We Travel Together: Examining the Drivers and Functions of Animal Movement in Biotic Seed Dispersal

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WE TRAVEL TOGETHER: EXAMINING THE DRIVERS AND FUNCTIONS OF ANIMAL MOVEMENT IN BIOTIC SEED DISPERsal

by

Binod Borah

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY in

Biology

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UTAH STATE UNIVERSITY Logan, Utah 2023
ABSTRACT

WE TRAVEL TOGETHER: EXAMINING THE DRIVERS AND FUNCTIONS OF ANIMAL MOVEMENT IN BIOTIC SEED DISPERSAL

by

Binod Borah, Doctor of Philosophy
Utah State University, 2023

Animal movement emerges from the interactions of multiple drivers, and contributes towards individual fitness and ecological services. Animal movement is vital for biotic seed dispersal, when animal vectors or seed dispersers disperse seeds to create the initial distribution of plant populations. Yet animal movement and plant ecology have run on parallel grounds where questions on drivers and implications of seed dispersers’ movement are treated as disparate topics. To have a generalized understanding of biotic seed dispersal, it is vital that we start establishing the links between drivers of animal movement and how it impacts initial seed dispersal patterns. In chapter 1, I developed a novel framework to integrate movement drivers into biotic seed dispersal studies. I proposed that we categorize the observed movement into their activity modes based on the distribution of fundamental movement elements, test what drivers give rise to these activity modes, and how these activity modes affect the emerging seed dispersal patterns. In chapter 2, I demonstrate that habitat conditions, an external driver of animal movement influence dispersers’ habitat choice and how they distribute their activities. I then show that both habitat choices and distribution of activities had non-random impacts on the conditions experienced by the dispersed seeds and their dispersal distances. In chapter 3, I
investigate how dispersers’ navigational capabilities used to track their resource locations and states influence their movement at multiple scales which in turn impact the seed dispersal patterns. In chapter 4, I tested how habitat loss and fragmentation can impact long-distance seed dispersal. I use a suite of simulations on artificial landscapes and showed that either fragmentation level or habitat amount or both can have distinct impacts on biotic seed dispersal. Finally, in chapter 5, I used multiple empirical datasets on bird-plant interactions, utilized allometric equations to estimate seed dispersal distances, simulated selective extinctions of large seed dispersers from hunting and other threats, and showed that plants with large fruits suffered stronger reduction in their long-distance seed dispersal which did not recover despite interaction rewiring. In conclusion, through my dissertation, I showed that movement drivers can significantly affect seed dispersers’ movement which can leave distinct signatures on seed dispersal patterns.

(212 pages)
Plants and frugivorous animals exist in mutually beneficial relations, as these animals feed on fruits, ingest the seeds, and carry them away from the parent trees. Such dispersion of seeds over space helps them colonize new habitats, escape high mortality rates near their parent trees, and avoid competition with conspecifics. Therefore, seed dispersing animal movement can be critical for the persistence of plant populations. Yet what drives such seed disperser movement is often less understood and how it affects seed dispersal is little explored. In my dissertation, I investigate multiple drivers of seed disperser movement, link movement to potential seed dispersal patterns, and how such movement and thus seed dispersal can be impacted by anthropogenic impacts. In chapter 1, I develop a framework that can allow us to couple seed disperser movement with the seed dispersal patterns, by using information from different movement drivers and characterizing movement into different activity modes. In chapter 2, I show that the external environment can be an important driver of a tropical seed dispersers’ movement and impact how far seeds are carried from their parent trees and the conditions they experience at their deposition sites. In chapter 3, I show that certain seed dispersers can account for multiple resource attributes while foraging, which in turn can affect their movement and hence seed dispersal patterns. Thus, seed dispersers’ navigational capabilities can play important roles in their seed dispersal services. In chapter 4, using computer simulations, I showed that habitat loss can have stronger impacts on seed dispersal patterns such as long seed dispersal
distances than habitat fragmentation, yet fragmentation impacts become more significant when
habitat amount fell below a threshold. Finally, in chapter 5, I showed that the loss of large
dispersers and therefore their movement from tropical ecosystems strongly reduced the long-
dispersal seed dispersal of large-fruited plants. In summary, through my dissertation I showed
that seed disperser movement is a critical component of plant seed dispersal.
ACKNOWLEDGEMENTS

It has been four wonderful years since I commenced my doctoral studies, and I am grateful for the support of several people throughout this venture. First, I would like to thank my advisor Dr. Noelle Beckman, who supported me wholeheartedly and had confidence in my abilities. Noelle, thank you for letting me pursue a research topic that I was unsure to begin with. My committee members were wonderful people, who pushed me to think beyond the obvious. Dr. Tal Avgar was a source of constant inspiration, who made me look at the bigger picture. I enjoyed my thoughtful discussion with Dr. Kezia Manlove.

I would like to thank the Biology department and the Ecology center for offering support for my research. My research would not have been possible without my collaborators, Dr. Meg Crofoot and Dr. Roland Kays. Thank you for kindly sharing your data. I would also like to thank the many people who made their data open source. My doctoral work made me realize the power of open data.

The Seedscape Research Group provided unbridled support, encouragement, and solidarity throughout my doctoral work. I big shout out to Elsa, Sarah, Rosemary, and Brynn. You all have been very kind. I owe a big thank you to Bryan, who would patiently help me with all my questions.

I am indebted to my families, in India and the USA. My parents, Rina and Debananda Borah and sister, Ponkhi have unwaveringly supported all my decisions, and I owe them for that. The kids and Kori, you all have brought warmth into my life. Our three dogs: Kola, Daku, and Hades have made me experience new joy. And finally, Wayne, you could not have been kinder, more patient, and supportive! This dissertation is the outcome of all that.
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INTRODUCTION

Biotic or animal-mediated seed dispersal is a critical ecosystem process that contributes towards individual fitness, plant population persistence, and community dynamics (Levine and Murrell 2003, Saastamoinen et al. 2018). Globally, around 52% of plants depend on animal vectors or seed dispersers to disperse their seeds (Aslan et al. 2013). This number rises to more than 80% in the tropics (Howe and Smallwood 1982). Animal movement is vital for biotic seed dispersal, as dispersers remove seeds from their parent trees, travel with them, and deposit these seeds to generate the initial spatial distribution of plants. Among the myriad of studies on biotic seed dispersal, several recently focused on how the observed movement affected seed dispersal patterns (Holbrook and Smith 2000, Campos-Arceiz et al. 2008). Some of these studies utilized dispersers’ gut retention time and their velocity to predict seed deposition sites along the observed movement trajectories, assuming random or selected start points (Stevenson and Guzmán 2008, Naniwadekar et al. 2019a). Other studies also used statistical movement models like Levy or Brownian walks to simulate disperser movement and seed dispersal patterns (Pires et al. 2017, Nield et al. 2020). However, amidst these advancements, we still lack clear understanding of what processes drive seed dispersers’ movement and how they affect the emerging dispersal patterns. In an attempt to make our knowledge about biotic seed dispersal more generalized and mechanistic, it is important to incorporate the drivers of disperser movement into seed dispersal studies.

Animal movement is the outcome of the interactions among several movement drivers (Nathan et al. 2008a). An individual can initiate movement when stimulated by its internal state, rely on its motion capacities to change its locations, use its sensory and cognitive capabilities to navigate while moving, and interact with the external environment comprised of both abiotic and
biotic components that further modify its movement. These drivers and their interactions that
give rise to the movement process are part of the new ‘movement ecology paradigm’ (Nathan et
al. 2008a). In my dissertation, I propose that the observed seed dispersers’ movement can
be considered as an emerging property and can be used as a template to connect movement
drivers with seed dispersal patterns.

The observed movement can be categorized into different canonical activity modes or
CAMs as described by Getz and Saltz (2008) and linked to the movement drivers. Different
CAMs are distinguished by their distribution of fine scale movement elements, including step
lengths, turning angles, directional bias, and stationary periods. Thus, the observed movement
can be categorized into activity modes such as foraging, traveling, resting etc. As seed dispersal
patterns can be strongly correlated to dispersers’ unique activities, the spatial distribution of
activity modes can have important consequences for how seed dispersal patterns emerge in the
landscape.

Among different external drivers of movement, habitat conditions are a major driver
(Graham 2001). Seed dispersers move among, select, and avoid different habitats. Such
movement patterns driven by habitat conditions result in non-random distribution of activity
modes and therefore seed dispersal patterns in the landscape. Tropical seed dispersers often
inhabit heterogenous forests, where habitat attributes like canopy height, cover, or terrain
ruggedness can vary (Hall et al. 1998). As seed dispersers navigate their external environment,
they exploit suitable habitats, explore habitats where conditions are unpredictable, and travel
through unsuitable habitats. Such activities can leave distinct signature on habitat conditions
experienced by dispersed seeds and their dispersal distances. Understanding how seed dispersers
select habitats, distribute their activities, and disperse seeds can also help towards forest restoration efforts, where we can create suitable conditions for biotic seed dispersal.

Movement facilitates seed dispersers in navigating their resource landscape, tracking, and exploiting their resources (Fryxell et al. 2005). Dispersers can use their sensory capabilities to detect visual or olfactory cues from resources or their cognitive capabilities to memorize both resource locations and attributes (Nevo and Ayasse 2020, Valenta and Nevo 2020). Thus, navigational capabilities can strongly drive movement, which in turn promotes individual survival and growth. Foraging movement can also impact seed dispersal patterns. Dispersers can make decisions at different spatial scales, selecting resources that can reduce travel cost or increase venture profitability, and travel directly between resources. Such movement can result in distinct seed dispersal patterns. Yet, both resource abundance and distribution can change, forcing dispersers to adapt and change their foraging and movement strategies. This can lead to substantial changes in seed dispersal patterns they generate.

In my first three chapters, I investigate how drivers of seed disperser movement affect the seed dispersal patterns they generate. I particularly focus on external drivers such as habitat conditions, and navigational drivers such as foraging decisions. I used two different primate species in my studies, as primates’ movement is shaped by external habitat conditions, they are known to reliably navigate for their resources, and disperse seeds in the process (Chapman and Russo 2007, Garber et al. 2009). To answer some of my questions, I used large observational datasets on animal relocations, remotely collected environmental data, novel statistical models, and integrated them together in simulation models to generate artificial seed dispersal patterns.

My last two chapter focuses on how anthropogenic activities affect biotic seed dispersal through its impacts on animal movement. Biodiversity is at an increasing risk today, as human
activities have expanded the anthropogenic landscape, where native habitats may now only co-occur as fragments. Habitat fragmentation and loss is a global threat, and their impacts on biodiversity is exhibited through reduction in population size, community richness, and genetic diversity (Fahrig 2003). Habitat fragmentation and loss can also affect biodiversity’s hidden components— the myriad ecological interactions such as biotic seed dispersal. The reduction and reconfiguration of native habitats will affect seed dispersers’ habitat choices, their activities, and movement patterns which in turn can change their ability to disperse seeds. It is urgent that we begin to understand how habitat fragmentation and loss can jointly and independently affect seed dispersal patterns. This can have important conservation implications such as setting aside land for conservation, their spatial configuration, and restoration efforts to improve and add habitats in anthropogenic landscapes.

However, anthropogenic impacts on animal movement can be more severe, where movement of specific disperser is rather lost from the ecosystem through disperser extinction with cascading impacts on seed dispersal. Human activities such as hunting disproportionately targets large seed dispersers, many of who can carry seeds relatively farther away from their parent trees (Bello et al. 2015, Peres et al. 2016). Their loss from communities can be detrimental to the entire plant community that interact with them (Donoso et al. 2020), yet plants with large fruits may disproportionately bear the brunt of their extinction. The situation can be even more dire if the ecological services rendered by large seed dispersers are rather irreplaceable and can’t be recovered by other dispersers that still persist in the community. Therefore, alterations or loss of animal movement will inevitably affect biotic seed dispersal.

In summary, my dissertation is a step towards coupling two seemingly disparate fields: animal movement and plant ecology that so far have run on parallel paths.
References


CHAPTER 1: STUDYING SEED DISPERSAL THROUGH THE LENS OF MOVEMENT ECOLOGY

Binod Borah, Noelle G. Beckman

Abstract

Frugivore movement plays a critical role in animal-mediated seed dispersal. Frugivores utilize resources that are heterogeneously distributed in the landscape and execute complex movement to exploit these resources. Employing the ‘movement ecology paradigm’, we discuss the drivers behind frugivore movement, categorize movement into canonical activity modes, and explore the potential impacts on seed dispersal effectiveness via removal and deposition of seeds. Among the movement drivers, frugivore physiology determines the goals, motion capacities determine how frugivores move across their heterogenous landscape, navigation capabilities determine how frugivores acquire and process both internal and external information that set them in motion, and biotic interactions further modulate frugivore movement. The movement process that emerges from the interactions of these drivers can be classified into different canonical activity modes that determine levels of seed removal and generate clumped, even, or other spatial distributions of seed deposition. We provide a novel framework to integrate movement drivers, frugivore activities, and seed dispersal services. We provide future directions utilizing advances in animal movement research to better understand the role of animal movement in the effectiveness of seed dispersal, highlighting potential impacts of increased anthropogenic activities. To advance a mechanistic understanding of animal-mediated seed dispersal, we encourage increased collaboration between animal movement and plant ecologists.
Introduction

Seed dispersal is a critical determinant of individual fitness (Saastamoinen et al. 2018) and contributes towards plant population persistence (Levin et al. 2003, Beckman et al. 2019) and community dynamics (Levine and Murrell 2003, Howe and Miriti 2004). Frugivorous vertebrates (or frugivores) play important roles in seed dispersal. Frugivores move seeds away from their parent locations and generate the initial spatial distribution of plants (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000, Clobert et al. 2012). Vertebrates disperse approximately 52% of plants globally (Aslan et al. 2013) and more than 80% of tree species in tropical systems (Howe and Smallwood 1982, Muller-Landau and Hardesty 2009). The movement of frugivores provides an important link among the different processes of seed dispersal, plant demography, and community dynamics. While mechanistic approaches to understanding animal-mediated seed dispersal have been proposed earlier ((Côrtes and Uriarte 2013), they often lump together the different movement drivers. Thus, we still have a limited understanding of how the underlying drivers of frugivore movements influence patterns of seed dispersal.

Several studies have investigated the consequences of frugivore movement on one or more components of seed dispersal effectiveness (Holbrook and Smith 2000, Morales and Carlo 2006, Campos-Arceiz et al. 2008, Nathan et al. 2008a, Stevenson and Guzmán 2008, Bravo 2009). Seed dispersal effectiveness (SDE) is the contribution of seed dispersal to the future reproduction of a plant (Schupp 1993, Schupp et al. 2010). It is quantified as the quantity (e.g., number of frugivore visits, number of seeds dispersed each visit) of seeds dispersed by a disperser times the quality of seed dispersal (e.g., gut or mouth treatment, quality of deposition sites, etc.) (Schupp 1993). Previous studies have focused on predicting spatial patterns of seed
deposition from observed frugivore movement within the SDE framework. For instance, some studies utilized frugivore velocity and gut retention time to predict seed deposition sites along observed movement trajectories of frugivores, assuming starting points of the movement trajectories as either random locations or foraging sites of the frugivore (Westcott et al. 2005, Phiphatsuwannachai et al. 2018). Other studies utilized statistical movement models such as Levy or Brownian walks to simulate frugivore movement and seed dispersal using parameters from observed data (Pires et al. 2017, Nield et al. 2019). For instance, (Pedrosa et al. 2019) used both Levy and Brownian walk models to simulate spatial distribution of seeds dispersed by mammalian dispersers in the Atlantic forests. In their empirically parameterized models, the authors found that Levy walk models resulted in longer median dispersal distances compared to that from Brownian models, which can have consequences for the quality of seed dispersal. However, these studies treat the drivers behind the observed movement patterns as latent.

A next step is to explicitly incorporate the drivers of frugivore movement into studies of seed dispersal. Observed movement patterns can be treated as an outcome of the interactions among different movement drivers. Therefore, we consider observed frugivore movement as an emerging property that provides the template to connect movement drivers with their consequences for seed dispersal. We can do this by building on the conceptual model of animal movement introduced by Nathan et al (2008a) that was mathematically described by Getz and Saltz (2008). As proposed by Nathan et al (2008a), the movement path of frugivores emerges from an individual’s internal state that stimulates movement (why move?), the frugivore’s motion capacity (how to move?), the frugivore’s navigation capacity to orient in space and time using sensory and cognitive capabilities (when and where to move?), and the frugivore’s interactions with the external environment (see Fig. 2 in Nathan et al 2008a). We can
mathematically characterize this observed movement of organisms by identifying their canonical activity mode (CAM) (Getz and Saltz 2008). Different CAMs are distinguished by their distribution of fine scale movement elements, including step lengths, turning angles, directional bias and stationary periods. For example, the movement of frugivores can be characterized as foraging if exhibiting short, tortuous steps; exploring if exhibiting long, directed steps; and resting if exhibiting stationary periods (Fig.1.1). The distribution of a frugivore’s CAM within a given landscape can have important consequences for seed dispersal, as the spatial distribution of seeds can strongly correlate with the frugivore’s activity mode. For example, foraging can result in higher seed removal and deposition rates at the spatial scale of fruiting tree patches, resting can cause clumped seed deposition under sleeping sites, and exploring can result in more uniform patterns of seed removal and deposition at much larger spatial scales (Table.1.1). Hence, a fruitful step towards making animal-mediated seed dispersal ecology more generalized and mechanistic is to incorporate the drivers of frugivore movement and characterize the observed movement into different CAMs in studies of seed dispersal (Getz and Saltz 2008).

Here, we propose a frugivore-centered, individual movement-based and process-oriented approach to studying the effectiveness of seed dispersal, focusing on seed removal and deposition patterns (Fig.2.1). We build on the previous work by (Côrtes and Uriarte 2013) who proposed a frugivore-centered framework to advance a mechanistic understanding of animal-mediated seed dispersal by integrating two existing frameworks, the movement ecology paradigm (MEP) along with the characterization of movement into CAMs; (Getz and Saltz 2008, Nathan et al. 2008a) and seed dispersal effectiveness (Schupp 1993, Schupp et al. 2010). We review existing literature since their seminal review and complement their work in the following ways: We first discuss the different patterns of observed frugivore movement and then consider
in detail the various drivers of movements, specifically, the internal states, motion capacities, navigation abilities of frugivores and their biotic interactions that influence seed dispersal. We focus our discussion on daily movements observed at fine spatiotemporal scales which influence the quantity of seeds dispersed and the quality of seeds dispersed at local spatial scales. Finally, we briefly summarize the potential anthropogenic impacts on frugivore movement and seed dispersal. In conclusion, we aim to encourage ecologists to break new ground and integrate frugivore movement in their seed dispersal research.

**Patterns of frugivore movements**

Patterns of animal movement influence patterns of seed dispersal across spatial and temporal scales. At large spatiotemporal scales, movements such as migration influence long-distance seed dispersal (Nathan et al. 2008b). For example, migratory passerines and waterfowls disperse few seeds much farther away than their average dispersal distances (Viana et al. 2016). Migratory movements can especially become critical for seed dispersal if migration time coincides with peak fruiting period (Hanya 2005). Long dispersal distances help plants to colonize new habitats or maintain connectivity in their metapopulation (Levine and Murrell 2003, Levin et al. 2003). At fine spatiotemporal scales, seed dispersal plays important roles in local population and community dynamics, as it mediates processes such as seed predation, competition, micro-habitat filtering that occur in the neighborhood of the dispersed seeds. Most studies of frugivores and seed dispersal focus on fine spatial scales (a few meters to kilometers) and short temporal scales (few days to weeks), and frugivores disperse majority of seeds by their daily movements (Nathan et al. 2008b, Côrtes and Uriarte 2013). We focus our subsequent discussion on fine spatiotemporal scales.
A preliminary step towards a mechanistic understanding of seed dispersal is to recognize the patterns of observed frugivore movements while foraging. These movement patterns can be described by a statistical movement model, that uses the observed distribution of step lengths and turn angles of the movement (Edelhoff et al. 2016). However, different movement models can produce similar distribution of step lengths and turn angles and thus CAMs. Therefore, it is important to understand the processes that generate these patterns.

Frugivore movement can be described by different movement models. In Levy walk, frugivores move with a series of short, tortuous steps that are connected by the occasional long and directed steps. Levy walk is considered a scale-free foraging movement (Boyer et al. 2006) where the distribution of step lengths follows a power law with a heavy tail. A similar pattern of short, tortuous steps and the occasional long directed steps is also generated by the ‘area restricted search’ model. Other models include the Brownian walk where the step lengths of a random movement is described a Rayleigh distribution, a correlated random walk model where successive turn angles are concentrated around zero that result in persistent movement direction, or a biased correlated random walk model, where in addition to directional persistence, frugivores can display biased movement towards or away from a goal, for e.g., roosting sites.

The patterns of step lengths and turn angles distributions in these movement models can be generated by fundamentally different processes. For instance, despite the similarities in the generated patterns, Levy walk assumes featureless environment, memoryless foragers, stationary behavioral state, and non-directional movement, some of which are now questioned on their biological basis (Reynolds 2008, Benhamou 2014). Whereas area restricted search emerges as the foragers interact with the resource environment. Particularly, area restricted search is considered an efficient strategy in a heterogenous resource landscape like a tropical forest where
tree species tend to be patchily distributed, occur in low densities, and fruit seasonally (Cartar and Real 1997, Condit et al. 2000, Roshier et al. 2008). In this movement model, frugivores move fast and straight when exploring their environment. However, movement speed is reduced, and tortuosity is increased when they discover a fruiting tree (Fauchald and Tveraa 2003). Therefore, observed movement patterns that follow an area restricted search can be classified as a distribution of between patches explorative and within patch exploitative CAMs. In light of this, the observed movement pattern of frugivores such as Spider Monkeys (*Ateles geoffroyi*) and African Elephants (*Loxodonta africana*) that were described by a Levy walk model (Ramos-Fernández et al. 2004, Dai et al. 2007) can also be described by movement models such as area restricted search. Interactions between the forager and the resource environment can also describe the patterns generated by the other models. In African savannahs, where resources are randomly distributed, Chacma baboons (*Papio ursinus*) moved with nearly uniform speed and the observed movement pattern followed a Brownian walk (Sueur 2011). Ochre-bellied flycatchers (*Mionectes oleaginous*), a small Australian frugivore bird, have been shown to exhibit a correlated random walk in which their turn angles were correlated as they moved directedly between known resource locations within their home ranges (Westcott and Graham 2000, Asensio et al. 2011).

Different movement models as described above result in different seed dispersal patterns with consequences for plant populations. For instance, area restricted search can generate long dispersal distances for seeds, critical for connectivity among populations or establishment of new populations. Brownian walk models, on the other hand, generate shorter dispersal distances and can be useful in understanding frugivore roles in local dynamics of plant populations. Ecologists can therefore utilize these models to simulate a range of possible frugivore generated seed
dispersal spatial patterns and investigate their ecological consequences. However, these movement models do not entirely capture the complexities of observed movement patterns that emerge from the interactions of various drivers.

In the subsequent sections, we discuss the internal states, motion capacities, navigational abilities, and biotic interactions that drive observed frugivore movements and their consequences for seed dispersal (Fig. 2.1).

**Why move? Internal drivers of movement.**

The internal state of frugivores incorporates a range of physiological and psychological states (Nathan et al. 2008a). These states drive the frugivore to attain a variety of goals, such as searching for food and mates or avoiding competition and predation, and give rise to distinct CAMs with implications for seed removal and deposition patterns. (Goossens et al. 2020).

