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Movement Ecology of Frugivores and Spatial Patterns of Seed Dispersal in a Cameroon Rainforest

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

Doctor of Philosophy in Biology

by

Nicholas Joseph Russo

2024

ABSTRACT OF THE DISSERTATION

Movement Ecology of Frugivores and Spatial Patterns of Seed Dispersal in a Cameroon Rainforest

by

Nicholas Joseph Russo
Doctor of Philosophy in Biology
University of California, Los Angeles, 2024
Professor Thomas Bates Smith, Chair

Tropical rainforests are among the most structurally complex environments on earth. In these ecosystems, animals disperse the seeds of up to 90% of tree species, a process that influences vegetation structure in turn. In this dissertation, I use animal tracking and remote sensing to reveal elements of a feedback loop between 3D rainforest structure and movements of seed-dispersing birds and bats in southern Cameroon.

In Chapter 1, I synthesize current research in a literature review that describes the feedback between vegetation structure and animal ecological roles. This chapter provides a worked example for applying the feedback loop concept to conservation problems.

In Chapter 2, I assess how 3D rainforest structure can shape seed dispersal patterns by influencing movements and habitat selection of black-casqued (*Ceratogymna atrata*) and white-thighed hornbills (*Bycanistes albotibialis*). The seed dispersal model in this chapter incorporates hornbill selection for canopy height, vertical complexity, and distance to canopy gaps in a framework that maps spatial probabilities of seed dispersal. In addition, the results show that white-thighed hornbills tend to avoid swamp habitats, while black-casqued increase their preference for swamps during the hottest temperatures—a key niche difference between the species.

In Chapter 3, I use recent advances in spaceborne remote sensing to show how 3D vegetation structure influences hammer-headed bat (*Hypsignathus monstrosus*) habitat selection over their full movement trajectories. Hammer-headed bats prefer swamp habitats, intermediate canopy height, and areas closer to canopy gaps.

Chapter 4 combines approaches from Chapters 2 and 3 to show how seed dispersal patterns by hornbills arise from diversity in both movement behavior and landscape-scale habitat selection. Black-casqued and white-thighed hornbills clustered into three “movement syndromes” based on variation in movement distances and home range size. Seed dispersal models involving hornbills from all three movement syndromes yielded the greatest diversity in both distances and directions of seed dispersal routes.

The results of this dissertation show the importance of movement behavioral diversity for seed dispersal and provide further evidence for a feedback loop between vegetation structure and animal ecological roles.

The dissertation of Nicholas Joseph Russo is approved.

Noa Pinter-Wollman

Nathan Jared Boardman Kraft

Thomas Welch Gillespie

Thomas Bates Smith, Committee Chair

University of California, Los Angeles

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Author contributions:

NJR, AF, NB, MW, EMO, SS, and TBS conceived the ideas and designed methodology; NJR, DLN, and NB collected the data; NJR and MN analyzed the data, NJR wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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When I reflect on the years of work that went into this dissertation, I think of the valuable mentorship I received from my advisor, Tom Smith. His “Tom-isms” guided me through six years of ambitious pursuits: Be tenacious; be a squeaky wheel. I thank Tom for his relentless optimism and big-picture thinking, which inspired me every day to become a thoughtful and persistent scientist.

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Russo, N.J., C.A.S.-J. Cheah, and M.W. Tingley. 2016. Experimental evidence for branch-to-bird transfer as a mechanism for avian dispersal of the hemlock woolly adelgid (Hemiptera: Adelgidae). *Environmental Entomology* 45:1107-1114.

SELECTED PRESENTATIONS

Ecological Society of America Meeting, Long Beach, CA, USA. 2024. *It takes a hornbill to build a village: Seed dispersal in a changing Afrotropical landscape.* Oral presentation using NASA Hyperwall.

Ecological Society of America Meeting, Long Beach, CA, USA. 2024. *Effects of 3D canopy structure on seed dispersal by hornbills in Cameroon.* Poster presentation.

Wilson Ornithological Society Meeting, Peoria, IL, USA. 2024. *Three-dimensional vegetation structure drives patterns of seed dispersal by African hornbills.* Oral presentation.

NASA Biological Diversity and Ecological Conservation Meeting, Silver Spring, MD, USA. 2024. *Understanding seed dispersers' movements and their consequences across rainforest gradients of structural and phenological diversity.* Oral presentation.

American Geophysical Union Meeting, Chicago, IL, USA. 2022. *Effects of 3D canopy structure on seed dispersal by hornbills in Cameroon.* Oral presentation.

Internet of Animals Symposium, Yale University, New Haven, CT, USA. 2022. *Movements of Congo Basin seed dispersers in relation to vegetation structure, phenology, and forest degradation.* Poster presentation.

Wilson Ornithological Society Meeting, Remote. 2021. *Movement ecology of hornbills and spatial patterns of seed dispersal in Cameroon*. Oral presentation.

Yale-Myers Forest Summer Seminar Series: Eastford, CT, USA. 2017. *Spring bird migration as a dispersal mechanism for an invasive insect pest.* Oral presentation.

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CHAPTER 1

Feedback loops between 3D vegetation structure and ecological functions of animals

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ABSTRACT

Ecosystems function in a series of feedback loops that can change or maintain vegetation structure. Vegetation structure influences the ecological niche space available to animals, shaping many aspects of behavior and reproduction. In turn, animals perform ecological functions that shape vegetation structure. However, most studies concerning three-dimensional vegetation structure and animal ecology consider only a single direction of this relationship. Here, we review these separate lines of research and integrate them into a unified concept that describes a feedback mechanism. We also show how remote sensing and animal tracking technologies are now available at the global scale to describe feedback loops and their consequences for ecosystem functioning. An improved understanding of how animals interact with vegetation structure in feedback loops is needed to conserve ecosystems that face major disruptions in response to climate and land use change.

INTRODUCTION

Global climate change and biodiversity loss have highlighted the need to understand how ecosystems function. Ecosystem functioning is largely driven by feedback loops between biotic and abiotic components, in which plants and animals influence each other and their environment in ways that change or sustain ecosystems (Schmitz 2010; Schmitz *et al.* 2018). Feedback processes have been documented in a variety of ecosystems. For example, tropical rainforests can be self-reinforcing in that evapotranspiration from vegetation forms clouds that lead to heavy rain, thus reinforcing the climate necessary for rainforests to persist (Wu *et al.* 2013; Zhu *et al.* 2023). Severe plant water stress of sufficient frequency and duration has the potential to disrupt this feedback and transform tropical rainforests to savanna-like ecosystems (Saatchi *et al.* 2021). How ecosystems persist or change can therefore depend on feedback loops among ecosystem functions.

Vegetation structure, defined here as the distribution of leaves, stems, and branches in three-dimensional (3D) space, including height, cover, and vertical and horizontal complexity (Valbuena *et al.* 2020), is an essential component of ecosystems that influences animal diversity and behavior (MacArthur & MacArthur 1961; Zellweger *et al.* 2013; Burns *et al.* 2020). Vegetation structure affects the distribution of microclimate refugia for animals (Scheffers *et al.* 2017), energetic costs of movement (McLean *et al.* 2016; Davies *et al.* 2017), spatial distribution of predation risk (Yovovich *et al.* 2021), and availability of preferred nest sites (Swift *et al.* 2017; Davies *et al.* 2019). In these ways, vegetation structure influences how and where animals move to find resources (Wittemyer *et al.*, 2019). In turn, vegetation structure itself is modified by animals, which can browse and trample vegetation, disperse seeds, and redistribute nutrients necessary for plant growth (Doughty *et al.* 2016a; Berzaghi *et al.* 2018; Davies *et al.* 2018). In terrestrial ecosystems, a feedback loop forms whereby vegetation structure influences the behaviors of animals, whose ecological functions, in turn, shape vegetation structure. Research typically investigates one or the other of these relationships without integrating them into a framework that describes the feedback explicitly.

Ecological functions of animals are often recognized in conservation strategies for their ability to sustain ecosystems or restore them to an earlier state of structure and functioning (Enquist *et al.* 2020; Malhi *et al.* 2022; Gordon *et al.* 2023). Some conservation strategies have benefited from acknowledging components of a feedback loop between vegetation structure and animal ecological roles, such as how landscapes can change after reintroducing animals (Gordon *et al.* 2023). Tools and methods now exist to describe animal-vegetation feedback loops and their importance for ecosystem functioning, with broad applications for conservation. Remote sensing has become central to research on animal-vegetation structure interactions, especially Light Detection and Ranging (lidar), which characterizes 3D landscape structure at local and global scales (Davies & Asner 2014; Dubayah *et al.* 2020). Similar advances in animal tracking, biologging, and big data processing (Ripperger *et al.* 2020; Jetz *et al.* 2022) will enable widespread evaluation of how animals respond to and shape vegetation structure.

Describing feedback loops between vegetation structure and animal ecological roles may reveal important aspects of ecosystem function as climate change, land use change, and other stressors threaten ecosystem productivity and stability. The primary goal of this review is to investigate the lines of research that form feedback loop components and synthesize results to describe such feedback loops in detail (**Fig. 1.1**). Because an animal-vegetation feedback loop will consist of different components and processes across ecosystems, a secondary goal is to review methods that can be used to better describe feedback loops in ecosystems and their potential applications. We first describe the essential functions of vegetation structure for habitat selection, movement, and other behaviors of animals, with a focus on terrestrial vertebrates. Next, we provide examples of how animals modify vegetation structure, both directly and indirectly. Drawing on remote sensing and animal tracking research, we then describe ways to measure the components of an animal-vegetation feedback loop and draw inferences. Finally, we discuss human impacts on animal-vegetation feedback loops and how using the feedback concept could improve conservation strategies. We conclude by outlining topics in need of further research to improve understanding of how animals interact with vegetation structure to shape and sustain terrestrial ecosystems.

HOW VEGETATION STRUCTURE INFLUENCES ANIMAL BEHAVIOR

The 3D structure of vegetation forms a major component of ecological niche space that species occupy and has led to important adaptations in animal behavior. Ecoregions with diverse vegetation structure broaden the diversity of movement strategies that are possible for animals to use, especially among arboreal lineages (Scheffers *et al.* 2017). Structural diversity also promotes functional diversity by increasing trophic niche space, (Pawar *et al.* 2012; Xing *et al.* 2023), a key factor driving variation in morphological form and ecological function (Pigot *et al.* 2020). Moreover, structural complexity of vegetation indicates potential risks and resource availability, albeit in environments where the cognitive load of memorizing the 3D environment is not too high (Fagan *et al.* 2013). The ways that vegetation structure influences animal behavior give rise to its ecological value for animals.

Vegetation structural attributes can influence habitat quality and the distribution of resources for animals (**Table 1.1**). Animals must weigh the benefits of accessing resources, such as prey or nesting sites, with the risks and energetic costs of moving towards them—a central tenet of Optimal Foraging Theory (MacArthur & Pianka 1966; Abrahms *et al.* 2021). Vegetation can decrease the energetic costs of movement by providing a substrate or increase them by cluttering movement paths. Monkeys and other arboreal animals move along canopy paths with high lateral connectivity, an attribute of 3D vegetation structure that aids in running, jumping, and brachiation (McLean *et al.* 2016). Aerial insectivores, however, often rely on open airspace to forage, and their movements may be hindered by vegetation (Sleep & Brigham 2003). Most research on animal movements in relation to 3D vegetation structure focuses on movement paths (McLean *et al.* 2016; Casalegno *et al.* 2017; Davies *et al.* 2017), but vegetation structure plays many functional roles that give rise to these movement behaviors.

Vegetation can provide shading for animals and create heterogeneity in microclimate within ecosystems. For example, moose seek taller and denser vegetation to avoid high summer temperatures (Melin *et al.* 2014), and arboreal animals track their thermal niche by moving vertically through vegetation, often seeking out tree cavities or denser vegetation during the hottest hours of the day (Scheffers *et al.* 2017; Scheffers & Williams 2018). Microclimates vary by ecosystem type, with open woodlands yielding greater diurnal variation in temperature and tall, closed canopy forests reducing temperature extremes below the canopy (Jucker *et al.* 2018; De Frenne *et al.* 2019, 2021; Vinod *et al.* 2023). Canopy gap openings (e.g., from treefall or crown damage) create additional variation in microclimates across time (Sprugel *et al.*, 2009; De Frenne *et al.*, 2021). Characterizing thermal variation in landscapes can lend insight into how 3D vegetation structure helps animals thermoregulate, especially as climate change necessitates adaptation or movement towards habitats with suitable microclimates (Davis *et al.* 2019; Zellweger *et al.* 2019).

