Amazona ventralis*	X	
	Hispaniolan Parakeet	*Psittacara chloropterus*	X	
Tyrannidae	Hispaniolan Pewee	*Contopus hispaniolensis*	X	
	Stolid Flycatcher	*Myiarchus stolidus*	X	I
	Loggerhead Kingbird	*Tyrannus caudifasciatus*	X	O
	Gray Kingbird	*Tyrannus dominicensis*	X	O
Vireonidae	Black-whiskered Vireo	*Vireo altiloquus*	X	O
Hirundinidae	Barn Swallow	*Hirundo rustica*		
	Caribbean Martin	*Progne dominicensis*		
Mimidae	Northern Mockingbird	*Mimus polyglottos*	X	
Turdidae	Rufous-throated Solitaire	*Myadestes genibarbis*	X	
	Red-legged Thrush	*Turdus plumbeus*	X	O

TABLE 1 Continued…

Dulidae	Palmchat	*Dulus dominicus*	X	I
Ploceidae	Village Weaver	*Ploceus cucullatus*	X	
Estrildidae	Scaly-breasted Munia	*Lonchura punctulata*	X	
Fringillidae	Antillean Euphonia	*Euphonia musica*	X	
	Antillean Siskin	*Spinus dominicensis*	X	
Passerellidae	Grasshopper Sparrow	*Ammodramus savannarum*	X	
	Rufous-collared Sparrow	*Zonotrichia capensis*	X	
Phaenicophilidae	Black-crowned Palm-Tanager	*Phaenicophilus palmarum*	X	O
Spindalidae	Hispaniolan Spindalis	*Spindalis dominicensis*	X	
Icteridae	Hispaniolan Oriole	*Icterus dominicensis*	X	
	Shiny Cowbird	*Molothrus bonariensis*	X	
	Greater Antillean Grackle	*Quiscalus niger*	X	
Parulidae	Common Yellowthroat	*Geothlypis trichas*	X	
	Black-and-white Warbler	*Mniotilta varia*	X	
	Louisiana Waterthrush	*Parkesia motacilla*		
	Ovenbird	*Seiurus aurocapilla*	X	
	Northern Parula	*Setophaga americana*	X	
	Black-throated Blue Warbler	*Setophaga caerulescens*	X	
	Yellow-rumped Warbler	*Setophaga coronata*	X	
	Prairie Warbler	*Setophaga discolor*	X	
	Yellow-throated Warbler	*Setophaga dominica*	X	
	Palm Warbler	*Setophaga palmarum*	X	
	Pine Warbler	*Setophaga pinus*	X	
	American Redstart	*Setophaga ruticilla*	X	
	Cape May Warbler	*Setophaga tigrina*	X	
Thraupidae	Bananaquit	*Coereba flaveola*	X	
	Black-faced Grassquit	*Melanospiza bicolor*	X	
	Greater Antillean Bullfinch	*Melopyrrha violacea*	X	
	Yellow-faced Grassquit	*Tiaris olivaceus*	X	I

TABLE 2. Plant taxa with the ripe fruits detected in neighborhood plots around focal trees during the *Guarea* fruiting period and corresponding attributes. Dry pulp mass per fruit (g) measures were used to estimate (Source = "estimated") fruit biomass from abundance surveys.

Family	Species	Form	Seeds per Fruit	Dry Seed Mass	Dry Pulp Mass	Source
Araliaceae	*Dendropanax arboreus*	T	6	0.011	0.067	field measures
Arecaceae	*Roystonea hispaniolana*	T	1		0.2	estimated
Cannabaceae	*Trema micrantha*	T	1		0.005	field measures
Clusiaceae	*Clusia rosea*	T	211	0.011	2.6	field measures
Euphorbiaceae	*Alchornea latifolia*	T	2		0.03	estimated
	Sapium jamaicensis	T	2		0.03	estimated
Fabaceae	*Inga laurina*	T			0.385	equivalent relative
	Inga vera	T	7.5	0.211	0.385	field measures
Lauraceae	*Ocotea coriacea*	T	1		0.155	equivalent relative
	Ocotea leucoxylon	T	1	0.182	0.155	field measures
Melastomataceae	*Miconia* spp.	S	11	<0.0001	0.001	field measures
Meliaceae	*Guarea guidonia*	T	3	0.27	0.15	field measures
	Trichilia pallida	T	2.6	0.041	0.02	field measures
Moraceae	*Ficus americana*	T	144	<0.0001	0.07	field measures
Piperaceae	*Piper aduncum*	S	1,268	<0.0001	0.025	field measures
Primulaceae	*Mrysine coriacea*	T	1	0.009	0.002	field measures
	Parathesis crenulata	S	1		0.014	equivalent relative
	Waulenia laurifolia	T	1	0.018	0.014	field measures
Rubiaceae	*Psychotria* sp.	S	2	0.01	0.002	field measures
Sapindaceae	*Cupania americana*	T	3	0.153	0.336	field measures
Santalaceae	*Phoradendron* spp.	S	1	0.02	0.02	equivalent relative*
Urticaceae	*Cecropia schreberiana*	T	226	0.001	0.87	field measures
Verbenaceae	*Citharexylum fruticosum*	T	2	0.035	0.07	field measures
Vitaceae	*Cissus* sp.	V	1	0.03	0.02	field measures

Life forms: T – tree, S – shrub, L – liana. Attributes listed here include mean number of seeds per fruit, mean dry mass of a single seed, and mean dry mass of pulp from one fruit. Most measures were taken from a field collection. For rare species or those that were otherwise difficult to collect, I first conducted a literature search that included the Frubase data set (Jordano 2007). Measures for *Phoradendron* spp. were taken from a representative of the genus from Frubase.

TABLE 3. AIC table with ranking and relative support of candidate models that predicted the visitation rate of seed dispersers to focal trees. Tree ID and Observer ID were included as random effects.

Candidate Model	k	ΔAICc	LogLik	weight
day from fruit period midpoint	5	0.0	21.9	0.997
full model	9	11.3	25.3	0.003
focal tree ripe fruit density	5	25.4	12.0	<0.001
calendar day	5	26.4	11.5	<0.001
heterospecific fruit biomass	5	26.6	11.4	<0.001
Guarea fruit biomass	5	26.7	11.3	<0.001
Intercept	4	37.6	0.0	<0.001

TABLE 4. Top candidate model (with >99% weight) summary for visit rates of avian seed dispersers to focal study trees based on a generalized linear mixed hurdle model. The zero-inflated component of the model considered the binary result of all data points (i.e., whether or not any seed dispersers visited during focal observation). The conditional model considered the magnitude of the response for all non-zero data (i.e., only observations with at least one visit). Bold print indicates confidence intervals that do not include zero.

Variable	Zero-Inflated Model			Conditional Model		
	Estimate	95% CI	z-score	Estimate	95% CI	z-score
Intercept	-0.080	(-1.932, 1.771)	-0.085	-0.309	(-1.022, 0.405)	-0.848
day from fruit period midpoint	**-1.873**	**(-3.641, -0.105)**	**-2.077**	**1.1762**	**(0.674, 1.678)**	**4.594**

TABLE 5. Generalized linear mixed model summaries for the effect of neighborhood fruit biomass of *Guarea* and heterospecific species on *Guarea* dispersers and other frugivorous birds, respectively. Bold print indicates confidence intervals that do not include zero.

Variable	Abundance of *Guarea* Dispersers			Abundance of Other Frugivores		
	Estimate	95% CI	z-score	Estimate	95% CI	z-score
Intercept	**0.638**	**(0.263, 1.01)**	**3.34**	**1.624**	**(1.38, 1.87)**	**13.20**
Guarea fruit biomass	6.80e-3	(-6.38e-3, 2.00e-2)	1.01	-2.256e-3	(-1.24e-2, 7.90e-3)	-0.44
heterospecific fruit biomass	4.43e-4	(-2.66e-4, 1.15e-3)	1.22	**6.53e-4**	**(1.64e-4, 1.14e-3)**	**2.62**
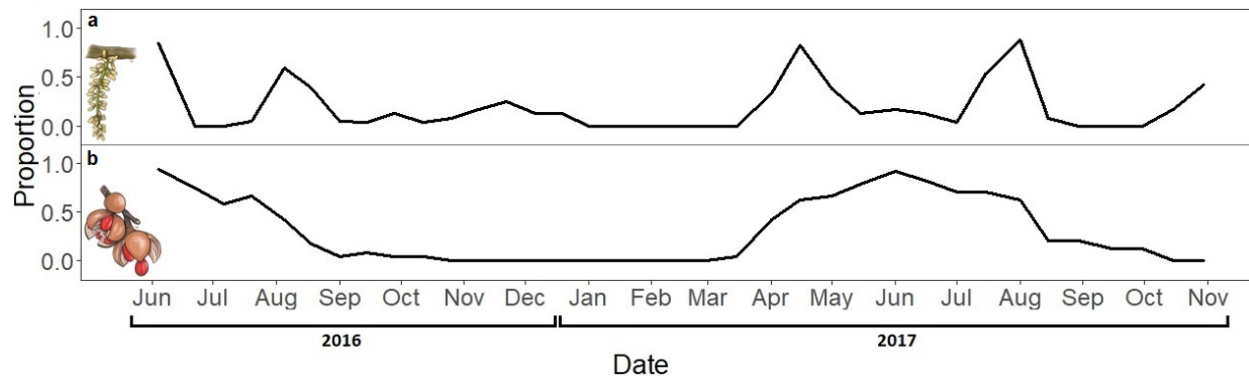
FIG. 1. (a) Blooming flower and (b) ripe fruit phenology observed in the *Guarea* study population (24 female trees) between June 2016 and October 2017 based on the proportion of individuals displaying reproductive characteristics on each biweekly survey.
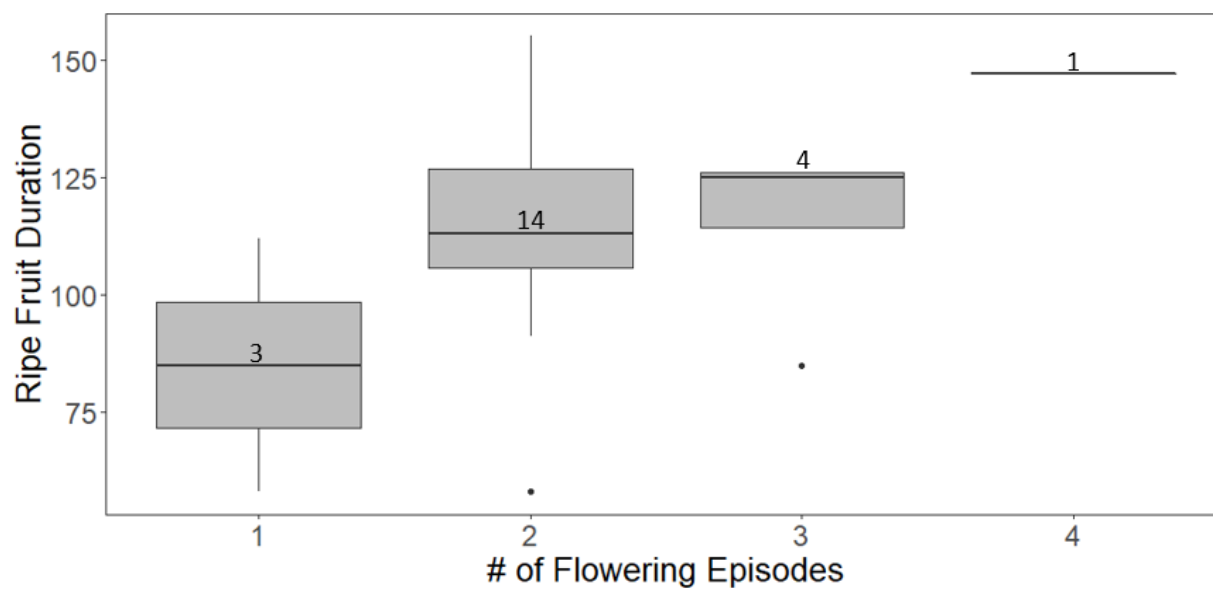
FIG. 2. The length of the ripe fruit phase of focal trees (i.e., number of days between first and last ripe fruits observed) by flowering frequency. Boxes show interquartile ranges with median line and with vertical lines showing minimum and maximum values. Sample size for each reproduction frequency class shown above the median marker. Two outliers are shown as black dots.
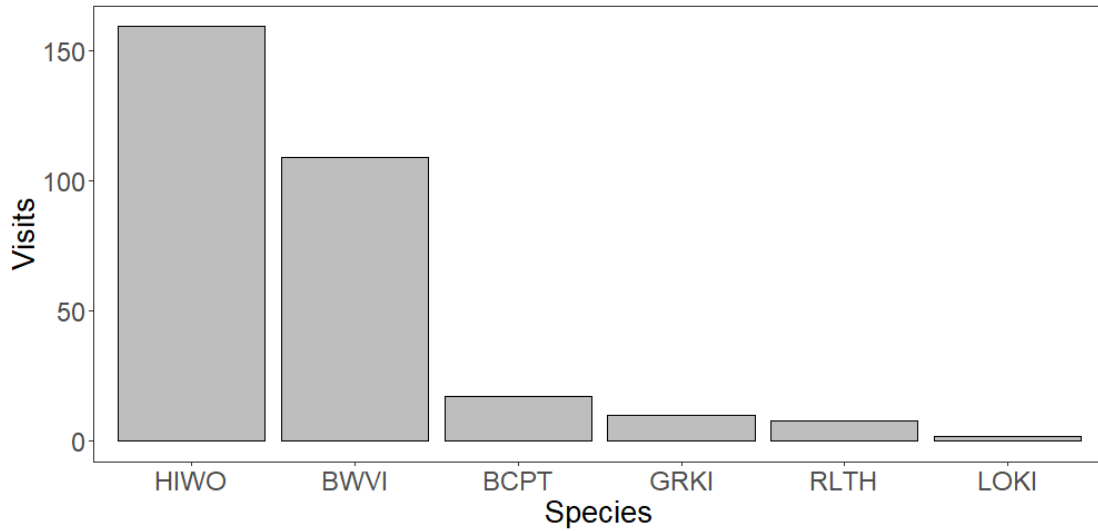
FIG. 3. Total visits to focal trees of all bird species that were observed feeding on *Guarea*. Species abbreviations: HIWO, Hispaniolan Woodpecker; BWVI, Black-whiskered Vireo; BCPT, Black-crowned Palm Tanager; GRKI, Gray Kingbird; RLTH, Red-legged Thrush (*Turdus plumbeus*); LOKI, Loggerhead Kingbird (*Tyrannus caudifasciatus*).
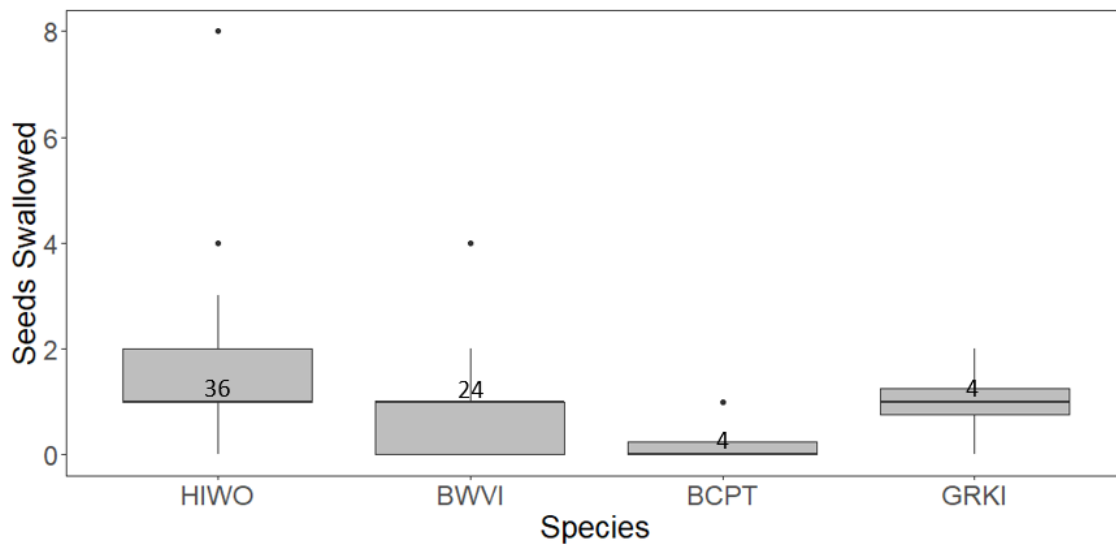
FIG. 4. The number of seeds swallowed by avian seed dispersers during visits for which individual activity at the tree was recorded. Sample size is indicated above median line as the number of individual birds for which behavioral observations were recorded. Species abbreviations are indicated on the legend for Fig. 3.
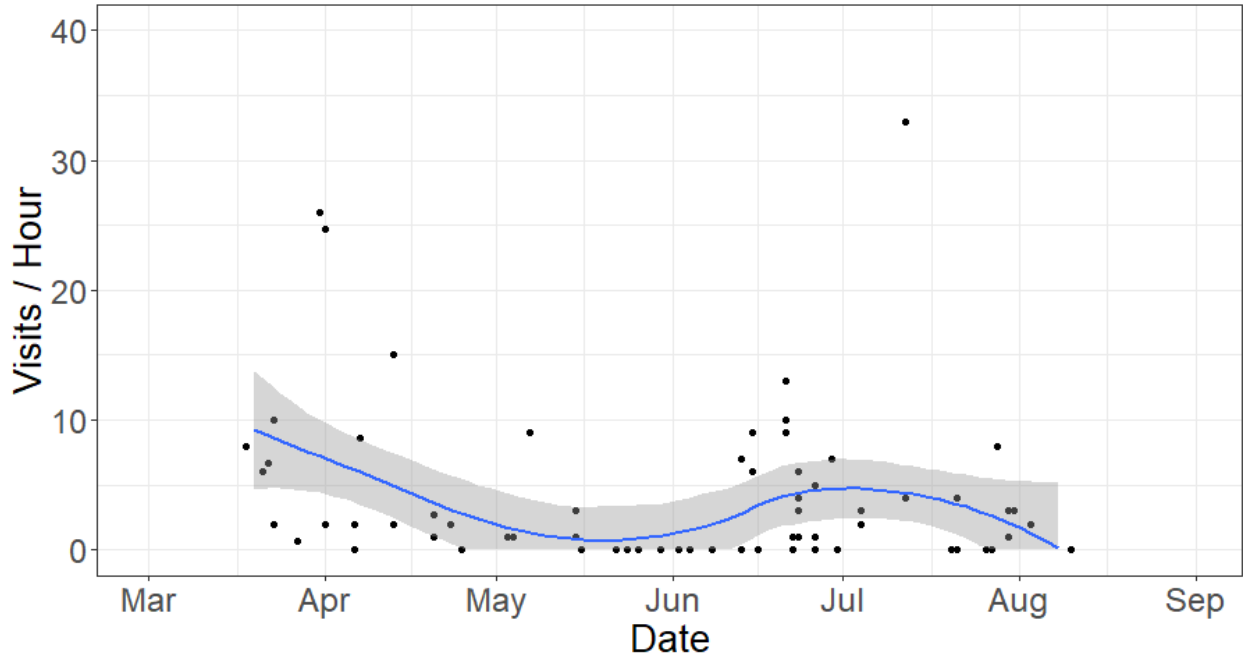
FIG. 5. Raw data on seed disperser visits to focal trees during the 2017 fruiting period with a fitted smoothing function (loess). The shaded gray region represents standard error. Visits were most frequent in foraging observations conducted near the beginning of the fruiting period when *Guarea* trees were first observed bearing ripe fruits. Visits declined into late May and June before reaching another peak extending through July and August.
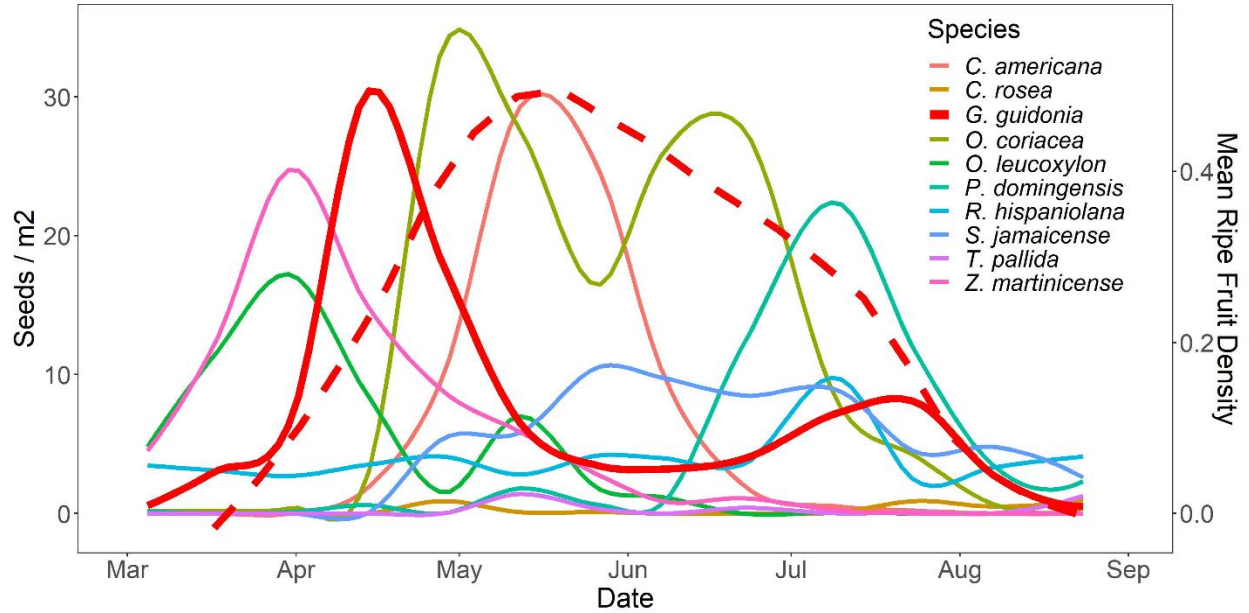
FIG. 6. Seed quantities sampled from traps (N = 20) at 14-day intervals throughout the *Guarea* fruiting period. A smoothing function (loess) was applied to better visualize peaks/troughs in the seed trap data. Displayed is a subset of species known from the diet of the two most important *Guarea* seed dispersers – Hispaniolan Woodpecker and Black-whiskered Vireo. The first peak in *Guarea* dispersal is in early April, but quickly diminishes as *Ocotea coracea* and *Cupania americana* become the most numerous seeds found in the traps. *Guarea* dispersal reaches a second, smaller peak during the month of July as these two species decline. Mean daily ripe fruit density for the *Guarea* study population is shown for reference (red dashed line) of relative *Guarea* fruit abundance in the study landscape.