Frugivores, like any living organism, require energy to maintain vital processes, and this internal stimulus mediates their movement. Hungry frugivores can remove more seeds from fruiting trees as they will consume more fruits to satiate their hunger. Hungry frugivores can also disperse seeds closer to their parent trees if they spent longer in the fruit tree patches for satiation, or farther from their parent trees if they exploit and move frequently among patches for satiation. Different physiological functions, such as thermoregulation and digestion, have competing demands on energy that could otherwise be allocated to movement. When movement becomes energy limited, a frugivore can stop moving to conserve energy. For instance, when ambient temperature is high, tropical frugivores experience higher energetic demands for thermoregulation, restricting energy allocations for locomotion (Korstjens et al. 2010). Consequently, to counter the heat load, frugivores cease movement, seek out shelter, and spend time resting. Such disperser movements interspersed with irregular periods of rest can result in
scatter dispersal of seeds. For example, seeds of *Virola calophylla* dispersed by Spider monkeys (*Ateles paniscus*) were deposited on average further from the nearest female tree under diurnal resting sites compared to sleeping sites (61 m vs 48 m, respectively, (Russo and Augspurger 2004). Likewise, assimilation of digestive nutrients can cause increased demand for oxygen (Karasov et al. 2011). Frugivores can prioritize blood flow to the gastrointestinal system for efficient digestion and reduce their movement. Consequently, seed passage time through the gut is reduced and dispersal distance can be shortened. Gut passage time of seeds in Mallard (*Anas platyrhynchos*) decreased with moderate activities (Kleyheeg et al. 2015). On the contrary, some frugivores prioritize movement and allocate energy to the locomotory system. In this case, seeds can be retained longer in the gut due to poor assimilation, causing an increase in dispersal distances. Common carps (*Cyprinus carpio*) experienced increased gut retention time for two riparian plant species during periods of high activities (Van Leeuwen et al. 2016). Finally, energetic demands increase with frugivore size with implications for seed dispersal effectiveness, especially for larger-seeded plants (Holbrook and Loiselle 2009, Campos-Arceiz and Blake 2011, Naniwadekar et al. 2019). Larger-bodied frugivores remove higher quantities of seeds, forage over larger areas (Mace and Harvey 1983), and tend to consume larger seeds (Naniwadekar et al. 2019) compared to smaller-bodied frugivores to meet increased energetic demands. The different physiological states experienced by the frugivore influences the frugivore’s CAM distribution, gut retention time, and, therefore, the number of seeds removed and the spatial deposition of seeds.

A frugivore’s daily CAM distribution and its impact on seed dispersal can be modified by their seasonal activities, such as breeding. In many species of rain forest birds, males display with other males in leks and females move among leks for mates (Karubian and Durães 2009).
During the breeding season, male manakins restrict their activities to their leks, removing most seeds from the nearby trees and depositing them in the leks, resulting in short dispersal distances and a clumped distribution of seeds (Karubian and Duraes 2009, Cestari and Pizo 2013, Ryder et al 2008). In contrast, females and juveniles move among multiple lek sites, removing and depositing seeds both near and away from leks, resulting in long dispersal distances and a uniform distribution of seeds (Théry 1992, Loiselle et al. 2007, Ryder et al. 2008, Tori et al. 2016). During the non-breeding season, manakins regardless of age and sex use both lek and non-lek areas variably, where they can remove and deposit seeds, thereby generating a more uniform distribution of seeds (Cestari and Pizo 2013). Post-mating physiological states can also alter frugivore activities. Lactating female squirrel monkeys (Saimiri oerstedii) foraged more frequently for fruits (Boinski 1988) and potentially removed more seeds. Female squirrel monkeys were also less stationary (Boinski 1988) and could contribute more towards dispersal of seeds. On the contrary, pregnant, and lactating female capuchin monkeys (Cebus capucinus) spent more time resting (Rose 1994) and therefore could contribute less to both seed removal and dispersal distances.

Psychological or behavioral states of the frugivore can affect the spatial distribution of seeds via a frugivore’s CAM distribution of movement elements (Zwolak and Sih 2020). Behavioral traits include boldness, timidness, fearfulness, etc and can vary among individuals within a population. Compared to timid frugivores, bold frugivores tend to be more active, exploring their environment by repeatedly turning and moving with longer steps into more diverse habitats (Zwolak and Sih 2020). Hence, bold frugivores may encounter more fruiting trees and carry seeds farther away, while timid frugivores may concentrate feeding at fewer
fruiting trees and disperse their seeds into more limited, specific habitat types through directed movements.

Behavioral states can also vary among species and depend on the environment context, resulting in interspecific differences in the distribution of CAMs and consequences for seed dispersal patterns. For instance, fear of predators causes some frugivores to abandon foraging in open areas for cover, whereas others can engage in vigilance activities in the same area. In Lahav Forest, Israel, Sapir et al. (2004) suggest Sylvia warblers utilized areas with high foliage density to avoid detectability by predators. Therefore, these frugivorous birds are likely to deposit more seeds in these microhabitats. On the contrary, bolder Turdidae chats preferred higher perches for vigilance and hence are expected to deposit more seeds under these locations (Sapir et al. 2004). Incorporating the role of fear in animal movement can thus offer some intriguing insights into seed dispersal.

**How to move? Role of motion capacity**

Motion capacity can interact with the external environment to create spatial heterogeneities in distribution of CAM movement elements such as step size or turn angles. Frugivores have evolved multitudes of locomotory adaptations such as climbing, quadrupedal walking, flying, and swimming, although tremendous variation can exist within each, in response to the external environment. These locomotory strategies influence seed dispersal, including the rate and pattern of seed removal and the rate and spatial pattern of seed deposition. Therefore, the capacity of the frugivore to move can have big effects on seed dispersal.

Non-volant arboreal frugivores have evolved different locomotion modes, including climbing, quadrupedal walking, brachiation, and leaping (August 1983) to move through the structurally complex vegetation layers of tropical forests (Chapman et al. 1997, Drake et al.
Many arboreal species, particularly primates, engage in suspensory locomotion and feeding using their prehensile tails (Fleagle and Mittermeier 1980). Leaping and bridging are common ways for primate species to cross tree fall gaps, a regular barrier to movement in tree canopies, but these modes are energetically costly (Cannon and Leighton 1994). Therefore, arboreal frugivores are likely to deposit fewer seeds in tree fall gaps. The location of suitable substrates for movement influences where arboreal frugivores will deposit seeds. Arboreal frugivores select substrates that support their body weight (Fleagle and Mittermeier 1980), and many primates use large lianas that facilitate vertical climbing as well as lateral movement among canopies (Manduell et al. 2012). Therefore, the spatio-temporal distribution of gaps and suitable substrates can partially explain why many arboreal frugivores use specific networks of routes to move in their habitats.

Terrestrial locomotion involves a diverse set of modes such as walking, running, and leaping. Among terrestrial vertebrates, energetic expenditure while walking is similar and only 30% of stored muscle energy is used (Cavagna et al. 1977). More energy is expended while running, but animals can cover greater distances. Overall, terrestrial locomotion can be cheaper than arboreal movement (Karasov 1992), and it is not limited by canopy features such as tree fall gaps. Compared to flat areas, locomotory cost of moving along landscape features such as hill slopes can be high. African elephants \((Loxodonta africana)\) incurred 2500% increase in energetic cost while moving along hill slopes compared to level walking (Wall et al. 2006). Therefore, terrestrial frugivores may avoid areas where costs of locomotion can be high, such as steep slopes, and remove and deposit fewer seeds in such areas.

Flight is a quick way to travel between two points and is energetically less expensive than terrestrial locomotion (Karasov 1992). CAM elements such as flight speed and maneuverability
are strongly determined by wing shape. Short, pointed wings with heavy wing load allow high speed and enables quick changes in directions. In contrast, long wings are used for slower flights (Farney and Fleharty 1969). Flight allows an animal to cross inhospitable environments and exploit resources inaccessible to terrestrial frugivores. Volant frugivores are therefore expected to disperse seeds to habitats that are disjointed by harsh environment. Some of these vertebrates are also more likely to carry seeds farther than other frugivores. Trumpeter hornbills (Bycannistes buccinator) carried seeds up to a distance of 8914 m in an agricultural landscape and frequently transported seeds between forest fragments (Lenz et al. 2011).

Frugivorous fishes constitute an important group of seed dispersers (Horn et al. 2011, Correa et al. 2015). Among fish species, CAM elements such as speed and turn angles depend on the mode of swimming. Fishes that primarily use their body and caudal fins to propel forward can swim faster but turn slowly. On the other hand, fishes that use their median and paired fins are slow swimmers but can turn rapidly (Breder Jr 1926). Swimming is energetically less costly than terrestrial locomotion (Stouffer 1940), and can result in long dispersal distances. In the Amazonian floodplains, the large-bodied characid Colossoma macropomum dispersed seeds to mean dispersal distances of 337-552 m (Anderson et al. 2011). The riverine fish Brycon guatemalensis carried seeds of Ficus glabrata in its gut for more than 30 hours. These fishes were recorded to swim longer distances upstream and therefore can disperse seeds farther away from the parent trees (Horn 1997).

**When and where to move? Role of navigation capacities**

Frugivores acquire information, provided by the external environment as well as internal cognitive abilities, to respond to their external environment and navigate towards resources. How frugivores detect, evaluate, and integrate different sensory cues and cognitive information will
determine their emerging CAMs and roles as seed dispersers. In the simplest of scenarios, frugivores may lack any external information or internal memory and engage in a ‘random search’. As they explore their environment, these naïve foragers can play important roles in long distance dispersal of seeds and generating a random distribution of deposited seeds. At the opposite extreme, frugivores may have perfect information of the resource landscape, exhibiting directed and recursive movements towards resources. In a simulated study, (John et al. 2016) showed that frugivores with memory repeatedly visited the same set of more profitable trees and ingested more seeds than naïve foragers. These repeated movements can result in increased seed deposition in some areas and clumped seed deposition across the landscape.

To acquire information of the external environment, frugivores rely on multiple sensory cues, including auditory, visual, and olfactory signals from resources as well as the non-resource environment. The strength of these sensory cues is scale-dependent, and their effectiveness depend on modulation by the external environment as well as individual frugivore perception. Auditory or olfactory cues provide information over larger spatial scales compared to visual cues (Dominy et al. 2001); this non-local information allows frugivores to navigate directly towards fruiting plants and can increase forager concentration at resources compared to local information ((Fagan et al. 2017). On the other hand, visual cues, such as fruit color, may be effective only at short distances in a tropical forest. Frugivores may be attracted to feeding calls of conspecific or heterospecific members that offer information about overall habitat quality (Reed and Dobson 1993, Koda 2012, Albrecht et al. 2018). Lemurs in Madagascar use olfactory cues, or specifically volatile organic compounds (VOCs) emitted from ripe fruit, to locate fruiting trees within patches; species with fruit dispersed by lemurs produced more VOCs compared to fruit dispersed
by birds (Nevo et al. 2018). In addition, olfactory cues can be the primary sensory drivers for frugivores that forage nocturnally, such as bats (Rieger and Jakob 1988).

Frugivores also rely on cognitive information for navigation (Chapman and Lefebvre 1990, Tomasello and Call 1997, Healy and Hurly 2004, Page et al. 2012). Fruiting in tropical forests can be predictable (Riotte-Lambert and Matthiopoulos 2020) because they are stationery in space and bear fruits for weeks before being depleted (Corlett 2011). Multiple trees in a neighborhood can fruit synchronously, have predictable renewal rates, and fruit in specific seasons (Snow 1965, Gorchov 1990). All these conditions can select for different types of memory in frugivores, including spatial and attribute memory (Garber and Paciulli 1997, Boinski and Garber 2000). With spatial memory, frugivores encode the locations of fruiting resources and other important landmarks (Fagan et al. 2013) that helps them orient with respect to their goals for moving. With attribute memory, frugivores encode features of fruiting resources such as abundance, type, and renewal rates (Fagan et al. 2013) that reduces the uncertainty in information that is location independent. Learning and retaining the renewal rates of resources reduces the chance of visiting an already exploited resource. Frugivores can memorize renewal rate either as a periodic event or one that is strongly associated with some environmental cues (Garber and Paciulli 1997). For instance, Grey-cheeked Mangabeys (*Lophocebus albigena*) frequently visited fruiting trees during warm periods when they anticipated fruit ripening due to higher temperature (Janmaat et al. 2006a).

Frugivores use external sensory cues and internal memory to varying degrees. As the strength of sensory cues decay with distance and memory decays over time, imperfect information of resource locations and availability can cause deviations from the frugivore optimal goals or travel paths. To supplement this imperfect information, primate species have
been observed to regularly sample the fruiting status of trees to gain information on new feeding locations or reinforce existing information, thereby offsetting additional movement costs (de Guinea et al. 2019, Souza-Alves et al. 2019). Accounting for resource monitoring while studying frugivore foraging behavior and seed dispersal can explain some of the variation observed in seed removal or deposition patterns.

**External drivers of movement: Biotic Interactions**

Frugivores engage with a variety of biotic interactions, including intra- and interspecific competition (Fleming 1979, Alcántara et al. 1997), facilitation (Saracco et al. 2004), and predation (Howe 1979) that can alter frugivore activities and drive movement patterns resulting in different CAMs. These external drivers of movement have implications for the quantity and quality of seed dispersal.

Frugivores may engage in intra- and interspecific competition (Fleming 1979, Alcántara et al. 1997). Over the period of an individual’s life span, resource defense and differential space use in response to competition can give rise to territoriality. How territory shapes seed dispersal depends on multiple factors, including movement attributes, aggression, and degree of resource monopoly (Karubian and Durães 2009). Territoriality restricts the spatial extent of movement but can cause recursions in movements. If the territory owner repeatedly moves among fruiting trees for patrolling, it can disperse seeds away from parent trees. However, few other frugivores will intrude to remove and disperse seeds from trees. For example, territorial Ruwenzori Turacos (*Musophaga johnstoni*) often drove away the Great Blue Turacos (*Corythaeola cristata*) from their territories (Sun et al. 1997). On the contrary, if the territory owner monopolizes few fruiting trees and spends longer durations in their defense, most seeds can end up beneath the parent trees. In this case, other opportunistic frugivores may intrude, feed on other resources that are
poorly defended, and disperse seeds away from the parent trees. Territoriality can also alter seed dispersal services in shared areas among frugivore neighbors. Neighboring Chimpanzee (*Pan troglodytes*) groups underused overlapping areas where territorial aggression can get lethal and fed less frequently while patrolling in these areas (Amsler 2010). On the other hand, Capuchin monkeys (*Cebus capucinus*) depleted fruiting trees to a greater extent in the peripheral areas of their home ranges (Tórrez-Herrera et al. 2020).

Facilitation can shape frugivore CAMs by affecting exploratory and foraging behaviors. Terrestrial vertebrates like Chital deer (*Axis axis*) aggregated around those fruiting *Phyllanthus emblica* trees that had the arboreal Hanuman langur (*Semnopithecus entellus*) feeding on them. These monkeys removed and dropped large number of fruits on the ground, and thereby facilitated their dispersal by the terrestrial seed dispersers (Prasad and Sukumar 2010). Similarly, the specialist tanager, *Spindalis portoricensis* discovered new foraging areas after they cued on the loud calls and joined flocks of the generalist heterospecific, *Nesospingus speculiferus* (Saracco et al. 2004). Therefore, facilitation promotes foraging activities in presence of mutualist partners and can cause increased seed removal or deposition rates as well as longer dispersal distances.

Risk of predation can have major influence on frugivore CAMs via changes in behavior. Animals move faster through areas where predation risk is high or avoid them (Gallagher et al. 2017). Taking advantage of this change in behavior, scatter hoarding rodents place caches in these areas to reduce risk of cache loss from pilferage (Steele et al. 2014). For frugivores, particularly solitary or smaller frugivores, foraging and vigilance are mutually exclusive activities. As such, frugivores can suspend feeding to look out for predators, become less detectable, or move away from feeding trees to seek refuge (Howe 1979).
The resulting movement path: Interactions among the drivers of movement

Frugivore internal states, motion, and navigational capacities will give rise to the realized movement path, which is simultaneously impacted by the external abiotic and biotic environment. This movement propagation process can be characterized by different CAMs, distinguished by their step lengths, and turn angle distributions. Different CAMs can result in distinct seed dispersal patterns (Fig. 1.2).

Frugivores may move directly towards their resources, resulting in nearly straight-line movement paths. Frugivores consider profitability and accessibility, among other factors when selecting resources (Levey et al. 1984, Martin 1985). Profitability of a resource can be measured as its net energetic yield after accounting for potential costs such as travel time, handling time, etc. (Levey 1987, Hegde et al. 1991, Witmer and Van Soest 1998). As a profitable foraging strategy, frugivores can use sensory cues to move in straight lines towards nearby resources. For instance, Capuchin monkeys moved to the closest resource when foraging (Janson and Byrne 2007). When such straight-line movements are observed towards resources that are beyond sensory perception, it is inferred that frugivores use a map-based navigation to forage. In such a navigation strategy, an animal has a long-term memory of the spatiotemporal features of the environment (or a ‘cognitive map’), allowing it to take shortcuts. Egyptian fruit bats (*Rousettus aegyptiacus*) used novel straight paths towards resources that were beyond their perceptual ranges (Toledo et al. 2020). When these bats were relocated, they returned to familiar fruiting trees from multiple directions using nearly straight line flights. Similarly, Tai Forest chimpanzees used shortcuts to visit distant fruiting trees, rarely reused routes, and approached fruiting trees from multiple directions (Normand and Boesch 2009). However, straight line traveling can also occur for other reasons. Many frugivores are territorial and maintain home
ranges. Such frugivores can travel in straight lines to frequently monitor their home ranges and reach range boundaries in shorter duration (Terborgh and Stern 1987). Alternatively, straight line travel can reduce backtracking and therefore the chances of encountering resources that were already depleted (Pyke 1978). The use of novel, straight lined paths to exploit resources can result in frugivore CAMs such as foraging, resting etc. to be more evenly spread in the landscape. As a result, they may encounter higher number of fruiting trees or deposit seeds evenly.

Several vertebrate frugivores can alternatively use route-based traveling to navigate in a tropical forest (Garber and Jelinek 2006, Valero and Byrne 2007). Routes can essentially connect resource patches or familiar landmarks distributed across the landscape. Route-based travelling therefore can be less cognitively demanding as frugivores can use few habitual routes. Routes can also lie among habitats such as ridges or tall canopy that facilitate movement. Therefore, route-based traveling can be treated as a spatial network where nodes are the resources (or landmarks), and the routes are the edges connecting them. Frugivores make important travel decisions at the nodes (or where two routes intersect). Saddle back Tamarins (Saguinus fuscicolis) significantly changed directions at these nodes and used familiar routes to exploit fruiting trees (Garber and Porter 2014). Routes can become well established over a period. Sympatric spider monkeys and woolly monkeys (Lagothrix lagotricha) used arboreal routes that ran along ridges in a study that spanned for eight years (Di Fiore and Suarez 2007). Frugivores that use habitual travel routes restrict their CAMs along these paths. For instance, White-bellied Spider monkeys mostly visited fruiting trees that occurred within 50m of their regularly traveled routes (Di Fiore and Suarez 2007). In this case, while the monkeys may feed on fewer trees, they can remove larger number of seeds from an individual tree. Route-based travel will result in a
spatially restrained seed shadow, as most seeds will be deposited along or close to these routes. Over a period, this can result in higher concentrations of seeds and later recruitment stages of fruiting trees around repeatedly used routes. Di Fiore and Suarez (2007) hence suggested that route travelling arboreal frugivores can contribute towards constructing or modifying ecological niches. In practice, frugivores are likely to use both straight line and route-based movement, but use them differentially over space. (Poucet 1993) suggested that frugivorous mammals like primates move in straight paths while navigating in small areas, particularly in core areas of their home ranges, and are more likely to use route-based travel in large areas and in the periphery of their home ranges.

Many frugivores make movement and foraging decisions based on one or more central locations (Chapman et al. 1989). These foragers display recursive movement to their central locations such as a nesting site, den, or roosting site (Kalina 1989, Suselbeek 2009, Rainho and Palmeirim 2011). Choosing foraging locations from a central location then assumes the form of a ‘traveling salesman problem (TSP)’, a mathematical algorithm. In a TSP, an individual chooses a set of destinations to visit and returns to the start point using the shortest route (Flood 1956). The navigation mechanism called ‘path integration’ involves continuous updating of the forager’s position through tracking and integrating of all distances and directional changes (Etienne and Jeffery 2004). However, errors can accumulate. Hence, central place foragers may also depend on visual cues or other mechanisms to navigate. Instead of planning for the entire route, as an approximation to the TSP, frugivores can plan for a few resources. Such ‘look ahead’ rules assume frugivores choose the shortest path to visit these resources. (Janson 2014) demonstrated that several primate species plan to visit two (and sometimes three) resources and use the shortest path connecting them.
Different spatial foraging models are employed to represent frugivore decisions on ‘where to move’. The observed movement process is either implicit or explicit and the models assume disparate perceptive or cognitive abilities. For example, the ‘gravity’ models are patch movement models, where frugivore movement between resources is not expressed. Gravity models are useful to test the influence of resource distribution and productivity and frugivore internal state and navigation on foraging decisions. For instance, these models can provide important insights into the optimal cache spacing hypothesis in scatter hoarding rodents and birds. This hypothesis predicts that scatter hoarding vertebrates distribute caches spatially to minimize travel cost, yet position them farther apart to deter pilfering individuals (Gálvez et al. 2009). Studies have shown that scatter hoarders recognize the reward from individual seeds, and place larger seeds farther away (and hence at lower densities) than smaller seeds (Kuprewicz and García-Robledo 2019). As many seed caches are never retrieved, such spacing patterns will subsequently influence plant spatial patterns. Alternative to gravity models, in ‘place utility models’, frugivore movements are explicitly expressed. In these models, frugivores estimate profitability of resource at every place in their perceptive or cognitive field and then the utility fields are added up across all resources (Janson 2000). Therefore, place utility models are based on gradient climbing where frugivores reconsider decisions as they move across the landscape. This can happen if frugivores initially navigated in a general direction towards resources based on cognitive information, but later turned towards specific resources as sensory information became more available. Spatial foraging models provide useful templates to contrast their predictions on frugivore resource selections or movements with the observed patterns and the effects of such movement on seed dispersal.
Future directions to advance our understanding of frugivore-mediated seed dispersal

Technological advancements have enabled nearly continuous records of frugivore movement using tracking devices such as GPS, harmonic radars, geo-locators, and RFID (radio frequency identification) (Spiegel et al. 2017). Many of these devices are now miniaturized and batteries have extended longevities. As a result, we can now monitor movements of many smaller frugivores, including migratory birds and bats. Additionally, secondary sensors such as accelerometers and thermometers provide additional physiological or environmental information (Kays et al. 2015). These can improve our understanding of frugivore movement considerably as we collect more information about the movement drivers.

Currently, it is possible to collect real time data from tagged animals using an existing network of satellites and cell phones (McClintock et al. 2015). These devices provide massive amount of data with increasing level of spatial accuracy, temporal resolution, and precision. These have placed ‘movement ecology’ in the realm of big data science (Kays et al. 2015). Sophisticated methods have been developed for movement data storage, management, and analysis (Hooten et al. 2017). State space models can be utilized to understand the latent behavioral states generating the observed movement data. Such models can inform us of the interactions between frugivore CAMs and the environment. Likewise, step selection analysis and other methods can help understand how frugivores prioritize space use within their habitats. Therefore, highly resolved movement data coupled with models can inform us what trees frugivores feed on, the type of environment they move through, and the quality of deposition sites and their distances from the maternal trees. As all these factors are critical for plant demography, advancement in frugivore movement studies can also help ecologists understand plant population ecology (Beckman et al. 2020b). Spatially explicit models incorporating
multiple layers of information can help us gain important insights. Spatial locations of fruiting trees and their attributes can be overlain on habitat features to create the landscape where frugivores forage. Data on frugivore abundance and their predator abundance can be used to account for biotic interactions. We can then follow individual frugivore movement and record their foraging activities as well as where they deposit seeds.

**Frugivore effectiveness as seed dispersers under local anthropogenic impacts**

Anthropogenic activities have impacted and altered 50 to 70% of Earth’s land surfaces (Tucker et al. 2018). Today, frugivores must navigate and move through a rapidly changing world. Consequently, their ecological roles as seed dispersers are also likely to change. Anthropogenic alterations of the environment create novel challenges by altering frugivore CAM elements. Human-made structures, such as roads, fences, and dams can impede terrestrial and aquatic frugivore movement (Laurance et al. 2009, Chen 2015). Other anthropogenic activities, such as logging and fragmentation of the landscape, can also influence CAMs. Many arboreal frugivores cannot cross large tree fall gaps (McLean et al. 2016), whereas several forest birds and mammals avoid the matrix surrounding forest fragments (Beyer et al. 2016). Human-modified landscapes may have fewer frugivore visits and frugivores that rapidly move through the modified landscape, resulting in less seed removal and deposition compared to intact landscapes. Human-made barriers in the landscape that impede movement can cause disjunct distributions of frugivore CAMs in the landscape and result in stark variations in the spatial distribution of deposited seeds, with some areas receiving disproportionately higher number of seeds than others. On the other hand, manmade features such as habitat corridors can facilitate animal movement and CAMs in an altered landscape (Pizo and dos Santos 2011). Therefore, corridors can enable flow of seed dispersal services in the landscape.
Anthropogenic impacts can create a landscape of fear (Suraci et al. 2019), where frugivores modify their behavior to avoid encountering humans. For example, yellow-breasted capuchin monkeys (*Sapajus xanthosternos*) avoided areas of high hunting risks (Suscke et al. 2020). Humans can also create a landscape of opportunities. For instance, food provisioning can attract frugivores to human settlements. Rhesus macaques (*Macaca mulatta*) fed infrequently on fruiting trees, dispersed seeds to shorter distances and deposited them in unsuitable habitats when provisioned by humans (Sengupta et al. 2015).