As animals balance the energetic and thermal costs of foraging, they must also consider predation risk. An animal's perceived risk is limited partly by its field of view, or viewshed, which is reduced in areas of high vegetation density (Aben *et al.* 2018). For example, lions (*Panthera leo*) make more kills in dense vegetation, allowing them to approach their prey more stealthily (Davies *et al.* 2016c). In response, African herbivores, on which lion prey, have been shown to flee from predator vocalizations more frequently in dense vegetation than in open habitats (Epperly *et al.* 2021). However, dense vegetation can also conceal prey. This function is vital for life stages more vulnerable to predation, such as juveniles who move to or are shepherded by parents to areas with greater protective vegetation cover (Davies *et al.* 2016b; Stillman *et al.* 2019). Whether vegetation cover lends an advantage to predator or prey may therefore depend on the hunting mode of the predator and defense mechanisms of the prey. Animal behavioral traits, such as ambush versus cursorial predation and running escape versus hiding, influence how risk and reward are perceived in the context of a habitat's vegetation structure (Davies *et al.* 2021).

The risks and rewards of animal reproduction are linked to all facets of habitat quality. Successful reproduction for animal pairs requires some combination of courtship, mating, defending territory, and rearing offspring. Vegetation structure can modulate behaviors of breeding individuals, such as by increasing conspicuousness of displaying males (Morales *et al.* 2008; Biagolini-Jr *et al.* 2021) or sheltering females (Morales *et al.* 2008) and indicating territory quality (Broughton *et al.* 2006). For cavity-excavating birds such as woodpeckers, breeding success depends on the availability of standing deadwood. Canopy height and heterogeneity metrics can indicate the distribution of this critical resource for reproducing birds, mammals, and insects (Martinuzzi *et al.* 2009; Carrasco *et al.* 2014; Stitt *et al.* 2021, 2022). In addition, insight from animal habitat selection can help identify minimum ecological requirements for population persistence, such as features of 3D vegetation structure necessary for survival and reproduction (Davies *et al.* 2017; Deere *et al.* 2020). Such thresholds in habitat selection related to vegetation structural metrics could help explain population declines and subsequent decreases in the ecological functions of animals.

HOW ANIMALS SHAPE VEGETATION STRUCTURE

Direct effects

Animals can shape vegetation structure directly through their behaviors (**Table 1.2**). Perhaps the most dramatic examples come from ecosystem engineers, which modify entire ecosystems. The sheer size of an animal can lead it to exert a substantial impact on vegetation structure due to its strength and metabolic needs (Enquist *et al.* 2020)—Asian elephants (*Elephas maximus*), for example, require 150 kg of vegetation per day, removing large swaths of vegetation as they browse (Vancuylenberg 1977). The loss of prominent ecosystem engineers is thought to account for significant differences in vegetation structure and composition between African and Neotropical humid forests (Doughty *et al.* 2016b). The outsized impact of ecosystem engineers can also facilitate behaviors of other animal species that further shape vegetation structure. Beavers (Castoridae), for example, cut down trees to dam riparian areas in temperate and boreal forests, consequently flooding surrounding forests and creating standing deadwood, or snags, that attract cavity excavators such as woodpeckers and benefit a variety of cavity-nesting species (Cockle *et al.* 2011; Brazier *et al.* 2021). While many effects of ecosystem engineers have lasting impacts on 3D vegetation structure, other effects may be more ephemeral, such as collapsing branches or removing leaves **(Fig. 1.2)**. Trampling of vegetation by large herbivores in forests creates well-worn paths that are used repeatedly. These “stigmergic paths” are used by a variety of animals and likely reduce the energetic costs of movement (Berdahl *et al.* 2018). The intensity of animal behaviors such as herbivory and trampling can dictate whether they have lasting impacts on vegetation structure (Geremia *et al.* 2019).

Indirect effects

While the direct effects of herbivory and ecosystem engineering by animals are readily visible in landscapes, animal-driven changes to 3D vegetation structure also arise from the indirect effects of actions that influence plant species composition, such as seed dispersal. Seed dispersal lays the template for 3D vegetation structure by influencing the floristic species composition of landscapes (Nathan & Muller-Landau 2000). Without seed arrival, there can be no woody plants. Seed-dispersers have been shown to impact the distribution of aboveground biomass and carbon storage in landscapes through models that simulate their extirpation (Bello *et al.* 2015; Osuri *et al.* 2016), but their impact on 3D vegetation structure through seed dispersal has not been explored empirically. Animals move with respect to vegetation structure for reasons outlined in the previous section, and about 50% of all plants rely on animals to disperse their seeds (Fricke *et al.* 2022). Controlled experiments or simulations that use standardized metrics of 3D vegetation structure (Valbuena *et al.* 2020) could reveal effects of this widespread ecosystem service on vegetation structure.

Animals also promote plant growth and shape plant species composition by distributing nutrients (Bauer & Hoye 2014). Nutrient transport by animals often occurs through the distribution of excreta, egesta, or carcasses (Bump *et al.* 2009; Doughty *et al.* 2016a; Ellis-Soto *et al.* 2021), and can serve as a critical link between aquatic and terrestrial ecosystems. Animal behaviors that alter the distribution of water and nutrients in nutrient-scarce environments can have a strong effect on plant communities. In African savannas, termite mounds create focal areas of soil that are rich in water and nutrients, enabling the growth of riparian tree species in drier habitats away from rivers (Davies *et al.* 2016a). Animals also modulate nutrient cycles in ecosystems through behaviors such as foraging and trampling soil (Schmitz *et al.* 2018). Carbon, nitrogen, phosphorus, and other nutrients released into the soil by live or dead animals can modulate primary production by plants (Schmitz *et al.* 2018), with potential cascading effects on vegetation structure.

Some animals play multiple roles in shaping vegetation structure. For example, African forest elephants (*Loxodonta cyclotis*) are both herbivores and seed dispersers, although they usually avoid browsing late-successional, slow-growing trees, which are unpalatable due to large amounts of defense compounds used to deter herbivory (Poorter & Bongers 2006). If these slow-growing saplings reach maturity, however, many will provide fruits for elephants. Elephants then sow the seeds of these late-successional trees in their nutrient-rich dung (Campos-Arceiz & Blake 2011; Berzaghi *et al.* 2019). In some cases, an animal species' ecological roles can have counteracting effects on vegetation structure. For example, seed-caching rodents limit seedling recruitment by predating on seeds but may also facilitate recruitment if seeds are left to germinate within their caches. Instances of seed predators neglecting their caches—by death or otherwise—are thought to allow large-seeded tree species to persist in the absence of seed dispersal by larger animals (Hirsch *et al.* 2012; Jansen *et al.* 2012). This interaction will need to be incorporated into models that predict changes in vegetation structure due to the loss of large frugivores that disperse the same trees (Gómez *et al.* 2019).

Predators also modulate vegetation structure indirectly by regulating population size and behaviors of herbivores. This effect has been detected in a variety of ecosystems, often following the loss or reintroduction of a key predator that changes herbivore foraging pressure (Beschta *et al.* 2018; Leo *et al.* 2019). Apart from the top-down effects of predation on vegetation structure, the very presence of predators imposes a “landscape of fear” response from prey, which alters their behavior to avoid predation risk. For example, pumas (*Puma concolor*) in California, U.S.A., kill deer away from human settlements, thereby creating refugia for deer near humans. In response, deer in human-dominated landscapes quadrupled their vegetation consumption (Yovovich *et al.* 2021).

Interactions between animals and abiotic and plant processes that shape vegetation structure

While animals play a pivotal role in shaping vegetation structure in many ecosystems, broader-scale patterns in vegetation structure are constrained by additional factors, such as climate, fire, soil, and plant competition. Moreover, vegetation structure is shaped by plant growth patterns adapted for sunlight capture, so that narrower, more conical trees are more abundant in temperate and boreal forests. In contrast, deeper and wider crowns are more common in tropical forests where sunlight is directly overhead year-round (Terborgh 1985). Crown architecture has important implications for dispersal mode—taller trees with small crown diameters are more conducive to wind dispersal, whereas trees with large, spreading crowns are more conducive to drop- or animal dispersal (Panzou *et al.* 2020). Accordingly, animals disperse an estimated 60-90% of trees in tropical rainforests, whereas wind is the dominant dispersal mechanism in most temperate and boreal forests (Howe & Smallwood 1982; Jordano 2013; Rogers *et al.* 2021). Animals are therefore expected to have an outsized impact on tropical tree composition—and hence vegetation structure—relative to wind. Asian tropical forests are a notable exception, however, because many are dominated by wind-dispersed Dipterocarps (Osuri *et al.* 2016). Still, the stature of Asian tropical forests is hypothesized to be driven by tall individuals in a diverse group of families, including those dispersed by animals (Banin *et al.* 2012).

Quantifying the relative role of animals in shaping vegetation structure will require reliable measurements of additional factors whose intensity varies by ecosystem type. Fire, for example, plays a dominant role in many dry ecosystems by transforming vegetation structure and releasing nutrients into the soil (Levick *et al.* 2009). Animals can influence fire regimes by modifying the amount, structure, and condition of fuels in the landscape (Holdo *et al.* 2009; Foster *et al.* 2020). Megaherbivores (>1000 kg) such as white rhinoceros (*Ceratotherium simum*) create grazing lawns of short grass that influence the behaviors of other grazers and lead to smaller, more heterogeneous fires (Waldram *et al.* 2008). African forest elephants browse paths along forest edges that limit wildfire spread (Cardoso *et al.* 2020). Capturing the complex interactions among plants, vegetation structure, and additional factors in a feedback loop will require drawing information from a variety of sources.

CHARACTERIZING FEEDBACK LOOPS BETWEEN ANIMALS AND VEGETATION

Considering vegetation structure and animal ecological roles in a feedback loop can increase understanding of processes that influence ecosystem functioning. Feedback in ecosystems can induce change or be self-reinforcing (**Fig. 1.3).** For example, outbreaks of spruce budworm in boreal forests defoliate spruce stands, thereby allowing broadleaf trees to establish under increased light conditions. These saplings are preferred by moose, whose browsing pressure transforms communities back to being spruce-dominant (Leroux *et al.* 2020). Feedbacks that maintain structure are more difficult to detect and may be evidenced by a perturbation or the loss of a species. Carnivores, for example, can control herbivore populations, which helps maintain vegetation structural diversity. This role often only becomes apparent after carnivores are extirpated from a system (Gable *et al.* 2020; Hoeks *et al.* 2020; Yovovich *et al.* 2021). Change-inducing feedback loops resulting from the functional extinction of animals can have important implications for carbon storage, nutrient cycling, and biodiversity. Still, they may not be detected for tens to hundreds of years, especially within forested environments, due to the slow growth of trees (Poulsen *et al.* 2013; Osuri *et al.* 2016; Peres *et al.* 2016; Berzaghi *et al.* 2019). Determining the timescale over which a feedback loop operates may present unique challenges. However, the processes that form a feedback loop may already be described for an ecosystem and simply need to be integrated into a framework that links them together (Borer *et al.,* 2021).

Testing for causal relationships

A feedback loop between animals and vegetation is circular in nature and demands an answer to a fundamental question: what evidence is needed to show that an animal species influences vegetation structure, and does not simply choose habitats with favorable structure? Addressing this and other outstanding questions requires appropriate experimental or statistical controls. Large-scale, long-term manipulation or natural experiments are often necessary to establish the direction of effects between animal behaviors and vegetation structure. For example, herbivory by elephants was confirmed as a critical driver of vegetation structure after comparing areas accessible and exclusionary to elephants for more than 60 years in South Africa (Davies *et al.* 2018). When *in situ* experiments are not feasible, however, computer simulations can predict changes in vegetation structure resulting from the functional extinction of animals that impact vegetation structure. Simulation approaches have shown that the loss of large frugivores in tropical forests leads to reduced seed dispersal and long-term losses in forest biomass and carbon storage (Bello *et al.* 2015; Osuri *et al.* 2016). The processes that influence 3D vegetation structure often do not occur independently, but this problem can be overcome by modeling interrelated factors through an analysis that identifies causal relationships. Structural equation models have proven useful in this regard because they allow researchers to hold statistical variables constant while modeling hypothesized cause-and-effect relationships and to then quantify the magnitude of effects in ecosystem processes with several components (Morante-Filho *et al.* 2018; Bernardi *et al.* 2019).