CHAPTER 3

SEASONAL DYNAMICS OF TROPICAL PLANT-FRUGIVORE NETWORKS:

EVIDENCE FOR COMPETITION AND TEMPORAL NICHE PARTITIONING

3.1 INTRODUCTION

Seed dispersal mutualisms between fleshy-fruited plants and frugivorous animals are widely distributed in terrestrial ecosystems, and their co-dependence is believed to play a prominent role in assembling communities over ecological and evolutionary time scales (McKey 1975, Howe and Smallwood 1982, Jordano 1987b). The growing application of ecological networks to describe mutualistic relationships between plants and their seed dispersers has expanded the ability of ecologists to understand how communities are organized in ways that permit inference about evolutionary history (Jordano 1987b, Guimarães et al. 2011), ecological function (Reiss et al. 2009), stability (Thébault and Fontaine 2010), and conservation in the face of global change (Beunen and Hagens 2009, Tylianakis et al. 2010, Harvey et al. 2017). Studies of mutualistic networks from a wide range of ecosystems have revealed recurrent architectural patterns of interaction topology, suggesting the mechanisms shaping communities may be fundamentally similar (Jordano et al. 2003, Bascompte and Jordano 2007). Networks are, nevertheless, limited in addressing ecological questions related to community organization and dynamics, since they typically offer only a snapshot into complex systems that are undergoing continuous change (Blüthgen 2010, Olesen et al. 2011, Timóteo et al. 2018). The variability in species composition across space and time is fundamental to ecology, and recent studies of mutualistic interactions have focused on how species interactions vary both in response to and independently of species composition (Jost 2007, Poisot et al. 2015). Despite widespread

recognition of this variation, little is known about the role of these temporal dynamics in shaping communities and the mechanisms underlying the variation in species interactions (CaraDonna et al. 2020).

Plant-frugivore networks tend to exhibit highly nested topology (Jordano et al. 2003), with poorly connected "specialist" species disproportionately linked to highly connected "generalist" species within the core of the network (Bascompte et al. 2003, Ruggera et al. 2016). The apparent asymmetric dependence between generalist and specialist species resulting from a nested assembly is hypothesized to stabilize mutualistic communities by minimizing competition and reducing the likelihood of extinction for peripheral species (Bastolla et al. 2009, Zografou et al. 2020). Modular topology, while less pronounced in smaller networks, is characteristic of networks derived from diverse plant-frugivore communities (Donatti et al. 2011). Modules in ecological networks represent compartments of a subset of species that interact more frequently with one another than with other species in the community, and these modules are regarded as the fundamental units of measurable ecological and evolutionary outcomes (Bascompte and Jordano 2007, Olesen et al. 2007).

Species occupying the same module are predicted to have redundant function with respect to their mutualistic partners, insofar as the removal or reduction of one consumer species in a module is hypothesized to be compensated for by another consumer that disproportionately uses a similar set of resources, and vice versa for resources critical to consumer life history (Winfree and Kremen 2009, Schleuning et al. 2015). When frugivore or plant taxa share the same module with other taxa within the same guild, their disproportionate interactions with shared mutualist partners present contexts in which indirect effects such as facilitation and competition are more likely to be realized (Simmons et al. 2018a). Facilitation among frugivore species can occur

through aiding in the discovery of and access to resources (e.g., mixed species flocks), leading to more efficient use of a resource (Tubelis 2004). Alternatively, exploitative competition can occur when frugivores consume and deplete limiting fruit resources at a cost to their competitors (Bonaccorso et al. 2007). Similarly, plants producing ripe fruits simultaneously in the community can either facilitate one another by attracting frugivores and increasing their respective seed dispersal (Wheelwright 1985b, Burns 2002), or detract from one another's seed dispersal services when frugivores are limiting (Thompson and Willson 1979, Burns 2005). While some of these previously described mechanisms of interspecific facilitation and competition in seed dispersal mutualisms are known, their broader influence and relevance to communities remain unresolved.

The relative importance of taxa in plant-frugivore networks and roles within the community are determined by numerous factors. One of the primary limitations to potential links among mutualistic partners is the mismatch between species based on traits and phenology (Jordano et al. 2003, Olesen et al. 2010). In plant-frugivore networks, such mismatches (often referred to as "forbidden links") can either be manifested by key morphological differences between plant and animal taxa, such as the gape width of a bird's bill being insufficient to process and swallow diaspores of particular plant species, or by phenological uncoupling in life history, whereby plants produce fruits during a season when they are unavailable to species that seasonally migrate away from the location. Moreover, not all species are equally, nor obligately, dependent on mutualistic services for survival and reproduction (Fricke et al. 2017). Many frugivores alter resource use seasonally depending upon energetic and nutritional requirements. In a Mediterranean landscape in Spain, Carnicer et al. (2009) showed how network structure can change markedly as a result of temporary diet shifts from fruit to insects. Accounting for the

recruitment benefits of animal-dispersed plants and the proportion of dietary frugivory of avian seed dispersers has also demonstrated that taxa with a greater dependence on mutualistic services tend to have more mutualistic partners and occupy more core network roles (Fricke et al. 2017).

Phenology is not only a potential driver of the number of mutualistic partners, but also shapes interactions and their organization at the scale of the community (Encinas-Viso et al. 2012). Networks commonly characterize species as being generalist or specialist in addition to other species-level and community-level properties based on topology (Bascompte 2007). Yet, many relevant ecological processes take place on notably short time scales (CaraDonna et al. 2020). For example, the period of ripe fruit availability for some plant species can be limited to only a few short days or weeks. Similarly, the availability of fruit resources on short time scales can determine settlement patterns by frugivores and duration of patch use (Foster 1977, Levey 1988, Marshall et al. 2013). When communities are represented by networks aggregated from interaction data across an extended time period, species with shared mutualistic partners are surmised to be affiliated through indirect interactions. Yet, only a subset of these interactions are likely to be active across shorter time scales, thereby overrepresenting the connectivity of the network and largely overlooking the continuity of indirect interactions (Fig. 7). The temporal plasticity of interactions is due in part to species turnover (e.g., migration or varying timings of ripe fruit phases) but is also determined by "rewiring" based on consumer preference and behavior (Poisot et al. 2012, 2015, CaraDonna et al. 2017). The extent to which facilitation and competition play a determinant role in interaction rewiring has hitherto not been investigated in seed dispersal systems to the best of my knowledge.

In this study, I applied multilayer network analyses to examine the temporal dynamics of six local communities within an insular Caribbean tropical forest landscape. Over the course of

one year, I monitored continuously the abundance, phenology, and interaction patterns between plants and frugivorous birds during successive visits to sites. My objectives were to (1) characterize the spatial and temporal variability and turnover of species composition and interactions in plant-frugivore networks; (2) determine the drivers of species' functional roles relative to temporal stability of networks; and (3) test the hypothesis that temporal networks are nonrandomly structured by indirect effects mediated through facilitation or competition.

3.2 METHODS

Study Area

I selected six sites on private farmlands in the highlands of the Rio Yaque del Norte watershed in the La Vega and Santiago provinces of the Dominican Republic within approximately 15 km of the town Jarabacoa. Sites ranged 500–800 m above sea level and were representative of Hispaniola's sub-montane tropical wet forest ecosystems, characterized by fragmented habitat with mixed small-scale agricultural use. Only farms – or a collection of neighboring farms – with ≥25 ha of land were considered for the study. These farmland areas were characterized predominantly by pasture matrix with low-lying patches and corridors of riparian broadleaf humid forest with other habitats including pine stands, savanna, and residential gardens. In each of the farms selected, I assigned a transect grid array to indiscriminately sample all habitats within the study area. At each farm, I established an array of four fixed 500-m transect lines spaced 100 m apart to reduce the likelihood of double-counting birds among transects during surveys (Bibby et al. 1998). Linear distance between transects was confirmed using a GPS unit (Garmin eTrex 20x, Olathe, KS; accuracy 2–3 m) to account for variable incline among sites. All woody plants ≥3 cm dbh within 2 m of the transect lines at each site

were uniquely marked and identified (total sampling area = 0.8 ha per site). The total marked

population of plants among all research sites was 1,805 plants from 62 taxa. Taxa were identified

using a field guide and by reference collections with the aid of botanists at the Dr. Rafael Ma.

Moscoso National Botanical Garden in Santo Domingo (Liogier 1996). All study sites were

monitored for 12 months to capture the complete annual phenology of plant and frugivorous bird

populations. Data collection consisted of paired abundance survey-foraging observations with

14–21 days between sampling rounds (N = 21) at each site.

Abundance and Phenology Surveys

To measure the abundance of potential seed dispersers, observers conducted avian

surveys within 50 m of the transect lines at each site. Surveys were conducted within the first 4

hours following sunrise and the order of transect visitation was randomized among sampling

rounds to minimize local detection bias based on time of day. Surveyors trained to recognize

local bird species by visual and auditory cues walked transect lines at a standard pace of ~ 11 m

min^{-1} to record and count detections of all bird species.

Fruit resource abundance was measured by visiting each of the plants marked on the

transects on the same day as avian surveys. Fruit quantities – measured separately for ripe and

immature – were estimated using a semi-logarithmic scale index ("fruit abundance index"; i.e., 1

= 1–10; 2 = 11–50; 3 = 51–100; 4 = 101–500; 5 = 501–1,000; 6 = 1,001–5,000; 7 = 5,001–

10,000; 8 = 10,000+) (Saracco et al. 2005, Blendinger and Villegas 2011).

Frugivory Observations

After completing the transect abundance surveys on the first day of the sampling visit,

observers sampled plant-frugivore interactions by observing foraging activity at marked focal plants the following day. All sites received equal sampling effort, with two observers devoting 5 hours to observations following sunrise. Foraging observations were assigned such that all species detected with ripe fruits were observed at least once at the site but with an upper limit of no more than five observations per plant species to avoid oversampling common plant species. In some cases, such as when few plants bore ripe fruits or rare species not represented in the marked population were incidentally detected near the transect trails, unmarked plants within view of the transects were also observed. Observations were made by an observer seated quietly at least 10 m away from the focal plant. The observer would commit a minimum of 15 min to observing the crown space of the plant to record and identify all avian visitors. All plants were monitored for 30 min unless there were no visits in the initial 15 min. By limiting observations to 15 min at plants where no visitors were observed, I could maximize the number of plants observed with interactions during a survey day, while also quantifying a representative sample of foraging interactions at the local site. For each avian visitor, the observer recorded the duration of the individual at the plant and whether the individual fed on fruits, did not feed, or the observer was unable to determine if feeding had occurred. For analyses, visits where fruits were not consumed were not used. Visits where observers were unable to determine whether fruit was consumed were included only if the bird species involved was known to consume fruits of the plant species being observed (i.e., a likely frugivory event, approximately 35% of observations).