Humans themselves or dispersal vectors associated with them can disperse seeds (Auffret et al. 2014). Motor vehicles can carry away seeds of several plants globally (Ansong and Pickering 2013). Likewise, organized movement of livestock across pastures can transfer millions of seeds regionally (Wessels et al. 2008). Human mediated seed dispersal can also be intentional for forestry or agricultural purposes or for the restoration of native plant communities (Bullock and Pufal 2020).

**Conclusion**

Building on Côrtes and Uriarte (2013), we provide a frugivore-focused discussion of seed dispersal, particularly emphasizing drivers of animal movement. To understand seed dispersal mechanistically, we need to examine frugivore movement and ecology in detail. We suggest future studies integrate the drivers of frugivore movement, particularly what motivates movement and how frugivores navigate their resource landscape, and consequences of this movement on seed dispersal. A way to accomplish this is to investigate how the distribution of a frugivore’s CAMs affect the quantity and quality components of seed dispersal effectiveness (SDE) for a given frugivore. Multiple frugivore species can disperse seeds of a single plant. While they may differ in their movement drivers, their movement process can be classified into
characteristics CAMs and linked to seed dispersal patterns. Therefore, CAMs provide us with a functional approach to study animal-mediated seed dispersal. We encourage an interdisciplinary approach (for strategies see (Beckman et al. 2020a)) where ecologists at the forefront of animal movement studies collaborate with plant ecologists to better understand animal mediated seed dispersal ecology.
References


Beckman, N. G. et al. 2020b. Introduction to the Special Issue: The role of seed dispersal in plant populations: perspectives and advances in a changing world. - AoB Plants 12: plaa010.


Cavagna, G. A. et al. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for


Kays, R. et al. 2015. Terrestrial animal tracking as an eye on life and planet. - Science, Jun 12; 348(6240)


tannin content, drives seed fate and survival in a tropical forest. - Ecosphere 10: e02551.


Nilsson, C. et al. 2005. Fragmentation and flow regulation of the world’s large river systems. -


Suraci, J. P. et al. 2019. Fear of humans as apex predators has landscape-scale impacts from

Suscke, P. et al. 2020. The role of hunting on Sapajus xanthosternos’ landscape of fear in the Atlantic Forest, Brazil. American Journal of Primatology, May; 83(5):e23243


Figures and Tables

![Diagram showing Canonical Activity Modes (CAMs) and Seed Dispersal Pattern]

Fig. 1.1: The observed movement of a frugivore segmented into different CAMs. Here CAM 1 is a resting state and the frugivore is stationary, CAM 2 is an exploratory stage characterized by long directed steps and CAM 3 is a foraging stage where the frugivore exploits resources with short, tortuous steps. Different CAMs can result in different seed removal and deposition patterns.
Fig. 1.2: A general framework coupling movement ecology with seed dispersal (modified from Fig. 2 in Nathan et al. 2008a). The external factors interact with the frugivore movement drivers. The emerging movement propagation process can be characterized by distinct canonical activity modes (CAMs) and linked to the resulting seed dispersal (seed removal and deposition) pattern.

Table 1.1: Different frugivore CAM types, their properties and potential seed removal and deposition patterns. This list of frugivore CAMs is not exhaustive.

<table>
<thead>
<tr>
<th>CAM type</th>
<th>CAM properties</th>
<th>Seed removal per fruit tree patch</th>
<th>Seed deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging</td>
<td>Short step lengths and large turn angles</td>
<td>High</td>
<td>Clumped</td>
</tr>
<tr>
<td>Activity</td>
<td>Description</td>
<td>Step Lengths</td>
<td>Turn Angles</td>
</tr>
<tr>
<td>----------</td>
<td>-------------</td>
<td>--------------</td>
<td>-------------</td>
</tr>
<tr>
<td>Resting</td>
<td>Both step lengths and turns angles are zero</td>
<td>Low</td>
<td>Clumped</td>
</tr>
<tr>
<td>Exploration</td>
<td>Long step lengths and small turn angles</td>
<td>Low</td>
<td>Uniform</td>
</tr>
<tr>
<td>Evasion</td>
<td>Long step lengths and small turn angles, biased away from a location or an area</td>
<td>Low</td>
<td>Uniform</td>
</tr>
<tr>
<td>Attraction</td>
<td>Long step lengths and small turn angles, biased towards a location or an area</td>
<td>Low</td>
<td>Uniform</td>
</tr>
</tbody>
</table>
CHAPTER 2: LINKING THE ENVIRONMENTAL DRIVERS AND FUNCTIONS OF SEED DISPERSERS’ MOVEMENT IN A TROPICAL FOREST

Binod Borah, Noelle G. Beckman

Abstract

Animal movement is driven by several processes and performs important ecological functions. Tropical seed dispersers move through their forested environment while they select or avoid different habitats, perform various activities, and disperse seeds. Understanding how the external environment drives dispersers’ movement and how it impacts seed dispersal patterns can establish stronger links between animal movement and their functional consequences on plant demography. Here we used high-resolution telemetry data of seed dispersers and lidar derived environment data; classified disperser movement into their activity modes; estimated their selection for different habitat conditions, and integrated them all into a seed dispersal model. We simulated dispersers’ movement driven by their habitat selection, and categorized into their activity modes in our model, and tracked where and how far they deposit seeds from their parent trees. Our seed disperser, spider monkeys selected for habitats with taller canopy and terrain ruggedness, mostly encamped, and deposited more seeds in these habitats compared to random foragers with no habitat affinities, but avoided treefall gaps, although deposited marginally fewer seeds there compared to random foragers. Spider monkeys also generated shorter seed dispersal distances than random foragers. In summary, external processes like habitat conditions can drive seed dispersers’ habitat selection, activities, and movement which in turn can leave distinct signatures on seed dispersal patterns. Thus, the links between drivers and functional consequences of seed dispersers’ movement need further exploration.
**Introduction**

Most tropical plants rely on the movement of frugivorous animals to disperse their seeds (Howe 1984, Côrtes and Uriarte 2013). Animal movement is influenced by several drivers, including the external environment (Nathan et al. 2008a). Animals use their movement to accrue benefits or avoid costs from their environment, such as forage for their resources and elude predators (Foley et al. 2015, Richardson et al. 2018, Pyke 2019). During movement, frugivorous animals deposit ingested seeds and generate the initial spatial patterns of plants that they ingest (Nathan and Muller-Landau 2000, Muller-Landau and Hardesty 2009). As these seed patterns determine the strengths of distant- and density-dependent demographic processes (Janzen 1970, 1971), movement of seed dispersing frugivores (or simply seed dispersers) is critical for plant population dynamics. Therefore, biotic seed dispersal is an important functional outcome of animal movement. However, studies investigating the drivers of movement and the roles of observed movements in vital ecosystems services, such as seed dispersal, have run on parallel paths. For instance, environmental features play major roles in animal movement, such as canopy height and cover in primates’ movements (McLean et al. 2016); vegetation and snow cover in terrestrial mammals’ movements (Avgar et al. 2013); or sea water temperature in marine mammals’ movements (Bestley et al. 2013), yet these studies did not explore the ecosystem services of movement. On the other hand, the observed movement determined the spatial components of seed dispersal patterns, such as seed dispersal distances or seed aggregation generated by birds (Holbrook and Smith 2000, Naniwadekar et al. 2019b), mammals (Campos-Arceiz et al. 2008), or fish (Anderson et al. 2011), yet the drivers behind the observed movements remain unknown in these studies. Therefore, the links between drivers and ecosystem services of animal movement are still missing. It is important to establish these links
as it can provide a more mechanistic understanding like how external drivers such as the environment can affect ecosystem services such as animal mediated seed dispersal.

A way to address this knowledge gap is to segment the observed animal movements, categorize them into what (Getz and Saltz 2008) had termed as canonical activity modes (CAMs), and understand how the external environment affect these modes and seed dispersal patterns through them (Borah and Beckman 2021). The observed movement can be segregated into step lengths which are the linear distances between two consecutive relocation points: step lengths are expected to be shorter when movement is slow (Schick et al. 2008, Wittemyer et al. 2019) and turn angles, which are the angular deviations between headings of two consecutive steps, and expected to have a wider distribution when movement is tortuous (Barraquand and Benhamou 2008). Observed movements then can be categorized into canonical activity modes (or simply activity modes or CAMs) based on distinct step lengths and turn angles distributions of the movement process and linked to the external environment. For instance, dispersers use short, tortuous steps when foraging in habitats with resources (Bell 1991). If a disperser forages frequently, it can deposit seeds nearer to parent trees. While these seeds may jointly experience a favorable habitat shared with their parent trees (Comita et al. 2007), they also encounter higher risks of mortality from biotic agents that are attracted to the same parent trees (Comita et al. 2014, Fricke et al. 2014). Similarly, if a disperser rests in areas with refuges and is stationary for a prolonged period, it can deposit seeds under its resting or roosting sites (Howe 1989). Such deposited seeds experience both the local environment of the resting site and pronounced conspecific negative density dependent effects (Fricke and Wright 2017). Dispersers also explore habitats where conditions are unpredictable (Bartumeus et al. 2005). If a disperser uses long, directed steps when exploring, it can deposit seeds farther away from their parent trees (Russo et
al. 2006). These deposition patterns increase chances of seeds experiencing habitat conditions different from their parents (Correia et al. 2018), but reduce the negative effects of both distance- and density-dependent effects on seeds. Thus, the external environment influences disperser movement and therefore the spatial spread of their activities. This spread emerges as dispersers move across and select different habitats. In summary, the distribution of seed disperser activity modes in conjunction with the distribution of habitat types will impact the local environment and dispersal distances of seed deposition sites.

Here, we study how activities and habitat selection of a Neotropical primate species—the Black-handed spider monkey (*Ateles geoffroyi*) impact seed deposition patterns in a tropical forest with heterogeneous successional patches. Spider monkeys have a highly frugivorous diet, disperse seeds of several plant species, generate long dispersal distances, and can enhance the germination success of the ingested seeds (Beckman et al. *in press*). However, how some of these seed dispersal patterns are influenced by the movement, habitat selection, and activities of these seed dispersers are not quite well understood. These primates are arboreal and prefer habitats that are productive and safe, such as tall canopy (Wallace 2008, McLean et al. 2016), facilitate navigation such as ridges (Gregory et al. 2014), and avoid habitats that are unproductive, riskier, and inhibit movement, such as tree-fall gaps (Brokaw 1982, Barnett et al. 2015, Madden et al. 2015). These habitat selection patterns will affect the distribution of activities of spider monkeys and hence their seed dispersal patterns including the local environment experienced by the seed deposition sites and seed dispersal distances. Therefore, we have the following hypotheses and predictions

1. Spider monkeys’ habitat selection will impact the spatial and temporal spread of their activity modes (CAMs) and hence the habitat characteristics of the seed deposition sites.
If spider monkeys prefer tall canopy for foraging, resting, and locomotion, we predict them to deposit more seeds under taller canopy. Also, we predict spider monkeys to deposit fewer seeds in the tree fall gaps compared to the understorey as they avoid them. Finally, we expect them to deposit more seeds in areas with high ruggedness. We also compared the environmental characteristics of the disperser generated deposition sites to the environmental characteristics of seed deposition sites generated by random foragers with no habitat preferences and environment dependent activity modes.

2. The spatial and temporal distributions of spider monkeys’ CAMs will also affect seed dispersal distances. Therefore, we predict that spider monkeys will generate shorter seed dispersal distances than those generated by random foragers with no habitat affinities. Additionally, we also compared the seed dispersal distances obtained from our stochastic simulations to dispersal distances obtained deterministically by tracing seed displacements on the observed trajectories from specific start points for time periods equaling the disperser’s gut retention time.

To test these predictions, we use an integrated approach employing remotely-sensed environmental data, field-based telemetric and vegetation data, novel statistical methods, and simulation models. We develop a spatially explicit, individual based model that integrates movement, habitat selection, and traits of the seed dispersers and simulates seed dispersal patterns from parent trees in the study location.

**Methods**

**Study area**
Our study area is located at Barro Colorado Island (BCI), Panama. The southwestern half of the 1560 ha island is covered with old growth tropical moist forests while late-secondary forest occurs on the northeastern half, a signature from past anthropogenic activities including agriculture, construction, and logging (Kenoyer 1929). Old-growth forests have higher densities of taller, larger trees, and greater vegetation cover at the higher canopies than the late-secondary forest. On the contrary, the late-secondary forest (>70 years) on the island has fewer emergent trees and lower average canopy height. The late-secondary forest is relatively young (Leigh 1999). Tree fall gaps can range from 25 m$^2$ to 1150 m$^2$ in sizes in the 50 ha plot (Schnitzer and Carson 2001), and occur in both old-growth and secondary forests. The topography of island is marked by a central plateau with sharp escarpments. BCI receives 2500 mm rainfall on average and experiences a distinct wet and dry season (December to April) (Windsor 1990).

Environmental Data

We used Lidar derived remotely sensed environmental data of the study area. This data includes 98% coverage of BCI (Asner et al. 2012). We used digital elevational and digital surface maps at 1m$^2$ resolution and calculated maximum canopy height of the study area from the differences between these two maps. We also estimated the absolute deviation of canopy height of each grid cell from the mean canopy height as a measure of canopy height variability. We characterized presence of tree fall gaps at 8m from the presence or absence of canopy cover at 8m or higher at 1m$^2$ resolution (McLean et al. 2016). If canopy cover was absent at 8m or higher, we treated the grid cell as a tree fall gap. Finally, we calculated the index of terrain or topographic ruggedness for each grid cell at 1m$^2$ resolution as the mean elevational differences from adjacent cells. Thus,
ridges and plateau edges will have higher ruggedness index values whereas ravines and low-lying areas will have lower values.

**Study species**

Our study species comprised of a primate species and an animal dispersed canopy tree. Black-handed spider monkeys are Neotropical in origin, arboreal in nature, and play important roles as seed dispersers. Spider monkeys (*Ateles geoffroyi*) are largely frugivorous and diurnal. They have a semi-brachiate locomotion and have home range size ranging from 88 ha to 1000 ha (Campbell 2000). Male spider-monkeys have larger home range than females (Fedigan et al. 1988). Spider monkeys feed on a wide range of fruits that includes as many as 130 plant species (Muller-Landau and Hardesty 2009). Their gut retention times can vary from 2.5 hours to 8 hours with most seeds deposited approximately after 4 hours (Lambert 1998, Link and Di Fiore 2006).

For our focal tree species, we selected the canopy tree *Dipteryx oleifera*. *D. oleifera* grows to a height of 40-50m and produces fruits that reaches maturation between January and April (Caillaud et al. 2010). These fruits are approximately 5cm in size (Vozzo 2002), major resources during the dry season, and can be dispersed by spider monkeys (Caillaud et al. 2010). In this study, we used the known patches of *D. oleifera* distributed over the entire island and obtained from high-resolution aerial photographs and vegetation plots (Hubbell et al. 1999, Condit et al. 2012). More details about the survey methods are available at (Garzon-Lopez et al. 2013) and (Caillaud et al. 2010).

**Movement data**
We collected relocation data from 8 individual spider monkeys using GPS tracking devices (e-obs GmbH, Gruenwald, Germany) from two field seasons: between December 2015 to April 2016 and December 2017 to June 2018. For our study, we selected relocation data from the dry season in BCI i.e., between the months December and April from both field seasons. We also discarded data where animal position was only partially recorded. This left us with 909,131 spider monkey relocation data, collected at 4 minutes intervals during the daylight hours (0600-1800 hr).

**Seed disperser activity mode model**

To investigate how the external environment influences seed disperser activity modes, we fit a hidden markov model (HMM) to the relocation data of all the 8 individual spider monkeys. HMM assumes the observed distribution of movement components (i.e., step lengths and turn angles) are conditional on a finite number of unobserved movement states, assumed to be a Markov chain and interpreted as movement behaviors or patterns (Langrock et al. 2012). The persistence or shift between these states are given by transition probabilities that can depend on the external environment.

Our model had two movement states. State 1 is interpreted as ‘encamping state’, such as foraging and resting, characterized by short step lengths and large turn angles. State 2 is interpreted as ‘traveling state, such as transit or extensive exploration, characterized by long step lengths and small turn angles. For this HMM, we used a gamma distribution and a von Mises distribution to fit the observed step lengths and turn angles, respectively. We used canopy height, cover, and terrain ruggedness as the covariate for transition probabilities between the two states. We used the Viterbi algorithm to estimate the most likely sequence of movement states to have
generated the observations. To fit the HMM models to our data, we used the R package ‘moveHMM’ (Michelot et al. 2016).

Habitat selection and movement model
To estimate effects of environmental conditions on habitat selection and movement, we used an integrated step selection analysis (iSSA) (Avgar et al. 2016) on individual relocation data of the 8 spider monkeys. The analysis estimates habitat selection and movement parameters simultaneously by comparing environmental variables associated with a used step to that of randomly generated available steps. We used a Gamma distribution and a von Mises distribution parametrized on observed step lengths and turn angles respectively to generate nine random available steps for each used step. For the main effects in the model, we included canopy height, cover, terrain ruggedness, step lengths and logarithms of step lengths (modifier of shape parameter of the underlying gamma distribution) (Signer et al. 2019). As we expected canopy height variability and cover to affect animal movement, we also included interactions between logarithms of step lengths and canopy height variability in the model. Habitat selection emerges when animals travel and explore their environment. Therefore, we analyzed habitat selection by spider monkeys as mediated by their underlying behavior (Picardi et al. 2022). For this, we fitted our iSSA model to daily relocation data of individual seed dispersers that was classified into the ‘traveling state (state 2)’ by the Viterbi algorithm. We used the R package ‘amt’ to fit the iSSA models to our data (Signer et al. 2019).

Seed dispersal model
The seed dispersal model is an individual based, spatially explicit, event driven and stochastic model. The purpose of this model is to simulate how individual frugivorous mammals spatially distribute ingested seeds while exhibiting different activities within their home range. The seed dispersers are characterized by species identity and their home range size. Intra specific differences exist in habitat selection, distribution of activity modes, movement capacities, and gut retention time. The external environment is characterized by the location of fruiting trees and the following habitat conditions: canopy height, tree fall gaps, and terrain ruggedness.

For our simulations, we selected the BCI island as our simulation landscape, as spider monkeys can range over the entire island during their daily activities. Our landscape consists of 20m*20m square grids. We selected this grid size which was larger than the mean step length and its standard deviation during the ‘encamping state’ of spider monkeys. This ensures individuals remain in the same grid cell when in the ‘encamping state’ i.e., when they were likely foraging or resting. Each square grid is characterized by its canopy height, canopy cover (presence or absence of a gap), and topographic ruggedness (Fig. 2.1b). This information was aggregated using the lidar derived digital elevational and surface maps of BCI. For the location of fruiting trees, we selected 500 adult *D.oleifera* trees located on the island. For these, we randomly selected 500 *D.oleifera* patches from our data and assigned the patch centroid as an adult tree.

The model integrates seed disperser activity modes (Fig. 2.1c) with their habitat selection (Fig. 2.1d). The probability of ‘encamping or ‘traveling’ activity modes emerging in a grid cell is based on its environmental covariates as estimated by the hidden markov model as follows.

$$
\gamma_{ij}^{t} = \Pr(S_t = j \mid S_{t-1} = i) = \frac{\exp(\eta_{ij})}{\sum_{k=1}^{N} \exp(\eta_{ij})}
$$
\[ \eta_{ij} = \begin{cases} \omega_0^{ij} + \sum_{l=1}^{p} \omega_l^{ij} w_{lt}, & \text{if } i \neq j \\ 0, & \text{otherwise} \end{cases} \]

Here \( \gamma_{ij} \) is the transition probability from states \( i \) to \( j \) at time \( t \) which is modelled as a function of the \( l^{th} \) covariate \( w_l \) with the parameter \( \omega_0 \) and \( \omega_l \). Here \( l = 1, 2, \ldots, p \). We used canopy height, canopy cover (presence of tree-fall gaps), and terrain ruggedness as the three covariates.

We parameterized habitat selection of an individual seed disperser for a landscape grid cell based on the cell’s canopy height, canopy cover, and terrain ruggedness and motion capacities of the individual using estimates from the integrated step selection analysis.

\[ \omega_i = \frac{\exp(\beta x_i + \theta y_i)}{\sum_{i=1}^{N} \exp(\beta x_i + \theta y_i)} \]  

(2)

Here \( \omega_i \) is the selection strength for the grid cell \( i \) based on the vector of habitat variables \( x_i \) and the discreet time movement kernel \( y_i \). The vector of habitat variables consisted of canopy height, cover and index of terrain ruggedness. The movement kernel consists of step lengths, logarithm of step lengths, and any spatial movement predictor with respect to grid cell \( i \). \( \beta \) is the parameter vector for habitat selection strength and \( \theta \) is the parameter vector for motion capacities.

An instance of the simulation model is initiated with an individual seed disperser located on a \( D.oleifera \) tree. Thus, each \( D.oleifera \) tree serves as a start point in our simulations (Fig. 2.1e). The simulation then proceeds as the disperser consumes fruits and ingest seeds from the fruit tree. Time is discreet in our model with each time step equivalent to four-minute intervals based on the resolution of the relocation data. For simplicity, we will track the possible trajectory of one single seed in the disperser’s gut until it is defecated (Fig. 2.1f). Post ingestion, the individual can continue to exploit the grid cell in its ‘encamping’ mode or switch to the alternate ‘traveling’ mode. The probability of persisting in a particular activity mode or transitioning to
the other activity mode is determined by the environmental covariates and governed by eq. 1. If the individual switches its activity mode, it can move and explore another grid cell that lies within its 95th quantile step length in its ‘traveling’ mode. We considered all grid cells that met this distance criteria as available grid cells (Merkle et al. 2014). An individual selects a grid cell from available grid cells based on its habitat suitability determined by the environmental covariates and governed by eq. 2. This process propagates, the individual selects different habitat types in the landscape, engage in different activity modes, and carries the seed in its gut for a time period equal to the gut retention time of the individual disperser species. We draw gut retention time from a gamma distribution parameterized to match observed species-specific gut retention time of spider monkeys (mean= 270 min, SD= 55 min). Therefore, the movement trajectory comprises of a sequence of ‘encamping’ and ‘traveling’ activity modes (Fig. 2.1f). The simulation concludes when the individual disperser defecates the seed and the movement trajectory ends at the seed deposition location. We recorded the spatial location of the deposition site and also its habitat conditions at 1m² resolution. For each individual seed disperser, we repeated the model simulation for each 500 D.oleifera fruit trees. Thus, for each individual seed disperser, we aggregated the dispersal distances and generated a dispersal kernel for the population of 500 D.oleifera trees. This amounts to 4000 seed deposition sites and seed dispersal distances generated by the 8 spider monkeys (Fig. 2.1g).

**Statistical analysis**

To test our predictions, we adopted a machine learning method—random forest analysis to assess the relative contributions of different parameters to the seed dispersal patterns. Random forest analysis is a recursive partitioning method that combines predictions from numerous
classification or regression trees and fits a single predictive model (Cutler et al. 2012). Random forest analysis is increasingly being employed in ecological studies for many benefits— it can handle non-linear, complex, and potentially collinear relationships between predictor variables; it can avoid the pitfalls of employing frequentist approach to analyze results from simulations, as sample size in simulations is arbitrary and frequentist methods can arrive at significant P values regardless of the effect size (Cutler et al. 2012). Random forest analysis has been used by studies looking at disease spread (White et al. 2018), species extinction (Cutler et al. 2012) etc.

To understand if animal identity— disperser or random forager and what habitat covariates influenced the seed deposition sites, we fitted random forest models with the number of seeds deposited per grid cell as the response variable and animal identity, canopy height, presence of gap, and terrain ruggedness as the predictor variables. To fit models, we discretized canopy height into three levels based on 25th and 75th quantiles: tall (> 29.84 m), medium (>17.27 m and <29.84 m), and short canopy (<17.27 m) and terrain ruggedness into three levels based on 25th and 75th quantiles: high (>0.26), medium (>0.09 and <0.26), and low ruggedness (<0.09).