Identifying causal relationships in animal-vegetation feedback loops is critical for modeling tipping points that induce ecosystem change. Alternative ecosystem states are possible when an environment is climatically suitable for more than one ecosystem type (Staver *et al.* 2011). While climate change, fire, and land use change can accelerate changes to alternative ecosystem states (Saatchi *et al.* 2021), the influence of animal-driven processes on the frequency of such changes needs further investigation. Ecosystem functioning is driven partly by productivity, stability, vulnerability to invasive species, nutrient dynamics, and feedback among these components (Tilman *et al.* 2014). Interactions between animals and their physical environment can bolster these functions by providing biotic resistance to invasive species (Boelman *et al.* 2007) or other agents of environmental change, thereby preventing ecosystem degradation and widespread changes to alternative ecosystem states.

Using remote sensing to uncover animal-vegetation structure relationships

A variety of data types are needed to describe feedback between animals and vegetation, and especially its effects on ecosystems. Remote sensing data are particularly useful because they allow researchers to quantify vegetation structure over broader landscapes than field data and with high three-dimensional detail. Many remote sensing techniques exist to measure vegetation structural attributes that influence or are influenced by animal behavior (**Fig. 1.4**). Lidar sensors mounted on aircraft or spacecraft can measure attributes of 3D vegetation structure such as vegetation height, fractional vegetation cover, and canopy complexity, and over scales relevant to habitat selection by wide-ranging animals (e.g., Davies & Asner 2014; McLean *et al.* 2016; Davies *et al.* 2017; Evans *et al.* 2020; Valbuena *et al.* 2020). While these metrics are often based on specific hypotheses of how vegetation structure influences animal behavior, the 3D nature of lidar point clouds can also be preserved in a principal component analysis to show which aspects of 3D structure and heterogeneity are important to animals (Ciuti *et al.* 2018). Finer-scale interactions between animals and vegetation structure can be described using data from drone-mounted lidar or Terrestrial Laser Scanning (TLS), a lidar mounted on a tripod that scans vegetation below the canopy (Blakey *et al.* 2017; Orwig *et al.* 2018). For example, lidar data acquired both above- and below-canopy are useful for quantifying how vegetation structure can aid or impede an animal’s line of sight, and therefore its ability to detect predators (Davies *et al.* 2016c, 2021; Aben *et al.* 2018). Lidar data are becoming more common for a variety of ecosystem types, but multiple lidar acquisitions per year are still rare. Such data can reveal how animal behaviors shape vegetation structure over time, and how animals shift their behavior in landscapes where vegetation structure changes seasonally.

Airborne lidar can help reveal drivers of animal behaviors that operate at a scale of several thousand hectares or less, but many phenomena are observable at an ecoregion or global scale. Animal migrations between continents, for example, would require acquisitions of 3D landscape structure data beyond reasonable operation of airborne lidar. Currently, there is no wall-to-wall global lidar product with regular collections. Therefore, other types of remote sensing data and analytical techniques may be necessary to overcome these limitations. Spaceborne lidar data are freely available for most temperate and tropical ecosystems through the Global Ecosystem Dynamics Investigation (GEDI) mission. While GEDI is contributing to important research in ecology and biodiversity, its spatial sampling regime (25 m diameter shots spaced 60 m apart) leaves gaps in spatial coverage. Machine learning can overcome this problem by fusing data from multiple sources to predict missing values of 3D structural attributes (Qi *et al.* 2019; Rishmawi *et al.* 2021). One approach used simulated data from GEDI and another satellite lidar aboard the Ice, Cloud, and land Elevation Satellite (ICESAT-2), and Synthetic Aperture Radar data to improve estimates of aboveground biomass compared to any sensor alone (Silva *et al.* 2021). ICESAT-2 is a spaceborne lidar that measures vegetation height and structure globally, but unlike GEDI, cannot penetrate dense canopies (Silva *et al.* 2021). Data from this sensor will be especially important for measuring vegetation structure over large scales in polar regions. Synthetic Aperture Radar (SAR) uses backscatter intensity to measure heterogeneity in habitat structure and is often used to map aboveground biomass (Mitchard *et al.* 2009). Unlike lidar, SAR is not limited by cloud cover, which makes it useful for interpolating vegetation structural metrics where gaps occur in lidar coverage in persistently clouded areas. The National

Aeronautics and Space Administration-Indian Space Research Organization SAR (NISAR) is planned to begin collecting L-band SAR data in 2023, providing global coverage of SAR data powerful enough to measure aboveground biomass from ground to canopy (Rosen *et al.* 2015). In addition, the Earth Explorer-7 Biomass mission is a P-band SAR that is expected to penetrate dense canopies well and contribute to understanding of 3D vegetation structure (Ustin & Middleton 2021).

Because airborne lidar scanners can be expensive to operate within a target ecosystem, techniques using optical data to map 3D vegetation structure can sometimes be a substitute. Structure from Motion (SfM) photogrammetry, a technique that maps 3D ecosystem structure from a patchwork of optical photographs collected using a drone, has proven useful in ecosystems with few woody plants, such as deserts, grasslands, and shrublands (Cunliffe *et al.* 2016; Forsmoo *et al.* 2018). In one study, SfM provided structural details for a savanna where an olive baboon troop was GPS-tracked at high spatiotemporal resolution, helping to show short-term attraction and repulsion to dense vegetation, roads, and other features of the landscape (Strandburg-Peshkin *et al.* 2017). Recent advances in commercial, high-resolution imagery can serve a similar purpose by providing textural details that correspond to canopy height (Csillik *et al.* 2020). Ultimately, the choice of remote sensing technique for characterizing animal-vegetation feedback loops will depend on budget and the spatial and temporal scales most appropriate for relating 3D vegetation structure to animal behavior.

Measuring animal movement and behavior

Recent advances in animal tracking promise to expand the possibilities for quantifying interactions between animals and 3D vegetation structure. Animals as small as 100 g can now be tracked over their lifetimes with solar-powered GPS tags (Jetz *et al.* 2022). Tracking the 3D movements of animals will be important for understanding the role of vegetation structure in shaping animal behavior. While animals moving through airspace have been tracked in 3D using tags that measure changes in air pressure and temperature (Shipley *et al.* 2017; Dreelin *et al.* 2018), 3D tracking has not typically been employed for animals moving primarily through vegetation (Belant *et al.* 2019; Hermans *et al.* 2023). The use of 2D tracking data to infer habitat selection or ecological functioning of animals is limited because animals often move through 3D space created by vegetation (Gámez & Harris 2022). Further developments in 3D tracking technology would enhance understanding of many topics discussed here.

Analyzing animal tracking data is equally important for understanding animal-vegetation feedback. The family of Habitat Selection Analyses (HSA) are often used to understand how animals move in relation to 3D vegetation structure (McLean *et al.* 2016; Davies *et al.* 2017; Zeller *et al.* 2017; Northrup *et al.* 2022). This approach compares animal positions, movement steps, or full movement paths to randomly generated options considered as available habitat. Recent advances have shown how HSAs can be used to generate predictions about animal movements and habitat selection (Potts *et al.* 2022). This application of HSAs is a promising avenue for inferring ecological functions from GPS data. Population-level estimates are often drawn from HSAs, but the importance of individual variation in movement behavior has increasingly been recognized as a key factor in ecological functions of animals (Shaw 2020). Individual personalities (e.g. boldness, exploratory behavior) can lead to different foraging patterns, space use, and reproductive behavior, all of which can influence their role in shaping vegetation structure (Spiegel *et al.* 2017; Stuber *et al.* 2022). Individuals may differ in home range size and the diversity of behaviors they exhibit. Home range, or the space animals use to survive and reproduce, is a useful and widely available metric that can help show how animals interact with vegetation structure through space and time (Jaap *et al.* 2023). The development of Continuous Time Movement Models has increased the reliability of home range estimates and other characteristics of movement behavior by reducing sensitivity of estimates to sampling regime and treating movement as a continuous process (Calabrese *et al.* 2016; Noonan *et al.* 2019). Through an individual movement track, it is also possible to identify a behavioral "syndrome," such as whether the individual is a central-place forager, nomadic, or migratory (Abrahms *et al.* 2017) and therefore how site fidelity relates to ecological function. The diversity of movement strategies within an animal population is an interesting area of further research with implications for how communities assemble and ecosystems function (Costa-Pereira *et al.* 2022).

Although GPS locations in themselves cannot capture many important aspects of animal behavior that might affect vegetation structure, machine learning can be used to infer behavioral states such as foraging or dispersing based on observed distributions of step lengths and turning angles, and where available, body orientation and acceleration. (Nathan *et al.* 2012; Torney *et al.* 2021; Yu *et al.* 2021). Hidden Markov Models, for example, estimate unobserved behavioral states using common metrics from GPS or accelerometer data (McClintock *et al.* 2020; Klarevas-Irby *et al.* 2021). Continuing to improve analysis methods for animal telemetry data will be important for quantifying the importance of vegetation structure for animal behavior, and how these behaviors in turn shape vegetation structure.

HUMAN IMPACTS THAT ALTER FEEDBACK LOOPS

Human disturbance alters or disrupts feedbacks between vegetation structure and animals by modifying vegetation structure directly and by influencing animal behavior (**Fig. 1.1**). Landscape modification by people is a primary source of change in vegetation structure, often with long-lasting effects (Lenoir *et al.* 2022). Direct human disturbance encompasses both human footprint and human presence; the former describes the transformation of landscapes through urbanization, natural resource extraction, agriculture, and hunting, whereas the latter describes how humans influence animal behavior simply by sharing space (Nickel *et al.* 2020). Both classes of human disturbance have been shown to impact the movement behavior of a variety of animal taxa, with activities such as recreation and hunting imposing the most substantial effects (Doherty *et al.* 2021). Animals either reduce their range in response to shrinking habitats (Tucker *et al.* 2018a; Hirt *et al.* 2021) or move long distances to find suitable habitats in disturbed landscapes (Doherty *et al.* 2021). Such effects on animal movements alter patterns of nutrient transport, seed dispersal, and other ecosystem services that maintain and regenerate vegetation (Bauer & Hoye 2014). While humans in many contexts have hunted wildlife sustainably for millennia, overhunting in fragmented landscapes has significant effects on animal populations and behaviors, and diminishes ecosystem services. For example, in seed dispersal networks of tropical forests, the largest frugivores are most at risk of being hunted by humans, yet they disperse the greatest proportion of large-seeded trees, which typically grow to the greatest sizes. Reduced recruitment of large trees not only disrupts interactions with the animals that depend on and disperse them, but can also initiate long-term consequences for regional and global climate because these trees hold the greatest capacity for carbon storage (Peres *et al.* 2016; Enquist *et al.* 2020; Rogers *et al.* 2021). The fruits of these trees may also balance the diets and economy of local people that ensure seed dispersal and cultivation (Van Zonneveld *et al.* 2018).

Downstream effects of human alterations to landscapes, such as climate change and wildfires, also significantly alter feedbacks between vegetation structure and ecosystem function. Fire-adapted and fire-naïve ecosystems alike are burning hotter, more extensively, and more frequently due to prolonged droughts and changes in human land use and management (Nimmo *et al.* 2021). These changes in fire regimes limit the ability of vegetation to recover and wildlife to recolonize habitats (Kelly *et al.* 2020), thereby disrupting feedback. Many animal species benefit from early successional habitat maintained by regular fires, but if fires are too frequent, characteristic plant species will not have time to mature and provision these species with food or shelter (Kelly *et al.* 2020). In contrast, ecosystems that depend on natural fires, such as savannas, may not burn if they are overgrazed by livestock (Veldhuis *et al.* 2019)—another human practice that disrupts vegetation-animal feedback. The consequent reduction or loss of fires and extirpation of wild herbivores leads to woody encroachment in savannas (Stevens *et al.* 2017). Changes in fire regimes can initiate a feedback loop whereby increases in woody encroachment reduce suitable habitat for herbivores that would otherwise prevent both woody plant recruitment and severe fires by creating heterogeneity in grassy fuel (Foster *et al.* 2020). Increased frequency and severity of fires imposed by human disturbance thereby threatens the balance between animals and vegetation structure.