Assembling Network Data

I compiled all network data into biadjacency matrices with columns representing frugivore species and rows representing plant taxa. Data for each of the six sites were compiled

in three ways by aggregating interactions recorded from: (1) clusters of 3 consecutive visits to each site (i.e., temporal network series for each of six sites), (2) all visits at each site (i.e., site networks), and (3) all visits to all sites (i.e., regional network). In the former-most approach described, temporal networks were partitioned into 7 periods representing a mean of 52 days in length (Yang et al. 2013). I chose to aggregate data in this manner to account for imperfect detection of species and their interactions during sampling rounds. I considered that shorter period lengths of 15–30 days (i.e., 1–2 visits per period) were likely to exclude sampling of certain plant species from the network whose ripe fruits were being dispersed by birds in the landscape but were either not yet ripe or already depleted in the select number of plants along my transects at the site. The chosen period length, therefore, offered sufficiently inclusive and realistic snapshots of all the taxa involved in frugivory during each period at a site.

Network-level Properties

I generated indices of network topology for all networks and temporal subnetworks using the "networklevel" function of the "bipartite" package (Dormann et al. 2008) in R 3.5.1 (R Development Core Team 2020). From these calculations, I examined weighted interaction nestedness to quantify the hierarchical organization of networks according to their core-periphery structure (Galeano et al. 2009). I assessed whether the temporal layers of each network were nested by comparing values with those of 1,000 null networks created with Patefield's algorithm (Patefield 1981), which randomizes interactions across the matrix while maintaining consistent marginal row and column totals. Weighted interaction nestedness (WIN) was considered statistically different from the null distribution of interactions if the z-score was +/- 1.96 standard deviations from the mean (Trøjelsgaard et al. 2015). Additionally, I analyzed the temporal

variability of network composition using a Beta-diversity approach developed by Poisot et al.

(2012), employing the "betalinkr" function, adapted for weighted networks by using a

partitioning approach that maintains a constant common denominator for the dissimilarity index

between the two networks. Link turnover between two network matrices (β_{WN}) was decomposed

into two underlying mechanisms: turnover caused exclusively by species turnover (β_{ST}) and

turnover caused by the rewiring of interactions between species present in both networks (β_{OS}).

(1) $\beta WN = \beta ST + \beta OS$

Species-level Properties

I used the "specieslevel" function of the package bipartite to generate summaries for the

relative importance and function of bird and plant taxa in each of the aggregated local networks.

I produced degree (i.e., number of mutualistic partners) and a weighted measure of strength (s) to

estimate the relative importance of particular species in the network based on the cumulative

proportional dependence of the members of the opposing guild on that species, measured by the

sum of the interaction frequencies (w) for each link (a) between species (i & j) (formula 2,

Bascompte et al. 2006, Gilarranz et al. 2012).

(2) $s_i = \sum_{j=1}^{N} a_{ij} w_{ij}$

Species degree was also calculated for the aggregate regional network for purposes of

comparisons among taxa in their overall number of documented mutualistic partners in the study

system.

To account for any phenological shifts in networks with time, I calculated species

multilayer versatility (hereafter "versatility") for each of the local networks. This metric is a

multilayer measure of centrality that quantifies the relative importance of species both through

their interactions within a layer of the network as well as between subsequent layers through their sustained presence within the system across time (De Domenico et al. 2015, Timóteo et al. 2018, Costa et al. 2020). I calculated versatility measures for each local network using the PageRank algorithm (Brin and Page 2012), which computes the steady-state solution of a random walk through existing intralayer edges with a probability p and a "teleportation" with a probability $1-p$ relative to any node in the multilayer network. The calculations were made using the program muxViz (De Domenico et al. 2015), after first transforming the biadjacency matrixes into a unipartite projection using Newman's method (Newman 2001) adapted for weighted networks (i.e., pairwise links quantified by interaction frequency) in the R package "tnet" (Opsahl 2009, 2013). Within the muxViz GUI, I selected the option "edge-colored network" for multilayer network type and chose ordinal interlayer links, which allows only teleportation of species state nodes between subsequent layers through time periods (i.e., layer "t" to layer "t + 1") with a value of 1 when those species are present in both layers.

I assessed the correlation of species degree, strength, and versatility values generated as well as compared their variability from plots. Furthermore, I used generalized linear mixed models (R package "lme4") to evaluate hypotheses of whether phenology or species attributes predict their function in plant-frugivore networks. Within the context of this study, I measured phenological variation as the coefficient of variation of the abundance of each species across temporal layers (out of a total of 7 periods ≈ 1 year), independently of whether or not interactions were recorded. Models were fitted separately for bird and plant taxa, using a Gamma error distribution. For the bird versatility dataset, models were fitted from combinations of fixed factors (phenology, body mass, and proportion dietary frugivory). Both body mass and proportion frugivory were obtained from Wilman et al. (2014). Models for plant versatility data

included combinations of fixed effects of phenology, seed diameter (measured from a field collection), and growth form (categorically defined as: 1 = tree, 2 = shrub, 3 = epiphyte/vine/mistletoe). All models included both site and species as random effects. I used R packages "bblme" and "MuMIn" for AIC model selection. I ranked a priori candidate models using Akaike's Information Criterion (AICc) values for small sample sizes (Burnham and Anderson 2003), and I considered all models with ΔAICc < 10 to show measurable support.

Multilayer Temporal Analysis

I applied a multilayer analysis of the local networks modeled as an ordinal progression through seven temporal layers. Within this framework, the temporal layers of the network were connected through a third dimension via interlayer edges. In addition to species being connected to other species' nodes through standard intralayer edges, each species was also assigned a "state node" that linked to its corresponding state node in previous and subsequent layers of the network, representing the persistence of that species in the system across time (Kivelä et al. 2014, Pilosof et al. 2017). For the analysis presented here, I weighted interlayer edges based on the change in relative abundance of species i between consecutive time periods: abundance i(t + 1)/abundance i(t) (Costa et al. 2020). For each layer of each local network, I used the median fruit abundance index value for the three ripe fruit counts from each marked plant along the study transects during each survey period and converted those values back to raw values (e.g., fruit abundance index of 3, 51–100 fruits, was assigned a value of 75) that were then summed to produce a site-level relative density estimate for each species. If a species was not involved in any of the two consecutive layers of the network, its interlayer edge for that step was set to 0. A Louvain algorithm (Blondel et al. 2008) was used in MATLAB (MathWorks, Inc.) to maximize

modularity over 1,000 runs using code originally from Jutla et al. (2014), later adapted for bipartite networks by Pilosof et al. (2017). Using this method, modules are resolved in such a way as to span across layers of the network while still allowing variation in their species composition among layers. To determine whether the observed modularity predicted by the algorithm differed from a randomly generated network, I compared observed modularity against the distribution of modularity values from 1,000 randomized networks, created with the Patefield algorithm in the R package "vegan" using the "r2dtable" option (Oksanen et al. 2015).

From the resulting modularity output for each network, species were assigned to modules with module membership permitted to vary dynamically among time periods. Using this output, I created a data array representing the co-occurrence of species membership in different temporal modules. I adapted the traditional format of species co-occurrence matrices to use "module ID x time period" in place of site, thus tracking the instances where different species occupy the same module during the same period. I used the R package "EcoSimR" to analyze the structure of temporal module co-membership to test the hypothesis that species were nonrandomly distributed. The "cooc null model" function was applied to bird and plant data sets separately, using the "SIM9" randomization algorithm (Connor and Simberloff 1979) to compare the observed C-score to a mean C-score of 1,000 randomized co-occurrence networks. The C-score was based on the mean number of checkerboards between all possible taxon pairs in a matrix (Stone and Roberts 1990). The standardized effect size and p-value were used to evaluate whether differences were statistically different (Gurevitch et al. 1992, Gotelli and McCabe 2002). An observed C-score significantly greater than the null indicated an exclusionary pattern with taxa sorted into the same modules less frequently than expected by chance, while a significantly lower score implied aggregation where species share module space more frequently

than expected by chance (Stone and Roberts 1990). Within this framework of temporal module co-membership, I interpreted exclusion patterns within an assemblage to imply a prevailing influence of competition and niche partitioning on communities, while aggregation would imply facilitation.

3.3 RESULTS

Over the annual sampling period, I recorded 7,697 frugivorous interactions from 2,025 focal observations on fruiting plants. The aggregate regional network from data compiled across all local networks included 53 plant and 44 bird species for a total of 356 unique pairwise interactions. Four resident frugivorous bird species were present consistently at local sites and accounted for 85% of all interactions in the regional data set: Palmchat (*Dulus dominicus,* Dulidae) 59.7%, Hispaniolan Woodpecker (*Melanerpes striatus*, Picidae) 9.1%, Black-crowned Palm Tanager (*Phaenicophilus palmarum*, Phaenicophilidae) 8.5%, and Black-whiskered Vireo (*Vireo altiloquus*, Vireonidae) 6.6%. The distribution of observed interactions among plant taxa was considerably more even, likely owing to their comparatively ephemeral and varied incidence of fruits among sites. The species with most frugivory events recorded included: *Roystonea hispaniolana* (Arecaceae) 13.6%, *Ficus americana* (Moraceae) 12.5%, *Cecropia schreberiana* (Urticaceae) 9.0%, *Cupania americana* (Sapindaceae) 8.3%, and *Clusia rosea* (Clusiaceae) 6.5%.

Network Patterns and Spatiotemporal Consistency

All but four of the 42 (6 x 7) subnetworks analyzed were significantly more nested than predicted by null networks and none were less nested (Table 6). Interaction turnover between

temporal layers of the network, on average, was attributed more to species turnover (mean β_{ST} = 0.411) than rewiring (mean β_{OS} = 0.344). Within the component of interaction turnover caused by species turnover, turnover of fruit resources was the primary contributor (mean $\beta_{ST.lower}$ = 0.322), while turnover of birds accounted for considerably less (mean $\beta_{ST.lower}$ = 0.049).

Species Roles

Species' versatility correlated strongly with both their degree and strength for both birds and plants (Fig. 8). In my analyses of species attributes as predictors of versatility, I found that phenology – expressed as the coefficient of variation of bird/fruit species abundance between periods – was consistently included in the top-ranked models for both plants and birds (Table 7). For both sets of taxa, species with higher temporal variation in abundance were less influential on the temporal cohesion of the network (Table 8). While traits did not predict versatility for birds, plant taxa with smaller seed diameter and larger growth forms (i.e., trees) had greater versatility.

Temporal Modular Structure

The overall multilayer networks were significantly more modular than expected by chance (Table 9). The number of modules identified from each local network ranged from 4 to 8 (median and mode = 5). I found statistically significant patterns of species co-occurrence in temporal modules in the local networks (Table 10). Bird assemblages from all six sites showed a statistically significant positive standardized effect size (i.e., exclusion pattern), indicating that species nonrandomly segregated from shared module membership across time periods. Two sites had plant assemblages exhibiting this same exclusion pattern, while the other four did not.

3.4 DISCUSSION

Despite the continuous turnover in species and their interactions, network structure remained relatively stable across temporal layers of the communities sampled. Nearly all subnetworks were more nested than expected, and deviations from nested configuration did not correspond to any specific period. Mutualistic networks, from both pollination and seed dispersal studies, are widely recognized for their nonrandom tendency toward a nested topology (Jordano et al. 2003). Past studies from pollination systems have identified the tendency of mutualistic networks across time to show consistent network-level topological properties such as nestedness, despite high variation in species composition and interaction among species (Olesen et al. 2011). Comparatively fewer studies from seed dispersal systems have examined temporal changes in interspecific relationships and resulting system-level properties. A study from a similar forest community to the present study, in the neighboring island of Puerto Rico, found no nested structure among birds and plants across temporal subnetworks (Yang et al. 2013). "Opportunistic attachment" has been proffered as a potential mechanism for assembly patterns observed in temporally variable pollination networks, where species flexibly change partner affiliation in a context-dependent manner as a result of consumer preference and rewiring interactions (CaraDonna et al. 2017, Ponisio et al. 2017). A substantial proportion of interaction turnover from the multilayer temporal networks was accounted for by rewiring, independent of species turnover, reflecting a high degree of plasticity and generality consistent with this pattern.

The species-level analyses conducted here underscore the importance of phenology in determining the role of species and their function within networks. Species with lower temporal variation in abundance consistently had greater versatility values and, thus, disproportionate

influence on maintaining other species in the network over time. The physical and ecological traits of species were useful predictors for plant taxa, but not birds. In the case of frugivorous birds, body size typically correlates strongly with bill gape width and, thus, determines the size of seeds and diaspores that are handled and swallowed (Wheelwright 1985a). Consequently, both large frugivores and small-seeded plants are likely to have disproportionate influence in dispersal networks mediated through a wider array of mutualist partners (Olesen et al. 2010). Plant taxa exhibited such a relationship with respect to their contribution to the temporal cohesion of networks, with small-seeded trees exhibiting disproportionate importance in multilayer networks. The abundance of large-bodied birds tends to be comparatively low in island ecosystems and anthropogenically disturbed areas (Heinen et al. 2018). Indeed, small-bodied birds in similar tropical landscapes are typically the most dominant and widespread seed dispersers in such anthropogenically disturbed systems (Emer et al. 2018). My study system is similarly dominated by small-bodied (< 100 g) seed dispersers typical of islands and from historic selective harvesting of larger native frugivores (e.g., Psittacidae, Columbidae, Trogonidae) as well as loss of forested habitat from human activities (Latta 2005).

The strong effect of phenological variability in abundance on species versatility is consistent with the results of previous studies of temporal networks in seed dispersal systems in which resident frugivore species and plants with extended fruit production typically occupy highly connected core roles within the community (Olesen et al. 2008, González-Castro et al. 2012, Yang et al. 2013). For example, species involved in frugivory over a protracted period of months in a network sampled from forests in Puerto Rico have a greater number of mutualist partners (Yang et al. 2013). Similarly, Costa et al. (2020) showed a strong correlation between the number of sample years that species engaged in frugivory/dispersal interactions and

versatility in an interannual temporal network from Portugal. Nevertheless, my study takes this question of temporal stability a step further by considering the consistency of consumer and resource abundance in the system at a seasonal temporal scale. Here, I showed that taxa with steady abundances contributed disproportionately more to the temporal dynamics and stability of communities, through providing consistent links with mutualistic partners across time periods.

All multilayer network models of the local communities produced in my analyses exhibited clear structuring of modules over time. Bird and plant species were less likely to co-occur in the same module at the various temporal intervals than expected by random chance. This finding implies a general tendency of species to partition interactions in such a way as to avoid sharing the same mutualist partners. While the specific mechanisms of module sorting are beyond the scope of the current study, the patterns are indicative of pronounced differences in the feeding niche and seed dispersal contributions of frugivores. Basic differences in feeding preferences caused by morphological and metabolic attributes likely play a fundamental role in module affiliation. The exclusionary patterns detected in avian modules, however, point to competition as a likely factor shaping temporal changes in resource preference. In a previous study at one of my research sites, I found evidence of competition among plants mediated through resource-switching behavior of avian frugivores where seed dispersal of *Guarea guidonia* was greatly reduced when ripe fruits of *Cupania americana* and *Ocotea* spp. became available in the landscape (Schubert and Walters 2022). Here, my temporal network analyses further show that avian species with considerable overlap in fruit resource use overall also partition their resource use over time and frequently sort into different modules from one another across periods. For example, Red-legged Thrush (*Turdus plumbeus*) and Black-crowned Palm Tanager fed on fruits of 22 shared species in the study region, representing 62.8% of the total

number of collective links. However, these two frugivores were placed in the same module in only 27.3% of co-occurrences in spatio-temporal subnetworks. The two frugivores tended to share the same module during periods when they fed on species such as *Cupania americana*, *Bunchosia glandulosa*, *Miconia* sp., and *Vitis* sp. but their differentiation was more likely to occur when Red-legged Thrush fed more heavily on such species as *Dendropanax arboreus*, *Chrysophyllum argenteum*, and *Ocotea* spp. and Black-crown Palm Tanager on *Phoradendron* spp., *Clusia rosea*, and *Guarea guidonia*. Previous studies have hypothesized that increasing fruit richness in a community should reduce interspecific competition among frugivorous birds through a reduction in dietary overlap (Blüthgen et al. 2007, Chama et al. 2013). My results further elucidate the importance of spatio-temporal context in this process and point to temporal switches in consumer-resource relationships as likely playing a prominent role in reducing competition.