We segregated the simulated results into two groups— test and train data by a 70:30 ratio. A random forest model with 1000 classification trees was fitted to the train data. We tested model performance through cross-validation using the test data. To estimated relative importance of covariates in determining model outcomes, we calculated variable importance scores. These scores are reported in terms of percentage increase in MSE (mean squared error) which corresponds to the increase in MSE of model predictions when a parameter is permuted randomly rather than using its given value. Our reported variable importance measures were not scaled by the standard error, as such measures can be less biased for correlated predictors.
To understand if simulated seed dispersal distances differed between dispersers and random foragers, we simply compared them between the two groups. Additionally, we also compared the simulated seed dispersal distances with dispersal distances obtained by tracing the disperser movement on the observed trajectories.

We used R statistical language for all the analysis (version 4.1.2, R Core Team 2021), and additional packages like raster (Hijmans et al. 2013), tidyverse (Wickham and Wickham 2017), and randomForest (Liaw and Wiener 2002).

**Results**

Our results from the models and the statistical analyses considered collectively demonstrate that seed disperser CAM, habitat selection, and their movement impact habitat characteristics of seed deposition sites and dispersal distances of seeds.

**Seed disperser activity mode model**

The HMM identified two underlying activity modes or states among 8 spider monkeys. The mean step length was shorter and turn angle sharper in the ‘encamping state’ (state 1) compared to that of the ‘traveling state’ (state 2). Mean step length ranges were 5.17m-8.02m for the ‘encamping state’ (state 1) and 27.43m-45.52m for the ‘traveling state’ (state 2). Similarly, the mean turn angle ranges were -3.12 rad-3.11 rad for the ‘encamping state’ (state 1) and -0.05 rad-1.24 rad for the ‘traveling state’ (state 2). We present the individual estimations in Table. S2.1.

Seed dispersers showed distinct associations between their CAMs and habitat conditions (Fig. 2.2). Spider monkeys were likely to continue in the ‘encamping state’ (state 1) under taller canopy. Spider monkeys were also more likely to switch to the ‘encamping state’ (state 1) from the ‘traveling state’ (state 2) as canopy height increased.
cover, spider monkeys were likely to continue with their previous CAM. Finally, Spider monkeys were also likely to switch to the ‘encamping state’ (state 1) when present in terrain with higher ruggedness. All spider monkey individuals had higher probabilities to persist in their current states than to switch states, which indicated that their activities occurred in bouts.

**Habitat selection and movement model**

Seed dispersers also showed distinct habitat selection (Fig. 2.3). Relative selection strength by all spider monkeys for habitats where canopy height (Fig. 2.3a) and terrain ruggedness (Fig. 2.3c) increased were positive where treefall gaps were present was negative (Fig. 2.3b). We found evidence that displacement rate differed with canopy height variability is some spider monkeys (37%) (Fig. 2.3f).

**Habitat characteristics of deposited sites**

Terrain ruggedness was the most influential environmental predictor that characterized the seed deposition sites and affected the number of seeds deposited, followed by canopy height and presence of treefall gaps (Fig.B.1). The identity of the animal, whether a primate seed disperser or a random forager also influenced the number of seeds deposited in a site.

Spider monkeys deposited more seeds in sites under tall canopy (30%, n= 1190) compared to random foragers that had no habitat affinities (21%, n= 832) as well as fewer seeds in sites under short canopy (20%, 870) when compared to random foragers (29%,1152). They also deposited marginally fewer seeds in sites under medium canopy (50%, 1990) compared to random foragers (50%, 2052) (Fig. 2.4a).
Spider monkeys deposited marginally more seeds under canopy cover where gaps are absent (97%, n=3911) compared to random foragers (96.6%, n=3865). Spider monkeys also deposited marginally fewer seeds in areas where gaps are present (3%, n=139) compared to random foragers (3.4%, n=171) (Fig. 2.4b).

Finally, spider monkeys deposited more seeds in sites present in high rugged terrain (26.8%, n=1073) compared to random foragers (24.7%, n=990), but fewer seeds in sites present in low rugged terrain (22.9%, n=919) compared to random foragers (25.9%, n=1036). Spider monkeys also deposited marginally more seeds in sites present in medium rugged terrain (51.4%, n=2058) compared to random foragers (50.2%, n=2010) as well as (Fig. 2.4c).

Seed dispersal distances
Spider monkeys dispersed seeds nearer (mean= 181.42m) to their parent trees compared to random animals with no habitat affinities (mean= 231.57) and the simulated seed dispersal distances were less variable (SD= 107.58m) compared to those generated by random animals (SD= 130.68) (Fig. 2.5).

We also found that simulated dispersal distances of disperser when we accounted for their habitat affinities and activity modes were shorter (mean= 181.42m) and less variable (SD= 107.58m) than the seed dispersal distances that were traced on the observed trajectories with random start points (median= 162.34, mean= 236.13m, SD= 270.20m) (Fig. 2.6).

Discussion
In our study, we demonstrated that in this tropical forest with mature and regenerating patches, external environmental features influenced the observed movement patterns of seed dispersers,
classified these movement patterns into activity modes, and showed that these modes affected the local environment of the seed deposition sites. Additionally, we also showed that disperser movement, habitat selection, and activity modes influenced the seed dispersal distances.

We found strong evidence that the local environment experienced by the seed deposition sites can be driven by seed dispersers’ habitat selection and the distribution of their activity modes. The seed disperser, spider monkeys strongly selected the tall canopy of the old growth and late successional forests (Fig. 2.3a). Tall canopies in tropical forest offer more resources and refuges (Davies et al. 2017, Deere et al. 2020). Therefore, spider monkeys can habitually forage or rest in areas with tall canopy trees. This was evident as spider monkeys persisted in or regularly switched to encamping activities under tall canopy (Fig. 2.2). Such activities are characterized by short steps, sharp turn angles, and stationary periods that increase time spent by dispersers and thus chances of depositing seeds under tall canopy. When we incorporated these results into our simulations, we found that spider monkeys deposited more seeds in areas under tall canopy when compared to random foragers that had no habitat affinities (Fig. 2.4a). Seeds deposited under tall canopy can experience strong biotic and abiotic conditions. Microhabitats under tall canopy can have higher densities of soil pathogens and invertebrates or limited light availability (Erwin and Ribeiro 1996, O’Hanlon-Manners and Kotanen 2004, Gommers et al. 2013). These biotic and abiotic conditions can ultimately affect the survival and recruitment of seeds.

Spider monkeys also selected habitats under canopy cover, persisted in their current activity modes under them (Fig. 2.2), and strongly avoided tree fall gaps (Fig. 2.3b). While spider monkeys can explore or exploit habitats under canopy cover, their arboreal movement are impeded by gaps that also offer fewer to no resources, and a physiologically stressful
environment from predation risk and high diurnal heat (Schultz 1998, Barnett et al. 2015, McLean et al. 2016, Davies et al. 2017). Our simulations showed that dispersers deposited fewer seeds in treefall gaps than under canopy cover (Fig. 2.4b). Both short and long-term seed trap data from the study area found that more animal dispersed seeds arrived in the canopy understory and fewer seeds were recorded in treefall gaps (Augspurger and Franson 1988, Puerta-Piñero et al. 2013). Yet spider monkeys deposited only marginally more seeds under canopy cover and fewer seeds in treefall gaps when compared to random foragers. One explanation for such lack of differences could be the low prevalence of gaps in tropical forest canopy. While vast extent of tropical forests can have canopy cover, treefall gaps constitute only a small portion of the canopy, and therefore even random foragers with no habitat affinities regularly come across canopy cover but encounter treefall gaps only infrequently. Therefore, any difference in number of seeds deposited in canopy cover and gaps between random foragers and dispersers may not be large. Seeds deposited in gaps than under canopy cover experience more light and other favorable conditions for recruitment (Roth 1943, Augspurger 1984, Denslow 1987), yet can be increasingly predated by vertebrate seed predators (Schupp and Frost 1989).

In addition, spider monkeys strongly preferred terrains with high ruggedness such as ridges and plateau edges (Fig. 2.3c), where they primarily remained in their encamping activities (Fig. 2.2). Distinct topographic features such as ridges can assist navigation during foraging while terrain slopes can impede foraging and other movement by imposing high energetic cost from climbing (Wall et al. 2006). Spider monkeys deposited more seeds in terrains with high topographic ruggedness than random foragers (Fig. 2.4c). This can further create strong spatial associations of trees with their habitats. Thus, habitat selection and distribution of activities of
seed dispersers together strongly affected the local environment experienced by the seed deposition sites which can have important implications for seed survival and recruitment.

Our simulations also provided evidence that dispersers’ habitat selection and associated activity modes can influence the seed dispersal distances, as they were shorter than dispersal distances generated by random foragers that had no habitat affinities and distributed their activities randomly in the landscape (Fig. 2.5). Strong habitat preference can restrict the activities of dispersers, particularly if such habitats occupy certain portions of the home ranges like patches of tall trees or ridges. If dispersers spend more time in such areas foraging, resting etc., do not navigate the landscape randomly, they are likely to deposit more seeds there, and generate shorter seed dispersal distances. We also found that our simulated dispersal distances were shorter than dispersal distances traced on the observed trajectories of focal individuals with random start points (Fig. 2.6). While we do not claim that estimating seed dispersal distances by only considering the observed trajectories to be erroneous, we want to highlight that such an observed trajectory is only but one realization of a stochastic movement process. Therefore, one may arrive at different conclusions if they consider such stochasticity in simulating the seed dispersal process. Our simulated seed dispersal distances incorporating spider monkeys’ activities, habitat selection, and movement matched several empirical findings. For instance, spider monkeys in Ecuadorian Amazon forests dispersed seeds within a range of 50m to 500m, with dispersal distances peaking at 245m (Dew 2008).

Different dispersal distances of seeds from parent trees can have important consequences for plant population, community dynamics and their spatial pattern. In our simulations, both seed dispersers carried seeds to distances where impacts of distant dependent mortality agents are likely to be weaker. Many of these agents, that include pathogens, fungi or insects concentrate
their activities around the parent trees and do not track seeds if they disperse a few tens of meters from their origin (Murphy et al. 2017).

Our study provided mechanistic links between the environmental drivers of seed dispersers’ movement, the local environment experienced by the deposition sites, or their spatial patterns. Yet there were several caveats in this study. We characterized our external environment with few variables, whereas other abiotic and biotic factors such as distribution of water holes, competitors can also impact animal movement. While we currently lack such data, many of them could be correlated with our used variables. Next, we did not consider navigational capabilities: one of the major movement drivers of our study species. Many arboreal species including spider monkeys can make foraging decisions based on resource locations and attributes, that can also influence the observed movement patterns (Cunningham and Janson 2007). We also did not consider intrinsic drivers of movement including physiological differences among individuals. Next, we acknowledge that our simulations did not incorporate typical behavior of species like spider monkeys that generate aggregated seed depositions under repeatedly used sleeping trees, as we were interested in seed dispersal patterns generated by transient behavior such as movement. Finally, while independent studies affirm our simulated patterns, we lacked observations on seed dispersal that were simultaneously collected with the movement data. In future, studies should incorporate more habitat variables, other movement drivers, and typical behavior such as roosting, while concurrently record information on seed dispersal. These efforts can be massive but successful from collaboration between movement and plant ecologists.

Through our study, we demonstrate the critical roles vertebrate seed dispersers like spider monkeys play in tropical forests. These seed dispersers rely on old growth forests and contributes to their maintenance and functioning through seed dispersal. Yet, several such seed dispersers
are threatened by human activities such as hunting. Hunting is imperiling 30% of primate species (Ripple et al. 2016), pushing their populations towards local extinctions and creating ‘empty forests’ (Redford 1992) where plants are severely dispersal limited (Bagchi et al. 2018). Therefore, for the persistence of tropical forests, and their ecosystem services such as carbon sequestration, populations of seed dispersers need to be strictly conserved.

Our study also highlights the conservation importance of old growth forests as habitats for large vertebrate seed dispersers. Yet human driven land use changes have drastically reduced the global extent of old growth forests, particularly in the tropics (Gibson et al. 2011). Therefore, extant old growth forests should be protected from any further loss. On the other hand, while several restorations projects of degraded and managed forests have been proposed and funded, focus should be paid to those that establish habitats for the seed dispersers and connectivity between the restored and the extant old growth forests (Deere et al. 2020).

Global biodiversity is at a critical point in the Anthropocene, and so are their ecological services. However, better understanding of how these services is rendered through animal movement can help policymakers, land use managers and conservationists to create better policies and practices to protect them.
References


Correia, M., R. Heleno, P. Vargas, and S. Rodríguez-Echeverría. 2018. Should I stay or should I go? Mycorrhizal plants are more likely to invest in long-distance seed dispersal than non-mycorrhizal plants. Ecology letters 21:683–691.


restoration for tropical mammals by detecting three-dimensional habitat associations.


Figures and Tables

(a) Animal movement
(b) Habitat data
(c) Hidden markov model (HMM)
(d) Step selection analysis

(e) Tree locations
(f) Seed dispersal model
(g) Seed deposition sites

Fig.2.1: Graphical summary of the seed dispersal model.
Fig. 2.2: The transition probabilities between the two movement states for the spider monkey individuals under different habitat conditions. Here state 1 is the encamping state and state 2 is the traveling state. The arrow points towards the direction of transition.
Fig. 2.3: Relative selection strength for different habitat conditions by spider monkey individuals. Here the error bars represent the 95% confidence interval of the mean coefficient. The horizontal line represents zero relative selection strength.
Fig. 2.4: Frequency plot of number of seeds deposited in a grid cell with different (a) canopy height, (b) presence or absence of treefall gaps, and (c) different terrain ruggedness by spider monkeys and random foragers with no habitat affinities.
Fig. 2.5: Density plots of simulated seed dispersal distances generated either by seed dispersing mammals or random foragers with no habitat affinities. Here the dashed lines represent the mean seed dispersal distances generated by spider monkeys (black) and random foragers (red).

Fig. 2.6: Density plots of simulated seed dispersal distances generated either by seed dispersing mammals or traced on the observed trajectories of individuals with specific start points. Here the dashed lines represent the mean seed dispersal distances when they were simulated (black) or traced on the observed trajectories (red).
CHAPTER 3: LINKING SEED DISPERSERS’ FORAGING DECISIONS AND MOVEMENT TO THEIR IMPACTS ON SEED DISPERsal PATTERNS

Binod Borah, Tal Avgar, Noelle G. Beckman

Abstract

Animal movement is essential for growth and survival, as it enables individuals to explore and exploit their resource landscape. Yet, some secondary outcomes of animal movement such as dispersal of seeds are also critical ecosystem processes. Foraging decisions and movement are multi-scaled, can reduce travel cost, or increase profitability of endeavors. Simultaneously, they also impact seed dispersal patterns. Here, we investigated the foraging decisions and movement of a tropical frugivore, White-handed gibbon (*Hylobates lar*), tested how these decisions and movement impacted simulated seed dispersal distances, and compared the dispersal distances with that generated by foragers who made random foraging decisions. Gibbons simultaneously discounted distant and previously exploited resources, and generated seed dispersal distances that were longer than that generated by foragers who did not account for these resource attributes. Moreover, through simulations, we compared seed dispersal patterns generated by gibbons that made informed decisions based on resource attributes and foragers that made random decisions and showed that gibbons generated relatively shorter seed dispersal distances when resources are clumped and either abundant or scarce, but relatively longer dispersal distances when resources are scattered. Therefore, we showed that foraging decisions, seed dispersers’ movement, and their dispersal services are strongly coupled. Thus, movement is functionally important for both activities such as foraging and the maintenance of critical services like seed dispersal.
Introduction

Animal movement is a vital process that influences individual fitness and population persistence (Fryxell et al. 2005, Revilla and Wiegand 2008, Morales et al. 2010). Movement enables animals to track and exploit their resource landscape (Fryxell et al. 2005) and contributes towards their growth and survival. Therefore, these benefits derived from foraging decisions and movement can be termed as essential outcomes. However, animal foraging decisions and movement can also have secondary outcomes that otherwise are vital ecosystem services. One such outcome is biotic seed dispersal (Herrera 2002, Côrtes and Uriarte 2013). Animals disperse seeds when they remove, carry, and deposit them away from their parent trees during their movements (Holbrook and Smith 2000, Russo et al. 2006). Dispersed seeds escape high mortality around parent trees (Janzen 1970, 1971), colonize suitable habitats (Schupp et al. 1989), and are vital for plant populations persistence (Howe and Miriti 2004). Therefore, movement couple animals’ tracking of their resource landscape to their seed dispersal services. As animals change foraging decisions and movement to adapt to their resource landscape, they also concurrently alter the spatial seed dispersal patterns. Yet, few, if any, studies have explored the links between the foraging decisions and movement of seed dispersers and the seed dispersal patterns incident on them.

A way to address this knowledge gap is by including seed dispersers’ foraging decisions and movement into seed dispersal studies. Foraging decisions and movement respond to resource attributes—their predictability and heterogeneity at multiple scales (Mueller and Fagan 2008) (Garber et al. 2009). At a large scale, foraging decisions and movement enable dispersers to explore the landscape, exploit resources in different ways, and uniquely influence seed dispersal patterns. In a tropical forest, trees are stationary, patchily distributed, and spatially predictable
resources (Condit et al. 2000, Roshier et al. 2008). Most tropical trees also synchronously bear fruits (Janmaat et al. 2012), often at the onset of wet seasons (Janmaat et al. 2006a). Individual trees are productive for weeks but can deplete and renew within days (Shukla and Ramakrishnan 1982, Howe 1984). At this large scale, dispersers can memorize spatial locations of these fruit tree patches, their renewal rates, and use sensory cues such as color or scent of fruits to locate patches (Nevo and Ayasse 2020, Valenta and Nevo 2020). They can either discount distant patches to reduce travel cost, select nearby patches, or avoid patches that were recently exploited to increase profitability. At a small scale, dispersers can move towards a fruit tree patch in a goal- oriented manner from their present location, aided by their spatial knowledge or sensory capabilities (Cunningham and Janson 2007b). Therefore, these foraging decisions and movement are essentially nested where dispersers can choose among the available resource patches in the landscape before they travel towards the selected patch.

These scale-dependent foraging decisions and movement of seed dispersers can impact patterns such as dispersal distances of seed deposition sites (Borah and Beckman 2021). If dispersers mostly feed and ingest seeds at nearby fruit tree patches, travel goal-oriented among them; they can have shorter displacements, and deposit most seeds close to their parent trees. If dispersers discount fruit patches that they recently exploited, travel towards renewed patches; they can have longer displacements, and disperse the ingested seeds farther away from their parent trees. Seed dispersers most likely weigh these different decisions, select one or more strategies that are optimal, and in the process of their movement leave distinct signatures on the seed dispersal distances.

Yet, resource predictability and heterogeneity can change through changes in their distribution and abundance. Such changes can be driven by both natural causes such as seasonal
patterns or anthropogenic causes such as deforestation. Seed dispersers must adjust to a dynamic resource landscape and respond with changing foraging decisions and movement that adapt to resource distribution and abundance, such as discounting distant resources when they are abundant yet scattered in the landscape. Expectedly, different foraging decisions and movements can cause different essential benefits. But we understand little how changing foraging decisions and movements in a dynamic resource landscape influence secondary outcomes like seed dispersal patterns. Therefore, it is important to test how resource distribution, abundance, and foraging movement can independently and jointly affect seed dispersal patterns.

In this study, we look at seed dispersers’ foraging movements, and their impacts on a seed dispersal metric: dispersal distances of seed deposition sites from their parent trees. We focus on frugivorous primates as they play important roles as seed dispersers in tropical forests worldwide (Chapman and Russo 2007). Primates can also forage efficiently and take into account multiple resource attributes such as distance to fruit tree patches or their rate of renewal (Janson and Byrne 2007, Trapanese et al. 2019). Specifically, we investigated the foraging movements of the White-handed gibbon (*Hylobates lar*), a vital seed disperser in Asian tropical forest using empirical data published by (Phiphatsuwannachai et al. 2018). In their study, the authors estimated the gibbons’ home range sizes, daily path lengths, and tortuosity as well as their seed dispersal distances. Building on these findings, we aim to link gibbons’ foraging movement to the spatial patterns of the dispersed seeds. For instance, gibbons potentially can account for resource attributes such as distances of fruiting trees from the foragers or history of past visits at the landscape (large) scale. Gibbons can also move directly towards resource patches at the local (small) scale (Asensio et al. 2011). Therefore, if gibbons relied on multiple resource attributes during foraging, move goal-oriented, their movement and resulting seed
dispersal patterns can be different from those that they could generate if they made random foraging decisions. However, if their resource landscape changes when resource distribution and abundance change, gibbons can likely respond by adapting their foraging movement, which in turn can affect the seed dispersal distances.

Therefore, we hypothesize and predict that:

1. Gibbons make foraging decisions to reduce travel cost and increase resource yield. Compared to a random forager, we predict that gibbons select nearby resource patches and discount resource patches that they recently visited.

2. Seed dispersers making foraging decisions based on distance and past visit to resource patches generate spatial seed distribution patterns that are different from patterns generated by seed dispersers making foraging decisions based on none of these attributes. We predict that dispersal distances will be shorter when frugivores simultaneously account for these two attributes than when they account for none of these attributes.

3. Gibbons’ foraging movement adapt to changes in resource distribution and abundance, which in turn affect their seed dispersal distances. We predict that when resources are abundant and clumped, gibbons forage and move over smaller area, and generate shorter seed dispersal distances. On the contrary, when resources are scarce and scattered, gibbons forage and move over larger area, and generate longer seed dispersal distances.

To test these hypotheses, we analyzed the observed daily movement patterns of a gibbon family, tested if gibbons based their foraging movements on distances to their resources or their past visits, and how gibbons put these decisions into effect by moving directly towards the chosen resources. We then developed a simulation model that incorporated the empirically derived gibbons’ foraging movements and tested if the simulated seed dispersal distances are
different if gibbons made random foraging decisions. In addition, we created *in silico* artificial resource landscapes, where we varied the resource distribution and abundance, and along with them, the foraging movements of the gibbons. We then tested how foraging movements in a novel resource landscape affected the emergent seed dispersal distances.

**Methods**

**Study areas**

Gibbon foraging, and movement data was collected from the Huai Kha Khaeng Wildlife Sanctuary (HKK) in Thailand by (Phiphatsuwannachai et al. 2018). The study area in HKK comprised of an evergreen forest with small patches of mixed deciduous forest. HKK experiences a dry and wet season annually and an average rainfall of 1552 mm. More details about the study area can be found at (Phiphatsuwannachai et al. 2018).

**Study species**

White- handed gibbon (*Hylobates lar*) is an arboreal and frugivorous primate. They live in small family groups (Brockelman et al. 1998) and our study group comprised of a mating pair (one adult male and one adult female) and their offspring. Gibbons primarily forage in the upper canopy and use brachiation to move (Michilsens et al. 2009, Singh et al. 2018). In our study, the gibbon family lived in the evergreen forest with a home range size of 12.4 ha (Phiphatsuwannachai et al. 2018). Gibbons are important seed dispersers, as they ingest and disperse seeds from a large variety of plants (McConkey 2000). They have a long gut retention time, estimated to average around 22 hours (McConkey and Chivers 2007).
Movement and foraging data

For our study, we used data published by Phiphatsuwanachai et al. (2018). In this study, the authors followed the gibbon family from sleeping site to sleeping site, on average for five consecutive days each month from January to June 2014. During the follow, the authors recorded the family location every fifteen minute. Therefore, there were 279 observation hours and 1186 locations recorded for the gibbon family. For the foraging data, the authors observed adult feeding on trees and recorded start and end time of feeding, type of food consumed, and species of the tree.

Movement parameters

We quantified two parameters from the observed movement data: step lengths defined as the linear distances between two consecutive relocation points (Schick et al. 2008) and turn angles, defined as the angular deviations between headings of two consecutive steps (Barraquand and Benhamou 2008).