Anthropogenic changes to landscapes can shut wildlife out of preferred habitats and force them closer to human settlements, which increases the risk of human-wildlife conflict and disease spillover. Such conflicts can emerge due to deforestation, which dramatically impacts vegetation structure across landscapes and may drive wildlife to alter the structure of other habitat types. For example, grey-headed flying foxes (*Pteropus poliocephalus*) have entered a change-inducing feedback loop in Australia after deforestation caused large roosting colonies ("camps") to form in urban areas where populations are sustained by fruiting and flowering trees (Williams *et al.* 2006; Boardman *et al.* 2021). In turn, burgeoning flying fox camps defoliate and break branches of urban trees, which—alongside perceived disease risk—prompts humans to move urban flying fox populations, a practice that merely spreads the problem (Hall 2002). In this way, the interactions between humans and flying foxes, precipitated by the ways this bat species modifies vegetation structure, could shift flying foxes from providing ecosystem services including seed dispersal and pollination of economically valuable trees to being responsible for ecosystem disservices, such as disease spillover (Eby *et al.* 2023).

USING FEEDBACK LOOPS IN CONSERVATION

Identifying critical links in the feedback between vegetation structure and animal behavior can improve biodiversity-focused conservation and restoration strategies, which often place a premium on habitat heterogeneity and the structural complexity of vegetation (e.g., Zellweger *et al.* 2013; Tuanmu & Jetz 2015; Martins *et al.* 2017; Erdős *et al.* 2018). Structural complexity is a strong driver of both biodiversity and ecosystem functioning, as it creates variation in both vertical and horizontal space for niche partitioning (Pawar *et al.* 2012; Larue *et al.* 2019; Oliveira & Scheffers 2019; Gámez & Harris 2022; Coverdale & Davies 2023). Accordingly, attributes of 3D vegetation structure such as height and complexity—both vertical and horizontal—have informed biodiversity-focused conservation of birds (Weisberg *et al.* 2014), mammals (Deere *et al.* 2020), and arthropod communities (Müller *et al.* 2014). Some studies have extended this approach to identify 3D structural attributes important for landscape connectivity and animal movement (Zeller *et al.* 2016; Casalegno *et al.* 2017; Guo *et al.* 2018), as well as species interactions (Sovie *et al.* 2020).

Managing land to encourage beneficial change-inducing feedback offers a process-oriented approach to restoring degraded ecosystems (**Fig. 1.5**). However, it is important to note that recent studies have challenged what is meant by “degraded,” highlighting that logged forests can still harbor diverse plant and animal communities with heightened flows of energy and nutrients (Malhi *et al.* 2022; Sullivan *et al.* 2022). These findings suggest that plant and animal ecological roles can be harnessed to restore degraded ecosystems. Structural attributes of vegetation promote the ecological roles of animals that rebuild or shape important aspects of an ecosystem’s vegetation structure. For example, perches and nest cavities can attract seed rain from birds and aid in the assisted restoration of tropical forests (González-Castro *et al.* 2018). In addition, planting fruiting trees in disturbed landscapes attracts a variety of frugivores that disperse seeds and accelerate reforestation (Carlo & Morales 2016; Corbin *et al.* 2016; Camargo *et al.* 2020). The lateral connectivity of tropical canopies promotes the movement of arboreal animals such as primates, which disperse seeds and consume foliage (McLean *et al.* 2016). Accordingly, artificial canopy bridges may support primate populations that contribute to forest recovery (Chan *et al.* 2020). Assisted reintroductions of species to landscapes can also promote change-inducing feedback that recovers past vegetation structure. One example from a South African savanna showed how elephant browsing behavior in densely vegetated areas contributed to an eventual increase in landscape openness through a change-inducing feedback loop (Gordon *et al.* 2023).

Conservation frameworks that show how animals contribute to all stages of plant community succession, such as through changes in the tempo, quantity, and diversity of seed dispersal, highlight the importance of feedback in restoring terrestrial ecosystems (Dent & Estrada-Villegas 2021). Findings from this review indicate that conservation efforts will benefit from considering all relationships in a feedback loop between vegetation structure and the ecological roles of animals. Such efforts have the potential to enhance strategies to protect or restore ecosystems by piecing together strategies that may have limited effects on their own.

Considering feedback between vegetation structure and animal behavior is particularly important in forecasting effects of global change, which can induce shifts to alternative ecosystem states. Ecosystem tipping points are typically brought about by a perturbation, such as extreme weather, land use change, pollution, or introduced species (Staver *et al.* 2011; Dakos *et al.* 2019). Such changes are already occurring in humid tropical forests—especially in the Amazon Basin—where a feedback cycle of drought, fire, and tree death transforms humid forests into more open woodlands (Saatchi *et al.* 2021). The feedback that sends these ecosystems into an alternative state will incur high costs for the planet because humid tropical forests harbor over half the world's carbon stocks and two-thirds of its biodiversity (Pan *et al.* 2011; Giam 2017). Similar change-inducing feedback may be occurring undetected in other ecosystems; a better understanding of how ecosystems function as a network of feedback loops can improve estimations of ecosystem tipping points and how additional factors, such as trait adaptation of plants and animals, can delay shifts among ecosystem states (Dakos *et al.* 2019). Priorities for future research include describing the nature of feedback loops between animals and vegetation structure, and how they behave in response to disturbance or assistance (**Fig. 1.6**). A primary goal of this line of thinking is improving how we monitor ecosystem health by estimating whether ecosystems are in a state of self-sustaining or change-inducing feedback. In this way, incorporating the animal-vegetation structure feedback loop concept into conservation decisions can help preserve the ecological processes that keep ecosystems intact.

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TABLES AND FIGURES

Table 1.1: Examples of animal behaviors influenced by vegetation structure.

Animal behavior	**Vegetation structural attributes**	**Example**	**Reference**
Movement	Distance to canopy gap, canopy height, crown density, canopy shape, canopy thickness	Monkeys seek canopy pathways with high lateral connectivity	(McLean *et al.* 2016)
Resting/Roosting	Canopy height, canopy cover, distance to canopy gap, number of canopy layers, max canopy volume:height ratio	Orangutans often build nests near canopy gaps and in forests with tall, uniform canopy	(Davies *et al.* 2019)
Foraging	Stem density, canopy cover, canopy height, canopy density, canopy gap volume	Stem density filters bat communities according to foraging niche	(Blakey *et al.* 2017)
Thermoregulation	Canopy height, density	Moose seek denser vegetation during the hottest hours of the day	(Melin *et al.* 2014)
Predator avoidance	Shrub cover	Ungulates flee more frequently in response to predator vocalizations in open habitat	(Epperly *et al.* 2021)
Territorial display	Vertical vegetation complexity	Display duration of blue-black grassquit increases with seed abundance and shadow intensity of vegetation	(Biagolini-Jr *et al.* 2021)

Table 1.2: Examples of animal ecological functions that influence vegetation structure.

Animal ecological function	Vegetation structural attributes	Example	References
Ecosystem engineering	Canopy height, coefficient of variation, percent canopy cover <0.5 m	Megafauna in African ecosystems reduce canopy height and increase height variability	(Davies *et al.* 2018)
Herbivory	Canopy height, cover, structural complexity	Savanna herbivores reduce canopy height and woody cover	(Levick *et al.* 2009)
Breaking/trampling vegetation	Branch thickness, branch fracturing	Orangutans break branches to build nests that comply with their weight	(Van Casteren *et al.* 2012)
Seed dispersal	Aboveground biomass	Reduction of seed dispersal by large frugivores is predicted to decrease aboveground biomass	(Peres *et al.* 2016)
Nutrient transport	Tree density	Nutrient-rich termite mounds diversify the spatial distribution of savanna vegetation	(Davies *et al.* 2016a)
Predation	Browsable plant density, bites available per plant, previous browse, percent browsed, bites taken per deer unit	Intense browsing by deer leads to bushier vegetation in sites where puma predation is less likely	(Yovovich *et al.* 2021)

Figure 1.1: 3D vegetation structure influences animal ecological functions, which can influence vegetation structure directly (e.g., herbivory, breaking/trampling) or indirectly (e.g., seed dispersal, nutrient transport). The black arrows represent this feedback loop. These feedback loops sit in the broader context of abiotic and anthropogenic factors, which can also influence vegetation structure and animal behavior.

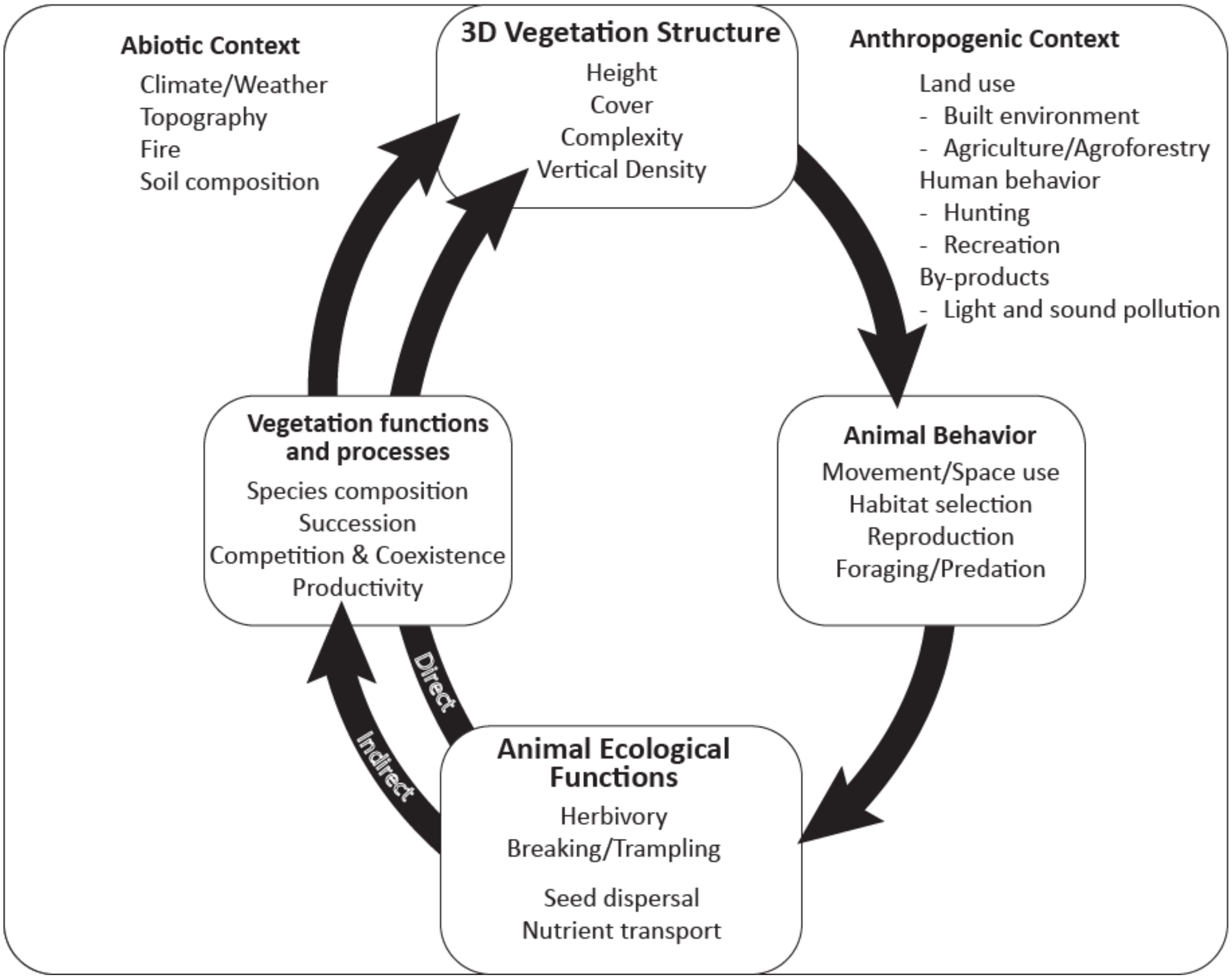


Figure 1.2: Examples of ecological functions of animals that influence vegetation structure and the approximate duration of the impact. Silhouettes downloaded from www.phylopic.org.