One of the principal challenges to assessing the effects of species attributes on ecological processes such as seed dispersal is the paucity of life history information on biota from vulnerable locations such as Hispaniola and other Caribbean islands. Of the 44 avian species identified in my networks, 14 of these were previously classified as not being frugivorous (Wilman et al. 2014). My a priori expectation of these taxa, based on published literature, was that they would have low mutualistic dependence. However, several of these species, most notably the two tody species (*Todus angustirostris* and *T. subulatus*) and the Bananaquit (*Coereba flaveola*) were among the most represented frugivores in my study system relative to interaction frequency and species importance measures. Such observations underscore the previous knowledge gap in the ecology of the birds of Hispaniola and suggest similar gaps across other Caribbean islands.

Modules identify contexts in which species are using a similar set of resources, or are being selected by a similar set of consumers, and are the fundamental network unit within which species potentially facilitate or compete with one another (Schleuning et al. 2015). Multilayer modules present an opportunity to examine the plasticity of species' niches through module membership. Nonrandom structuring of module composition of avian and, to a more limited extent, plant taxa in my study provide strong support for temporal niche partitioning, suggesting that competition rather than facilitation structures species relationships and their variability across time through behavioral and resource-selection patterns of frugivores.

My results reveal novel insights into how temporal dynamics are realized within communities of plants and their seed dispersers. By nature of the diffuse, generalized relationships between plant and frugivore taxa arrayed in complex networks, for every direct pairwise interaction, many other indirect links are formed. Although indirect interactions in mutualistic communities have been recognized for their role in shaping stable systems and long-term dynamics leading to coevolution among taxa (Stachowicz 2001, Bastolla et al. 2009, Guimarães et al. 2017), the ecological consequences of short-term dynamics that vary across space and time remain poorly understood.

Despite increasing recognition of the temporal variation in species interactions of mutualistic networks, few studies have empirically addressed the factors or mechanisms that contribute to the temporal plasticity of mutualistic relationships in plant-frugivore communities (CaraDonna et al. 2020). Functional redundancy—whereby taxa exhibit overlap in their mutualistic partners rather than exclusive relationships—is a well-recognized feature of plant-frugivore networks that is associated with greater stability and robustness to extinction events (Bastolla et al. 2009, Brodie et al. 2014). The prevalence of functional redundancy and high

degree of convergence observed in plant and animal morphologies in mutualistic networks has led previous studies to infer that interspecific facilitation is likely more influential than competition in the assembly and evolution of communities (Rathcke 1983, Ghazoul 2006, Albrecht et al. 2015). However, short-term community dynamics of mutualistic systems, such as those detailed in the present study, present a contrary outlook. Further studies of the temporal dynamics within plant-frugivore networks are needed to determine the consistency of these patterns in other mutualistic communities as well as to further elucidate the ecological and evolutionary significance of indirect interactions.

TABLE 6. Nestedness values for all temporal subnetworks and significance scores based on null models. Values identified as significantly different than null expectation are shown in bold face.

Site	Period	Nestedness	Mean Null (95% CI)	SD	z-score
Hatillo	1	**0.4125**	**0.3235 (0.2887, 0.3636)**	**0.0197**	**4.5146**
Hatillo	2	**0.4520**	**0.2868 (0.2634, 0.3134)**	**0.0136**	**12.1898**
Hatillo	3	0.5156	0.5481 (0.4791, 0.6304)	0.0382	-0.8499
Hatillo	4	**0.5567**	**0.4513 (0.3944, 0.5152)**	**0.0313**	**3.3693**
Hatillo	5	**0.7825**	**0.5417 (0.4563, 0.6547)**	**0.0509**	**4.7315**
Hatillo	6	**0.5062**	**0.3494 (0.3104, 0.3905)**	**0.0207**	**7.5770**
Hatillo	7	**0.6095**	**0.4497 (0.3995, 0.5003)**	**0.0267**	**5.9878**
Brache Farm	1	0.3879	0.4043 (0.3570, 0.4577)	0.0262	-0.6272
Brache Farm	2	**0.5356**	**0.4548 (0.3892, 0.5325)**	**0.0366**	**2.2082**
Brache Farm	3	**0.5187**	**0.2953 (0.2631, 0.3293)**	**0.0176**	**12.7128**
Brache Farm	4	**0.6266**	**0.4086 (0.3660, 0.4563)**	**0.0238**	**9.1545**
Brache Farm	5	**0.8364**	**0.6311 (0.5686, 0.7119)**	**0.0363**	**5.6600**
Brache Farm	6	0.6942	0.6328 (0.5600, 0.7123)	0.0396	1.5503
Brache Farm	7	**0.5915**	**0.4453 (0.3968, 0.5013)**	**0.0265**	**5.5113**
Las Auyamas	1	**0.5656**	**0.4531 (0.3962, 0.5135)**	**0.0305**	**3.6824**
Las Auyamas	2	**0.3919**	**0.2483 (0.2230, 0.2759)**	**0.0141**	**10.1471**
Las Auyamas	3	**0.4465**	**0.3659 (0.3238, 0.4093)**	**0.0215**	**3.7417**
Las Auyamas	4	**0.6125**	**0.4822 (0.4259, 0.5394)**	**0.0293**	**4.4440**
Las Auyamas	5	**0.6764**	**0.5405 (0.4731, 0.6106)**	**0.0363**	**3.7460**
Las Auyamas	6	**0.6434**	**0.4889 (0.4272, 0.5589)**	**0.0341**	**4.5303**
Las Auyamas	7	**0.4201**	**0.3376 (0.3022, 0.3767)**	**0.0195**	**4.2399**
Llano de Higos	1	0.5400	0.5147 (0.4510, 0.5910)	0.0353	0.7162
Llano de Higos	2	**0.5344**	**0.4239 (0.3750, 0.4796)**	**0.0273**	**4.0533**
Llano de Higos	3	**0.5159**	**0.3792 (0.3324, 0.4301)**	**0.0247**	**5.5281**
Llano de Higos	4	**0.6361**	**0.4896 (0.4235, 0.5733)**	**0.0391**	**3.7501**
Llano de Higos	5	**0.7175**	**0.5224 (0.4589, 0.5852)**	**0.0313**	**6.2407**
Llano de Higos	6	**0.6176**	**0.5257 (0.4579, 0.6100)**	**0.0388**	**2.3701**
Llano de Higos	7	**0.6518**	**0.4801 (0.4211, 0.5420)**	**0.0316**	**5.4356**
Vazquez Farm	1	**0.7306**	**0.5768 (0.5118, 0.6537)**	**0.0370**	**4.1575**
Vazquez Farm	2	**0.4389**	**0.3469 (0.3132, 0.3817)**	**0.0178**	**5.1655**
Vazquez Farm	3	0.5200	0.5029 (0.4354, 0.5814)	0.0374	0.4576
Vazquez Farm	4	0.6100	0.5275 (0.4430, 0.6284)	0.0479	1.7220
Vazquez Farm	5	**0.5680**	**0.3930 (0.3508, 0.4402)**	**0.0230**	**7.6043**
Vazquez Farm	6	**0.7029**	**0.5859 (0.5046, 0.6731)**	**0.0426**	**2.7471**
Vazquez Farm	7	**0.4784**	**0.4086 (0.3593, 0.4626)**	**0.0265**	**2.6373**
Vera del Yaque	1	**0.4999**	**0.3906 (0.3499, 0.4408)**	**0.0244**	**4.4800**
Vera del Yaque	2	**0.5458**	**0.4076 (0.3617, 0.4608)**	**0.0257**	**5.3829**
Vera del Yaque	3	**0.4968**	**0.3362 (0.2974, 0.3809)**	**0.0212**	**7.5653**
Vera del Yaque	4	**0.5152**	**0.4184 (0.3763, 0.4660)**	**0.0236**	**4.1043**
Vera del Yaque	5	**0.5862**	**0.3798 (0.3431, 0.4168)**	**0.0185**	**11.1284**
Vera del Yaque	6	**0.6048**	**0.4566 (0.4151, 0.5000)**	**0.0218**	**6.7981**
Vera del Yaque	7	**0.6055**	**0.4720 (0.4228, 0.5218)**	**0.0250**	**5.3315**

TABLE 7. AIC table showing the ranking and relative support of candidate models to predict the temporal versatility of frugivorous birds and plants. Site ID and Species ID were included as random effects.

Frugivore Taxa					Plant Taxa				
Model	K	ΔAICc	LogLik	Weight	Model	K	ΔAICc	LogLik	Weight
Phen	3	0.0	22.3	0.43	Phen+Diam+Form	5	0.0	17.5	0.706
Phen+Frug	4	0.7	23.0	0.30	Phen+Form	4	2.9	15.0	0.168
Phen+Mass	4	2.1	22.3	0.15	Phen+Diam	4	4.8	14.0	0.063
Phen+Mass+Frug	5	2.6	23.1	0.12	Phen	3	4.8	12.9	0.063
Intercept	2	42.5	0.0	<0.001	Diam+Form	4	21.9	5.5	<0.001
Frug	3	43.1	0.7	<0.001	Form	3	26.8	2.0	<0.001
Mass+Frug	4	44.2	1.2	<0.001	Diam	3	27.3	1.7	<0.001
Mass	3	44.2	0.2	<0.001	Intercept	2	28.6	0.0	<0.001

TABLE 8. Model-averaged summaries of variables across candidate models in predicting the temporal versatility of bird species in local networks. Parameters with coefficient estimates whose confidence intervals do not overlap zero are in bold.

Frugivore Taxa					Plant Taxa				
Variable	β	SE	95% CI	z-score	Variable	β	SE	95% CI	z-score
Intercept	**-2.47**	**0.230**	**(-2.93, -2.02)**	**10.68**	**Intercept**	**-1.79**	**0.48**	**(-2.73 -0.85)**	**3.74**
Phenology	**-0.482**	**0.065**	**(-0.609, -0.354)**	**7.40**	**Phenology**	**-0.377**	**0.073**	**(-0.521, -0.232)**	**5.09**
Mass	-0.0085	0.0420	(-0.181, 0.119)	0.840	**Form**	**0.318**	**0.181**	**(0.080, 0.647)**	**1.75**
Frugivory	0.0029	0.0047	(-0.003, 0.017)	0.532	**Diameter**	**-0.165**	**0.122**	**(-0.400, -0.030)**	**1.35**

TABLE 9. Mean Q values and 95% confidence intervals for each site, and the resulting number of modules identified by the Louvain algorithm. All observed values were significantly different from their respective nulls.

Site Code	Q_{obs} (95% CI)	Q_{null} (95% CI)	# modules
Hatillo	0.5021 (0.4974, 0.5054)	0.3575 (0.3487, 0.3670)	5
Brache Farm	0.4964 (0.4957, 0.4968)	0.4840 (0.4833, 0.4847)	6
Las Auyamas	0.5105 (0.5058, 0.5140)	0.3127 (0.3034, 0.3233)	4
Llano de Higos	0.5276 (0.5239, 0.5305)	0.4625 (0.4573, 0.4686)	5
Vazquez Farm	0.5390 (0.5317, 0.5433)	0.3818 (0.3728, 0.3911)	5
Vera del Yaque	0.5070 (0.5063, 0.5076)	0.4952 (0.4942, 0.4963)	8

TABLE 10. Standardized effect size values of C-score generated from 1,000 simulated modularity co-occurrence matrices for each of the six sites. An observed C-score significantly greater than the null indicated an exclusionary pattern (i.e., competition) with taxa sorted into the same modules less frequently than expected by chance, while a significantly lower score implied aggregation (i.e., facilitation) where species share module space more frequently than expected by chance Statistically significant statistics are presented in bold text.

Site	Frugivore Taxa			Plant Taxa		
	Obs. C-score	Null C-score	p-value	Obs. C-score	Null C-score	p-value
Hatillo	**6.4923**	**3.247**	**<0.001**	4.3494	-0.8024	0.805
Brache Farm	**6.4**	**1.450**	**0.048**	5.2387	1.314	0.096
Las Auyamas	**8.5692**	**2.012**	**0.034**	4.3219	1.329	0.114
Llano de Higos	**6.7489**	**4.945**	**<0.001**	**6.0936**	**2.741**	**0.01**
Vazquez Farm	**6.2933**	**2.539**	**0.019**	**5.1046**	**1.665**	**0.049**
Vera del Yaque	**7.6797**	**3.142**	**<0.001**	3.8369	1.422	0.116
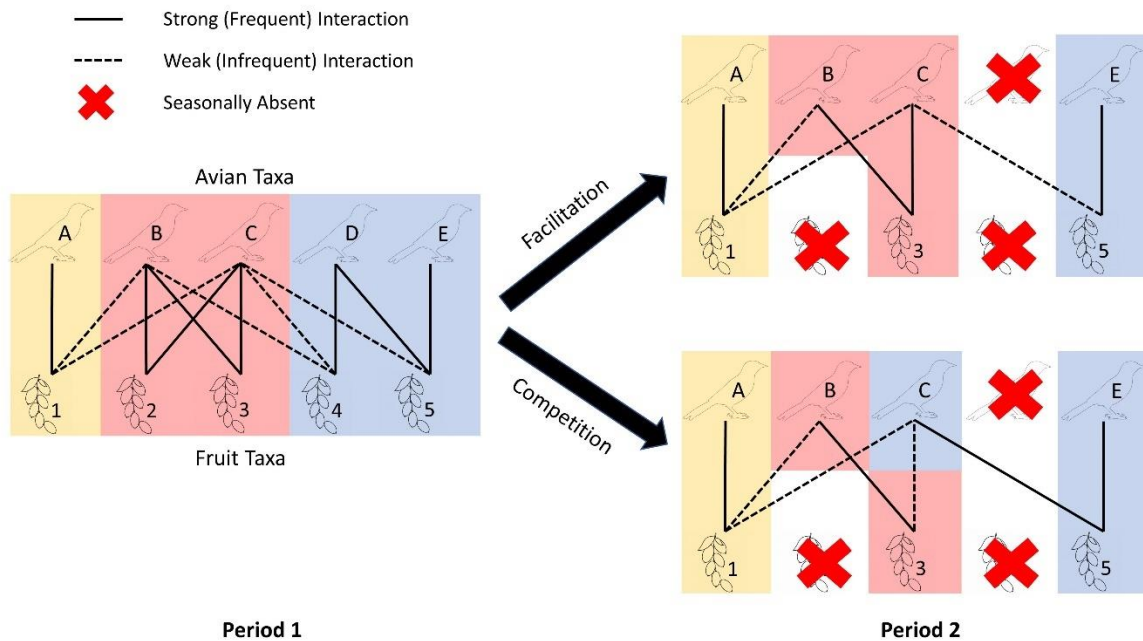
FIG. 7. A simple model community of birds and plants is presented as a temporal network with two periods. Species are sorted into modules – here coded by color – based on the relative frequency of interactions among taxa. In this example, community context shifts from a period of all taxa active in the system to a period when several taxa have migrated away from the site or ceased to fruit. Resource availability becomes increasingly constrained for two generalist species, Bird B and C, from which one of two responses are possible. Under the facilitation scenario, both Bird B and C continue to interact with their remaining preferred resource (Fruit 3). Under the competition scenario, Bird C is an inferior competitor to Bird B for the preferred resource and shifts to consuming Fruit 5, changing module affiliation in the network.
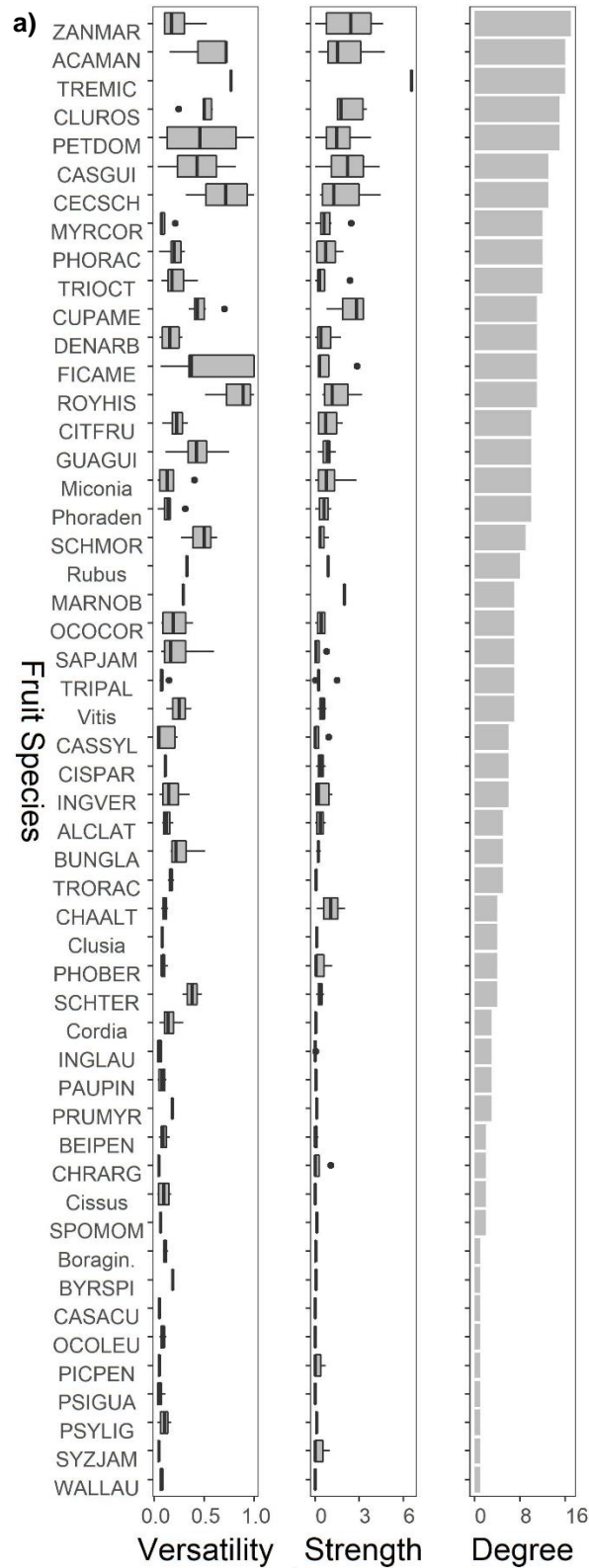
FIG. 8. (a) Measures of species importance for plant/fruit taxa. Degree as a sum of all known mutualistic partners. Strength as a measure of the species' cumulative proportional contribution to bird species diets. Versatility as a multilayer centrality demonstrating species' importance to the temporal cohesion of the network.
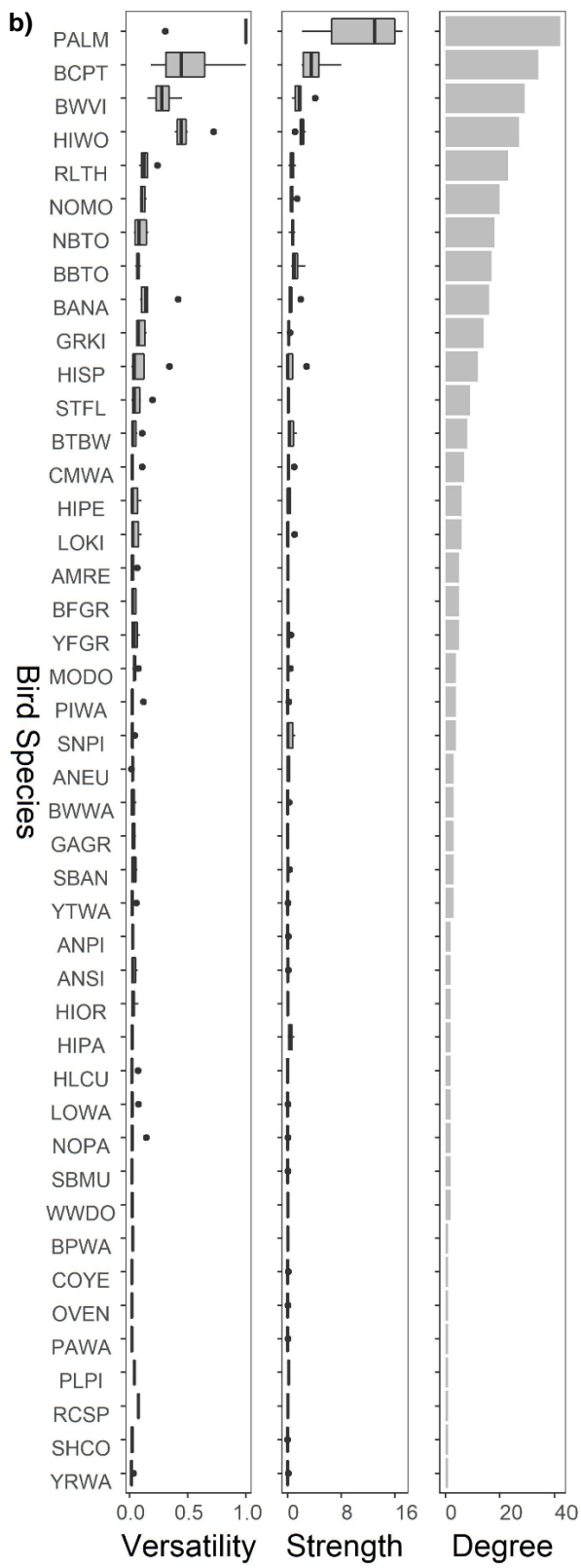
FIG. 8. (b) Measures of species importance for plant/fruit taxa. Degree as a sum of all known mutualistic partners. Strength as a measure of the species' cumulative proportional contribution to feeding visits to plant species. Versatility as a multilayer centrality demonstrating species' importance to the temporal cohesion of the network.