Patch to patch movement model

To test if gibbons selected resource patches based on their distances from their current patch or recent visitations, we used a patch-to-patch movement model (Merkle et al. 2014). For this, we first laid a grid over our study area. We based the grid cell size on the median step size of gibbons calculated from the movement data and fixed cell dimensions to 40 m x 40 m. We then assigned all recorded fruit trees to individual grid cells based on their relative positions and distances from the grid centers. We defined each such cell where at least one fruit tree occurred as a resource patch. This definition had couple of advantages. First, tropical fruit trees tend to
occur as clumped resources (Condit et al. 2000, Roshier et al. 2008). Therefore, our definition of a grid as a patch was biologically appropriate. Such a grid cell would also include any fruit trees that were not recorded but occurred in the proximity of recorded conspecific trees due to their aggregation. Next, a grid would enclose any small-scale foraging activities at the resource patch that we did not explicitly consider here. Finally, this method of cataloguing resource distribution from consumer behavior (consumer-centric method) had been shown to be comparable to vegetation plot estimation, particularly when home ranges were small and resource environment was moderately rich (Wessling et al. 2022). Gibbons are highly mobile and territorial, and expected to exploit most available resources within their small home ranges (Brockelman et al. 2014).

We then segregated the foraging data by months, and each month consisted of on average five consecutive observation days. We considered all patches that were visited at least once during this brief observation period as available for that duration. This significantly reduced chances of erroneously including patches that did not have fruit trees during that period. Then, for each resource patch, we calculated its Euclidean distance to all the other available resource patches and whether the resource patch was visited the previous day. Next, we looked at all observed incidences of patch-to-patch movement i.e., movement from one resource grid to another. For each such observed incident, we generated all possible patch to patch movements. We considered all patches that were within 95\textsuperscript{th} quantile step length of gibbons from the current patch for the possible patch to patch movements (Merkle et al. 2014). We then compared the observed to all possible patch to patch movements using conditional logistic regressions with the following covariates: a) inter-patch distance, b) past visit, and c) both inter-patch distance and past visit as the explanatory variables. In this analysis, each observed patch movement and the
associated possible patch movements were included as a unique stratum. We estimated model parameter using maximum likelihood and calculated 95% confidence intervals of estimated parameters.

We also identified all the sleeping sites of the gibbon family from the relocation data, assigned these sites to individual grid cell, and calculated their distances from all the available resource patches. We tested whether foraging decisions if gibbons were at a sleep site were different from foraging decisions if gibbons were at a resource patch. For this, we included the interaction between sleep site and distance to available patches as an additional covariate in our model. However, we did not find any significant interaction and dropped this term from our models (Table S3.1).

Selection of sleep sites
To test how the gibbons selected their sleep sites at the end of their daily activities, we first calculated the distance between the last foraging patch visited during the daily travel to all the sleep sites. We then fitted a conditional logistic regression and compared the observed movement between the foraging patch and a sleep site to all the possible movement between the patch and sleep sites. In this regression, the distance between the patch and the sleep sites was the explanatory variable and each observed patch to sleep site movement and the associated possible patch to sleep sites movements were included as a unique stratum. We estimated model parameter using maximum likelihood and calculated 95% confidence intervals of estimated parameters.

Seed dispersal simulation model
We created a seed dispersal simulation model that integrates the parameters from the patch-to-patch and patch to sleep site models to simulate the gibbon family’s foraging decisions and movement at the landscape scale, uses gibbon movement parameters to simulate inter-patch trajectories at the local scale, and combines these movements with gut retention time to generate seed dispersal patterns. The seed dispersal model is individual based, spatially explicit, and event driven. The purpose of this model is to understand the effect of foraging decisions and movement of seed dispersers on the spatial distribution of dispersed seeds in their resource landscapes. We used a single metric: dispersal distances of seed deposition sites to quantify the spatial distribution of seeds.

The model consists of the same empirical and gridded landscape of the study area. The landscape has 588 grid cells and each grid cell is 40m in dimension. As initial conditions, we populated the landscape with resource patches (grids) whose spatial locations were identical to the empirical resource grids. This spatial distribution of resource patches was also distinct for each month and determined by the empirical data. At the start of a model run, gibbons were located at a sleeping site, that was randomly chosen from the set of sleeping sites derived from the empirical data (Fig. 3.1a).

In our simulations where gibbons were informed about their resource attributes, they selected patches in the landscape based on distance to patches from their current resource patch (or sleeping site) and past visits to these patches (Fig. 3.1b). The canonical form of this decision was given by the equation

\[
S_i = \frac{\exp(\alpha D_i + \beta v_i)}{\sum_{i=1}^{N} \exp(\alpha D_i + \beta v_i)}
\]  

Here, \(S_i\) is the strength by which gibbons select the resource patch \(i\) from all ‘N’ available patches, \(D_i\) is the Euclidean distance of the patch from the gibbons’ location and \(v_i\) indicates if
the resource patch was visited the previous day. \( \alpha \) and \( \beta \) are the parameters estimated from the patch-to-patch movement model that mediates the relative strength of selection based on distances and past visits respectively. Each day initiates from one of the gibbons’ sleeping locations. The gibbons make a foraging decision governed by equation 1, maximizes \( S_i \), and select a resource patch from the available patches. We considered all resource patches that were within the 95\(^{th}\) quantile step length as available resource patches and included the current patch among the available patches. However, we did not allow any back-and-forth movements between two patches, as primates rarely trace their daily paths (Van Schaik et al. 1983). Once a patch is selected, the gibbons then travel from their current patch to the selected patch (Fig. 3.1c). The process is repeated, multiple patches are visited (Fig. 3.1d), and at the end of the day, gibbons select a sleep site from their current patch (Fig. 3.1e). This selection of sleep site is governed by the equation

\[
S_j = \frac{\exp(\gamma d_j)}{\sum_{j=1}^{\kappa} \exp(\gamma d_j)}
\]

(2)

This sleep site acts as the start point for the next day’s simulations. Therefore, every day, gibbons make unique foraging decisions and movement. We simulated foraging decisions and movements for five consecutive days monthly for five months, for a total of twenty-five days.

To simulate the small-scale gibbon movement between any two known locations (resource patch-resource patch or sleep site-resource patch), we simulated empirically informed random trajectories using the modified random trajectory generator (RTG) algorithm (Unterfinger 2018). The algorithm generates trajectories between two successive points (A and B) in a stepwise procedure with discrete time steps. From the start point (A), a probability surface of the possible next locations is created, based on the empirically derived distributions of
step lengths and turn angles. This surface is intersected with the probability surface of the end point (B), which is a pull towards the point (B) and derived based on the distributions of step lengths, turn angles, and distances to the target at the end of each successive steps. The joint probability surface is used to select the next point in the trajectories (Fig. 3.1c). The procedure is repeated for \( n \) steps until the target is reached. In our simulations, we employed the algorithm to simulate random trajectories between any two resource patches (or sleep site-resource patch) with an average of five successive steps. We selected five steps based on the predicted values from a linear regression model where inter-patch distance was the explanatory variable and number of steps was the response variable (Table S3.2). The model predicted 5-6 steps when patch distances ranged between 100-200m. As animal movement has an inherent stochasticity and gibbons can use different trajectories between any two resource patches, we simulated multiple (\( n=20 \)) trajectories between any two points.

As the next step, we constructed the daily travel paths of the gibbons. For this we randomly picked the trajectories between any two points (sleep site-resource patch or resource patch-resource patch), and combined them to create a ‘travel path’ (Fig. 3.1f). In our simulations, gibbons visited 8-10 patches daily, and their travel starts and ends at a sleeping site. Therefore, our daily travel paths were created by combining 8-10 random trajectories generated by the modified random trajectory generator (RTG) algorithm. For each day, we created 100 different daily travel paths.

To generate seed dispersal by gibbons, we assumed gibbons ingested seeds from trees in each resource patch during their daily activities. Thus, everyday gibbons ingested seeds from 8-10 resource patches. Each ingested seed is in motion in the gibbons’ gut for a time period equal to a gut retention time that is randomly drawn from a gamma distribution (Guttal et al. 2011)
parameterized to reflect the gibbons’ empirical gut retention time (mean= 21 hours, SD= 2 hours). At the end of this time period, gibbons deposit the seeds. As gibbons have a long gut retention time, these deposited seeds were most likely ingested the previous day. We recorded the ingestion locations on the gibbons’ daily paths. For the location of each such ingestion site, we recorded the location where the seed was deposited on the daily paths. Thus, each day we recorded 8-10 deposition sites (Fig. 3.1f).

When gibbons foraged randomly in our simulations, we repeated the same procedure. However, now gibbons selected resource patches randomly rather than accounting for their attributes like distances to patches or whether they were recently visited.

Finally, using the locations of the seed ingestion and deposition sites, we calculated seed dispersal distances as the distance between a seed deposition site and its ingestion site (Fig. 3.1g), and created dispersal kernels (Fig. 3.1h) for both our informed and random foraging decisions and movement simulations.

**Seed dispersal in dynamic landscape model**

To test how changing resource distribution and abundance along with foraging strategies of seed dispersers affect seed dispersal distances, we extended the seed dispersal simulation model and incorporated dynamic resource landscapes where both resource distribution and abundance changed independently, foraging strategies of seed dispersers, and their movement into the model. Here, we used landscapes with square grids. Each grid size was 40m and there were 289 grids. Our landscapes had binary values: we designated grids that were resource patches as 1 and non-resource patches as 0. We defined resource distribution as its spatial configuration in the landscape and simulated it using the Hurst exponent, and resource abundance as the total number
of resource patches. Hurst exponent (H) is a real number in the interval (0,1); a high value of H represents a clumped resource landscape whereas a low value of H represents a scattered resource landscape (Tracey et al. 2014, de Souza et al. 2020). We changed both the resource distribution and abundances of resources. We had three levels of resource distribution: clumped (H= 0.9), intermediate aggregation (H= 0.5), and scattered (H= 0.1) and three levels of resource abundance: low (10 patches), intermediate (25 patches), and high (50 patches). Therefore, we had nine resource landscapes with distinct resource distribution and abundance (Fig. 3.2). We simulated four different foraging strategies: i) when foragers discount distant resource patches ii) when foragers avoid resource patches that were exploited the previous day iii) when foragers discount both distant resource patches and patches that were exploited the previous day and iv) dispersers choose resource patches randomly. We parameterized each unique foraging decision by the estimates from the corresponding patch-to-patch model estimates (Table S3.1), simulated these four foraging decisions and disperser movement on each of the nine resource landscapes for 10 consecutive days. Therefore, we had 36 distinct simulations for a total of 360 simulated days.

Disperser movement between patches was simulated in the same manner as in the seed dispersal simulation model using the modified empirically informed random trajectories simulator. Dispersers started their daily movement from one of the 25 randomly selected sleeping sites (Fig.C.1), visited 8-10 patches daily, ingested and deposited seeds during the process, and ended daily activities at one of the sleep sites. We recorded the locations of these ingestion and deposition sites and calculated the dispersal distances.

Statistical analysis
We compared the simulated seed dispersal distances generated by the gibbon family with the 
dispersal distances generated by foragers that make random decisions, and calculated their 
respective 25\textsuperscript{th} quantile, median, and 95\textsuperscript{th} quantile seed dispersal distances. To estimate the 
relative contribution of resource distribution, abundance, and disperser foraging strategy on seed 
dispersal distances, we used random forest analysis, a machine learning method (Cutler et al. 
2012). We used the simulated seed dispersal distances as the response variable and resource 
patch distribution, their abundances, and foraging strategy type as predictors. We separated the 
simulated results into two groups—test and train data by a 70:30 ratio. We then fitted a random 
forest model with 1000 classification trees to the train data. We tested model performance 
through cross-validation using the test data. To estimate relative importance of covariates in 
determining model outcomes, we calculated variable importance scores. These scores are 
reported in terms of percentage increase in MSE (mean squared error) which corresponds to the 
increase in MSE of model predictions when a parameter is permuted randomly rather than using 
its given value. Our reported variable importance measures were not scaled by the standard error, 
as such measures can be less biased for correlated predictors.

All modeling, simulations, and analysis were done using the R statistical software 
(version 4.1.2, R Core Team 2021).

**Results**

**Movement and foraging attributes**

The median, mean, and 95\textsuperscript{th} percent quantile step lengths of the gibbon family were 32.76 m, 
42.52 m, and 110.37 m, respectively at a resolution of 15 minutes. The median, mean, and 95\textsuperscript{th} 
percent quantile of turn angles for this gibbon family were -0.01 rad, -0.001 rad, and 2.59 rad,
respectively. Gibbons on average visited 27 (SD: 15.52) resource patches during the observation period per month with a total of 73 resource patches across all five months. Mean interpatch distance was 191.70 m (SD: 108.82 m).

**Patch to patch movement model**

Gibbons selected resource patches that were nearer to their current patch. With increase in distance of patch from the gibbons’ current location by one meter, its (log) odds of getting selected ($\beta_{distance}$) decreased by an average -0.017 (95% CI: [-0.018, -0.015]). Gibbons avoided resource patches that they visited the previous day. Patches visited the previous day compared to the non-visited patches, have their (log) odds ($\beta_{past}$) decreased by an average -0.53 (95%CI: [-0.92, -0.14]). We provide coefficient estimates of all fitted patch to patch models in Table S3.1

**Selection of sleep sites**

At the end of their daily travel, gibbons selected a sleep site that was nearer to their current location compared to all available sleep sites. With increase in distance of a sleep site from the gibbons’ current location by one meter, its (log) odds of getting selected ($\beta_{sleep\ site}$) decreased by an average -0.011 (95% CI: [-0.02, -0.01]).

**Dispersal distances of seeds**

The 25th quantile, median, and 95th quantile seed dispersal distances generated by the gibbons were 80m, 120m, and 240m respectively (Fig. 3). The 25th quantile, median, and 95th quantile seed dispersal distances generated by the forager that made random decisions were 40m, 72.39m, and 339.41m respectively (Fig. 3).
Simulated seed dispersal in dynamic landscape

Resource abundance was the most influential predictor that affected the simulated seed dispersal distances, followed by resource aggregation and foraging strategy (Fig. C.1).

When dispersers discounted distant resource patches, the median seed dispersal distances generated when a) when resource abundance is high and distribution is clumped: 56.56m b) when resource abundance is high and distribution is scattered: 182.81m c) when resource abundance is low and distribution is clumped: 109.68m and d) when resource abundance is low and distribution is scattered: 233.23m (Fig. 3.4).

When dispersers discounted resource patches they exploited the previous day, the median seed dispersal distances generated when a) when resource abundance is high and distribution is clumped: 329.84m b) when resource abundance is high and distribution is scattered: 126.49m c) when resource abundance is low and distribution is clumped: 143.97m and d) when resource abundance is low and distribution is scattered: 361.71m (Fig. 3.4).

When dispersers discounted both distant and previously exploited resource patches, the median seed dispersal distances generated when a) when resource abundance is high and distribution is clumped: 178.88m b) when resource abundance is high and distribution is scattered: 200m c) when resource abundance is low and distribution is clumped: 102.34m and d) when resource abundance is low and distribution is scattered: 279.83m (Fig. 3.4).

When dispersers chose resource patches randomly, the median seed dispersal distances generated when a) when resource abundance is high and distribution is clumped: 329.84m b) when resource abundance is high and distribution is scattered: 94.61m c) when resource
abundance is low and distribution is clumped: 164.92m and d) when resource abundance is low and distribution is scattered: 172.29m (Fig. 3.4)

**Discussion**

In this study, we showed that seed dispersers’ foraging decisions influence their movements in the landscape, which in turn impact seed dispersal patterns such as their dispersal distances. The gibbon family strongly accounted for spatial resource heterogeneity and the temporal predictability of the resource state. When these foraging decisions were incorporated in a simulation of gibbon movement, they resulted in characteristically different seed dispersal patterns—dispersal distances were longer than seed dispersal distances generated when gibbons selected resource patches randomly. In addition, resource distribution and abundance affected simulated seed dispersal distances through dispersers’ foraging decisions and movement.

**Discounting of resources**

The gibbon family considered distances to their resource patches, selected nearby patches, and discounted patches that are farther away from their current patches. Discounting distant patches reduces travel cost (Teichroeb and Aguado 2016), decreases delay to next resource (Tobin et al. 1996), and increases resource exploitation (Ramos-Fernández et al. 2004). Therefore, this foraging rule can be profitable when resources such as fruit trees are patchily distributed in the landscape and foragers need to exploit multiple resource patches daily. In a study conducted over 10 years, wild capuchin monkeys mostly moved to their nearest resources (C.H. Janson, unpublished data). While foragers can still select for more distant but productive patches (Cunningham and Janson 2007), evidence overwhelmingly support that different taxon employ
such distance-based discounting of resources (Bernays et al. 1997, Asensio et al. 2011, Rainho and Palmeirim 2011).

Whether gibbons discount distant patches or other mechanisms lead to similar resource use patterns depend on how they acquire and process information about their resources. Sensory cues such as visual and olfactory signals from fruit trees can assist gibbons in navigating their resource landscapes (Garber and Hannon 1993, Dominy et al. 2001). Yet, sensory cues operate at small spatial scales. In tropical forests, visual cues from fruit trees are obstructed by dense vegetation and effective over tens of meters whereas olfactory cues can operate only over relatively larger scales (Dominy et al. 2004). Therefore, if gibbons primarily use sensory cues to navigate, they acquire resource information from small areas and use nearby resources. In this case, patterns of resource use that can appear as distance-based discounting of resources are rather the limits of gibbons’ navigation capabilities. On the other extreme, gibbons can have a spatio-temporal map of their resources that can influence foraging decisions. Use of such maps appear to be prevalent among primates (Poucet 1993, Normand and Boesch 2009). In an experimental setup, juvenile chimpanzees (*Pan troglodytes*) memorized the locations of resources and travelled along the shortest path connecting multiple resources (Menzel 1973). In the wild, female chimpanzees positioned their nests enroute to profitable resources like fig trees and started their activities early in the day when such resources were ephemeral (Janmaat et al. 2014). Gibbons, who are close relatives of chimpanzees likely can commit the locations of resource patches to their memory. This cognitive capability referred to as working memory (Fagan et al. 2013) enables them to reliably estimate distances of available resources and discount those that entails higher travel costs.
Past visits to resource patches also influenced foraging decisions. The gibbon family avoided resource patches that they visited the previous day. The evergreen forest in our study area has a higher fruit tree density (Steinmetz et al. 2013) and the gibbon family maintained a smaller home range (Phiphatsuwannachai et al. 2018). In such a resourceful habitat, foragers can substitute recently depleted patches with new or replenished patches. Gibbons utilized only 38% of the trees that they exploited the previous day (Phiphatsuwannachai et al. 2018).

The cognitive mechanisms that enable gibbons to avoid or select recently exploited resources are complex. If their decisions are based on resource profitability, they must also retain additional information such as resource renewal or depletion rates. Such cognitive abilities are referred to as attribute memory (Fagan et al. 2013) and used to store information about resource profitability, synchronicity, or renewal rates. Frugivorous primates that possess relatively larger brains and live in dynamic yet fairly predictable environments can perform such cognitive tasks (DeCasien et al. 2017). For instance, gray-cheeked mangabeys (Lophocebus albigena) avoided fruit trees that were recently exploited. Mangabeys also seemed to anticipate the quality of fruit trees by using their memory of the latest fruiting state and avoided trees that offered poorer rewards (Janmaat et al. 2006).

**Heterogeneity in foraging decisions and implication on seed dispersal patterns**

When we incorporated gibbons’ foraging decisions and their movement into our seed dispersal simulation model, the simulated seed dispersal patterns were longer than dispersal distances had the gibbons made random foraging decisions (Fig. 3.3). This was contrary to our predictions, as we expected that if gibbons discounted distant patches, it could limit the spatial extent of their foraging (Rainho and Palmeirim 2011), caused smaller displacements from their feeding
locations, and thereby reduced seed dispersal distances. However, such a foraging strategy could quickly deplete locally available patches and reduce their profitability. In our study, gibbons avoided resource patches that they visited the previous day. As gibbons carried seeds for long duration and as they were displaced farther from the fruit trees located in the recently visited patches; they carried seeds over longer distances. Therefore, while gibbons discounted both distant and recently exploited resource patches, these foraging decisions cumulatively caused gibbons to explore larger areas than foragers that make random decisions, and disperse seeds over longer distances.

**Effect of resource distribution and abundance**

Resource distribution, abundance, and foraging strategy independently and jointly affected simulated seed dispersal distances. When resource patches were clumped, their abundance was either high or low, foragers that made informed decisions based on resource attributes generated shorter seed dispersal distances than foragers who chose resources randomly (Fig. 3.4). In an abundant resource landscape where resources are clumped, foragers can meet their requirements by exploiting a smaller portion of the landscape. They can discount distant patches, avoid recently exploited patches, and travel shorter distances to encounter new patches. Several studies demonstrated that animals become territorial when their resources are abundant and clumped (Enoksson and Nilsson 1983, Macdonald 1983, Valeix et al. 2012). On the other hand, in a scarce resource landscape where resources are clumped, foragers are simply forced to exploit the small area where resources are available. As a consequence of foragers exploiting smaller areas, seed dispersal distances are reduced. When resource patches were scattered, their abundance was either low or high, foragers that made informed decisions based on resource attributes generated
longer seed dispersal distances than foragers who chose resources randomly (Fig. 3.4). In such a resource landscape, foragers have to explore larger areas to meet their requirements. They can discount distant patches, avoid recently exploited patches, yet have to travel longer distances to encounter new patches, particularly in a scarce resource landscape, and therefore carry seeds farther away from their parent trees. Thus, resource distribution and abundance that can change in response to several drivers including anthropogenic land use changes such as deforestation disparately affect seed dispersal patterns. Here, we showed that such effects on seed dispersal distances are mediated through foraging decisions and movement of the seed dispersers.

**Implications for plant demography**

The spatial patterns generated by seed dispersal are important for plant demography, particularly for the growth and survival of early life stages. Gibbons carried seeds more than 100 meters away from their parent plants in our simulations. Seeds dispersed away from parent trees over these distances can escape mortality agents such as fungi and pathogens (Murphy et al. 2017). Moreover, the different seed dispersal distances generated under different conditions of resource distribution, abundance, and foraging strategies can leave disparate signals on the spatial distributions of plants.

**Empirical evidence**

Our estimated seed dispersal parameters from our simulations corresponded with other simulated and field-based estimates. In our simulations, gibbons in the evergreen forest dispersed seeds to distances (median: 120m, quartile: 80-165m) that broadly matched the seed dispersal distances reported by Phiphatsuwanachai et al. (2018) in their study (median: 163m, quartile: 66-271m).
While our objective was to contrast the seed dispersal distances generated under different resource conditions and foraging decisions, we believe our simulations can reasonably reproduce empirical patterns of seed dispersals generated from the observed movement, while simultaneously explore how resources drive dispersers’ movement. Our simulated seed dispersal distances were slightly shorter than those reported by (McConkey and Chivers 2007) from Borneo. However, the gibbons in Borneo had much larger home ranges than those from the present study area (Cheyne et al. 2019), which could significantly impact seed dispersal distances.

Caveats

Nevertheless, the study has several assumptions. We assumed that gibbons had perfect knowledge of their resource distribution. While this may not be true, gibbons in our study area had smaller home ranges that could promote reliable ecological knowledge. Next. We did not consider non-foraging movements in our simulations. Besides, gibbons can also deposit seeds in their sleeping sites, but we did not investigate such non-movement related seed dispersal. In future, we would like to include further details, including productivities of resource patches, within patch gibbon movements, external environmental conditions such as canopy cover or additional field-based estimates of seed dispersal patterns generated by the gibbons.

Conclusions

In our study, we show that gibbons making foraging decisions in their resource landscape can account for resource attributes, move goal-oriented among resource patches at local scale, which in turn can influence the seed dispersal distances. We demonstrate that disperser movement not
only facilitates meeting its essential foraging goals, but also creates important secondary outcomes like seed dispersal. However, resource distribution and abundance can change, often caused by anthropogenic impacts, which can affect foraging decisions and movement of the seed dispersers that in turn can alter seed dispersal distances. Thus, seed disperser movement is vital for the persistence of plant populations, particularly in a rapidly changing world. It is imperative that we study seed disperser movements in details. This will not only augment our knowledge about animal-mediated seed dispersal, but also help us implement effective plans to conserve these critical ecological processes.
References


Fig. 3.1: Graphical summary of our seed dispersal simulation model.
Fig. 3.2: The simulated resource landscapes with varying resource distribution and abundances. Resource distribution is controlled by the Hurst component (H). Here the columns are different levels of resource distributions: scattered (H=0.1), moderately aggregate (H=0.5), and clumped (H=0.9). The rows are the different resource abundances (A): low (A=10 patches), moderate (A=25 patches), and high (A=50 patches).
Fig. 3. 3: Density plots of simulated seed dispersal distances when gibbons accounted for resource attributes, made informed foraging decisions, and when gibbons made random foraging decisions. The dashed lines represent the median dispersal distances when gibbons made informed (black) and random (red) foraging decisions.