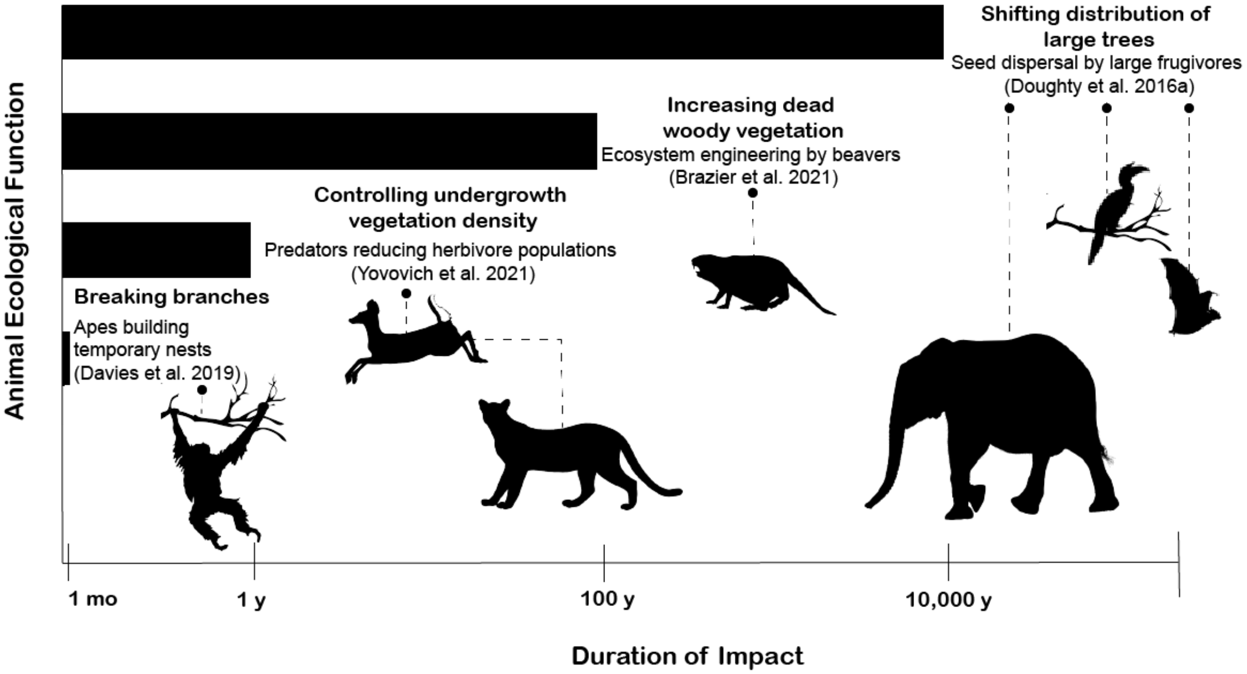


Figure 1.3: Change-inducing vs. self-sustaining feedback. **1)** Change-inducing feedback loop in which a top predator (gray wolf; *Canis lupus*) is extirpated from a boreal forest and the ensuing breakdown of a trophic cascade leads to reduced understory cover. **2)** Self-sustaining feedback loop in which seed dispersers are attracted to a tropical humid forest with tall canopy and disperse seeds of trees that become adults and contribute to canopy height. Created with BioRender.com and Adobe Illustrator.

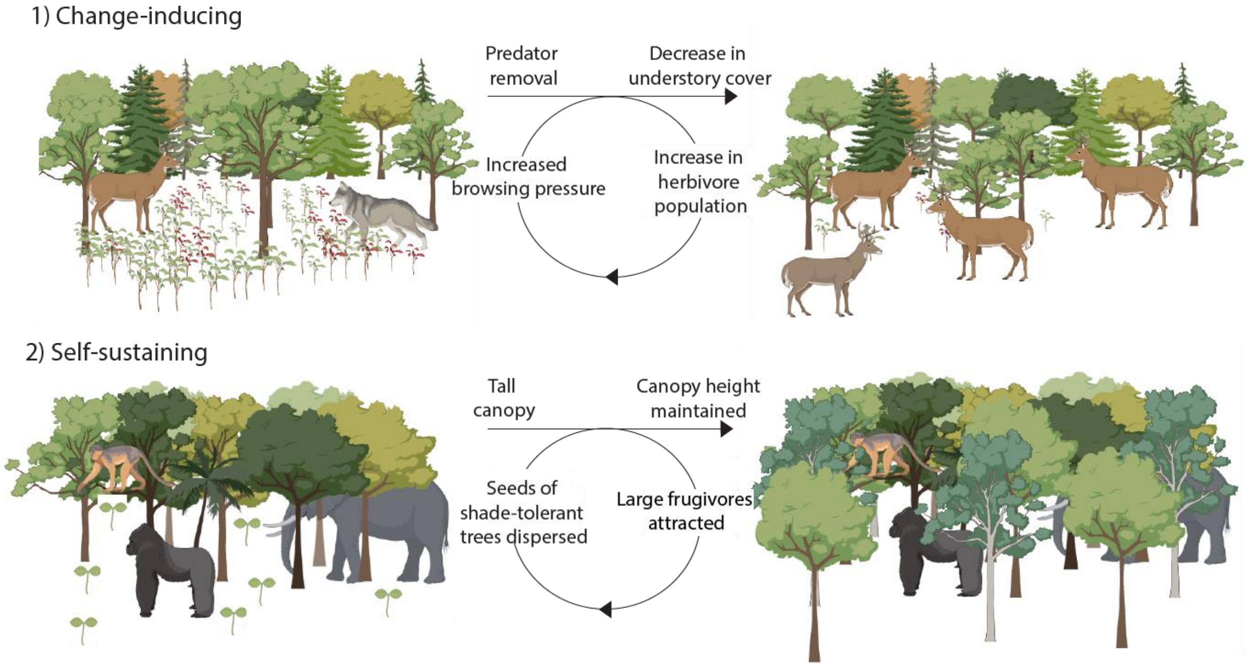
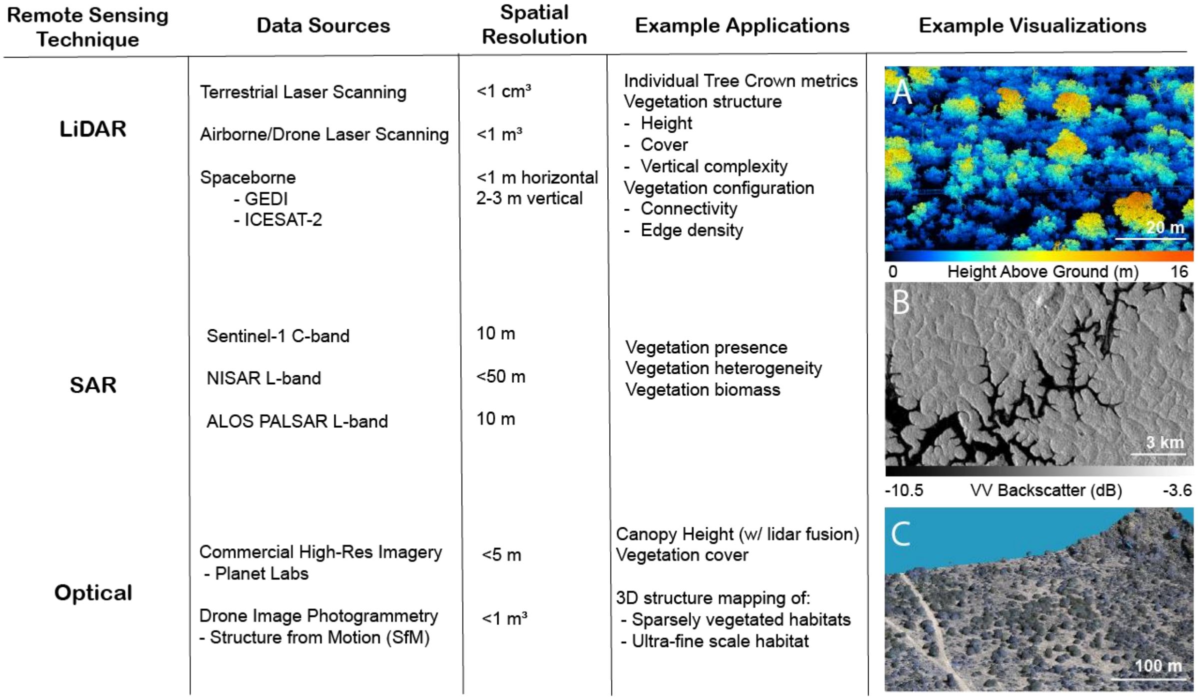


Figure 1.4: Measuring 3D vegetation structure with lidar, synthetic aperture radar (SAR), and optical data. **A)** An aerial view of 3D vegetation structure measured with airborne lidar in Kruger National Park, South Africa, colored according to vegetation height**. B)** A map of Vertical-Vertical (VV) backscatter values for a composite image of the Dja River in eastern Cameroon, using Sentinel-1 C-band SAR. Here it is possible to see the river slicing through a landscape of tropical humid forests and swamps. **C)** SfM rendering of 3D habitat structure in Mpala Research Centre, Kenya (data from Strandburg-Peshkin *et al.* 2017). GEDI: Global Ecosystem Dynamics Investigation; ICESAT-2: Ice, Cloud, and land Elevation Satellite; NISAR: NASA-ISRO Synthetic Aperture Radar; ALOS PALSAR: Advanced Land Observing Satellite Phased Array type L-band Synthetic Aperture Radar; SfM: Structure-from-Motion.



Remote Sensing Technique	Data Sources	Spatial Resolution	Example Applications	Example Visualizations
LiDAR	Terrestrial Laser Scanning Airborne/Drone Laser Scanning Spaceborne - GEDI - ICESAT-2	<1 cm^3 <1 m^3 <1 m horizontal 2-3 m vertical	Individual Tree Crown metrics Vegetation structure - Height - Cover - Vertical complexity Vegetation configuration - Connectivity - Edge density	A
SAR	Sentinel-1 C-band NISAR L-band ALOS PALSAR L-band	10 m <50 m 10 m	Vegetation presence Vegetation heterogeneity Vegetation biomass	B
Optical	Commercial High-Res Imagery - Planet Labs Drone Image Photogrammetry - Structure from Motion (SfM)	<5 m <1 m^3	Canopy Height (w/ lidar fusion) Vegetation cover 3D structure mapping of: - Sparsely vegetated habitats - Ultra-fine scale habitat	C

Figure 1.5: Using the feedback loop approach to inform conservation of an African savanna. In this worked example, we demonstrate the components of a feedback loop between 3D vegetation structure and ecological functions of animals. This example demonstrates a way to address the challenge of woody encroachment in a savanna by initiating a change-inducing feedback loop, including examples of patterns and processes that can be measured to describe the feedback. In this example, reintroduced African savanna elephants are attracted to dense vegetation, where they browse and knock down trees, creating more open vegetation structure and attracting other herbivores, which contribute to further increases in vegetation openness by browsing and grazing in areas where they can easily find forage and detect predators. This figure draws from many examples in African savannas, with the examples in **Steps 1** and **6** from inside and outside the Nkuhlu herbivore exclosure in Kruger National Park, South Africa; the example in in **Step 2** of rewilding in South Africa from Gordon et al. (2023), Photo: Bernard Dupont, CC BY-SA 2.0 via Wikimedia Commons; elephant tracking data in South Africa in **Step 3** from Thaker *et al.* (2019); tree density data in **Step 4** from Gordon *et al.* (2023), and viewshed in **Step 5** from (Davies *et al.* 2016c).