CHAPTER 4

SELECTIVE FRUGIVORY DRIVES COLONIZATION AND DIVERSITY OF SEED

DISPERSAL IN A HETEROGENOUS TROPICAL LANDSCAPE

4.1 INTRODUCTION

In ecosystems with flora dominated by taxa that produce fleshy fruits, plant-frugivore

seed dispersal mutualisms play a central role in structuring community composition (Jordano

1987b, Jordano et al. 2003, Vázquez et al. 2009). Seed dispersal is widely regarded as an

important process in maintaining gene flow in plant populations and facilitating colonization

among disjointed patches of suitable habitat (Nathan and Muller-Landau 2000, Nathan et al.

2008). Plants also account for most of the biomass and, hence, disproportionately influence

ecosystem functioning in terrestrial systems (Hooper and Vitousek 1997). Animal seed

dispersers, therefore, operate as mobile links by providing connectivity for plant populations

between patches and driving colonization and recruitment patterns (Lundberg and Moberg 2003).

Anthropogenic effects are broadly recognized for their ability to cause rapid changes to the

atmosphere, natural landscapes, and biodiversity and are increasingly seen as a threat to the

integrity of ecosystems through the disruption of core ecological processes (Dirzo et al. 2014,

Hautier et al. 2015). Understanding the function of frugivorous animals as seed dispersers in

human-modified landscapes is essential for predicting the consequences of land use change on

the resilience of biodiversity in tropical forests (McConkey et al. 2012, Kueffer and Kaiser-

Bunbury 2014). The progressive loss of frugivorous animals, resulting from such pressures as

habitat destruction and hunting pressures, can feed back to cause a loss of seed dispersal

functioning, with measurable negative effects on plant populations (Caughlin et al. 2015,

McConkey and O'Farrill 2016). Seed dispersal mutualisms in most plant communities, particularly in tropical ecosystems, are realized through interactions with highly diversified assemblages of frugivorous animals (Howe and Smallwood 1982, Jordano 1987b, Schleuning et al. 2012). Examining the interactions among plants and frugivores through networks has become an established approach to understanding ultimate factors influencing the co-dependence of taxa (Fricke et al. 2017) as well as proximate factors such as feeding preferences and their relationship with seed dispersal (Donatti et al. 2011, Simmons et al. 2018b). Empirical research relating community-level interaction patterns of frugivory to realized seed dispersal patterns, however, remains understudied.

Field investigations linking frugivory to seed dispersal from focal plant species or subsets of taxa and their corresponding seed dispersers have largely provided a basis for understanding how interactions with fruits ultimately translate to deposition and recruitment patterns. Examining seed dispersal at the scale of an individual plant affords opportunities to characterize the seed shadow, a spatially explicit representation of the locations where seeds are deposited (Nathan and Muller-Landau 2000). At the scale of a population or species, spatial data on seed dispersal can be aggregated to estimate dispersal kernels (Jordano et al. 2007). Given that plants with fleshy fruits are heavily dependent on frugivorous animals for seed dispersal, an increase in the rate of frugivory is expected to translate to an increase in seed dispersal away from the parent plant (Carlo and Morales 2008). Independently of the feeding rates at fruit-bearing plants, the diversity of frugivorous taxa consuming fruits can also influence seed dispersal patterns. For example, frugivorous birds in the Brazilian Atlantic Forest produce complementary and synergistic positive effects on recruitment (Rother et al. 2016). Seed disperser taxa are differentially influenced by traits such as body size and home range relative to propagule

movement over a variety of distances and frequencies within particular habitats (Bueno et al. 2013).

Despite a coupling of increasing seed dispersal with fruit abundance, this effect is often attenuated by seed disperser behavior. High fruit abundance can lead to satiating effects on frugivore feeding rates (Hampe 2008, Naoe et al. 2018). A diminishing functional response of frugivores to increasing resource density can be driven by numeric constraints on local population or behavioral and physiological constraints to particular fruits and their accumulation of toxic or deleterious secondary compounds (Whelan et al. 1998, Nelson and Whitehead 2021). Seed dispersal in a human-modified forest landscape in Puerto Rico was shown to produce an anti-apostatic pattern, or rare-biased pattern cascading to the stage of seedling recruitment (Carlo and Morales 2016, Morán-López et al. 2018a, 2018b). Frugivores provide an equalizing mechanism whereby rare taxa become disproportionately more represented in the community because of selective dispersal. This pattern of dispersal can augment populations of rare taxa that have otherwise been in decline (Chesson 2000).

Long-distance seed dispersal, including the delivery of seeds beyond the boundaries of forest fragments to other patches in the landscape, is critical to the persistence of plant populations (Cain et al. 2000). The ability of frugivorous animals to travel through and use non-native or anthropogenic habitats is often critical to facilitating cross-patch connectivity of plant communities. Although many studies have addressed seed dispersal patterns and connectivity in heterogenous landscapes for focal taxa (Levey et al. 2008, González-Varo et al. 2017), how the relationship between spatial complexity and mutualistic interactions at the community scale translates to the seed dispersal process remains poorly understood. Interaction frequencies of frugivory are frequently used as a proxy for direct measures of seed dispersal, serving as an

approximation of the quantitative component of seed dispersal effectiveness (Schupp 1993, Vázquez et al. 2005a). However, the relationship between community-level frugivory patterns at source plants and seed dispersal patterns in the landscape have rarely been explored simultaneously.

In this study, I investigated the extent to which fruit abundance and interactions with avian frugivores determined seed dispersal patterns in a heterogenous landscape. I predicted that the quantity of seeds dispersed would be proportionate to fruit production and that the relative role of frugivory would become increasingly important for dispersal that involved the colonizing of novel patches. I also considered the potential for seed dispersal of groups of taxa to be co-dependent in their transport to different habitat types, which could reflect common movement paths of their shared seed dispersers. Finally, I followed the trajectory of seed dispersal to examine the prospective consequences for biodiversity.

4.2 METHODS

Study Area

My study was carried out on private farmlands in the Rio Yaque del Norte watershed in the La Vega and Santiago provinces of the Dominican Republic. The region consists of fragmented remnant and secondary tropical wet forest scattered across hilly terrain ranged 500– 800 m above sea level The primary local land use is cattle ranching, but small agricultural plots and pine plantations are also maintained.

Abundance and Phenology Surveys

Trained observers carried out phenological surveys and frugivory observations along

fixed transects for a 12-month period at six sites from 2018 to 2019 (Chapter 3). I quantified fruit

abundance on marked plants along four 4 m x 500 transects at each site and recorded frugivory

rates using focal observations at plants with ripe fruits. Ripe fruits were quantified using a semi-

logarithmic scale index ("fruit abundance index" [FAI]; i.e., 1 = 1–10; 2 = 11–50; 3 = 51–100; 4

= 101–500; 5 = 501–1,000; 6 = 1,001–5,000; 7 = 5,001–10,000; 8 = 10,000+) (Saracco et al.

2005, Blendinger and Villegas 2011). Focal observations of up to 30- min durations were made

by observers at plants bearing ripe fruits to quantify the number of frugivorous birds arriving to

forage (N = 2,025 observations, Chapter 3).

Seed Collections

I deployed seed traps along the survey transect grid of three sites to continuously sample

seed rain across the landscape simultaneously with observations of phenology and frugivory. The

seed traps, elevated 1 m off the ground with PVC posts, were fitted with fine screen mesh (1

mm) with a surface area of 0.5 m^2 screen seed traps (1 m tall, mesh). Traps were placed at 50-m

intervals along each of four 500-m transects (i.e., 25 m, 75 m, 125 m… 475 m) for a total of 40

traps per site. Placement was made independently of habitat type to obtain a proportionate

sample of seeds falling in all cover types in the landscape. In locations with a vegetated

overstory, traps were placed strictly at the 50 m marker. In the case of open fields and other

habitats where natural perching structures were scarce, traps were adjusted by moving up to 10 m

to the nearest potential perching structure. If no such perch was present nearby, the trap was left

to sample seed rain in the open. Habitat types were classified based on the vegetation features

within a 10-m radius of the trap. These included pasture, successional, pine stand, forest edge,

and forest interior (Table 11).

The contents of seed traps were collected, identified, and quantified every 14–21 days, concomitant with phenology and frugivory surveys. Seed taxa were identified based on a photographic taxonomic guide made from a botanical collection from the study area. Each sample was classified by mode of dispersal. I recorded gravity-dispersed seeds, winged seeds dispersed by wind, and epizoochorous seeds (e.g., burrs), but excluded these in my analyses to focus on dispersal by frugivores. When seed samples from fleshy fruits were observed to be covered in undigested fruit pulp or epicarp, observers verified whether a plant of this species was in the overstory above the trap and classified these as gravity-dispersed. Furthermore, I used the vegetation surveys from the 10-m radius surrounding each trap to identify seeds as "colonists" if a reproductive plant from its species was not present in the plot. Since the seeds of some related species are visibly indistinguishable, I grouped these into broader taxonomic units by genus and family when relating seed dispersal data to fruit abundance and frugivory data (Table 12).

Statistical Analyses

To evaluate the effects of fruit abundance on the quantity of seeds dispersed into the landscape, I examined the seed trap data at two levels. First, I considered the total number of discrete seed samples of each plant species deposited into seed traps. I chose to analyze quantity of samples rather than quantity of seeds to prevent pseudoreplication, since instances of dispersal taxa with small seeds can produce samples of dozens and even up to hundreds of seeds than taxa with larger seeds, and quantity of seeds is not likely to scale with recruitment potential at the fine scale of area represented by my seed traps. Records of seed taxa deposited in traps were tallied by their presence in independent fecal clusters on the surface of a trap irrespective of the quantity of seeds in each sample. If multiple seeds of a given taxa were lying loose in the seed trap, these

were recorded as a single sample.

I compiled data from transect phenological surveys and frugivory observations to determine their relationship to seed dispersal patterns. For each taxon recorded from the seed traps, I estimated its local abundance at the three study sites. Estimates were derived by aggregating the FAI measures of individual marked plants of each taxon, such that one cumulative score was used for each of 7 periods (see Chapter 3). This was done to avoid factoring in double counts of ripe fruits that persisted across consecutive surveys only 2–3 weeks apart. Frugivory measures were summarized based on interaction data from across all six sites in the regional data. I calculated frugivory rates for each plant taxon based on the number of visits from confirmed avian seed disperser species divided by the cumulative minutes of observation on focal plants. The degree value of each plant taxon was determined based on the total known number of avian seed disperser species (Chapter 3).

Using seed taxa for which both fruit abundance and frugivory data were available, I modeled their effects on the seed dispersal. I fit the data on number of seed samples per species with generalized linear models with a Poisson distribution, using mean FAI, degree, and frugivory rate as explanatory variables. Models were run using package "lme4" and "bbmle" for AIC model selection in R 3.5.1 (R Development Core Team 2021). As an alternative for comparison, I fitted the same models to a subset of the data set which only included colonist samples that were confirmed to have dispersed to a trap with no neighboring plant of that taxon.

To determine the effect of birds on spatial seed dispersal patterns, I modeled the seed traps as a spatial network between classified habitats and plant taxa based on the composition and frequency of seed samples arriving to seed traps. I created an adjacency matrix by aggregating traps from each habitat type and quantified links from plant taxa based on the

number of samples collected. I then tested the extent to which the distribution of seeds deposited

in these traps took on a modular pattern, with nonrandom tendencies of taxa to cluster together in

their delivery to habitat types, by using package "bipartite". I applied Beckett's DIRTLPawb+

algorithm to compute weighted modularity for the seed-habitat network (Beckett 2016). The

observed modularity parameter was compared with the modularity of 100 null models, created

using the "r2dexternal" function to weight nodes based on the cumulative abundance of fruit taxa

across all three sites as well as the number of seed traps sampling each habitat type. Finally, I

used package "vegan" to calculate Shannon diversity (H') and Pielou's evenness for fruit and

seeds at each site.

4.3 RESULTS

I collected 19,480 seeds from 2,206 discrete samples, representing 67 distinguishable

taxa with characteristics of zoochory in seed traps. Of the total number of samples, 1,402

(64.4%) were identified as colonizing a site with no neighboring reproductive stems of its taxa.