Fig. 3. 4: Boxplots of simulated seed dispersal distances when resource distribution and their abundance are altered independently and gibbons adopt different foraging strategies based on resource attributes. When gibbons adopt: (a) ‘Distance’ strategy, they discount distant resources; (b) ‘Memory’ strategy, they avoid resource patches that they exploited the previous day; (c)
‘Coupled’ strategy, they discount distant resources as well as avoid previously exploited resources and; (d) ‘Random’ strategy, they do not account for resource attributes. Here, the columns are the three levels of resource abundances and rows are the three levels of resource distribution.
CHAPTER 4: IMPACTS OF HABITAT FRAGMENTATION AND LOSS ON LONG-DISTANCE SEED DISPERsal ARE MEDIATED THROUGH SEED DISPERsERS’ MOVEMENT

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Abstract

Habitat fragmentation and loss can disparately impact ecological interactions like biotic or animal-mediated long-distance seed dispersal, which can be similar to their impacts on different biodiversity metrics. Yet, we know little how long-distance seed dispersal respond to habitat fragmentation and loss, often due to our inability to observe these interactions across multiple landscapes with different levels of fragmentation and habitat loss. As a way around this, here we simulated multiple artificial anthropogenic landscapes, replicated different levels of habitat fragmentation and loss, and tested how they marginally and jointly affect long-distance seed dispersal. In our simulations, a medium sized avian seed disperser moved within the landscape and dispersed seeds of trees it fed on. During its movement, the disperser preferred the habitat fragments over the matrix, regularly performed encamping activities in the fragments, and traveled through both the fragments and the matrix. The dispersers’ movement was dictated by a correlated random walk, which was tortuous while encamping in the fragments, but directed while traveling, although travel speed was slower in the fragments than in the matrix. We found that dispersers had smaller displacements from their movements in landscapes with high habitat amount, which caused shorter long-distance seed dispersal, but longer displacements in landscapes with low habitat amount, which caused longer dispersal. Impacts of fragmentation on long-distance seed dispersal became apparent at low and intermediate habitat amount. When habitat amount was low and fragments were scattered, long-distance seed dispersal was
relatively shorter than that when fragments were clumped. However, the opposite pattern was observed in the landscapes when habitat amount was intermediate and fragmentation level varied. Thus, the impact of habitat fragmentation and loss on long-distance seed dispersal can differ. This can have important implications for conservation actions planning to protect and restore this critical ecological interaction.

**Introduction**

Habitat fragmentation and loss is globally pervasive, and together imperil biodiversity (Ellis et al. 2010). Several studies concluded that habitat loss such as clearing of forest have stronger negative impacts on different biodiversity metrics than habitat fragmentation or the ‘breaking apart’ of the habitat by different land use types, collectively referred to as the matrix (McGarigal and McComb 1995, Fahrig 1997, Flather and Bevers 2002). Yet fragmentation effects on biodiversity can persist (Hiebeler 2000) and become more apparent at low habitat amount (Andren 1994, Fahrig 1998). While these metrics: population size, species richness, or genetic diversity effectively highlight how habitat fragmentation and loss is a growing global threat (Fahrig 2017), they are silent about the impacts on different ecological interactions that are also crucial parts of biodiversity. One such interaction is animal-mediated seed dispersal that contributes significantly towards biodiversity, particularly in the tropics (Howe and Smallwood 1982, Muller-Landau and Hardesty 2005). Among several pathways, habitat fragmentation and loss can disrupt animal-mediated seed dispersal by affecting the animal vectors or seed dispersers. As an extreme impact, it can cause the extirpation of seed dispersers (Cordeiro and Howe 2003) with cascading effects on seed removal, dispersal distances etc. (Martínez and García 2015, Jones et al. 2017, Nield et al. 2020). However, habitat fragmentation and loss can also impact the habitat choices, behavior, and movement patterns of seed dispersers that in turn
affect seed dispersal. Relatively fewer studies have explored the relative impacts on seed dispersal patterns such as long-distance dispersal of seeds (LDD) when dispersers’ habitat choices, behavior, and movement patterns respond to both habitat fragmentation and loss.

Habitat choices, behavior, and movement patterns of seed dispersers respond to the different habitat conditions present in a fragmented landscape. Dispersers’ habitat choices are affected by habitat conditions. The remaining habitat fragments can differ from the matrix in several abiotic and biotic attributes. The fragments have more heterogeneous vegetation structure (Laurance et al. 2018) and therefore higher availability of resources (Keuroghlian and Eaton 2008, Pozo-Montuy et al. 2011), suitable microhabitats (Stratford and Stouffer 2015), or lower predation risk than the matrix (Lendrum et al. 2018), that can prompt dispersers to frequently use these habitats. These habitat choices in turn affect the dispersers’ behavior and movement patterns. Dispersers exhibit more encamped behavior like foraging in the habitat fragments, move slow and tortuously in them to remain longer (Goodwin and Fahrig 2002, Hein et al. 2005), but primarily travel through the matrix, and move fast and directly to quickly pass through it (Schultz 1998, J. Haynes and T. Cronin 2006). Habitat conditions can also affect its permeability to animal movement. In the forest fragments, dense vegetation cover can impede disperser movement and reduce their speed whereas the matrix can be more permeable (Cline and Hunter Jr 2014). Therefore, the prevailing habitat conditions influence dispersers’ habitat choices, behavior, and their movement patterns.

The distribution of habitat choices, behavior, and different movement patterns in the landscape will depend on the landscape features: fragmentation level and habitat amount, and influence long-distance seed dispersal. Fragmentation level determines the spatial configuration of the habitat fragments embedded within the matrix whereas habitat amount determines the total
area of fragments in the landscape. For the same habitat amount, when the fragments are
spatially scattered; or for the same level of fragmentation, when habitat amount is low; dispersers
encounter more of the matrix. In these circumstances, dispersers can either reside longer in the
habitat fragments, have smaller displacements from their movement, and disperse seeds over
relatively shorter distances or they can navigate the matrix with long, directed steps, have larger
displacements, and disperse seeds over long distances. On the contrary, if fragments are spatially
aggregated or habitat amount is high, dispersers encounter less of the matrix. They can either
travel through the forested areas, have large displacements from their movement, and disperse
seeds farther away or they can frequently perform encamping activities like foraging with short,
tortuous steps, have smaller displacements, and disperse seeds over relatively shorter distances.
Therefore, the marginal impacts of fragmentation level and habitat amount on long-dispersal
seed distance can differ, depend on relative frequencies of dispersers’ habitat choices, behavior,
and movement patterns that determine their displacements, and can moderate their joint effects
on long-distance seed dispersal.

Here, using simulations, we test how landscape features: fragmentation level and habitat
amount affect the long-distance seed dispersal of a plant species, mediated through its dispersers’
habitat choices, behavior, and movement patterns. In our simulations, dispersers primarily travel
in the matrix and use long, directed steps to move through it. Dispersers prefer to reside in the
forest fragments, regularly exhibit encamping behavior like foraging in them, and move with
short, tortuous steps. Dispersers also travel in the fragments, but their movement is slower in the
fragments. With these conditions, we tested how dispersers’ habitat choices, behavior, and
movement patterns affect long-distance seed dispersal in landscapes where we independently
varied both the fragmentation level and habitat amount.
Specifically, we hypothesized and predicted that:

1) Dispersers prefer the fragments than the matrix. Habitat fragments are more resourceful and less risky than the matrix that elicit more encamping behavior like foraging and short, tortuous movement in dispersers. On the other hand, dispersers primarily travel through the matrix with quick, directed movement. Additionally, habitat fragments are less permeable to animal movement than the matrix. Therefore, dispersers have smaller displacements and generate relatively shorter long-distance seed dispersal in landscapes with either low or high habitat amount compared to landscapes with intermediate habitat amount. Dispersers also have smaller displacements and therefore shorter long-distance seed dispersal in landscapes where fragments are scattered than in landscapes where they are more clumped.

Methods

Artificial landscapes

For our simulations, we used artificial landscapes that had experienced habitat fragmentation and loss. Our landscapes had 129 rows and columns of square grid cells, and individual cell size was 100m. Our landscapes were binary— where a grid cell can either be part of a habitat fragment or the matrix. We varied fragmentation level and habitat amount independently in the landscapes. The level of fragmentation i.e., the spatial configuration of forest fragments was controlled by the Hurst component (Tracey et al. 2014, de Souza et al. 2020). Low values of Hurst component results in high fragmentation level, where forest fragments were scattered, whereas high values of Hurst component results in low fragmentation level, where forest fragments were clumped. We selected three levels of forest fragmentation i.e., Hurst component values: high (0.1), intermediate (0.5), and low (0.9). The habitat amount was controlled by assigning fixed
proportion of the grid cells as habitat fragments. We simulated three levels of habitat amount: high (0.75), intermediate (0.5), and low (0.25). Thus, in total we had nine different landscapes with unique combination of fragmentation level and habitat amount (Fig.D.1).

**Disperser and plant species**

We considered an avian seed disperser in our simulations of long-distance seed dispersal. Birds are important seed dispersers (Sekercioglu et al. 2016), and show varying responses to habitat fragmentation and loss (Osuri et al. 2020). Moreover, information on different traits—body mass, gut retention time etc. that influence long-distance seed dispersal are readily available for birds.

Our seed dispersers are a mid-sized bird species that has a body mass of 100g. The bird species is more fragment dependent, prefers the habitats therein, and forages in the fragments. It can also tolerate the matrix, and makes forays through it. Seeds of our plant species are dispersed by the bird. We randomly placed 25 individual plants in the landscapes. However, we maintained a buffer of around two kilometers between the outermost individual and the landscape boundaries to avoid any edge conditions.

**Gut retention time**

To estimate mean gut retention time of the bird species, we first used the following allometric equation where the body mass of the bird was the predictor.

\[ GRT (h) = 4.5BM^{0.5} (kg) \]

This is an empirically derived relation obtained from the feeding trials of 34 frugivorous bird species (sample size= 37, \(R^2= 0.69, p< 0.001\)) in their natural environment (Sorensen et al.
We then drew gut retention time values from a gamma distribution whose shape (k) and scale (θ) were given by

\[ k = \frac{\bar{t}^2}{s^2} \]
\[ \theta = \frac{s^2}{\bar{t}} \]

Here, \( \bar{t} \) is our estimated mean gut retention time and \( s \) is the standard deviation that we fixed at 30 minutes. Gamma distribution was found to be a good approximation for gut retention times distribution (Guttal et al. 2011).

**Movement parameters and habitat preferences of dispersers**

We simulated correlated random walks of the dispersers in the landscapes. In a correlated random walk, the direction of movement is correlated (Kareiva and Shigesada 1983). We used two movement components: step length and turn angle to characterize bird movement. Step lengths are the linear distances between two consecutive relocation points (Schick et al. 2008) whereas turn angles are the angular deviations between headings of two consecutive steps (Barraquand and Benhamou 2008b). Our simulated movement was affected by both bird behavior and the habitat permeability. Birds can either encamp or travel in the landscapes. Birds regularly exhibit encamping behavior like foraging in the habitat fragments, and its movement during encamping is characterized by short step lengths and large turn angles. The habitat fragments are also less permeable, and when birds travel through them, they move with short step lengths and small turn angles. Birds tend to rapidly travel through the matrix, and its high permeability assists quick movement. Therefore, movement in the matrix is characterized by relatively longer step lengths that that in the habitat fragments and small turn angles.
We drew step lengths from a gamma distribution (Avgar et al. 2017) whose shape (k) and scale (θ) were set to 1 and 2 respectively and multiplied by a scale parameter dependent on both the disperser behavior and habitat permeability (Fig. 4.1b). Larger values of scale parameter result in larger step lengths. We drew the turn angles from a von Mises distribution (Duchesne et al. 2015) with mean 0 (i.e., left and right turns are equally likely) and concentration parameter that was dependent on the disperser behavior (Fig. 4.1b). Larger values of concentration parameter result in smaller values of turn angles aggregated around the mean whereas smaller concentration parameter results in wider range of values of the turn angles. If the disperser was encamping in the habitat fragments, the scale parameter was set to 5 and the concentration parameter was drawn from a uniform distribution between 0.1 and 0.2 (Fig. 4.1e). If the disperser is traveling through the habitat fragments, the scale parameter was set to 10 whereas if it was traveling through the matrix, the scale parameter was set to 20 (Fig. 4.1e). If the disperser were traveling, the concentration parameter was drawn from a uniform distribution between 0.8 and 0.9 (Fig. 4.1e).

Dispersers chose between the two habitat types: the habitat fragments and the matrix, and decide to either remain in the habitat fragments or move into the matrix and vice versa during the movement process. We set the probability that the disperser would remain in the habitat fragments than to move into the matrix as 0.8 (Fig. 4.1d). Therefore, the probability that the disperser would remain in the matrix than to move into the habitat fragments was fixed at 0.2.

LDD simulation
The purpose of the model is to understand how landscape features: fragmentation level and habitat amount interact with dispersers’ habitat choice, behavior, and movement and influence long-distance seed dispersal (LDD) of plants.

The simulation model comprises of the artificial landscape, individuals of the plant, and the bird species (Fig. 4.1a). An instance of the model proceeds in time steps of ten minutes and runs for a time period set to the gut retention time of each bird. For each ten minutes interval, we simulated a correlated random walk of the disperser. The random walk consists of ten steps, each step has a resolution of a minute. The movement components of the random walk: step lengths and turn angles (Fig. 4.1b) are determined by the dispersers’ behavior—encamping or traveling (Fig. 4.1c) and habitat conditions of the disperser’s present location. At the end of each random walk, dispersers make a habitat choice, depending on the habitat conditions of the grid cell where the walk ends and the grid cell where the disperser is currently in (Fig. 4.1d). The dispersers’ movement propagate in the landscape through their habitat selection. The model instance ends once the disperser deposits the seed. We record the location of the seed deposition site.

For the 25 adult trees of the large-fruited plants, we simulated 50 seed dispersal events from each tree by the disperser. Therefore, we had 1250 dispersal events. We calculated dispersal distances as the euclidean distance between the deposition location and the tree location. We then estimated long-distance seed dispersal for each of the adult tree as the 95th quantile of its dispersal distances (Fig. 4.1f) (Pires et al. 2018).

**Statistical analysis**

To test if displacements from disperser movement differed among the landscapes with different fragmentation level and habitat amount, we used a subset of the simulated data by randomly
selecting 10 of the 50 random correlated walk that the disperser initiated from each individual plant. We had 250 correlated random walks in total. We then calculated the displacements resulting from each correlated random walk at ten minutes interval.

To test how long-distance seed dispersal is affected by landscape features, we used random forest analysis—a machine learning approach (Cutler et al. 2012). We used long-distance dispersal of the 25 individual plants as the response variable and fragmentation level and habitat amount as predictor variables. We separated the simulated results by a 70:30 ratio into two groups—test and train data. We then fitted a random forest model with 1000 classification trees to the train data. We used the test data to evaluate model performance through cross-validation. We calculated variable importance scores to estimate relative importance of covariates in determining model outcomes. These scores are reported in terms of percentage increase in MSE (mean squared error) which corresponds to the increase in MSE of model predictions when a parameter is permuted randomly rather than using its given value. Our reported variable importance measures were not scaled by the standard error, as such measures can be less biased for correlated predictors.

We performed all analysis and simulations using the R statistical software (version 4.1.2, R Core Team 2021)

Results

Displacements from dispersers’ movement

Movements of dispersers in landscapes with high habitat amount had shorter median displacements ($d_{med} = 103.27m$), a higher percentage of smaller displacements ($p_{<100m} = 47.2\%$), but a smaller percentage of larger displacements ($p_{>300m} = 2\%$) than in landscapes with
intermediate \( (d_{\text{med}} = 136.34 \text{m}, p_{<100\text{m}} = 33.9\%, \text{and } p_{>300\text{m}} = 12.5\%) \) or low habitat amount \( (d_{\text{med}} = 173.31 \text{m}, p_{<100\text{m}} = 24.8\%, \text{and } p_{>300\text{m}} = 18.5\%) \) (Fig. 2). Movement in landscapes with high or intermediate habitat amount also had smaller percentage of zero displacements \( (0.9\% \text{ and } 0.8\%) \) than in landscapes with low habitat amount \( (1.5\%) \) (Fig. 4.2).

Movement in landscapes with intermediate fragmentation level had longer median displacements \( (d_{\text{med}} = 140.05 \text{m}) \), a smaller percentage of shorter displacements \( (d_{<100\text{m}} = 31.6\%) \), but a higher percentage of longer displacements \( (d_{>300\text{m}} = 12.7\%) \) than in landscapes where fragments were scattered \( (d_{\text{med}} = 127.71 \text{m}, p_{<100\text{m}} = 36.7\%, \text{and } p_{>300\text{m}} = 10.5\%) \) or fragments were clumped \( (d_{\text{med}} = 122.07 \text{m}, p_{<100\text{m}} = 37.8\%, \text{and } p_{>300\text{m}} = 9.6\%) \) (Fig. 2). Movement in landscapes with intermediate fragmentation level also had smaller percentage of zero displacements \( (0.5\%) \) than in landscapes with scattered \( (1.8\%) \) or clumped fragments \( (1\%) \) (Fig. 4.2).

We provide different estimates of dispersers’ displacements in Table S4.1

**Long-distance seed dispersal**

Habitat amount was the more important predictor variable in explaining the variation in long-distance seed dispersal than fragmentation level (Fig. D.1).

Long-distance seed dispersals generated by dispersers were shorter in landscapes with high habitat amount \( (\text{median} = 125.21 \text{m}) \) when compared to landscapes with intermediate \( (\text{median} = 232.50 \text{m}) \) or low habitat amount \( (\text{median} = 240.55 \text{m}) \) when all levels of fragmentation were considered (Fig. 4.3).

Long-distance seed dispersals generated by dispersers were shorter in landscapes with low fragmentation level \( (\text{median} = 129.58 \text{m}) \) when compared to landscapes with intermediate...
(median = 225.79m) or high fragmentation level (median = 193.23m) when all amounts of habitat were considered (Fig. 4.3).

Long-distance seed dispersal in landscapes that experienced both intermediate level of fragmentation and habitat loss was longer (median= 230.30m) than in landscapes that either experienced high (median= 194.38m) or low (median= 122.24) level of fragmentation and habitat loss (Fig. 4.3).

Fragmentation affected long-distance seed dispersal when habitat amount was low or intermediate, but these patterns were contradictory. When habitat amount was low, long-distance seed dispersal was shorter when fragmentation level was high compared to when fragmentation level was intermediate or low. On the contrary, when habitat amount was intermediate, long-distance seed dispersal was longer when fragmentation level was high (median= 382.11m) or intermediate (median= 230.30m) compared to when fragmentation level was low (median= 125.65m) (Fig. 4.3).

**Discussion**

Using a suite of simulations, in this study we showed that habitat amount in a landscape had a stronger effect on long-distance seed dispersal. Interestingly, dispersal distances were shorter when habitat amount was higher. The effects of fragmentation became apparent only at intermediate and low habitat amount. When fragments were scattered, long-distance seed dispersal was relatively longer in landscapes with intermediate habitat amount but shorter in landscapes with low habitat amount. Our simulations additionally showed that the effects of landscape features: fragmentation level and habitat amount on seed dispersal distances were
mainly mediated through dispersers’ habitat choices and the distributions of movement parameters: step lengths, turn angles, and the resulting displacements.

Habitat amount was a stronger predictor of the variability in long-distance seed dispersal. Long distance seed dispersal in landscapes with high habitat amount was shorter than that in landscapes with intermediate and low habitat amount. Habitat amount can affect long distance seed dispersal by influencing seed dispersers’ behavior and movement. In landscapes with high habitat amount, dispersers regularly exhibit encamping behavior like foraging and move slow and tortuously, which is characterized by short steps and large turn angles. Habitats such as forest fragments can be relatively resource rich and animals perform such ‘area restrictive’ movement when they frequently encounter resources during foraging (Fryxell et al. 2005, Boyer et al. 2006, Paiva et al. 2010). Area restrictive movements allow animals to remain in their preferred habitats (Adler and Kotar 1999), exploit resources effectively (Haskell 1997), and can result in smaller displacement. As such dispersers generate shorter seed dispersal distances in these landscapes.

High habitat amount can also exert a permeability effect on animal movement. Forested habitats can be less passable to animal movements as vegetation cover in forested habitats can impede dispersers’ navigation capabilities or motion capacities that collectively influence the movement process. Thick vegetation can impair vision and cause birds to undertake shorter flights (Aben et al. 2021). It can also slow down their flight. Flight speed of several birds were slower in the forest cover than in the matrix in an Afro-tropical fragmented landscape (Habel et al. 2019). While vegetation cover can allow dispersers to move over extended areas in fragmented landscapes, these effects on long-distance seed dispersal can be countered if movement is short and slow through dense vegetation and dispersers deposit seeds before they
travel farther in the landscapes. In summary, dispersers either performed area restrictive or had slower, directed movements in habitat fragments that caused smaller displacements of dispersers. This was evident from the higher proportion of small displacements (<100m) in landscapes with high habitat amount. Smaller displacements in turn result in relatively shorter long-distance seed dispersal.

On the contrary, dispersers carried seeds over longer distances in landscapes with low habitat amount. The matrix which is more extensive in such landscapes can exert its own behavioral and permeability effect on animal movement. The matrix can be relatively resource poor, as land use practices such as agriculture can clear most of the native vegetation and severely deplete resources such as fruit trees (Harvey et al. 2006). The matrix can also be a riskier environment, as its more homogenous vegetation cover like monoculture may provide fewer refuges from predators (Estrada et al. 1997). As such, dispersers can move through the matrix quick and directedly and reduce time spent in these unfavorable habitats. The matrix can also be more permeable to animal movement. When vegetation such as cultivated crops replace the native cover, it offers a relatively homogenous environment that may cause less impediment to animal movement (Cline and Hunter Jr 2014). Thus, a resource poor, riskier, and structurally simplified matrix can cause dispersers to move quick and directedly through it, achieve larger displacements, and carry seeds farther away in the landscapes.

Fragmentation had contrasting effects on long-distance seed dispersal at low and intermediate habitat amount. When habitat amount was low, long-distance seed dispersal was shorter in landscapes when fragments were scattered than they were clumped. Fragmentation can lead to abrupt changes in habitat configuration at low and intermediate habitat amount by severing connectivity among patches (Turner 1989) and impacting dispersers’ habitat choices.
and movement. When fragments are isolated, scattered, and surrounded by an extensive matrix; they can also become less available for the dispersers. Dispersers can experience suboptimal conditions for movement through the matrix if extended time in the matrix causes stress (Tuff et al. 2016), makes movement energetically costly (Schtickzelle et al. 2006), and exposes the dispersers to higher predation risks (Pietrek et al. 2009). Under these circumstances, dispersers may rather reside longer in isolated fragments and delay their movement. Longer residence periods can cause shorter displacements. In landscapes with low habitat amount and scattered fragments, there was a higher proportion of zero and shorter displacements. Short displacements in turn can cause relatively shorter long-distance seed dispersal.

The opposite patterns occurred when habitat amount was intermediate i.e., long-distance seed dispersal was longer when fragments were scattered in the landscape. In these landscapes, while the dispersers encountered the matrix, they also encountered more habitat fragments, which can act as stepping stones and facilitate movement. Stepping stones are particularly important for the movement of forest dependent birds, many of who have modest dispersal capabilities in human-modified landscapes (Sekercioglu 2007). Thus, fragmentation impacts on long-distance seed dispersal are dependent on habitat amount.

Our results can have important conservation implications. We show that in landscapes with intermediate habitat loss, habitat fragments can facilitate disperser movement through the matrix. In such landscapes, conservation plans should aim to maintain the spatial configuration of the landscape and preserve the remaining fragments. When habitat amount in low, restoration plans can increase habitat amount by improving degraded areas and adding to the remaining habitats. Yet such efforts should also pay attention to how habitat fragments are positioned in the landscape, as landscape configuration are critical for ecological processes like seed dispersal at
low habitat amount. Priority should be given to save small fragments that can serve as stepping stones, as small fragments are often at higher risks of being lost (Riva et al. n.d.). When habitat amount is high, conservation efforts should focus on maintaining habitat quality, as forest dependent dispersers rely heavily on these habitats.

However, the results from our study should be considered with its assumptions. We considered binary landscapes in our simulations and assumed that within habitat variation, either in the fragments or the matrix did not exist. In reality, both habitat fragments and the matrix can be highly heterogenous in their quality, which in turn will affect the movement parameters and therefore seed dispersal. Considering this variation in habitat quality in the form of a continuous landscape can further improve our understanding about how landscape features can affect animal movement and their functional roles in seed dispersal.