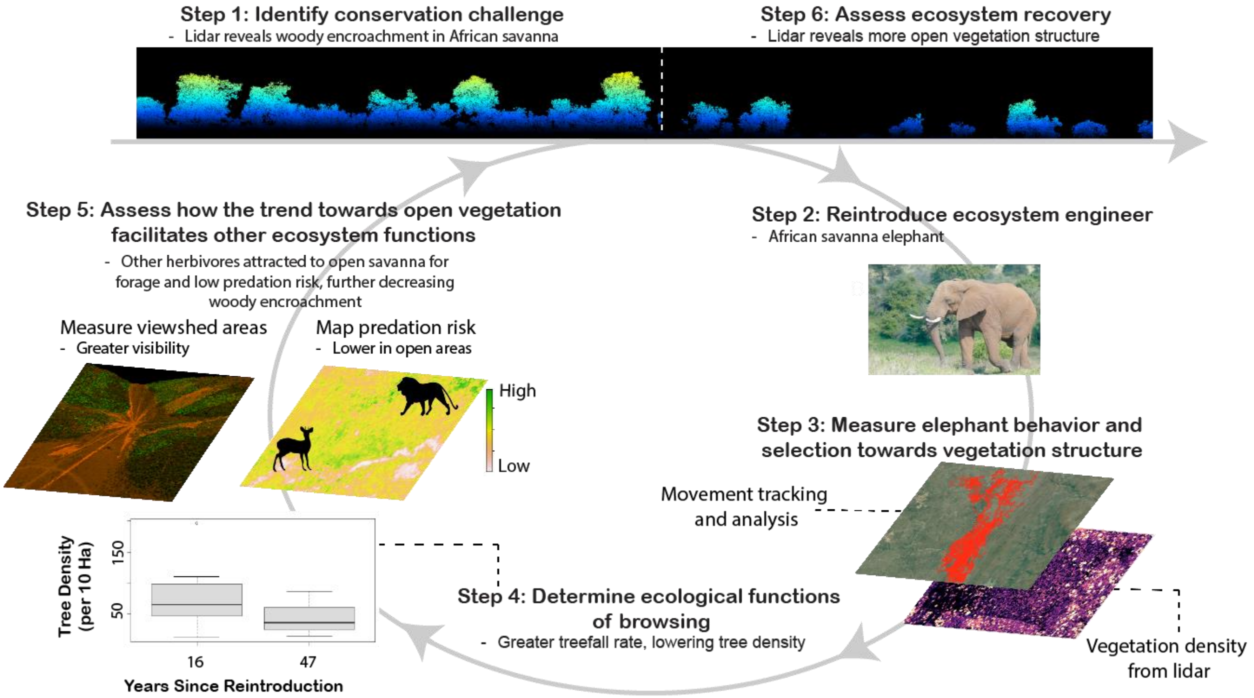

Step 1: Identify conservation challenge
- Lidar reveals woody encroachment in African savanna
Step 6: Assess ecosystem recovery
- Lidar reveals more open vegetation structure
Step 5: Assess how the trend towards open vegetation facilitates other ecosystem functions
- Other herbivores attracted to open savanna for forage and low predation risk, further decreasing woody encroachment
Measure viewshed areas
- Greater visibility
Map predation risk
- Lower in open areas
High
Low
Step 2: Reintroduce ecosystem engineer
- African savanna elephant
Step 3: Measure elephant behavior and selection towards vegetation structure
Movement tracking and analysis
Vegetation density from lidar
Step 4: Determine ecological functions of browsing
- Greater treefall rate, lowering tree density
Tree Density (per 10 Ha)
150
50
16
47
Years Since Reintroduction

Figure 1.6: Outstanding Questions

1) How can a feedback loop be identified as self-reinforcing or change-inducing?
2) When do feedback loops switch from self-reinforcing to change-inducing, or vice versa?
3) Do animal functions render vegetation structure more resilient to perturbations?
4) What is the influence of animals on vegetation structure relative to other factors at different spatial and temporal scales?
5) Is vegetation structure shaped primarily by many weak interactions or a few strong ones?
6) Which ecosystem types are shaped most strongly by animal influences on vegetation structure?
7) How has coevolution shaped interactions between animals and vegetation structure?
8) How can animal-vegetation structure interactions contribute to biological and functional diversity of ecosystems?
9) Animals can homogenize or diversify vegetation structure—how should each type of role be prioritized in conservation efforts?
10) Can feedback loops be leveraged to increase delivery of ecosystem services, for example increased agricultural yields or decreased risk of zoonotic spillover?
11) How do dynamics in human presence (e.g. recreation or poaching) influence feedback loops between animals and vegetation structure?

CHAPTER 2

Three-dimensional vegetation structure drives patterns of seed dispersal by African hornbills

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ABSTRACT

Three-dimensional (3D) vegetation structure influences animal movements and, consequently, ecosystem functions. Animals disperse the seeds of 60-90% of trees in tropical rainforests, which are among the most structurally complex ecosystems on Earth. Here, we investigated how 3D rainforest structure influences the movements of large, frugivorous birds and resulting spatial patterns of seed dispersal. We GPS-tracked white-thighed (*Bycanistes albotibialis*) and black-casqued hornbills (*Ceratogymna atrata*) in a study area surveyed by Light Detection and Ranging (LiDAR) in southern Cameroon. We found that both species preferred areas of greater canopy height, and white-thighed hornbill preferred areas of greater vertical complexity. In addition, 33% of the hornbills preferred areas close to canopy gaps, while 16.7% and 27.8% avoided large and small gaps, respectively. White-thighed hornbills avoided swamp habitats, while black-casqued increased their preference for swamps during the hottest temperatures. We mapped spatial probabilities of seed dispersal by hornbills, showing that 3D structural attributes shape this ecological process by influencing hornbill behavior. These results provide evidence of a possible feedback loop between rainforest vegetation structure and seed dispersal by animals. Interactions between seed dispersers and vegetation structure described

here are essential for understanding ecosystem functions in tropical rainforests and critical for predicting how rainforests respond to anthropogenic impacts.

INTRODUCTION

Seed dispersal by animals is essential for maintaining the structure and composition of tropical rainforests, which harbor over half the planet's carbon stocks and two-thirds of its biodiversity (Pan *et al.* 2011; Giam 2017). Between 60 and 90% of trees in tropical forests depend on animals to disperse their seeds away from specialist predators and competing conspecifics to areas where they can germinate (Janzen 1970; Schupp *et al.* 2010; Rogers *et al.* 2021). Climate and land cover change reduce the structural complexity of rainforests (Saatchi *et al.* 2021), decreasing their value for wildlife (Deere *et al.* 2020) and impacting seed dispersal capabilities of trees (Tucker *et al.* 2021). Although changes in the ecological roles of animals are thought to result from forest degradation, quantifying these relationships has proven challenging (Poulsen *et al.* 2013; Davies & Asner 2014; Malhi *et al.* 2022). A clearer understanding of these relationships can yield insights into possible feedback mechanisms between vegetation structure and seed dispersal by animals (Russo *et al.* 2023).

Vegetation structure exerts a strong influence on ecosystem functioning by modulating plant productivity (Larue *et al.* 2019) and influencing animal behavior (Davies & Asner 2014). Light Detection and Ranging (LiDAR), a 3D mapping technique, has helped reveal how vegetation structure influences animal behavior, such as by indicating predation risk (Davies *et al.* 2016c) and reducing energetic costs of movement (McLean *et al.* 2016; Wittemyer *et al.* 2019). LiDAR data acquired with unoccupied aerial vehicles (UAV-LiDAR) enable fine-scaled characterization of 3D vegetation structure from ground to canopy (Boucher *et al.* 2023).

Attributes of 3D vegetation structure, including height, cover, and vertical complexity, are components of ecological niche space that give rise to functional diversity of plants (Valbuena *et al.* 2020) and habitat partitioning by animals (MacArthur 1958). Vegetation structure also shapes the distribution of microclimates in ecosystems, reducing temperature extremes and shaping the 3D distributions of animals (Scheffers *et al.* 2014, 2017). How animals interact with vegetation structure also influences their ecological roles, such as nutrient transport and seed dispersal (Wittemyer *et al.* 2019).

Animal species differ from each other in habitat selection, but intraspecific variation may underlie additional functional diversity in ecosystems (Shaw 2020). Population-level estimates of habitat selection, while useful, may fail to reveal diversity in movements of individual animals (Shaw 2020; Costa-Pereira *et al.* 2022). Individual variation in movement behavior has important implications for population persistence due to its influence on population connectivity, gene flow, dispersal, and colonization events. However, it is less understood how movement variation leads to diversity in ecological roles and resulting effects on ecosystems (Shaw 2020). Ignoring individual variation in movement behavior likely weakens the predictive power of models that characterize animal ecological roles (Potts *et al.* 2022; Potts & Luca 2023). Consequences of such generalizations can lead to misguided conservation efforts, highlighting the need for intensive sampling of animal populations with high intraspecific variation.

Predictions of wildlife responses to global change are limited by geographical sampling biases. Animal tracking data from the tropics—and particularly Central Africa—are poorly represented in global databases (Kays *et al.* 2022). However, African hornbill movements have been studied over the past 30 years at increasingly finer spatial and temporal resolution, providing a unique opportunity to study their role in seed dispersal and forest recovery

(Holbrook & Smith 2000; Holbrook *et al.* 2002; Lenz *et al.* 2011; Chasar *et al.* 2014; Mueller *et al.* 2014). Black-casqued (*Ceratogymna atrata*) and white-thighed hornbills (*Bycanistes albotibialis*) are obligate frugivores of mature and degraded rainforests that collectively disperse the seeds of at least 50 tree species (Whitney *et al.* 1998) and may undertake long-distance movements of 100 km or more during the food-lean dry season (Holbrook *et al.* 2002). These characteristics, combined with gut passage times of up to six hours, enable hornbills to disperse seeds over long distances (Holbrook & Smith 2000; Holbrook *et al.* 2002).

Given that both hornbill species consume fruits of the upper canopy (Hardesty & Parker 2002) and require large trees for nesting cavities (Stauffer and Smith 2004), one might expect tall canopies to attract both species. While adult female hornbills are confined to nest cavities for months at a time, they may fly long distances during the longest dry season (December-March), and their annual home ranges average four times greater than adult males (Holbrook *et al.* 2002; Chasar *et al.* 2014). Hornbills have a large body size (>1 kg) and must frequently flap their wings to generate lift. Because vegetation structure can increase or decrease energetic costs of movement (McLean *et al.* 2016; Davies *et al.* 2019), hornbills may move among vegetation in an energy-efficient way. For these reasons, we expected 3D vegetation structure to influence hornbill movement behavior and resulting patterns of seed dispersal.

Here, we explored which attributes of 3D vegetation structure and habitat type influence hornbill movements, examining differences among individuals and between species. We then tested whether vegetation structure influences energetic costs of movement by relating hornbill activity levels to weather conditions and 3D structural metrics of selected habitats. Finally, we simulated spatial patterns of seed dispersal for hornbill-dispersed trees based on hornbill habitat selection, movement behavior, and gut passage times of seeds, showing how 3D vegetation structure influences seed dispersal by hornbills.

MATERIALS AND METHODS

Study site

Our study took place in the Dja Faunal Reserve in southern Cameroon, which consists primarily of mature lowland tropical rainforest mixed with inselbergs (rocky outcroppings that rise above the canopy) and *Raphia* palm-dominated swamps. Spanning 5,260 km^2, it is one of the largest protected areas of Africa's Congo Basin. There are two rainy and two dry seasons annually, with maximum and minimum rainfall occurring in September and May, respectively (Whitney *et al.* 1998). All hornbills were captured on the 25 km^2 Bouamir study area located near the center of the Dja Reserve (3°11' N, 12°48' E; maximum elevation 760 m). Bouamir includes a network of former hunting trails and numerous inselbergs that facilitate ground-based animal tracking (Holbrook & Smith 2000). A drone-mounted LiDAR scan of the 25 km^2 research site was completed in March 2022 using a Dji Zenmuse L1 waveform scanner, with an average point cloud density of 300 points · m^{-2}.

GPS tracking

Using canopy mist nets (Russo *et al.* 2024a), we captured 16 black-casqued and five white-thighed hornbills **(Fig. S2.1**) and tracked each bird with a 27g (n=18) or 25g (n=3) solar-powered transmitter (e-obs, GmbH, Munich, Germany, www.e-obs.de) from April 2022-April 2024. Tag mass was well under 3% of each animal's body mass, the highest recommended percentage (Wilson *et al.* 2021). Transmitters were attached using a backpack harness made from 1.12 cm (0.44") tubular Teflon ribbon (Bally Ribbon Mills; Kenward 2001) with 36.29 kg (80 lb.) strength nylon trammel line (Avinet) reinforcing the interior. The reinforcement was designed to withstand the wear from a hornbill's initial attempt to remove the harness without compromising the bird's well-being (see **Fig. S2.2** for an assessment). All capture and tracking methods were approved by the University of California, Los Angeles Animal Research Committee, under protocol #2019-037-01. We performed all field research with permission from Cameroon's Ministry of Scientific Research and Innovation (permit #15/MINRESI/B00/C00/C10/C13) and Ministry of Forestry and Wildlife (permit #1470/PRBS/MINFOF/SETAT/SG/DFAP/SDVEF/SC/ENJ).