In total, 48 seed taxa matched taxa identified from survey transects, and an additional 14 taxa

were unable to be identified (Table 12). These unidentified taxa, judged to likely be dispersed by

frugivores, represented 2.5% of samples collected. Wind-dispersed seeds, classified based on

morphology, were similarly rare at 1.2% of samples. The most abundant fruit taxa across the

three sites were *Cecropia schreberiana*, Primulaceae spp., *Inga* spp, and Melastomataceae spp.

(Fig. 9a). Taxa accounting for the greatest quantities of seed samples included *Cecropia

schreberiana*, *Zanthoxylum martinicense*, *Ficus* sp., and *Scheflerra morototoni* (Fig. 9b).

Fruit abundance, frugivory rates, and degree value were all variables selected in the top

model and positively predicted the number of seed samples deposited in traps for plant taxa

(Tables 13-14). When considering only colonist seed samples, the best candidate model included only frugivory rate and degree, which were positive predictors. While a model including all three variables carried substantial model weight, the addition of fruit abundance had a negligible increase on the maximized log-likelihood and was, therefore, interpreted as an uninformative parameter (Arnold 2010).

The composition of seed rain was significantly compartmentalized among the habitat types in the landscape than predicted by null models ($z = 14.94$). I identified three modules of seed deposition by habitat: (1) forest interior with forest edge habitats, (2) successional, and (3) pine savanna with pasture habitats (Fig. 10). These modules revealed disproportionate rates of seed dispersal by common sets of taxa. Furthermore, I observed greater diversity and evenness of seed sample composition than fruit composition at all three sites (Table 15).

4.4 DISCUSSION

The selective feeding behavior of birds likely outweighs the effects of their abundance on dispersal patterns of fruits at increasing distances. When accounting for seeds belonging to colonizing species, fruit abundance was not included in the top model and did not predict seed dispersal rates. This finding aligns well with the long-tailed pattern often associated with the dispersal kernel of most species, with decreasing frequency of seeds reaching greater dispersal distances from the fruit source (Pegman et al. 2017). Dispersal by frugivores generated non-random deposition patterns across habitat types in the environment. Moreover, all three communities exhibited a markedly greater increase in diversity measures in the composition of seed rain compared with the composition of fruits along survey transects.

I expected that fruit abundance would likely have a strong effect on the quantity of seeds

dispersed into the environment. Indeed, the most abundant fruit, *Cecropia schreberiana*, accumulated both the greatest number of total seed samples and colonist samples in collection traps. Beyond this one species, however, the relationship between fruit abundance and seed dispersal was relatively weak. Some of the most pervasively dispersed seeds were from fruits that were relatively rare, most notably *Schefflera morototoni*, *Ficus* sp., and *Clusia* spp. One important consideration in these patterns is the relationship between seed dispersal and phenology. I found previously that plant species' degree value was predicted by the period length of available fruits in the landscape (Chapter 3). This accumulation of greater mutualist partner diversity is due, in large part, to fruits being available over a longer temporal window that allows frugivores greater opportunities to discover fruit (Yang et al. 2013, Costa et al. 2020). Consequently, plant species are likely to accumulate interactions with a greater number of seed dispersers with greater exposure to seasonal contexts, such as coinciding with regional or latitudinal migrants. Plant taxa with more known seed dispersers had both greater dispersal overall and a greater likelihood of colonizing new patches. This finding is consistent with previous research showing that species richness of frugivore assemblages positively relates to the colonization potential of seeds in the landscape (García and Martínez 2012). My data support the logical extension of this pattern, such that the diversity of seed dispersers of particular plant species in plant-frugivore interaction networks indeed has functional consequences on colonization rates and could, therefore, be a useful predictor of the seed dispersal process as well as processes such as succession and species invasion.

Rather than dispersing in a diffuse and random manner across the varying habitats in the environment, plant taxa showed a disproportionate tendency to cluster with a similar set of other taxa in their arrival to specific habitats. Interdependence of dispersal between taxa can have a

variety of causes. The tendency of frugivores to select complementary fruit items in their diet can lead to co-dispersal of seeds to microsites, as well as contagious dispersal whereby nearby fruit trees act as foci for seed deposition when frugivores are drawn to the area to feed (Schupp et al. 2002, Kwit et al. 2004). Habitat preferences, more generally, of particular frugivores are likely drivers of modular seed dispersal patterns. However, discerning the relative roles of frugivorous bird species in producing spatially biased seed dispersal patterns by habitat remains an elusive challenge. In this study region, the Palmchat (*Dulus dominicus*) is responsible for an estimated 60% of all seed dispersal and makes frequent movements between forest patches with abundant fruit resources and pastures where birds maintain large colonies atop palm trees (Chapter 3). Other highly active seed dispersers such as the Black-crowned Palm Tanager (*Phaenicophilus palmarum*) and Black-whiskered Vireo (*Vireo altiloquus*) were primarily detected in forested areas, and likely contribute more spatially restricted seed shadows. One emerging tool that could resolve spatial networks of seed dispersal in plant-frugivore communities is the use of environmental DNA techniques, which can readily be applied to identify the source of plant propagules and seed dispersers based on DNA collected from seeds and corresponding fecal residues (González-Varo et al. 2014, 2017). Such applications offer a promising framework for connecting spatial patterns of seed dispersal mechanistically with frugivory at the community scale through combining sampling approaches (Quintero et al. 2021).

Finally, I found that frugivorous birds acted as a selective filter on seed dispersal rates of the plant community, producing a seed rain more diverse than would be expected based on landscape fruit composition. A similar diversifying pattern of seed dispersal has been observed in Puerto Rico and the Brazilian Atlantic Forest, where birds consistently disperse proportions of seeds more diverse than the fruits available locally (Carlo and Morales 2016, Camargo et al.

2022). While the realized effect of these seed dispersal patterns on recruitment remains unclear in this system, particularly given that management practices outside current standing forests are largely unfriendly to recruitment (e.g., cattle grazing and weeding), my data suggest high potential for forest recovery in disturbed landscapes.

TABLE 11. Descriptions of habitat classifications across the study sites.

Site	Description	Traps per Site		
		JB	LH	VY
Forest Interior	closed canopy forest > 5 m	9	2	3
Forest Edge	forested area within 10 m of non-forested cover (e.g., pasture)	10	7	2
Successional	shrub canopy or presence of small trees (< 5 m) lacking closed canopy	5	11	15
Pine Savana	pines measuring > 10 m, pasture grass and scattered shrub understory	6	5	11
Pasture	actively grazed grasslands, sparsely vegetated with palms and live fences	10	15	9

TABLE 12. All fleshy-fruit plant taxa identified from seed traps.

Species	Family	SpeciesCode
Acacia mangium	Fabaceae	ACAMAN
Alchornea latifolia	Euphorbiaceae	ALCLAT
Beilschmiedia pendula	Lauraceae	BEIPEN
Bunchosia glandulosa	Malpighiaceae	BUNGLA
Capsicum sp.	Solanaceae	CAP
Casearia aculeata	Salicaceae	CAS
Casearia arborea	Salicaceae	CAS
Casearia guianensis	Salicaceae	CAS
Casearia sylvestris	Salicaceae	CAS
Cecropia schreberiana	Urticaceae	CECSCH
Chamissoa altissima	Amaranthaceae	CHAALT
Chrysophyllum argenteum	Sapotaceae	CHRARG
Cissampelos pareira	Menispermacae	CISPAR
Cissus sp.	Vitaceae	CIS
Citharexylum fruticosum	Verbenaceae	CITFRU
Clidemia spp.	Melastomataceae	Melastom
Clusia rosea	Clusiaceae	CLU
Clusia sp.	Clusiaceae	CLU
Cordia sp.	Boraginaceae	COR
Cupania americana	Sapindaceae	CUPAME
Dendropanax arboreus	Araliaceae	DENARB
Dendropemon emarginatus	Loranthaceae	DENEMA
Ficus americana	Moraceae	FICAME
Guarea guidonia	Meliaceae	GUAGUI
Inga laurina	Fabaceae	ING
Inga vera	Fabaceae	ING
Margaritaria nobilis	Phyllanthaceae	MARNOB
Miconia sp.	Melastomataceae	Melastom
Myrsine coriacea	Primulaceae	Primul
Ocotea coriacea	Lauraceae	OCOCOR
Ocotea leucoxylon	Lauraceae	OCOLEU
Parathesis crenulata	Primulaceae	Primul
Paullinia pinnata	Sapindaceae	PAUPIN
Petita domingensis	Lamiaceae	PETDOM

TABLE 12 Continued…

Phoradendron berteroanum	Santalaceae	PHO
Phoradendron racemosum	Santalaceae	PHO
Phoradendron sp.	Santalaceae	PHO
Picramnia pentandra	Picramniaceae	PICPEN
Piper spp.	Piperaceae	PIP
Prunus myrtifolia	Rosaceae	PRUMYR
Psidium guava	Myrtaceae	PSIGUA
Psychotria spp.	Rubiaceae	PSY
Roystonea hispaniolana	Arecaceae	ROYHIS
Rubus sp.	Rosaceae	RUB
Sapium jamaicensis	Euphorbiaceae	SAPJAM
Schefflera morototoni	Araliaceae	SCHMOR
Schinus terebinthifolius	Anacardiaceae	SCHTER
Solanum sp.	Solanaceae	SOL
Spondias sp.	Anacardiaceae	SPO
Trema micrantha	Cannabaceae	TREMIC
Trichilia pallida	Meliaceae	TRIPAL
Trichostigma octandrum	Petiveriaceae	TRIOCT
Trophis racemosa	Moraceae	TRORAC
Vitis sp.	Vitaceae	Vitis
Wallenia laurifolia	Primulaceae	Primul
Zanthoxylum martinicense	Rutaceae	ZANMAR

TABLE 13. AIC table showing the ranking and relative support of candidate models to predict the number of seed samples deposited in traps for each plant taxa.

All Seed Samples (N = 1,762)					Colonist Seed Samples (N = 1,320)				
Model	K	ΔAICc	LogLik	Weight	Model	K	ΔAICc	LogLik	Weight
Abun+Deg+Frug	3	0.0	528.0	99.99	Deg+Frug	2	0.0	432.5	0.75
Deg+Frug	2	9.2	522.2	0.01	Abun+Deg+Frug	3	2.2	432.6	0.25
Abun+Degree	2	83.2	485.2	<0.001	Abun+Degree	2	136.6	364.1	<0.001
Degree	1	85.1	483.1	<0.001	Degree	1	139.4	361.6	<0.001
Abun+Frug	2	825.8	113.9	<0.001	Abun+Frug	2	631.7	116.6	<0.001
Frug	1	900.1	75.6	<0.001	Frug	1	645.2	108.7	<0.001
Abun	1	979.9	35.7	<0.001	Abun	1	849.6	6.5	<0.001
Intercept	0	1049.1	0.0	<0.001	Intercept	0	860.4	0.0	<0.001

TABLE 14. Summaries of the top models for predicting the number of seeds samples of plant taxa found deposited in traps. Parameters with coefficient estimates whose confidence intervals do not overlap zero are in bold.

	Total Seed Samples				Colonist Seed Samples		
Variable	β	SE	95% CI	Variable	β	SE	95% CI
Intercept	**2.087**	**0.069**	**(1.95, 2.22)**	**Intercept**	**1.714**	**0.081**	**(1.55, 1.87)**
Abundance	**0.072**	**0.020**	**(0.03, 0.11)**	Abundance	NA	NA	NA
Degree	**0.151**	**0.005**	**(0.14, 0.16)**	**Degree**	**0.153**	**0.006**	**(0.14, 0.17)**
Frugivory	**0.561**	**0.054**	**(0.45, 0.67)**	**Frugivory**	**0.749**	**0.055**	**(0.64, 0.86)**

TABLE 15. Summary of diversity measures of fruit abundance and seed rain by site for fleshy fruit taxa. Sampling area for fruits per site was 8,000 m^2 and 20 m^2 for seeds.

	Fruit Composition			Seed Composition		
Site	Quantity	H' (Richness)	Evenness	Seeds (Samples)	H' (Richness)	Evenness
Jose Brache	47,800	2.214 (34)	0.628	9,368 (1,110)	2.883 (43)	0.767
Llanos de Higos	40,700	1.501 (26)	0.461	2,711 (348)	3.106 (45)	0.816
Vera del Yaque	68,200	1.235 (33)	0.353	3,825 (503)	3.110 (40)	0.843
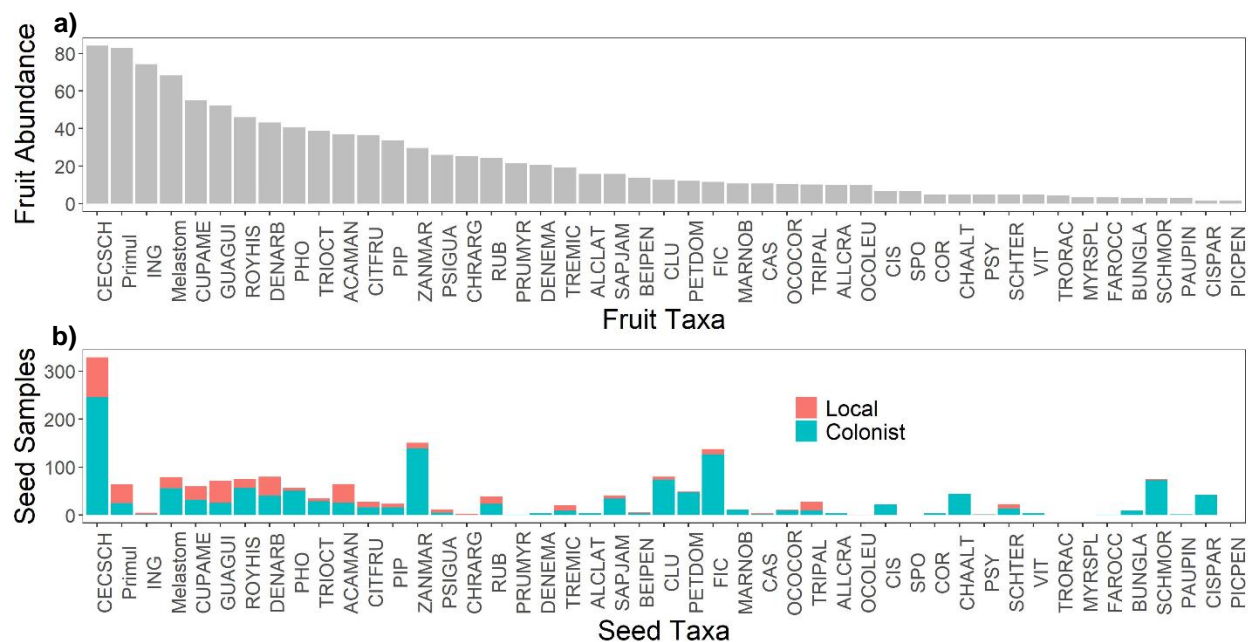
FIG. 9. A graphical comparison of (a) fruit abundance shown on a logarithmic scale and (b) quantity of recorded seed samples for taxa identified as dispersed by frugivorous birds in the study region.
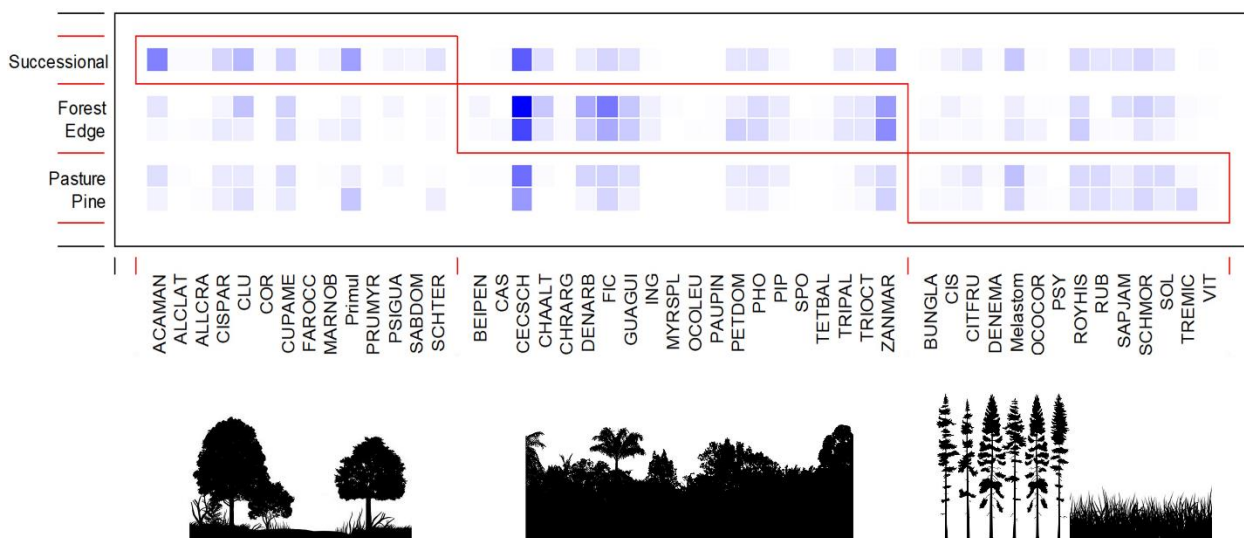
FIG. 10. An adjacency matrix between habitat types and seed taxa, organized by maximum modularity. Increasingly dark shades of blue for cells reflects greater quantities of seed samples. The observed pattern of taxa deposited across habitat types was significantly more modular than the values produced by null models.