Habitat loss have stronger negative impacts on biodiversity metrics such as population sizes, species richness, or genetic diversity than fragmentation. Yet effects of fragmentation on these metrics become apparent when habitat loss falls below a threshold (Fahrig 1997). These patterns emerge as the remaining fragments may be too small to sustain viable populations (Debinski and Holt 2000), or individuals suffer higher mortalities in the matrix (Niebuhr et al. 2015). Here we show that habitat loss also has stronger impacts on ecological process like long-distance seed dispersal, whereas fragmentation impacts on seed dispersal become apparent and can differ when habitat loss also becomes more severe. Therefore, we demonstrate that not just biodiversity metrics, but ecological processes like seed dispersal may respond similarly to habitat loss and fragmentation. In conclusion, any conservation efforts aim to mitigate biodiversity loss from habitat loss and fragmentation may also benefit the ecological processes like seed dispersal.
References


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**Fig.4.1:** Graphical summary of the long-distance seed dispersal (LDD) simulation model.

**Fig.4.2:** Histogram of displacements of dispersers in landscapes with different levels of fragmentation (rows) and habitat amount (columns). Here displacements are calculated at the end of a 10 min correlated random walk that started from an individual tree. The dotted lines represent the median displacements.
Fig.4. 3: Density plots of long-distance seed dispersal of all individual plants in landscapes with different levels of fragmentation (rows) and habitat amount (column). Here the dotted lines represent the median long-distance seed dispersal of the plant populations.
CHAPTER 5: LARGE-FRUITED TROPICAL PLANTS SUFFER STRONG REDUCTIONS IN THEIR LONG-DISTANCE SEED DISPERSAL FROM THE DEFAUNATION OF THEIR LARGE SEED DISPERSERS

Binod Borah, Noelle G. Beckman

Abstract

The loss of large frugivorous birds can have cascading effects on the entire plant community as it loses their seed dispersal services, yet some plant species may disproportionately suffer the consequences. Plants with large fruits primarily interact with large birds and therefore can suffer stronger reduction in their long-distance seed dispersal when these birds go extinct. Yet, ecological interactions between plants and extinct birds can rewire with extant birds, if the latter are morphologically similar to the extinct birds; although whether rewiring can successfully mitigate losses in ecological functions is debatable. Here we used interaction data from ten Andean bird-plant seed dispersal networks, estimated plant species specific long-distance seed dispersal using a trait-based framework, simulated various scenarios where large birds went extinct, and tested if plants with larger fruits suffered stronger reduction in their long-distance seed dispersal. We found that large-fruited plants suffered nearly 50% reduction in their long-distance seed dispersal when few of the largest birds (≥300g) went extinct and no interactions rewiring occurred, which was also surprisingly similar to the reduction in their long-distance dispersal when interactions selectively rewired between plants and the extant bird species. When extinction pressure was more severe (25 and 50% loss of the largest birds), large-fruited plants suffered over 50% reduction in their long-distance seed dispersal which was also greater than that if birds randomly went extinct. Therefore, large birds are functionally important to large-
fruited plants, generate greater long-distance seed dispersal whose loss are irrecoverable if they
go extinct, and therefore merits stronger actions for their conservation.

**Introduction**

Large frugivorous birds are critical for biotic seed dispersal. Large birds travel farther (Tucker et al. 2019) and carry seeds longer in their guts (Godínez-Alvarez et al. 2020)—factors that contribute towards long-distance seed dispersal of plants. These long-distance seed dispersals maintain genetic connectivity (Martínez-López et al. 2020), rescue local populations from extinctions (Lesser and Jackson 2013), and enable species to track their suitable niche under climate change (Dyer 1995). Yet large birds are vulnerable to anthropogenic impacts. Threats such as hunting, habitat loss, and fragmentation can cause the local extirpation of large birds (Malhi et al. 2014, Young et al. 2016). Analyzing data collected from 6214 bird species, Gaston and Blackburn (1995) reported that birds that were threatened with extinction had three times the geometric mass compared to birds that were not threatened. Eventually, the loss of large birds can affect several ecological processes including long-distance seed dispersal of the plants with which they interact.

Several traits can mediate interactions between frugivorous birds and plants. One such trait is fruit size. The average diameters of fruits strongly correlate with the gape widths of their avian consumers and determine the set of seed dispersers (Wheelwright 1985). As a consequence of such size coupling, while both small and large birds can ingest and disperse seeds of small-fruited plants, seeds of large-fruited plants are mostly dispersed by large birds. Therefore, large bird extinction can impact the entire plant community. Donoso et al. (2020) simulated extinctions of large birds from several plant communities in the Andes and found that median
long-distance seed dispersals of these plant communities were reduced. These losses ranged between 20% to 80% when only 20% of the largest birds went extinct from the local communities. Yet, when large birds become extinct, different plants within a community can experience different degree of losses in their long-distance seed dispersal. This present study aims to quantify these variable losses using a trait-based framework, linking fruit size of plants to the changes in their long-distance seed dispersal driven by large bird extinction.

Particularly we investigated if large-fruited plants experienced greater changes in their long-distance seed dispersal compared to small-fruited plants from the local extinctions of large birds. Such changes will depend on both the severity of the extinction pressure as well as interaction rewiring: the establishment of new interactions among the remaining species (Raimundo et al. 2018). When the extinction of large birds is less severe and only a subset of large birds become extinct, the large-fruited plants can potentially interact with the remaining large birds that are morphologically similar to extinct birds (Dehling et al. 2016), and experience only small changes in their long-distance seed dispersal. Yet, studies looking at loss of these ecological functions (or network structures) do not account for any potential rewiring (Mello et al. 2011, Vidal et al. 2014, Donoso et al. 2020), and thereby can overestimate any potential changes. However, when extinction pressure is more severe and all large birds are lost, rewiring may no longer occur between large-fruited plants and the remaining medium and small birds (Wright 2003). Under such scenarios, large-fruited plants can suffer greater changes to their long-distance seed dispersal. For instance, in Tonga, at least eight large pigeon and dove species have gone extinct, and the richness of the frugivore community reduced by over 50%. As no extant birds on the island have gapes wide enough to handle large fruits, seeds of several large-fruited plants are no longer dispersed by the remaining bird species (Meehan et al. 2002).
To test our predictions, we used data from 10 weighted bird-plant networks from the Andes (Dehling et al. 2021). The Andes harbor the highest diversity of frugivorous birds. This region also faces strong defaunation pressure from hunting, forest loss, and degradation, and have substantially lost its forest cover (Shanee 2012, Aide et al. 2019, Clerici et al. 2019). We simulated size-selective extinction of birds from individual networks, estimated and recorded the changes in long-dispersal seed dispersal of individual plant species using a trait-based framework, and related these changes to the fruit sizes of the plant species. We categorized our simulations into two groups: 1. When size-selective extinction of birds is less severe and interactions rewire within the networks. We compared the resulting changes in long-distance seed dispersal to that when no such interactions rewiring occurred. 2. When size-selective extinction of birds is more severe and interactions rewiring is not feasible. We compared the resulting changes in long-distance seed dispersal to that when extinctions of dispersers are random.

Specifically, we hypothesized that seeds of large-fruited plants are primarily dispersed by large birds because of strong size coupling, whereas seeds of small-fruited plants are dispersed by both small and large birds. We predicted that 1) when extinction pressure on large birds is less severe and interactions rewiring occur, long-distance seed dispersal of large-fruited plants experience smaller changes compared to when no such rewiring occur 2) When extinction pressure is more severe on large birds that precludes rewiring, long distance seed dispersal of large-fruited plants experience greater changes compared to when birds become randomly extinct.
Methods

Plant-frugivore networks

We used data from ten weighted bird-plant networks from the Andes (Dehling et al. 2021). The weights in these networks were the frequencies of visits between a plant and a bird species. Birds are critical seed dispersers (Sekercioglu et al. 2016), and information on their traits that influence long distance dispersal such as body size and gut retention time are readily available from the literature.

For each network, we recorded their geographical locations and habitat type, calculated the birds, plants, and interactions richness, and collected information on sampling time (Table 5.1). More details about sampling methods are available in (Dehling et al. 2021).

Trait data

We collected data on bird mass from the Elton trait data base (Wilman et al. 2014). All morphological plant traits were provided by Dehling et al. (2021) which were measured in the field. For each plant recorded in the networks, the fruit diameter was recorded.

Community wide long-distance seed dispersal

We calculated plant species specific long-distance seed dispersal generated by their seed dispersers. We defined long-distance dispersal as 0.95 quantile of all seed dispersal distances for a plant species (Pérez-Méndez et al. 2016, Pires et al. 2018).

To estimate seed dispersal distances, we employed a trait-based framework previously used by Donoso et al. (2020) and Sorensen et al. (2020) which is based on the allometric relationship between bird species body mass (BM) and the two important components of seed
dispersal: gut retention time and flight speed. This framework ensures that body mass, an easily identifiable predictor can be used to reliably estimate biological parameters of seed dispersal processes in species rich communities.

We estimated the mean gut retention time for each bird species using the following allometric equation between gut retention time (GRT) and body mass (BM)

$$\text{GRT (h)} = 4.5BM^{0.5}(\text{kg})$$

This relation was empirically derived from the feeding trials of 34 frugivorous bird species (sample size= 37, $R^2= 0.69$, p< 0.001) in their natural environment (Sorensen et al. 2020). For each species, we then drew 1000 gut retention time values from a gamma distribution whose shape (k) and scale (θ) were given by

$$k = \frac{\text{GRT}^2}{s^2}$$

$$\theta = \frac{s^2}{\text{GRT}}$$

Here, GRT is our estimated mean gut retention time for each bird species and $s$ is the standard deviation that we fixed at 750 seconds following Sorensen et al. (2020). Gamma distribution was found to be a good approximation for the distribution of gut retention time (Guttal et al. 2011). To estimate mean flight speed for each bird species, we used the following allometric equation between flight speed (FS; in no wind conditions) and body mass (BM)

$$\text{FS (m s}^{-1}) = 15.7BM^{0.17}(\text{kg})$$

These flight speeds were derived by Alerstam et al. (2007) using aerodynamic measures from wind tunnel experiments, and broadly apply to all bird species. Slight variations around the mean estimates of flight speed did not affect estimates of long-distance seed dispersal (Sorensen et al. 2020). For each bird species, we then drew 1000 flight speed values from a normal distribution
(Bruderer and Boldt 2001) whose mean was set to the estimated mean flight speed and standard deviation was set to $2.35 \text{ ms}^{-1}$ as estimated by (Alerstam et al. 2007) in their study of flight speed.

We combined the gut retention times and flight speeds of each bird species to estimate 1000 seed dispersal distances and generate dispersal kernels. We accounted for resting periods of birds and their non-directional movements by multiplying each dispersal distance with a calibration term that was derived following Schurr et al. (2009) using the equation

$$z = fc \times (254340)BM^{0.67}$$

where $z$ is the seed dispersal distance (m), $f$ is the time allocated to movement as a constant fraction of gut retention time, $c$ is a straightness factor that determines if movement occurs in a straight line ($c$ is 1 if movement is straight), and $BM$ is the body mass (kg). The product of $f$ and $c$ is the calibration term and after comparing the ratio between the derived seed dispersal distances to empirical dispersal distances, the calibration term ‘fc’ was estimated to be 0.002 (Donoso et al. 2020, Sorensen et al. 2020).

Next, we calculated dispersal kernels of each plant species. For this, we aggregated all dispersal distances by individual plant species and calculated the $95^{\text{th}}$ quantile of these values as the long-distance seed dispersal of individual plant species.

Our allometric approach to estimate long-distance seed dispersal may be a reasonable approximation given that most bird species in our study are canopy foragers that use flight as the mode of locomotion. These allometric relationships were derived from a broad group of birds with similar body size ranges. While birds can also regurgitate seeds and carry them only over small distances, long-distance seed dispersal are rare events and can occur when dispersers occasionally carry seeds with non-interrupted travel.
Relationship between fruit sizes and number of interaction partners of plants

For each network, we fitted a Poisson regression with a log link function with the number of interaction partners of a plant species as the response variable and its fruit size of plant species calculated as the mean fruit diameter as the predictor variable.

Relationship between size coupling between birds and plants and their interaction frequencies

We defined size coupling between a pair of bird and plant as the difference between the bill width and fruit diameter. Therefore, for the observed interactions, size coupling will be a positive number, and expected to be larger when the bird is large with wider gape and the fruit is small. For each network, we fit a poisson regression with a log link function, with the frequencies of interactions between a bird-plant pair as the response variable and size coupling as the predictor variable.

Extinction simulations

We simulated local extinction of large birds from their individual networks (Fig. 5.1a) to assess how plants with different fruit sizes experience reduction in their long-distance seed dispersal from the loss of large frugivorous birds. First, we arranged all bird species from a network in a descending order based on their body mass. Next, we simulated local extinction of frugivorous bird species in order of size, starting with largest species first unless otherwise noted. We referred to this as the ‘downsizing’ of the seed disperser community. To quantify changes in long-distance dispersal across all networks due to extinction, we calculated the percentage changes in long-distance dispersal event after every extinction compared to the original network.
We quantified changes in long-dispersal dispersal for different levels of downsizing under the following two extinction scenarios:

\textit{a) Mild downsizing with and without interactions rewiring:} Under this scenario, we considered the local extinction of a large bird with body mass greater than 300g from each community. We then calculated the long-distance seed dispersal of each plant species in the community when interaction rewiring was i) present (Fig. 5.1b) and ii) absent (Fig. 5.1c).

For scenarios in which interaction rewiring was present, we considered interactions to rewire between the remaining bird and plant species based on morphological similarities among birds (Vizentin-Bugoni et al. 2020). In other words, extant birds were more likely to interact with plants that lost a disperser if the extant bird species shared similar traits with the extinct bird species. Using a trait-based framework, we defined morphological similarity between a pair of birds as similarities between their gape widths as gape widths correlate with body sizes among birds. We used gape width data of birds from each network, measured their similarities using euclidean distances, employed fuzzy set theory, and created matrices of fuzzy sets. In a fuzzy set, an element belongs to the set with certain degree: if the element has a value 1, it is a complete member; if it has a value 0, it is not a member; and if it has any value between 1 and 0; it is a fuzzy member of the set (Maiers and Sherif 1985). Here, each bird species is a fuzzy set, and other birds belong to this set with values ranging between 0 (no similarity in gape width) and 1 (complete similarity in gape width) determined by their gape width similarities. Therefore, higher the value of an element in the fuzzy set of a bird, the higher is the similarity in gape widths between the focal bird species with the other species. If a fuzzy set of a bird has several high values, the bird species has similar gape widths with many other birds in the network, and if that bird becomes extinct, its plant partners have high chances of rewiring with other similar bird.
species. We drew from a multinomial distribution and distributed the lost interactions between an extinct bird and the plant species among the extant birds

\[ P = \left[ \frac{n!}{(n_1! \times n_2! \times \ldots \times \eta_k!)} \right] \times \left( p_1^{n_1} \times p_2^{n_2} \times \ldots \times p_k^{n_k} \right) \tag{1} \]

where the size ‘n’ was set equal to the number of lost interactions, to be distributed among ‘k’ classes where k was the number of extant bird species and the probability of successful interaction \( p_1, p_2, \ldots, p_k \) for the k classes was determined by the fuzzy set of the extinct bird.

We ran a set of simulations for scenarios of interaction rewiring present or absent. For networks where more than one large bird (>300g) was present, we calculated long-distance seed dispersal of plant species in separate simulations when each of the bird species became extinct and all other bird species were present (or when each of the bird species went extinct sequentially in order of size), determined the percentage change in long-distance dispersal for each such extinction, and calculated the average change in long-distance dispersal for each plant species. Additionally, we also repeated the same extinction scenario and recorded the change in long-distance seed dispersal, but this time considered the extirpation of only the largest bird in the community. Notes, with scenarios of rewiring absent, plants that lost all their dispersers would suffer the complete loss of their long-distance seed dispersal, i.e., hundred percent change in their long-distance seed dispersal.

b) Severe downsizing with no rewiring: For this, we considered i) 25 percent (Fig. 5.1c) and ii) 50 percent extinction (Fig. 5.1d) of the largest birds from the ordered list in each network.

Concomitant to these downsizing extinction events in each network, we also simulated 1000 random extinction events, where birds were randomly removed from the network. Again, we calculated the percentage differences in long-distance seed dispersal from the original network
for each plant species after the extinction events. For plant species that lost all their dispersers, this change in long-distance seed dispersal would be hundred percent. We did this for both the downsizing and random extinction events.

**Statistical analysis**

We fitted generalized additive model (GAM) to the percentage changes in long-distance seed dispersal with fruit size ratio—calculated by diving the fruit size of a tree species by the largest fruit size present in the community, as the predictor variable for each network. GAM is a generalized linear model that includes a sum of smooth functions of covariates. GAM offers better fit to non-linear trends in data, control of predictor functions smoothness to prevent model overfit, and easily interpretable results (Hastie 2017). We used a thin plate smoothing spline (TPSS) as the smoother functions and restricted maximum likelihood (REML) as the fitted method. For each gam model, we selected an optimal number of basis functions that control model fit based on visual inspection of diagnostic plots. We then predicted 100 values using each model. We then aggregated these predicted values from all networks, calculated their mean, and the 95% confidence interval around the mean. We compared these estimates between the i) mild downsizing events with ‘rewiring’ and ‘no rewiring’ (Figs. 5.1a, b) and ii) severe and random downsizing events (Figs. 5.1c, d).

**Results**

**Bird-plant networks**

Mean number of bird species recorded was 38 (SD: 13.87) and plant species was 30.37 (SD: 13.36) in the bird-plant networks. The mean number of interactions recorded was 1446.5 (SD:
1538.66). All but one networks were sampled from forest interior habitats (Table 5.1). All networks were well sampled and the mean sampling hour was 606 hours (SD: 224.22 hours).

Trait data
The mass of the largest bird in the networks ranged between 118g and 1770g (mean: 875.20g). The number of birds in each network that were over 300g ranged between 0 and 4 (mean: 2.2). Average mass of bird in these networks ranged between 39.61g and 127.84g. The body masses of birds (n=170) roughly followed a log-normal distribution (Fig. E.1) and a majority of bird species had body mass equal to or less than 100g (78.8%, n=134) whereas few species had body mass that exceeded 300g (7%, n=12).

The largest fruits in the bird-plant networks have diameters that ranged between 16.9 mm and 33.4 mm (mean: 23.06 mm). The average fruit diameter ranged between 6.2 mm and 9.9 mm.

Fruit sizes and number of interaction partners of plants
In 50% of the networks (n=5), plants with larger fruits have fewer birds as partners. When the relationships between number of interaction partners and fruit diameter were statistically significant, slope values were negative (Fig. 5.2). Estimates from GLM regression between number of partners and fruit diameter are provided in Table S5.1.

Size coupling between birds and plants and their interaction frequencies
In 80% of the networks (n=8), there were fewer interactions between birds and plants when there were larger size couplings i.e., when the differences between gape width of birds and sizes of
fruits were larger. Slope values were negative when the relationships between interaction frequencies and difference between bill width and fruit diameter were statistically significant (Fig. 5.3). Coefficient estimates from GLM regressions are provided in Table S5.2.

**Extinction scenarios**

*a) Mild downsizing with and without interactions rewiring:*

Large-fruited plants suffered considerable changes in their long-distance dispersal when few large birds with body mass greater than 300g went extinct from their communities. Plants with fruits whose sizes were in the upper quartile (seed size ratio ≥ 0.75) suffer 10% or more reduction in their long-distance dispersal (Fig. 5.4). Plants with the largest fruits (seed size ratio=1) suffered close to 50% reduction in their long-distance dispersal under mild downsizing (Fig. 5.4). Losses in long-distance dispersal when few of the largest bird species were extirpated appeared to be similar under both scenarios when interactions wired or did not wire after extinction events (Fig. 5.4).

*b) Severe downsizing with no rewiring:*

When downsizing was severe and many large birds went extinct with no interaction rewiring, plant with large fruits suffered considerably more reduction in the LDD compared to plants with small seeds. These losses were higher than that expected if birds went extinct randomly (Fig. 5.5). When birds were ordered from largest to smallest and 25% of the birds from each community went extinct from this ordered list, plants with fruit sizes in the upper quartile (seed size ratio ≥ 0.75) suffer over 50% reduction in their LDD, whereas plants with fruits in the lower quartile (seed size ratio ≤ 0.25) suffered less than 50% reduction in their LDD.
When 50% of bird species went extinct from the ordered list, plants with fruit sizes in the upper quantile suffered more than 50% loss in their LDD, whereas plants with fruit sizes in the lower quartile also suffered 50% or less loss in their LDD.

**Discussion**

In this study, we used a trait-based framework and a suite of simulations and showed that large frugivorous birds are critical long-distance seed dispersers in tropical forests. Large-fruited plants experienced reduction in their long-distance seed dispersal when a few of the largest birds from the disperser community became extinct. This loss in long-distance seed dispersal was further exacerbated for large-fruited plants when severe extinction pressure eradicated more larger birds. Moreover, even when interactions rewired selectively among the plants and remaining birds after a large bird became extinct, we found similar reduction in long-distance seed dispersal of large-fruited plants. Therefore, large birds can be irreplaceable in generating long-distance seed dispersal of large-fruited plants.

The reduction in long-distance seed dispersal of large-fruited plants was determined by the severity of size biased extinction events of dispersers. Our simulations showed that long-distance seed dispersal of large-fruited plants was very sensitive even to mild extinction pressure. When few and the largest birds over 300g became extinct, large-fruited plants suffered nearly 50% reduction in their long-distance seed dispersal. A similar reduction in long-distance seed dispersal of large-fruited plants was observed even when the single largest bird species was extirpated from the community (Fig.E.2). Other studies have demonstrated losses in long-distance seed dispersal triggered by large disperser extinction, both from contemporary ecosystems: the extinction of the largest lizard species caused fewer long-distance seed dispersal
events of the plant *Neochamaelea pulverulenta* in the Canary Islands (Pérez-Méndez et al. 2016) as well as pre-historical ecosystems: the extinction of Pleistocene megafauna like ground sloths and gomphotheres significantly reduced the long-distance seed dispersal of plants they dispersed (Pires et al. 2018). In this study, we further demonstrated that reductions in long-distance seed dispersal caused by large dispersers extinctions were disproportionately experienced by large-fruited plants.

When extinction events became more severe, large fruited plants experienced further losses to their long-distance seed dispersal. As more large birds became extinct from the communities, long-distance seed dispersal of large-fruited plants reduced by more than 50%. Thus, large-fruited plants respond strongly to large bird losses, and this can be attributed to two factors: the body mass distribution of birds in the disperser communities and the number of partners that large-fruited plants have. Body mass of birds are log-normally distributed (Fig.E.1) and only few bird species exceed a large threshold weight (300g in this study, 12 species). Thus, large birds are rare in their communities. However, several large-fruited plants interact mostly with these few large birds as they have wider gapes that can swallow large fruits, or large birds prefer these fruits, and disperse their seeds. Thus, large-fruited plants either solely or disproportionately interact with few large dispersers (Figs. 5.2, 5.3). Seeds of large-fruited plants from the Lauraceae, Palmae, Myristicaceae, and Meliaceae families are primarily dispersed by few large and frugivorous tropical bird species (Stiles 1993). Ecologists have long debated the adaptive benefits or costs that large-fruited plants accrue from having fewer large dispersers (McKey 1975, Howe and Estabrook 1977). It can be beneficial for the plants as large birds travel farther (Tucker et al. 2019), have large home ranges (Schoener 1968), therefore can carry seeds over longer distances, and provide reliable dispersal services. In such scenarios, loss of large
birds can erode these adaptive benefits that large-fruited plants enjoy by interacting with large birds. On the contrary, having few large dispersers can be costly for plants, as large birds are relatively rare in the disperser community and ultimately contribute little to dispersal services. In such cases, loss of large birds can farther exacerbate the situation, ‘makes the poor poorer’, and potentially leaves large-fruited plants with no viable partners. Regardless of whether large-fruited plants having few large birds as dispersers is adaptively beneficial or detrimental to them, the loss of these partners can significantly change long-distance seed dispersal of these plants.