All transmitters were programmed to record a GPS fix every 5 minutes from 5:45-18:30 local time, which corresponds with both species' peak period of activity (French & Smith 2005). At three lower battery levels, the tags were programmed to lower GPS fix rates to 30 or 120 minutes or 24 hours. We retrieved all GPS data using a handheld BaseStation in the study area or remote downloads via local cell networks when birds left the study area. We collected over 250,000 GPS points and 707,000 accelerometer bursts from the tagged hornbills and tracked each hornbill over a period ranging from three to 23 months (**Fig. S2.1**).

Habitat selection analyses

We conducted an integrated Step Selection Analysis (iSSA) for each hornbill to determine the attributes of vegetation structure that best predict their movements (Thurfjell *et al.* 2014; Avgar *et al.* 2016). Variables included canopy height, vertical forest structural complexity, distance to small canopy gaps (≥50 m^2), and distance to large canopy gaps (≥500 m^2), all of which were produced at 10 m resolution from the 3D LiDAR point cloud (**Table S2.1)**. Canopy gaps were defined as areas with no vegetation above 5 m from the ground, consistent with a standard definition of forested habitat (Hansen 2013). We limited model selection to covariates we expected to influence hornbill behavior, and covariates with a high Pearson correlation coefficient (>0.6) were not included together in models to avoid collinearity between covariates (**Table S2.2**). This practice resulted in the use of a single metric for vertical complexity. Based on field observations and initial data exploration, we hypothesized that black-casqued hornbills select swamps more often during hotter afternoon temperatures. Accordingly, we included a term for the interaction between temperature and swamp habitat (taking on 0 or 1) in iSSAs for hornbills of both species. Swamp habitats were classified based on a Convolutional Neural Network applied to a cloud-free Sentinel-2 image. Temperatures were measured using a DAVIS Vantage Pro 2 weather station (Deblauwe *et al.* 2023) within the study area every 15-60 minutes throughout the hornbill tracking period and matched to hornbill GPS data based on timestamp. We note that temperature was recorded in an area of open canopy rather than swamp habitat, and that diurnal temperatures vary among habitat types. We scaled and centered canopy height, vertical complexity index, temperature, and both "distance to gap" variables prior to model fitting.

We resampled all hornbill tracks to a 30 min fix rate, then used an iSSA to compare the habitat metrics at the destination of an observed step to those of 10 alternative steps while accounting for movement behavior (step length and turning angle; Signer et al. 2019). Habitat selection results were insensitive to a higher number of random control steps (n = 100 steps; **Figs. S2.3 and S2.4**), so we continued analyses with 10 random steps for the sake of computing efficiency. The randomly generated steps represented paths to habitats potentially available to the animal, whose lengths and turning angles are drawn from the observed distributions. Each iSSA contained a habitat selection function that estimated the animal's preference for habitat characteristics:

$$w(x) = \exp\left(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots \beta_n x_n\right)$$

where $w(x)$ is a value approximating the likelihood of a location being chosen, x_n are the predictors (i.e., habitat metrics) and β_n are the model coefficients estimated by fitting a conditional logistic regression (Thurfjell *et al.* 2014; Fieberg *et al.* 2021). We fit models using the "fit_issf" function in the "amt" R package (version 0.2.1.0; Signer *et al.* 2019). We only report results from analyses with no issues estimating β coefficients and 95% confidence intervals; as a result, only hornbills with at least 1000 GPS locations within the study area were used in the analysis (n = 18).

We estimated population-level coefficients for black-casqued and white-thighed hornbills using generalized linear mixed-effects models (GLMMs) that avoid pseudoreplication by fitting random slopes for each individual (Muff *et al.* 2020). We used the same model structure as the individual iSSAs to generate selection coefficients and 95% confidence intervals for each covariate. To further illustrate the interaction between temperature and selection for swamp habitat, we binned temperatures into four categories that correspond roughly to quartiles of the range of temperatures experienced by the hornbills on the study site (<22, 22-25, 25-27, and >27° C) and estimated each species' strength of selection for swamp habitats. All GLMMs were fit using the "glmmTMB" R package (version 1.1.7; Brooks et al. 2023). We also estimated means of each coefficient using inverse-variance weighted linear modeling (Dickie *et al.* 2020) and tested for differences between species using ANOVA.

Behavioral valuation of the landscape

We used accelerometer measurements to address the hypothesis that 3D vegetation structure influences energetic costs of flight. Each tag recorded a burst of accelerometer measurements every 10 min from 5:50-18:30 local time. Bursts consisted of a raw measurement in the x, y, and z axis every second for 20 seconds. We converted raw accelerometer values to units of gravity (g) and then calculated Overall Dynamic Body Acceleration (ODBA) using the default transformation for e-obs tags within the "ACCstats" function in in the "moveACC" R package (Scharf 2022). ODBA is the non-vectorial sum of absolute acceleration values of all three axes, and because it is related to activity levels, ODBA serves as a useful proxy for energy expenditure (Lopez-Lopez *et al.* 2022).

We used linear mixed-effects models to investigate predictors of ODBA, including all 3D structural variables used in habitat selection analyses, as well as rainfall (mm), temperature, and a binary variable for swamp habitat. We fitted a model to each hornbill species separately, with individual hornbill ID as a random effect, using the "lme4" R package (version 1.1.34; Bates *et al.* 2015). For each species, we generated a model with each combination of predictors and ranked all candidate models using the Akaike Information Criterion corrected for small sample size (AICc), implemented with the "dredge" function in the "MuMIn" R package (version 1.47.5; Bartoń 2023).

Modeling seed dispersal

We derived seed dispersal models for six combinations of hornbill and tree species, incorporating gut passage time of seeds and population-level means of habitat selection. Gut passage times were obtained from a captive feeding experiment involving both species of hornbill (Holbrook & Smith 2000). For example, *Staudtia kamerunensis* seeds passed through the digestive tract of a black-casqued hornbill 345 ± 39 min after consumption and 162 ± 8 min for white-thighed. We developed a simulator that predicts seed dispersal patterns for a fruiting tree based on hornbill movement behavior, selection for attributes of 3D vegetation structure, and gut passage time of seeds (**Fig. 2.1**). For each hornbill species, we estimated population-level selection for attributes of 3D vegetation structure using a GLMM that treats individual hornbill ID as a random effect (Muff *et al.* 2020), but these models were agnostic to time and therefore did not contain an interaction term for temperature and swamp habitat. Because simulations themselves are used to evaluate the goodness-of-fit of step-selection models (Signer *et al.* 2024), we evaluated the movement models used for seed dispersal simulations by comparing the distribution of habitat covariates at simulated locations to those of both observed and available locations, thus blending the approaches of (Fieberg *et al.* 2018) and (Fieberg *et al.* 2024). This approach is a visual check as to whether each hornbill species selected for or against a habitat feature at the population level, and whether this relationship is captured well by the simulations. We then generated a redistribution kernel from iSSA coefficients that influenced habitat selection significantly ($p<0.05$) and simulated 100 hornbill trajectories per tree using the "amt" package (version 0.2.0.1; Signer *et al.* 2019, 2024). Although fruiting trees vary widely in total frugivore visits, many trees receive at least 100 visits during their fruiting period (French & Smith 2005). We simulated spatial patterns of seed dispersal surrounding the crown of one individual of three different tree species in the hornbill diet (*Staudtia kamerunensis*, *Xylopia hypolampra*, and *Maesopsis eminii*) as a Poisson point process with intensity λ (Baddeley & Turner 2005). Tree locations were selected from a network of individuals monitored for a concurrent project on fruiting phenology. Each simulation included 50 movement steps of 20-minute duration, with the starting turn angle based on a random uniform distribution. For each simulation, we assigned a probability of seed deposition at each movement step by fitting a gamma distribution to the gut passage times and standard errors reported by Holbrook and Smith (2000). We estimated and smoothed kernel density estimates of seed dispersal events by weighting each movement step according to the probability of deposition based on gut passage time using the “spatstat” package (version 3.0-6; Baddeley and Turner 2005). The final product for each hornbill-tree pair (n=6) was a spatially explicit map of seed dispersal events based on 100 simulated trajectories originating from a fruiting tree. All analyses were conducted using R version 4.3.1 (R Core Team 2023).

RESULTS

Hornbill habitat selection

All hornbills preferentially moved among areas with greater canopy height except for one hornbill that frequented the open-canopy research camp (ID: 11847) and another that was tracked on the study site only as a juvenile (ID: 9895; **Fig. 2.2A**). Eight hornbills selected habitats with greater vertical complexity (**Fig. 2.2B**). At the population level, only white-thighed hornbills preferred habitats with higher vertical complexity (**Table 2.1**). Based on coefficients estimated from inverse variance-weighted linear modeling, we found that white-thighed hornbills were associated with forests of greater canopy height (ANOVA: $F_{2,16}$ = 130.13, p<0.001) and vertical complexity (ANOVA: $F_{2,16}$ = 19.6, p<0.001) than black-casqued.

Hornbills showed a variety of responses to both large and small canopy gaps. Six hornbills (33.3%) selected areas closer to small canopy gaps, while five (27.8%) appeared to avoid them **(Fig. 2.2C).** Three of the hornbills (16.7%) appeared to avoid large canopy gaps (**Fig. 2.2D)**, which included inselbergs, the research camp, and large treefalls. Six hornbills (33.3%)

were attracted to these landscape features. Notably, three birds preferred areas closer to small gaps while avoiding large gaps (ID: 8970, 8976, 11852), and two birds displayed the opposite relationship (ID: 8972, 8973). In addition, we detected no significant response of either species to small or large canopy gaps at the population level (**Table 2.1**). Black-casqued hornbills were more likely to use swamps during hotter temperatures, while white-thighed hornbills avoided them (**Table 2.1; Fig. 2.3**). Black-casqued hornbills' preference for *Raphia*-dominated swamp forests and white-thighed hornbill's tendency to avoid these habitats is a major behavioral difference between the two species (**Fig. 2.4**).

Behavioral valuation of the landscape

Black-casqued hornbills exhibit their lowest activity levels—as measured by ODBA—during hotter temperatures (**Fig. S2.5A**) and when they were within swamp habitats (**Fig. S2.6**). White-thighed hornbills also exhibited their lowest activity levels during hotter temperatures **(Fig. S2.5B**), but no other predictors were included in the top GLMM. We found clear support for the top model of both black casqued (**Table S2.3**) and white-thighed hornbill ODBA (**Table S2.4**), with the second-best model differing by 8.42 and 6.15 AIC_c units, respectively. No 3D structural variables were consistently included in top models of ODBA for either species.

Modeling seed dispersal

We generated a spatially explicit model of seed deposition probabilities for three species of hornbill-dispersed trees occurring within the Bouamir Research Site, using canopy height, vertical complexity index, habitat type (swamp vs. non-swamp), and the distribution of step lengths and turn angles as predictors (**Fig. 2.5**). We omitted both 'distance to canopy gap' variables because they were not significant predictors of either species' movements at the population level. In evaluating the underlying movement models, we saw concordance between the values at used locations and those of simulated locations (**Fig. S2.7**). The intensity (λ) of the Poisson point process underlying each model represents the average probability of seed dispersal per 10 m pixel and ranged from $7.33 \cdot e^{-5}$ for *Staudtia kamerunensis* dispersed by white-thighed hornbill (**Fig. 2.5B**), to $1.31 \cdot e^{-4}$ for *Maesopsis eminii* dispersed by either hornbill species (**Fig. 2.5E, F**). The median simulated dispersal distances ranged from 457.59 to 687.85 m for hornbill-tree species pairings (n=6), and the maximum simulated dispersal distance ranged from 2391.70 to 2972.31 m (**Fig. S2.8**).

DISCUSSION

Our results show that vegetation structure plays an important role in the movement decisions of seed-dispersing hornbills and resulting spatial patterns of seed dispersal. Black-casqued and white-thighed hornbills prefer tall canopies but individuals of both species vary in their attraction to canopy gaps. These findings suggest that the 52 species of trees known to be dispersed by hornbills will likely arrive at areas with greater canopy height, and that variation in movement behavior among individual hornbills may increase the possibility of seeds dispersing to areas suitable for germination. Although relatively small sample sizes of hornbills introduce some limitations to this study, the strength of selection for attributes of 3D vegetation structure indicate strong individual- and population-level patterns. The results of this study point to the importance of 3D vegetation structure in shaping seed dispersal capabilities of tropical trees, an ecological process that shapes vegetation structure in turn.