CHAPTER 5

DIET-BASED DISCRIMINATION OF BROADCASTED BIRD SOUNDS INFLUENCES

USE OF FOREST RESTORATION PLOTS BY FRUGIVOROUS BIRDS

5.1 INTRODUCTION

Frugivorous birds are the most ubiquitous and diverse class of vertebrate seed dispersers across the world's tropical forests, providing a foundational ecosystem service for the maintenance of biodiverse floral communities and the biota these habitats sustain (Fleming and Kress 2011). Despite widespread protection and conservation efforts, modern day tropical forests continue to be lost at disproportionately high rates (Spracklen et al. 2015). Many conservationists and researchers have touted the potential for restoration programs to recover forest resources and preserve biodiversity (Gardner et al. 2009, Chazdon 2017). Regeneration of functioning forests in degraded landscapes is, nevertheless, inhibited by many challenges that exacerbate the time and investment required to achieve successful restoration outcomes (Holl 2017). In recent decades, many developing nations in tropical regions have seen a resurgence in the recovery of secondary forests due to shifting urbanization of human populations and more efficient agricultural land use (Rudel et al. 2002, Meyfroidt and Lambin 2011). Much of this recovery has come from natural regeneration on abandoned agricultural lands, providing evidence for the potential resilience of tropical forest communities (Poorter et al. 2016). More recently, natural resource managers and ecologists have expanded their focus on assisted and passive restoration methods to increasingly recognize the role of animal mutualists and the integrity of these complex systems as vital to restoring seed dispersal and regeneration processes (Kaiser-Bunbury et al. 2010, Ribeiro da Silva et al. 2015, Howe 2016, Raimundo et al. 2018). However, the

specific mechanisms by which communities of seed dispersers such as birds respond to stimuli and environmental conditions associated with management interventions remain poorly understood.

Seed dispersal is one of the most critical and fundamental limiting factors in the regeneration of tropical forest in degraded landscapes (Wunderle 1997). Once deforested, land with a history of prolonged agricultural or other human use largely destroys the existing seed bank, thus, making regeneration almost entirely dependent on new seed inputs (Zimmerman et al. 2000). The extent of deforestation in the local surroundings of a particular site can also limit the number and species of seeds likely to recolonize, with seed rain, regeneration potential, and diversity all potentially diminishing with increasing distance to the nearest forest fragment (Cubiña and Aide 2001, Muniz-Castro et al. 2006, Lopes et al. 2012, Oliveira et al. 2018). In tropical regions, the majority of native tree species are adapted to produce fleshy fruits to promote seed dispersal by frugivorous animals (Howe and Smallwood 1982). This dependence on frugivores creates a negative feedback dynamic of seed dispersal with respect to habitat quality, since patch use by potential seed dispersers is typically low in deforested or sparsely vegetated areas with few fruit resources (Terborgh 2013). Interventions that encourage frugivorous animals to use restoration sites are, therefore, frequently recommended as a strategy to augment seed dispersal and accelerate natural regeneration (Wunderle 1997, Howe 2016).

Artificial perches for birds have been increasingly offered as a measure to promote seed dispersal in restoration projects (Holl 1998, Guidetti et al. 2016). Frugivorous birds are prolific seed dispersers because of their ubiquity in most ecosystems and their vagility across habitat boundaries and among fragments (Pizo and dos Santos 2011, Vélez et al. 2015, González-Varo et al. 2017). Natural perches, such as isolated trees, are known to attract disproportionate

quantities of seed deposits from transient avian visitors in relatively open landscapes, and these perches may act as nuclei for plants, compared to negligible recruitment in the surrounding matrix (Toh et al. 1999, Pausas et al. 2006, Schlawin and Zahawi 2008, Derroire et al. 2016). In sites where natural perches are scarce or unavailable, artificial perches can potentially recreate these attractive effects on birds, thereby augmenting seed dispersal and regeneration. Many studies have evaluated the effect of artificial perches on bird behavior, seed dispersal, and seedling recruitment in different sites across the globe with varying results. A consistent finding among studies is that a greater number and diversity of seeds are dispersed below perches compared to control spaces with no perches (Holl 1998, Scott et al. 2000, Vicente et al. 2010, Graham and Page 2012, Athiê and Dias 2016, Ferreira and de Melo 2016). While the effectiveness of perches as a conduit to plant regeneration has been highly variable across studies, a meta-analysis by Guidetti et al. (2016) of field experiments using artificial perches showed consistent increases in both seed dispersal and seedling recruitment across temperate and tropical sites on multiple continents.

Despite a growing consensus of the positive effect of perches on frugivore visitation and seed dispersal in targeted restoration areas, most investigations exploring the factors affecting the affinity of birds to be attracted to such areas and their contributions to seed dispersal in degraded landscapes, more generally, have focused on structural features of landscapes such as the degree of habitat fragmentation and distance of perches from the nearest forest fragment or seed source (Holl 1998, Alencar and Guilherme 2020). One aspect determining bird movement behavior through degraded landscapes that remains largely unknown with respect to seed dispersal, however, is the effect of sound. Numerous experimental studies have shown that broadcasted sounds can influence animal movement behavior (reviewed in Williams et al. 2021). For

example, broadcasted frog calls can increase colonization of unoccupied restored ponds (James et al. 2015), and there is ample evidence from marine reef systems that broadcasts of healthy and more auditorily complex soundscapes increase recruitment of fish and invertebrate larva to degraded habitat (Lillis et al. 2013, Butler et al. 2016, Anderson et al. 2021). Social information from the sounds of both conspecific and heterospecific species has also been shown to influence habitat selection by birds (Szymkowiak 2013, Andrews et al. 2015, Schofield et al. 2018). In the case of frugivorous birds, which often congregate where ripe fruits are available, the sounds of other frugivorous birds can trigger directional movement towards potential resources, increasing local foraging effort (Gu et al. 2017). Other experimental research has shown that frugivorous bird sounds can increase the number of birds and feeding activity at fruiting trees (MacDonald et al. 2019). Social information conveyed through sound, therefore, likely plays a role in how avian seed dispersers navigate and use restoration areas, but I am unaware of any studies that have tested such ideas experimentally under field conditions.

I designed an experiment to evaluate the effect of broadcasted avian sounds on the attendance of potential seed dispersers to artificial perches for forest restoration sites in the central Dominican Republic. Using prior data collected from the study area on the frugivorous diet and feeding tendencies of the avian community, I curated multiple audio playlists of bird calls stratified by taxa based on their degree of frugivory. I predicted that broadcasts more generally would elicit an increase in the number of frugivorous bird visitors and that the response would be greatest when sounds of frugivorous taxa were played.

5.2 METHODS

The study was conducted in an agricultural region in the foothills of the Cordillera

Central of the Dominican Republic on the island of Hispaniola, 500–700 m above sea level surrounding the town of Jarabacoa, La Vega Province. The native biome of this region is evergreen, broadleaf tropical humid forest. Mean annual precipitation is 1340 mm and, while winter (Jan–Feb) and summer months (Jun–Aug) are comparatively drier, there is no consistent wet or dry season, and mean monthly rainfall does not fall below 70 mm. Nearly all forests in the region have been logged historically or converted for agricultural (e.g., pasture and cropland), agroforestry (e.g., coffee and cacao), or pine timber plantations. Remaining native vegetation consists mostly of small fragments of preserved secondary forests along streams and rivers on private farms, which is due in large part to federal law prohibiting the cutting of trees alongside river and stream banks (Law 64-00).

I conducted my experiments in the context of an ongoing small-scale forest restoration project managed in cooperation with local landowners and a watershed conservancy, Plan Yaque Inc. Five restoration plots (0.1–0.25 ha) were established in the years 2017–2018, in recently active cattle pastures located near small headwater streams using barbed wire fences to exclude livestock grazing. During or shortly after establishing the plots, 6–8 artificial perches were installed in each plot. Each perch was constructed from bamboo poles with the base pole standing 5 m tall and three smaller 1-m poles fitted as crossbars 1-m apart in height down from the top of the base pole (Fig. 11). Seedling quadrats measuring 4 x 4 m were delineated using buried PVC tubes as corner-posts with the perch at the center. An equal number of control seedling quadrats were established haphazardly in the plot space ≥5 m from the nearest perch. No existing woody seedlings were present in the quadrats during initial plot installations.

The data collection for this study took place in two phases. Over the long term, I monitored seedling establishment in perch and control quadrats. I censused the quadrats after 12

or 24 months during the summer of 2019, depending on whether the associated perches were deployed in 2017 or 2018. Additionally, I conducted an experiment on bird behavior, testing the effect of sound broadcasts on avian activity in the plot. Each plot was visited four times April–July 2019 to conduct experiments, such that each of four playback treatments were performed once in each plot. The order of experiment for each site was randomized. These treatments consisted of four different call broadcasts of birds based on their degree of frugivory (i.e., number of fruit species in diet) as determined by foraging observations from another study at these sites (Chapter 3): generalist frugivores (>20 fruit species), specialist frugivores (<5 fruit species), nonfrugivores, and silence as a control (Table 16). I expected avian visitors to respond to these treatments to proportionately to the level of frugivory of the birds on the playlist, here measured by the diversity of fruit taxa in their diet. Each experiment was composed of a playlist of 100 min with five 10-min tracks, each corresponding to a particular bird species, separated by 10 min of silence. Bird sounds were downloaded from xenocanto.com from the Dominican Republic. The species selected for this stimulus were common residents of all five sites based on my prior surveys. Furthermore, I intentionally excluded including sounds from Northern Mockingbirds (*Mimus polyglottos*) and Gray Kingbirds (*Tyrannus domincensis*) which I already observed to be common users of the perches during the pilot phase of my study in the prior year. I included a variety of calls for each species (e.g., song, contact calls, other social noises), but excluded sounds known to signify territorial conflict, alarm, or distress. Maximum sound decibel intensity was standardized among the different tracks using audio editing software Audacity and looped to produce uninterrupted sound during the 10-min tracks of active broadcast. The speaker was placed at a central location between the perches in the plot at the beginning of each experiment. A 10-min silence was added to the beginning of the playlist, accounting for the

disturbance of an observer entering the plot to place the speaker. To record avian activity, I deployed digital video cameras mounted on a tripod at the edge of the plot with all perches in view, 10–40 m away. Video footage was later reviewed on a computer screen to record the number and species of avian visitors to the perches (defined as individuals who landed on the perch). Video time stamps were aligned with the playlist to determine whether birds arrived during broadcast of a particular bird call or during a silent period in addition to tallying their visits more generally. Review of all video footage was conducted by two observers, independently, to ensure repeatability of detection and identification of taxa. During these experiments, I also maintained 0.5 m^2 screen seed traps (1 m tall, 1 mm mesh), whose contents were collected on each visit to the site.

To analyze the effect of the treatment of bird sound broadcast on the number of visits to the restoration plots, I used package 'lme4' in R 3.6.2 (R Development Core Team 2021) to model the data using a generalized linear mixed model with a Poisson distribution. Treatment group was used as a fixed effect with restoration plot ID as a random effect. A post-hoc tukey test was applied to distinguish treatment groups whose mean number of avian visitors significantly diverged from one another.

5.3 RESULTS

A total of 191 visits from 10 frugivorous bird species were recorded in the restoration plots from 33.3 hrs of video footage (Table 17). One species with one recorded visit, the American Kestrel (*Falco sparverius*), was excluded from the analyses due to being the only species not known to disperse seeds. Northern Mockingbirds and Gray Kingbirds were the most frequent in the plots, accounting together for 65% of all visits. All treatment groups with bird

sound broadcast resulted in a greater number of visitors to the perches on average than the control group (Table 18, Fig. 12). However, only the specialist playlist resulted in a significantly greater visit rate from the control.

A total of 186 samples, including 1,171 seeds, from 29 taxa were collected during the 2019 summer period (Table 19). The number of seeds collected by site over the monitoring period was highly correlated to the overall number of recorded visits during experiments (coef = 0.924, t = 4.1965, p-value = 0.02469). The majority of seeds dispersed to the plots were native species, with only three being exotic.

Seedling establishment in the restoration plots was infrequent, with only 68 seedlings in 75 quadrats (0.057 seedlings/m^2). Most seedlings (81%) were of two exotic species, *Psidium guava* and *Leucaena leucocephala*, with a smaller number of native seedlings from four species. Overall, only 4 out of 47 quadrats under perches (8.5%) saw establishment of native seedlings in their understory. Native seedling taxa included *Clidemia* sp., *Cupania americana*, *Guarea guidonia*, and *Zanthoxylum martinense*. However, no native species were detected in any of the control quadrats in open pasture spaces. Seedlings of exotic species were similarly frequent among perch and control quadrats, though nearly all such seedlings were recorded at two of the five sites.

5.4 DISCUSSION

My results provide support for the hypothesis that bird sounds attract visits by avian seed dispersers to artificial perches. All experiments with bird sounds resulted in a greater average number of visits than the control experiment without sound. The two frugivorous bird sound treatment groups averaged a greater number of visits; however, contrary to my expectations, only

sounds from the specialist frugivore playlist rather than the generalist frugivore treatment attracted significantly more birds than the control group. In plant-frugivore communities, generalists with a highly diversified diet of fruit species tend to be more dependent on fruit resources as a significant proportion of their diet, whereas birds with few links to plant species may either be true specialists or more omnivorous (Mello et al. 2015). Consequently, generalists are expected to spend time foraging mostly in habitat patches with abundant fruit resources. Most of the patterns in visitation to my restoration plots were driven disproportionately by species that prefer relatively open habitats rather than forest (i.e., mockingbirds, flycatchers, and grassquits). One possible reason that the generalist playlist did not have the greatest attractive effect is that these taxa may be unlikely to respond strongly to cues of frugivores that spend most of their time foraging in contiguous forest. The generalist playlist did, however, attract generalist bird species that had not been previously observed in the plots prior to beginning the experiments.

I found an expected strong correlation between the cumulative number of visits to restoration plots and the number of seeds collected during the three-month monitoring period. The relationship between frequency of bird visits to restoration areas and seed deposition has been shown consistently in other similar field experiments (Holl 1998, Carlo and Morales 2016). While the recruitment of native species seedlings was limited, the absence of native seedlings in control quadrats away from perches demonstrated clear, albeit weak, effect of avian seed dispersers on seedling composition.

The role of birds and other animal seed dispersers in propagating exotic species is well documented and presents a potential pitfall of integrating animal-facilitated seed dispersal into restoration plans (Heleno et al. 2010). Notable exotic species regularly found in seed traps

included *Acacia mangium* and *Rubus* sp.; however, these were not found to establish within the restoration plots. The growth of exotic species in my restoration plots was primarily accounted for by *Psidium guava* and *Leucaena leucocephala*. While the native distribution of *P. guava* is uncertain, I have classified it as exotic because of its tendency to grow in feral, semi-cultivated fields and to readily invade pastures. In previous surveys in the study area, I only rarely observed dispersal of *P. guava* by birds, suggesting its rapid dispersal is primarily accounted for by gravity, livestock, and humans. Nevertheless, some research has shown that *P. guava* invasions can accelerate succession and increase seedling biodiversity in the long-term (Zahawi and Augspurger 1999). *Leucaena*, which was only present at one site, is a highly invasive leguminous shrub that spreads primarily by abiotic dispersal.

My study focusing on the short-term response of birds to auditory stimuli has shown that frugivorous birds are likely to use social information from the sounds of other birds when directing their movements and use of isolated perches in deforested landscapes. There are several key consequences of this finding for the process of seed dispersal. First, my results are consistent with the limited research that is available on the response of frugivorous birds to sound. MacDonald et al. (2019) found that broadcasting the calls of frugivorous birds increases the overall attendance and fruit consumption of birds at fruiting trees, hypothesizing that sound stimuli could provide a catalyst for birds to sample unfamiliar fruits. By extension of this pattern, I predicted frugivorous birds could also use social information in directing flight paths and perching between feedings, thus becoming more prone to explore recently disturbed landscapes and novel structures and initiating seed dispersal in targeted areas. During my initial non-systematic observations during the first several months following perch installation, I observed primarily Northern Mockingbirds, flycatchers (Tyrannidae), and grassquits (Tiarus spp.) using

perches. None of the species included in the generalist frugivore playlist were observed using plots prior to conducting sound experiments. The majority of visits from these taxa were evidently drawn to the plot in direct response to the broadcasted call of their own species during the generalist playlist. However, several of these visits occurred during the control experiment or during broadcasts that did not include their own species call. Further data are needed to determine whether particular taxa are attracted to abandoned pastures at different rates, but I predict that such a period could be shortened by broadcasting bird calls.