The severe negative impacts of large bird extinctions were further underscored by the lack of role interaction rewiring played in mitigating the losses in long-distance seed dispersal of large-fruited plants. Such rewiring can happen through density compensation: when loss of one species is followed by increase in abundances of other species which in turn increases interaction frequencies (Walker 1992, Peres and Dolman 2000), or per-capita compensation: when loss of one species is followed by behavioral changes in other species which in turn forges new interactions and increases frequencies of existing ones (Brosi and Briggs 2013), or both. Interaction rewiring can make mutualistic animal-plant networks tolerant to species loss (Bastolla et al. 2009, Thébault and Fontaine 2010). Rewiring prevented secondary loss of species from pollinator-plant networks when any pollinator or plant species was removed from them (Kaiser-Bunbury et al. 2010) and maintained network structure which is determined by the organization of the species (nodes) and their interactions (edges) (Lau et al. 2017). Thus, interaction rewiring can help networks recover their structures after species loss and turn some species’ roles redundant in maintaining these structures (Memmott et al. 2004, Bascompte 2009, Mello et al. 2011). Yet, interaction rewiring may be inadequate in shielding networks from losses in particular functions caused by species extinctions, such as loss of pollination services when
specialized pollinators become extinct (Biesmeijer et al. 2006), or loss of long-distance seed dispersal of large-fruited plants when large birds become extinct. This inadequacy can be explained by the fact that such species like large birds only interact infrequently with their plant partners, probably driven by their low abundances. When large birds become extinct and their interactions are redistributed among the remaining birds, each species may only gain few interactions which may not be enough to recover functional losses. Interaction rewiring was less effective in contributing to network robustness when species with fewer interactions were removed in pollinator-plant networks (Kaiser-Bunbury et al. 2010). Here, we show that it can also be ineffective in recovering some functional losses in disperser-plant networks.

Threats to large birds can be manifold. Large birds are selectively targeted for hunting for higher rewards per unit effort (Owens and Bennett 2000, Osuri et al. 2020). Such hunting practices are prevalent across most of the tropics (Fa et al. 2002, Peres and Palacios 2007), and even inside protected areas (Harrison 2011). Severe hunting pressure can quickly extirpate large birds from their local ecosystems as they are relatively rare and have slow regeneration time (Marquet et al. 1995). Other traits of large birds also make them vulnerable to human impacts. Large birds have larger home ranges and hence more susceptible to habitat modifications such as forest loss, degradation, and fragmentation. Although they can occur in anthropogenic landscapes, large birds were primarily absent from small forest fragments (Cordeiro and Howe 2003, Melo et al. 2010) that may have insufficient resources to support them. As large birds navigate these landscapes, they may also encounter more threats in the matrix (Peres 2001). Thus, several factors can threaten large birds and their ecological services like seed dispersal.

The reduction in long-distance seed dispersal of large-fruited plants can impact plant populations, communities and the ecosystem. Plant populations that experience strong reduction
in their long-distance seed dispersal may fail to colonize new habitats, track suitable niches under climate change, and face increased genetic isolation (Nathan et al. 2008d, Schurr et al. 2009). Large-fruited plant populations can incur many of these costs because of their reduced long-distance seed dispersal. Such population level effects can alter community properties. Large fruits also have large seeds (Primack 1987). Large seeds can outcompete smaller seeds while they establish (Leishman et al. 2000), yet their failure to reach certain habitats can allow smaller seeds to colonize such areas and change community composition (Coomes and Grubb 2003).

Finally, such changes in plant community composition also alter ecosystem services. Large fruit and seed sizes in woody plants are strongly correlated with wood density which in turn is positively related with their ability to sequester carbon (Bello et al. 2015, Peres et al. 2016). If plant communities lose more large-fruited plants as their long-distance seed dispersal fail, they may also fall short to provide reliable ecological services. While many processes such as establishment, recruitment, growth to adult stage can affect plant demography post seed dispersal (Schupp and Fuentes 1995b, Wang and Smith 2002), it is apparent that reduced long-distance seed dispersal of large-fruited plants can leave distinct marks on their populations, communities, and ecological services.

While our study demonstrated that loss of large birds can severely reduce long-distance seed dispersal of large-fruited plants, we arrived at these conclusions with the following assumptions. First, we assumed that in all our simulated dispersal events, birds ingest seeds and disperse them after seeds pass through their guts. However, several large bird species also disperse seeds by regurgitating them. Regurgitation time is shorter than gut passage time (Fukui 2003) and hence do not contribute towards long-distance seed dispersal in our simulations. Next, large birds from genera *Penelope*, *Aburria*, and *Chamaepetes* generally do not fly long distances.
While these birds frequently fly short distances when they forage etc., they can also infrequently fly over much longer distances using a series of short flights and disperse seeds over longer distances (Remsen Jr and Cardiff 1990). Finally, we did not consider how species abundances can affect interaction rewiring as we lacked such data from these networks. However, interaction rewiring models that only consider morphological features such as gape widths similarities can be reasonable approximations of how interactions can potentially rewire in the networks (Vizentin-Bugoni et al. 2020). In future, studies designed to collect data on species habitat selection, abundances can address some of these issues.

In conclusion, our study overall demonstrated that large birds are critical members of the seed disperser community in tropical forests, and their roles particularly affect the long-distance seed dispersal of large-fruited plants. While it is widely acknowledged that large birds are threatened by hunting, habitat loss, and other anthropogenic impacts and their extinction is a visible component of biodiversity loss, the loss of functional outcomes such as long-distance seed dispersal accompanying large bird extinctions is less appreciated and can remain hidden (Valiente-Banuet et al. 2015). Thus, our study makes the case to protect large birds to conserve vital ecological functions like seed dispersal.
References


Fig. 5.1: Graphical display of the extinction simulations from (a) an intact bird-plant community. Extinction scenarios were categorized into mild downsizing where birds over body mass 300g selectively went extinct and interactions either (b) rewired or (c) did not rewire with the extant dispersers; or severe downsizing where (c) 25% or (d) 50% of the largest birds went extinct. We estimated the change in long-distance seed dispersal of plants with different fruit sizes for different extinction scenarios.
Fig. 5.2: The relationship between fruit diameter of a plant species and its number of partners. The shaded region represents the 95% CI around the mean estimate. Each individual panel represents a bird-plant network.
Fig. 5.3: The relationships between interaction frequencies between a plant and its partners (response) and the difference between their bill widths and the plant’s fruit diameter (predictor). The shaded region represents the 95% CI around the mean estimate. Here each panel represents a bird-plant network.

![Diagram showing relationships between interaction frequencies and fruit diameter](image)

Fig. 5.4: Percentage change in LDD when both interactions rewired or failed to rewire between extant birds and plant species. Here multiple large birds heavier than 300g went extinct from each community.

![Percentage change in LDD](image)

Fig. 5.5: Percentage change in LDD when (a) 25% of the largest birds went extinct from each community and (b) 50% of the largest birds went extinct from each community with no interaction rewiring. Corresponding to these severe extinction events, we also Percentage change in LDD when (a) 25% of the largest birds went extinct from each community and (b) 50% of the largest birds went extinct from each community with no interaction rewiring. Corresponding to
these severe extinction events, we also recorded percentage change in LDD when birds rather randomly went extinct from each community.

Table 5. 1: Information on network attributes (Dehling et al. 2021)

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SUMMARY

Animal movement that allows them to change their spatial locations over time is a ubiquitous part of life on earth. For an individual, its movement can be fundamental for its survival, growth, and contributions towards its populations. Yet, apart from these essential outcomes, animal movement also provides secondary services, many of which are vital for ecosystem functioning. One such secondary service is biotic or animal-mediated seed dispersal which in the tropics assume greater importance as 70-80 percent of tropical woody plants rely on animals to disperse their seeds. Animal-mediated seed dispersal is dictated by vector movement, as animals remove seeds from their parent trees, travel with them, and deposit these seeds in other locations. However, our understanding of animal-mediate seed dispersal is still limited as knowledge about what drives seed dispersers’ movement and the links between these drivers and the patterns of seed dispersal are only emerging.

Several processes can act at different scales to drive animal movement. These processes can be categorized into four fundamental drivers: internal, motion capacities, navigational, and the external environment. In the first chapter, using the ‘movement ecology paradigm’, I proposed a novel framework that integrates the movement drivers with the functional roles of animal movement in seed dispersal ecology. I suggest that the observed movement can be categorized into different activity modes based on the distributions of movement components, which then can be coupled to the movement drivers. These activity modes then can be linked to seed dispersal patterns such as seed removal rates, dispersal distances, and seed deposition.

In the second chapter, I showed that how habitat conditions, one of the external processes, can drive seed dispersers’ movement and in turn affect seed dispersal patterns. I showed that spider-monkeys, a tropical seed disperser strongly preferred habitats with taller
canopy and higher ruggedness, and avoided tree fall gaps. Their habitat selection drove the movement process which we categorized into different activity modes. These activity modes had strong relationships with the prevailing habitat conditions. Spider-monkeys mostly encamped in habitats with taller canopy and higher ruggedness but both encamped and travelled under canopy cover. Together, habitat selection and activity modes caused strong spatial signatures in seed dispersal patterns. Spider-monkeys deposited more seeds in habitats with taller canopy and higher ruggedness than random seed dispersers with no habitat affinities that also distributed their activities randomly in the landscape. Spider-monkeys also deposited fewer seeds in treefall gaps than random seed dispersers, but this difference was only marginal. Additionally, spider monkeys generated shorter seed dispersal distances than random seed dispersers. In summary, external processes like habitat conditions can drive seed dispersers’ habitat selection, activities, and movement which in turn can leave distinct signatures on the habitat conditions experienced by the dispersed seeds or their dispersal distances. In this chapter, I used high resolution telemetry data, and lidar derived environment data, along with novel statistical methods, and simulation models.

In the third chapter, I explored how seed dispersers’ navigational capabilities drive their movement at different spatial scales and in turn affect the seed dispersal patterns. Dispersers can navigate their resource landscape, make foraging decisions to reduce travel cost, and increase profitability of endeavors. Dispersers’ navigation capabilities: the ability to detect sensory cues or to memorize locations or attributes of resources aid in these foraging decisions, drive the movement process at different scales, and in turn affect seed dispersal patterns. I showed that White-handed gibbon, a tropical seed disperser discounted distant resources in the landscape, avoided resources that it recently exploited, and moved directly between resource patches.
When I incorporated these movement patterns in a simulation model, I found that gibbons generated longer seed dispersal distances than any disperses that made random foraging decisions. Thus, foraging decisions based on resource attributes and driven by dispersers’ navigation can affect seed dispersal patterns. I also showed that resource aggregation and abundance together with dispersers’ unique foraging decisions can generate different seed dispersal distances. Gibbons that made informed decisions based on resource attributes generated relatively shorter seed dispersal distances than foragers that made random decisions when resources are clumped and either abundant or scarce, but relatively longer dispersal distances when resources are scattered. Thus, movement is functionally important for both the fitness of the animals and the maintenance of critical services like seed dispersal.

Today, several ecosystems including those in the tropics face rising risks from anthropogenic actions. Large scale habitat fragmentation and loss are widespread, affects animal movement, and detrimental to ecological interactions like animal-mediated seed dispersal. Not only habitat fragmentation and loss exacerbate extinction risks of seed dispersers, they can also restrict their movement and alter their distribution of activities. Such impacts in turn will change the seed dispersal patterns. In addition, hunting of seed dispersers, particularly the selective targeting of large seed dispersers can impact their ecological services. Disruptions of seed dispersal services can be detrimental to the entire plant community, yet some plants like those that bear large fruits may especially suffer the negative consequences of large seed disperser extinction.

In the fourth chapter, I examined how dispersers’ habitat selection, behavior, and motion capacities interact with their external environment in simulated fragmented landscapes and affect long-distance seed dispersal of plants. Particularly, I tested how different levels of habitat
fragmentation and loss affect long-distance seed dispersal. I simulated multiple artificial landscapes with varying levels of fragmentation and habitat loss. I found that long-distance seed dispersal was relatively shorter in landscapes with high habitat amount since dispersers had smaller displacements from their movement, likely because they performed more encamping activities or moved slower in habitat fragments. The opposite pattern was observed in landscapes with low habitat amount, as dispersers moved quickly through the matrix which also promoted faster movement. Contradictory effect of fragmentation was observed in landscapes with low and intermediate habitat amount. When habitat amount was low and fragments were scattered, long-distance seed dispersal was relatively shorter than that if fragments were clumped. In such landscapes, dispersers preferred to remain longer in isolated fragments than to move into the matrix and achieved shorter displacements. When habitat amount was intermediate, scattered fragments potentially acted as stepping stones and promoted disperser movements, as they achieved longer displacements and generated relatively longer seed dispersal distances.

In the fifth and final chapter, I tested how loss of large seed dispersing birds from their communities can disproportionately reduce long-distance seed dispersal of large-fruited plants. I accounted for interaction rewiring, where plants rewired their lost interactions with extant dispersers based on their morphological similarities with the extinct dispersers. I found that even when few of the largest dispersers were lost, large-fruited plants suffered nearly 50% reduction in their long-distance seed dispersal. Surprisingly, interaction rewiring was unable to mitigate this functional loss, as I observed similar reduction even when interactions rewired between plants and the extant dispersers. Under severe extinction pressure, where 25% and 50% of the largest dispersers were lost, large-fruited plants suffered over 50% reduction in their long-distance seed dispersal, which was also considerably higher than that if dispersers rather
randomly went extinct. Therefore, large birds are functionally important to large-fruiting plants, generate greater long-distance seed dispersal whose loss are irrecoverable if they go extinct, and therefore merit stronger actions for their conservation.
APPENDICES

Appendix A: License for Chapter 1

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## Appendix B: Figures and Tables for Chapter 2

Table B. 1: HMM estimates of step lengths and turn angles from the two movement states of individual spider monkeys. Here state 1 is the encamping state and state 2 is the traveling state.

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<tr>
<td>Emma 5762</td>
<td>coef</td>
<td>9.789281</td>
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<tr>
<td></td>
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<td>7.277471</td>
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<td>0.488716</td>
<td>0.322825</td>
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<tr>
<td>Greg 4689</td>
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<td>7.093821</td>
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<td>0.010967</td>
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<tr>
<td></td>
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<td>5.446995</td>
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<td>1.120578</td>
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<tr>
<td>Inez 5213</td>
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<td>8.028345</td>
<td>38.55452</td>
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<td>-0.05237</td>
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<tr>
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<td>sd</td>
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<td>30.24108</td>
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<td>Zola 5212</td>
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<td>Kyle 4692</td>
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<td>Veruca 4690</td>
<td>coef</td>
<td>7.497348</td>
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<td>5.687674</td>
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</tr>
</tbody>
</table>

Fig.B.1: Relative importance of the variables in predicting the number of seeds deposited in a grid cell by spider monkeys as estimated by random forest analysis.
Appendix C: Figures and Tables for Chapter 3

Table C. 1: Estimates of the patch-to-patch conditional logistic models with the different predictor variables and their interactions.

<table>
<thead>
<tr>
<th>Model</th>
<th>Predictor variable</th>
<th>Coefficient estimate</th>
<th>95% CI</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Distance</td>
<td>-0.019</td>
<td>[-0.02, -0.014]</td>
<td>0.003</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>2</td>
<td>Past visit</td>
<td>-1.21</td>
<td>[-1.87, -0.55]</td>
<td>0.33</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Distance</td>
<td>-0.018</td>
<td>[-0.025, -0.02]</td>
<td>0.003</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>3</td>
<td>Past visit</td>
<td>-1.18</td>
<td>[-1.85, -0.52]</td>
<td>0.33</td>
<td>0.004</td>
</tr>
<tr>
<td>4</td>
<td>Distance</td>
<td>-0.019</td>
<td>[-0.025, -0.013]</td>
<td>0.003</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>SleepSite</td>
<td>0.313</td>
<td>[-1.79, 2.42]</td>
<td>0.292</td>
<td>0.771</td>
</tr>
<tr>
<td></td>
<td>Distance: SleepSite</td>
<td>0.006</td>
<td>[-0.03, 0.042]</td>
<td>0.335</td>
<td>0.737</td>
</tr>
</tbody>
</table>

Table C. 2: Linear regression model estimates with inter-patch distance as the explanatory variable and number of steps that the gibbons take as the response variable.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>95% CI</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.38</td>
<td>[2.04, 2.71]</td>
<td>0.16</td>
</tr>
<tr>
<td>Distance between patches</td>
<td>0.021</td>
<td>[0.01, 0.024]</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Variable Importance

- Abundance
- Aggregation
- Strategy

%HoMSE
Fig. C.1: Variable importance derived from random forest analysis with simulated seed dispersal distances as the response variable and resource abundance, aggregation, and foraging strategy as the three predictor variables.

Fig. C.2: Random locations of the 25 sleep sites located in our simulated landscapes.
Appendix D: Figures and Tables for Chapter 4

Supplementary material

<table>
<thead>
<tr>
<th>A= 0.25</th>
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<tr>
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<td><img src="image8.png" alt="Image" /></td>
<td><img src="image9.png" alt="Image" /></td>
</tr>
</tbody>
</table>

Fig.D.1: The 9 different landscapes with variable fragmentation level (rows) and habitat amount (columns). The fragmentation level is determined by the Hurst component.
Fig.D.2: Variable importance derived from random forest analysis with long-distance seed dispersal as the response variable and habitat amount and fragmentation level as the predictor variables.
Appendix E: Figures and Tables for Chapter 5

Fig. E.1: Body mass distribution of Andean frugivorous birds (n= 170 species). The body masses are log transformed.

Fig. E.2: Percentage change in LDD when both interactions rewired or failed to rewire between extant birds and plant species. Here the largest bird from each community heavier than 300g went extinct.
Table E. 1: Coefficient estimates of GLM regressions between number of interaction partners and fruit diameter from the 10 bird-plant networks.

<table>
<thead>
<tr>
<th>Networks</th>
<th>Intercept</th>
<th>Slope</th>
<th>Lower CI (slope)</th>
<th>Upper CI (slope)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bolivia_edge</td>
<td>1.01</td>
<td>0.02</td>
<td>-0.01</td>
<td>0.05</td>
<td>0.05</td>
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<tr>
<td>Bolivia_forest</td>
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<td>-0.06</td>
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<td>0.96</td>
</tr>
<tr>
<td>Colombia1</td>
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<td>0.01</td>
<td>-0.01</td>
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<tr>
<td>Colombia2</td>
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<td>-0.09</td>
<td>-0.16</td>
<td>-0.03</td>
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</tr>
<tr>
<td>Ecuador1</td>
<td>2.42</td>
<td>-0.05</td>
<td>-0.08</td>
<td>-0.02</td>
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</tr>
<tr>
<td>Ecuador2</td>
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<td>-0.04</td>
<td>-0.09</td>
<td>0.005</td>
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<tr>
<td>Ecuador3</td>
<td>0.73</td>
<td>0.005</td>
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<td>0.07</td>
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<tr>
<td>NW_Argentina</td>
<td>1.74</td>
<td>-0.04</td>
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<td>0.01</td>
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<tr>
<td>Peru1</td>
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<td>0.001</td>
<td>-0.01</td>
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<td>Peru2</td>
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<td>-0.05</td>
<td>-0.09</td>
<td>-0.02</td>
<td>0.001</td>
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</tbody>
</table>

Table E. 2: Coefficient estimates of GLM regressions between interactions frequencies and difference between bill width and fruit diameter from the 10 bird-plant networks.

<table>
<thead>
<tr>
<th>Network</th>
<th>Intercept</th>
<th>Slope</th>
<th>Lower CI (slope)</th>
<th>Upper CI (slope)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bolivia_edge</td>
<td>-0.014</td>
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<tr>
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<tr>
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<td>0.05</td>
<td>0.04</td>
<td>0.07</td>
<td>3.95E-14</td>
</tr>
<tr>
<td>Colombia2</td>
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<td>-0.02</td>
<td>-0.04</td>
<td>-0.01</td>
<td>0.0001</td>
</tr>
<tr>
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<td>-0.16</td>
<td>-0.12</td>
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</tr>
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</tr>
<tr>
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<tr>
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<td>-0.08</td>
<td>-0.07</td>
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</tr>
<tr>
<td>Peru2</td>
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<td>-0.02</td>
<td>-0.03</td>
<td>-0.01</td>
<td>1.77E-07</td>
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</tbody>
</table>
CURRICULUM VITAE

Binod Borah

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EDUCATION

Utah State University, Logan, Utah
Ph.D. student in Biology Department and Ecology Center
Jul 2018-To date

Tata Institute for Fundamental Research, Wildlife Conservation Society-India Program & National Centre for Biological Sciences, Bangalore, India
Masters in Wildlife Biology & Conservation, Full Tuition Scholarship of $3700
Dissertation Title: Impacts of selective logging on understorey mixed-species bird flocks

National Institute of Technology, Jalandhar, India
Bachelor of Technology, Mechanical Engineering,
Jun 2005-Jun 2009

RESEARCH EXPERIENCE

Ph.D. Researcher
Jan 2019-To date
• Working on a collaborative project on two- species competitive metacommunity and employing stability analysis to investigate species coexistence
• Leading a collaborative project that incorporates animal space use in determining seed distribution in tropical forests through inverse modelling
• Working on a collaborative project investigating how frugivore mammals’ sensory perceptions and memory impact their space use pattern and ecological services such as seed dispersal

MSc Researcher
Oct 2015-May 2017
• Investigated the impacts of selective logging on mixed-species bird flocks, especially responses of interspecific associations in mixed-species flocks to logging using a network analytical framework.
• Investigated the possible drivers of these responses such as prey (arthropod) abundance through repeated sampling

PROFESSIONAL EXPERIENCE

Utah State University
Aug 2018-Dec 2018
Teaching Assistant, BIOL 1615
• Instructed three sections of undergraduate students on project development, synthesis of results and writing scientific reports involving in class experiments

Guest Lecturer, IELI 2310
Oct 2018
• Presented basic concepts of ecology to a class of international students

Guest Lecturer, BIOL 3200
Mar 2019
• Taught advanced ecological concepts such as plant-animal interactions

Eaglenest Wildlife Sanctuary
Oct 2016-Mar 2018
Independent Consultant, Arunachal Pradesh, India.
• Provided consultation to local management authority in drafting the decadal management plan. Ensure goals set forth in the plan are optimal and scientifically robust for the conservation of the sanctuary and its rich biodiversity
• Spearheaded conservation outreach campaign for the local communities

**Forest Landscape Restoration Program, International Union for Conservation of Nature, India Intern**
Jun 2017-Oct 2018

• Assimilated information from multiple partners and draft report for policy makers

**Nature Conservation Foundation Research Assistant, Mysore, India**
Jan 2014-Jun 2014

• Conducted field work and analyze data estimating distribution of five sympatric species of hornbills in North-East India using occupancy sampling

• Organized conservation themed workshops at numerous schools

**Wildlife Conservation Society- India Program Research Assistant, Bangalore, India**
Jan 2013-Dec 2013

• Conducted field work and analyze data for distribution and population estimation of tigers and their prey using distance sampling, occupancy sampling and capture-recapture sampling

**GRANTS**

**World Wildlife Fund-India, Small grant program**
Jun 2016-Jun 2017

• Received $3500 for research into the impacts of selective logging on mixed-species bird flocks

**MacMohan Research Award**

• Received $1000 as student scholarship from the Biology Department, Utah State University  Mar 2019

**JOURNAL ARTICLES**


Borah, Binod, Velho, Nandini and Srinivasan, Umesh “A socio-economic survey of the newly constituted Singchung Bugun Village Community Reserve, Arunachal Pradeh, India” *Current Science*, 2020

Borah, Binod, Beckman, Noelle “Studying seed dispersal through the lens of movement ecology”, Oikos, 2021

Borah, Binod, Beckman, Noelle “Bird movement in agricultural landscape are mediated by their traits” (in review)

Borah, Binod, Beckman, Noelle “Linking the environmental drivers and functions of seed dispersers’ movement in a tropical forest” (in prep)

Borah, Binod, Beckman, Noelle “Seed dispersers foraging decisions and movement impact seed dispersal patterns” (in prep)

Borah, Binod, Beckman, Noelle “Defaunation of large birds have stronger impacts on long-distance dispersal of large-fruited plants” (in prep)
PROFESSIONAL SERVICES
• Biology Graduate Students Association at Utah State University: Vice President
• College of Science Graduate Students Council at Utah State University: Graduate representative
• Biology department seminar committee at Utah State University: Student representative

MENTORSHIP
• Justin Tirell- undergraduate researcher, Biology department, Utah State University
• Camilla Moses- undergraduate researcher, Biology department, Utah State University
• Shaleena Phinya- Green hub fellow, India

REFERENCES
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