As the importance of seed dispersal mutualisms has become increasingly recognized in the long-term success of tropical forest restoration (Howe 2016), there is a corresponding need to understand the mechanisms driving the behavior of seed dispersers. Negative feedback effects of population reduction and biodiversity losses in communities of plants and their seed dispersers are well recognized (Harrison et al. 2013, Caughlin et al. 2015). As tropical forests are converted for agricultural or other human uses and remaining forest fragments suffer from defaunation due to hunting and habitat loss, the loss of seed dispersal links can cause further cascading loss of other species in the community (Farwig and Berens 2012). Furthermore, major disturbances to ecosystems can render a species "functionally extinct" despite sustaining a viable population at the local scale (McConkey and O'Farrill 2016). Soundscapes are known to have measurable impacts on the ecology and behavior of birds. For example, anthropogenic noise alters the effort and performance of singing birds (Duquette et al. 2021). Similar disruptions of sensory information, such as the reduction of sounds following disturbances like deforestation, could inhibit cues that inform movement and foraging effort. Conversely to the strong negative feedback effects on wildlife and seed dispersal as ecosystems become degraded, positive feedback mechanisms are likely equally pivotal to the long-term success of restoration and

recovery.

Finally, my results add further clarity to the net positive effect of artificial perch installation in restoration plots. Based on the response of the avian community in my experiments, sound broadcasts can increase the frequency of perch use by birds. Applications of this dynamic could include direct interventions in restoration settings to promote seed dispersal by birds through sustained broadcasts. Alternatively, even limited use of broadcast in the early timeframe following initial preparation of restoration sites could serve to acclimatize birds to novel structures to more readily recruit avian visitors.

TABLE 16. A list of bird species' sounds used for the playback experiments. Degree indicates the number of fruit species on which the bird is known to feed in the study region.

Bird Species	Frugivory Level	Degree
Vervain Hummingbird (*Mellisuga minima*)	Nonfrugivore	0
Village Weaver (*Ploceus cucullatus*)	Nonfrugivore	0
Antillean Mango (*Anthracothorax dominicus*)	Nonfrugivore	0
Scaly-breasted Munia (*Lonchura punctulata*)	Nonfrugivore	0
Cattle Egret (*Bubulcus ibis*)	Nonfrugivore	0
Antillean Siskin (*Spinus dominicensis*)	Specialist	2
Smooth-billed Ani (*Crotophaga ani*)	Specialist	3
Hispaniolan Parakeet (*Psittacara chloroptera*)	Specialist	2
Antillean Euphonia (*Euphonia musica*)	Specialist	3
Hispaniolan Oriole (*Icterus dominicensis*)	Specialist	2
Red-legged Thrush (*Turdus plumbeus*)	Generalist	23
Black-whiskered Vireo (*Vireo altiloquus*)	Generalist	29
Palmchat (*Dulus dominicus*)	Generalist	47
Black-crowned Palm Tanager (*Phaenicophilus palmarum*)	Generalist	34
Hispaniolan Woodpecker (*Melanerpes striatus*)	Generalist	27

TABLE 17. Summary of visits by avian seed dispersers.

Bird Species	Visits	Conspecific Attraction (%)	Cumulative Time (min)	Sites
Northern Mockingbird (*Mimus polyglottos*)	78	—	76.0	3
Gray Kingbird (*Tyrannus dominicensis*)	46	—	155.7	4
Hispaniolan Pewee (*Contopus hispaniolensis*)	20	—	24.6	4
Yellow-faced Grassquit (*Tiarus olivaceus*)	15	—	11.1	2
Black-crowned Palm Tanager (*Phaenicophilus palmarum*)	11	8 (72%)	13.5	2
Palmchat (*Dulus dominicus*)	9	7 (78%)	10.8	3
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	5	—	8.5	1
Broad-billed Tody (*Todus subulatus*)	3	—	1.5	3
Red-legged Thrush (*Turdus plumbeus*)	2	2 (100%)	1.2	1
Hispaniolan Woodpecker (*Melanerpes striatus*)	1	0 (0%)	0.8	1
Black-faced Grassquit (*Tiarus bicolor*)	1	—	0.5	1

"Conspecific Attraction" denotes a tally of the instances in which birds arrived during the track of the call of their own species.

TABLE 18. Post-hoc pairwise comparison test (Tukey) showing the differences between the mean number of bird visits during experiments from different treatment groups. Significant differences are highlighted in boldface.

Comparison	β Estimate (95% CI)	P
Control – Nonfrugivore	0.4763 (-0.1982, 1.151)	0.2665
Control – Specialist	**1.0054 (0.3738, 1.637)**	**0.0003**
Control – Generalist	0.5612 (-0.1128, 1.235)	0.1408
Nonfrugivore – Specialist	**0.5291 (0.0583, 1.000)**	**0.0203**
Nonfrugivore – Generalist	0.0848 (-0.440, 0.6098)	0.9759
Specialist – Generalist	-0.4442 (-0.912, 0.0239)	0.0702

TABLE 19. A list of seed taxa and quantities collected. Morphospecies are unidentified taxa. Exotic species are marked with *.

Family	Taxa	Form	Quantity of Seeds
Moraceae	*Ficus* sp.	Tree	374
Melastomataceae	*Miconia/Clidemia* spp.	Shrub	192
Fabaceae	*Acacia mangium**	Tree	129
Lamiaceae	*Petitia domingensis*	Tree	89
Solanaceae	*Solanum torvum*	Shrub	82
Urticaceae	*Cecropia schreberiana*	Tree	74
Rosaceae	*Rubus* sp.*	Shrub	64
Santalaceae	Phoradendron	Parasite	36
Primulaceae	*Myrsine/Wallenia* sp.	Tree	32
Cannabaceae	*Trema micrantha*	Tree	19
Salicaceae	*Casearia* spp.	Tree/Shrub	12
Malpighiaceae	*Bunchosia glandulosa*	Tree	7
-----	Morphospecies 2	-----	7
Euphorbiaceae	*Margaritaria nobilis*	Tree	7
Meliaceae	*Guarea guidonia*	Tree	5
Euphorbiaceae	*Zanthoxylum martinicense*	Tree	5
Menispermaceae	*Cissampelos pareira*	Vine	4
-----	Morphospecies 1	-----	3
Araliaceae	*Dendropanax arboreus*	Tree	3
Petiveriaceae	*Trichostigma octandrum*	Liana	2
Euphorbiaceae	*Sapium jamacensis*	Tree	2
-----	Morphospecies 3	-----	2
Sapindaceae	*Cupania americana*	Tree	1
Amaranthaceae	*Chamissoa altissima*	Vine	1
Verbenaceae	*Citharexylum fruticosum*	Tree	1
Cucurbitaceae	*Momordia charantia**	Vine	1
Arecaceae	*Roystonea hispaniolanum*	Tree	1

FIG. 11. Perch design diagram with an example photo from the field.

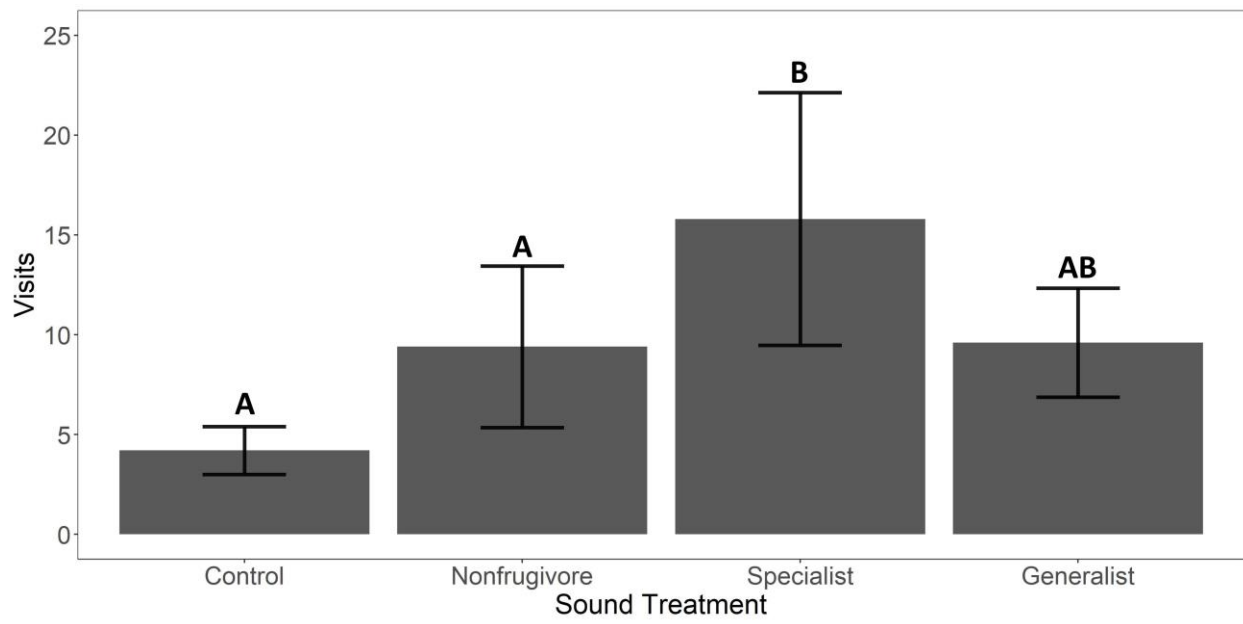

FIG. 12. Bar plots showing the variation of visit frequency to restoration plots for the different sound broadcast experiments (N = 5) with bars displaying standard error. Pairwise comparisons from a post hoc Tukey test are indicated by letters.

CHAPTER 6

CONCLUSION

Through my studies of plant and frugivore populations in the Rio del Yaque watershed (La Vega, Dominican Republic), I documented substantial diversity of avian and plant taxa involved in the processes of frugivory and seed dispersal across the region and numerous previously undescribed mutualistic relationships among species. Furthermore, these communities showed substantial variation in both across locations as well as between the time periods over which they were observed. In addition to uncovering the biodiversity of flora and avifauna in a region previously underrepresented in scientific literature, my studies have uncovered novel insights into the ecology of frugivory and seed dispersal. My research illustrates the complex role of phenology on the dynamics of tropical plant-frugivore networks in its influence over the plasticity of plant and seed disperser relationships as well revealing the relationship between empirical measures from interaction networks and the process of seed dispersal.

I found that plants with subannual reproduction and the resulting extended temporal availability of ripe fruit displays subject them to highly variable contexts of differential seed dispersal frequency, driven by the selective preferences of frugivorous birds. While I hypothesized that local scale fruit abundance at focal trees and neighboring plants would have a pronounced influence on foraging rates of *Guarea guidonia*, I found that landscape-level availability of alternative fruit resources was most likely responsible for dramatic intra-seasonal changes in frugivory at this focal species.

Based on my findings from the population study of *Guarea guidonia* and determining that the effects of fruit availability on avian frugivore behavior were likely occurring on a larger spatial scale than local plant neighborhoods, I proceeded to design a community-level study of

plant-frugivore networks replicated across six farmland sites to investigate the how phenological variation affects the temporal dynamics of interactions among taxa. I found that local networks tended to remain consistently and nonrandomly nested across time, despite persistent changes in community composition and rewiring of species interactions. Species with low phenological variation in abundance had disproportionate influence on the temporal cohesion and stability of networks. I found significant multilayer modular structure in all six local networks with a consistent pattern of exclusion, in which taxa belonging to the same guild were less likely to co-occur within modules than expected by random chance. These results suggest competition and temporal niche partitioning as likely mechanisms structuring plant-frugivore networks. My results provide a new perspective on how short-term, seasonal dynamics shape communities and provide empirical evidence for competition rather than facilitation as the major driver of temporal plasticity in mutualistic networks.

I supplemented my efforts to monitor local plant-frugivore networks across an annual period with systematic measures of seed dispersal in the landscape of three of these communities. I examined the roles of fruit abundance and frugivory on seed dispersal patterns, finding that characteristics of plants based on frugivory and network measures predict their propensity to colonize novel patches in a heterogenous landscape and that seeds of subsets of taxa are disproportionately delivered to particular habitat types.

Finally, given prior results suggesting strong indirect effects on the seasonal dynamics of plant-frugivore interaction networks, I sought to explore a possible mechanism driving movement behavior of birds and seed dispersal patterns through the implementation of sound broadcast experiments in forest restoration plots. Hypothesizing that the most prolific avian seed dispersers in the community would likely produce strong auditorial cues to other birds of feeding

opportunities, I quantified the attractive effects of broadcasts from avian species with varying levels of frugivory to potential avian seed dispersers visiting artificial perches in restoration plots. While I was unable to detect differences among responses to broadcasts from different levels of frugivory, I found that bird sounds produce a pronounced increase in avian visitors to perches in open fields than under control conditions with no added sound. These findings underscore the need to consider indirect effects that drive behavior beyond solely pairwise consumer-resource relationships and offer insight into previously understudied links between seed dispersal and sound ecology.

The investigations from this dissertation have marked an effort to resolve the ecological complexity of relations between plants and their avian seed dispersers in a region where these were previously undocumented. In addition to contributing new, highly resolved data set to the field of seed dispersal research, this work has sought to address knowledge gaps related to ecological networks. Examining processes such as frugivory and seed dispersal in large and diverse communities, however, inherently comes with numerous challenges and limitations. I have focused on study designs involving data collection of frugivory interactions at focal plants and seed deposition to collection traps. Data concerning the specific treatment of seeds and quality of dispersal by specific frugivorous bird species was not experimentally tested (Schupp 1993, Schupp et al. 2010). For example, we were unable to consistently distinguish legitimate seed dispersers that swallow seeds from those that ingest pulp without transporting the seed (e.g., fruit thieves) (Blendinger and Villegas 2011). The integrity of seeds and relative viability for germination following handling and digestion may also vary considerably, depending on the species responsible for dispersal (Traveset et al. 2007). Further study on the variation of specific traits and behaviors of seed dispersers represented in my data could provide important insights

into the extent of their contributions as mutualists or even antagonists to plants with which they interact.

Several other aspects of this study system remain open for further study. First, my investigations have focused on birds as seed dispersers, as they account for the vast majority of contributions to seed dispersal in the humid forests of the Dominican Republic. However, I have recorded observations outside of systematic data collection on dispersal by bats (*Artibeus jamaicensis*) and lizards (*Anolis* spp.). While the contributions of these groups to frugivory and seed dispersal appear to be small and not likely to greatly sway the major patterns uncovered by my work, their consideration in future studies could offer important advances. Beyond these groups of native seed dispersers, introduced animals in the region such as livestock, rats, mongoose, and humans are also likely overlooked as seed dispersers and seed predators (Miceli-Méndez et al. 2008, Carlo et al. 2013).

In focusing on the dynamics of plant-frugivore networks and resulting seed dispersal patterns, my investigations have alluded to some open-ended problems in seed dispersal research. The first relates to the challenge of spatial scale. In attempting to uncover effects of competition or facilitation between plant species for seed dispersal in Chapter 2, we were unable to detect any influence of fruits from trees in neighboring plots on the focal species, despite a strong signature for competition from landscape-level seed dispersal data. Only upon broadening the scale of vegetation and avian sampling in Chapter 3 did we detect indirect effects in our primary analysis. This dilemma conveys the importance of spatial scale in study design on both the likely result as well as its interpretation. The presence, magnitude, and direction of effects among species are likely to differ in a context-dependent manner at relatively fine vs. broader spatial scales (García and Ortiz-Pulido 2004). Defining appropriate scales, therefore, is critical to

study design. Nevertheless, there is no consensus for what scales is most appropriate for particular questions or how these might differ with respect to inferences made for ecological vs. evolutionary processes.

Species form the fundamental unit of mutualistic networks, but it must be acknowledged that populations are not monolithic in their properties. Intraspecific variation in the traits and behaviors of plants and animals are widespread for both animals and plants (Zwolak 2018, Snell et al. 2019), and individuals can have a different composition of mutualistic partners or contributions to frugivory and seed dispersal. This variance is largely ignored by the traditional network approach, despite it being the substrate upon which natural selection acts in seed dispersal systems. Integrating these elements into community-level studies, thus, presents a major challenge to the field.

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SELECTED PUBLICATIONS

Schubert, S. C., and E. L. Walters. 2022. Subannual phenology and the effect of staggered fruit ripening on dispersal competition. Biotropica 54:31–41.

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