Canopy height was an important driver of habitat selection by hornbills, which select fruits from trees that occupy the upper canopy of Cameroon's rainforests (Hardesty & Parker 2002). The fruiting trees that attract hornbills tend to be among the tallest in the landscape, as slow-growing trees characteristic of mature forests (Whitney *et al.* 1998; Sonké & Couvreur

2014). Tall trees can also indicate potential nesting habitat because hornbills require large tree cavities, and nesting trees tend to be taller than surrounding trees (Stauffer & Smith 2004). Canopy height is typically associated with vertical vegetation complexity (Gouveia *et al.* 2014). However, we did not find a strong correlation between these variables, and hornbills showed a broader variation of habitat selection in relation to vertical vegetation complexity. Because hornbills rarely descend below the upper canopy, where denser vegetation can restrict flight paths, it is possible that individual birds that selected for greater vertical vegetation complexity—including all five white-thighed hornbills—might not be selecting for vegetation structure in the vertical column, but instead associating with structurally complex habitats, such as transitional habitats between forest and swamp or inselberg grasslands.

Three-dimensional vegetation structure influences the behavior of animals in a landscape by indicating reward and risk (Wittemyer *et al.* 2019). It is difficult to measure all landscape characteristics that may influence animal behavior, so we encourage researchers to formulate hypotheses based on observations of the study species. In this study, we found that individuals of both hornbill species showed positive and negative selection for distance to canopy gaps of large ($\geq$500 m^2) and small areas ($\geq$50 m^2). Gap edge specialists may seek fruits of trees that are associated with inselberg edges, such as *Lannea welwitschii*, *Eribromum oblongum*, and *Maesopsis eminii* (Whitney & Smith 1998), or perhaps early colonizing tree species that produce fruits abundantly in canopy gaps, such as *Musanga cecropioides.* Canopy gaps could also present hornbills with an energy-expensive crossing or expose them to one of their main predators, the crowned eagle (*Stephanoaetus coronatus*; Rainey *et al.* 2004). Gap-avoiding hornbills may respond to the risks of visiting canopy gaps or the potential energy costs of moving across them (Davies *et al.* 2019; Gaynor *et al.* 2019). It might be expected that canopy gaps increase the energetic costs of flight, while taller canopies help decrease them. Still, we found no 3D structural attributes that predicted the Overall Dynamic Body Acceleration (ODBA) of hornbills, a proxy for energy use. Hornbills that did not move preferentially towards or away from canopy gaps may use an optimal foraging strategy that balances predation risk with the rewards of finding food (Abrahms *et al.* 2021). Taken together, these results suggest that hornbills can routinely deposit seeds in canopy gaps, provided perches are available.

Black-casqued and white-thighed hornbills are thought to be functionally similar as seed dispersers, given the extensive overlap in their diets (Whitney & Smith 1998; Whitney *et al.* 1998). However, black-casqued hornbills prefer *Raphia* palm-dominated swamps over other habitat types during hotter times of day, while white-thighed hornbills appear to avoid them altogether. This finding highlights an important niche difference between related species that can lead to a functional difference in seed dispersal beyond the differences in gut passage times of seeds. It is not immediately clear why white-thighed hornbills avoid *Raphia* swamps, because both species have been observed gathering mud from swamps for their cavity nests during the onset of the breeding season (May-July) and consuming fruits of *Raphia monbuttorum* (Whitney *et al.* 1998). However, some white-thighed hornbills may not have a large enough gape to consume the fruits (Whitney & Smith 1998; Whitney *et al.* 1998). Black-casqued hornbills are larger than white-thighed and behaviorally dominant at fruiting trees (French & Smith 2005). This behavioral hierarchy could extend to *Raphia* palm fruits or perhaps resting locations with cool temperatures and low predation risk. Indeed, we found that black-casqued hornbills exhibited their lowest activity levels within swamp habitats. These findings shed light on the importance of *Raphia* swamps for black-casqued hornbills, especially as climate change brings greater temperature and precipitation extremes to the region (Réjou-Méchain *et al.* 2021). An interesting avenue for further research would be to explore how temperature—mediated by vegetation structure—influences habitat and nest site selection of hornbills.

Three-dimensional vegetation structure is known to influence animal distributions, behavior, and niche differences, but few studies extend the importance of 3D vegetation structure to ecological functions performed by animals (Davies & Asner 2014). In this paper, we demonstrated how 3D vegetation structure can modulate seed dispersal patterns by influencing animal dispersers' behavior. Characterizing 3D structure with UAV-LiDAR was easier and less costly than airborne LiDAR and enabled more granular descriptions of vertical and horizontal complexity that revealed differences in habitat selection between species and among individuals. There is growing interest in the predictive power of Step Selection Analyses, a standard method to analyze habitat selection of animals based on movement data (Potts *et al.* 2022). Recent advances in simulating animal movements based on habitat selection (Signer *et al.* 2024) enabled this paper's seed dispersal modeling framework. Mechanistic models of seed dispersal are becoming increasingly detailed in predictions of the spatial distribution of seed deposition probabilities (Kleyheeg *et al.* 2017; Van Toor *et al.* 2019; Nield *et al.* 2020; Borah & Beckman 2021; Treep *et al.* 2021). To our knowledge, we present the first model that links coefficients from an iSSA with gut passage times to predict spatial patterns of seed deposition. This framework enables practitioners to include any variables of interest that influence habitat selection and movement behavior of seed dispersers in predictions of seed dispersal patterns.

Seed dispersal gives rise to the intricate 3D structure of tropical rainforests, which creates heterogeneity in vertical and horizontal space for the most diverse biological communities on Earth. These ecosystems are threatened by myriad factors, including logging, mining, infrastructure expansion, and commercial agriculture (Barlow *et al.* 2018). While hornbills show clear patterns of habitat selection in a mature rainforest, they encounter human-dominated landscapes when they fly long distances during food-lean times, and some populations rely on forests and swamps near rural villages to survive and reproduce (Chasar *et al.* 2014). Across the tropics, human pressures curtail animal movements and reduce seed dispersal distances (Tucker *et al.* 2021). We have built a predictive model that can be used to understand how changes in 3D structure can affect seed dispersal, an important aspect of ecosystem structure and function. We encourage the use of this framework to characterize seed dispersal in other systems, as well as other ecosystem subsidies distributed by animals (Ellis-Soto *et al.* 2021). Given the role of natural seed dispersal in forest restoration, the modeling framework presented in this paper may also serve as a useful tool for proactive ecosystem management (Estrada-Villegas *et al.* 2023). Ecosystem functioning arises from the interactions among primary producers, consumers, and abiotic factors (Schmitz 2010; Schmitz *et al.* 2018). An intimate understanding of these interactions is necessary to predict the future of ecosystems in response to global climate and land use change.

ACKNOWLEDGMENTS:

This work would not have been possible without the contribution of several local forest guides in Cameroon. We thank them for sharing their knowledge of the forest with us: Mbembo Luc, Dando Daniel, Abah Armand, Eloumo “Elgas” Gaston, Obam Lundi, Ngong Antoine, Amiezeh David, Mbengue Moise, Manga Michel, and Biango Felix. We also thank the Republic of Cameroon and the Ministries of Scientific Research and Innovation (MINRESI) and Forestry and Wildlife (MINFOF) for permission to conduct this research and to conservator Oum Njock Gilbert for permissions and matching us with helpful eco-guards, including Mekok Alfred, Doumba “Calao Vert” Olivier, Mevoula Bertrand, and Samuah Harvilange. We thank the Congo

Basin Institute and e-obs for logistical support. Finally, we thank Tegueu Prudence, Hongie Mandela, Tekam Antoine, Tegebong Valorian, and Ninying Benedicta for their assistance in tagging and tracking hornbills. We thank Francis Forzi for assistance with canopy netting. This work was funded by a grant from the NASA ROSES program; the NSF Graduate Research Fellowship Program; Walder-Christensen Foundation; Greenville Zoo; Explorers Club; American Philosophical Society; Sigma Xi; Association for Tropical Biology and Conservation; American Ornithological Society; Animal Behavior Society; IDEA Wild; and the UCLA Dept. of Ecology and Evolutionary Biology. Sophie Philips provided helpful statistical support. We also thank numerous instructors and participants at the AniMove Summer School for their advice, including Tal Avgar, Hannah Williams, and Geneviève Degré-Timmons. We thank Vincent Deblauwe and Hannah Stouter for access to and assistance with field station weather data, Lebienfaiteur Sagang for assistance with data acquisition, and Pierre Ploton for assistance with data processing. We thank members of the UCLA Center for Tropical Research for their helpful comments on all aspects of this project.

TABLES AND FIGURES

Table 2.1: Population-level estimates (β) of habitat selection and movement behavior for both hornbill species. Estimated coefficients of selection and standard error (in parentheses) for each predictor of movement steps are based on a generalized linear mixed-effects model with random slopes for each individual hornbill. BCH = Black-casqued hornbill; WTH = White-thighed hornbill; The number of asterisks (*) after a coefficient estimate correspond to significance at the level of 0.05, 0.01, and 0.001, respectively.

Covariate	**BCH**	**WTH**
Canopy Height	0.260 (0.018)***	0.337 (0.042)***
Vertical Complexity Index	0.019 (0.018)	0.189 (0.026)***
Distance to gap ≥50 m^2	-0.023 (0.035)	-0.0002 (0.047)
Distance to gap ≥500 m^2	-0.043 (0.050)	-0.009 (0.035)
Swamp	0.379 (0.074)***	-0.708 (0.092)***
Temperature:Swamp	0.160 (0.018)***	0.079 (0.072)
log(Step Length + 1)	0.002 (0.009)	-0.012 (0.010)
cos(Turn Angle)	-0.278 (0.087)***	-0.120 (0.028)***

Figure 2.1: Workflow for generating spatially explicit seed shadow models based on hornbill habitat selection and gut passage times of seeds.

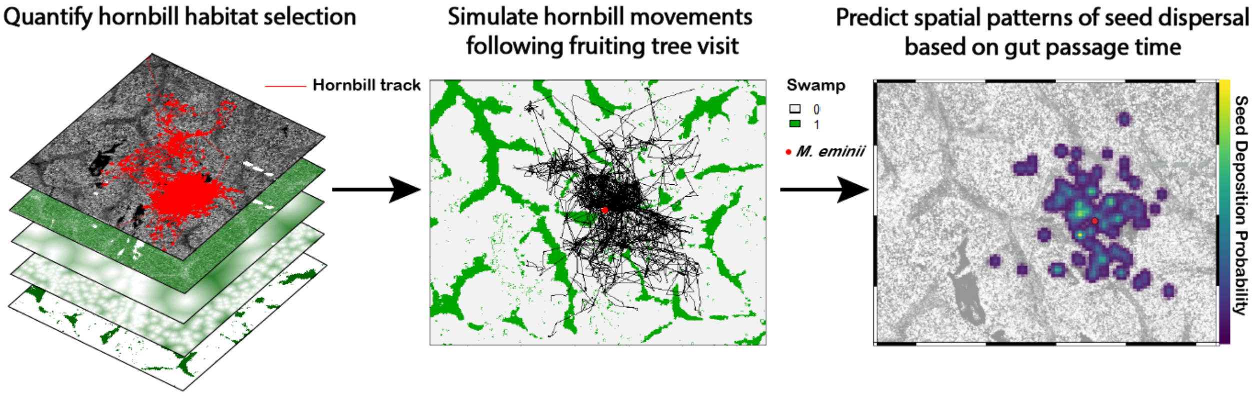


Figure 2.2: Hornbill selection for 3D structural attributes at 10 m resolution, including **A)** Canopy height, **B)** Vertical Complexity Index, **C)** Distance to small canopy gaps (≥50 m^2), and **D)** Distance to large canopy gaps (≥500 m^2). Coefficients of habitat selection (β) and 95% confidence intervals for each individual hornbill in the study are based on an integrated Step Selection Analysis (BCH = Black-casqued hornbill, WTH = White-thighed hornbill). The dotted line at x=0 in each plot represents no selection. Note that the range of values in the x and y axes differs for each plot.

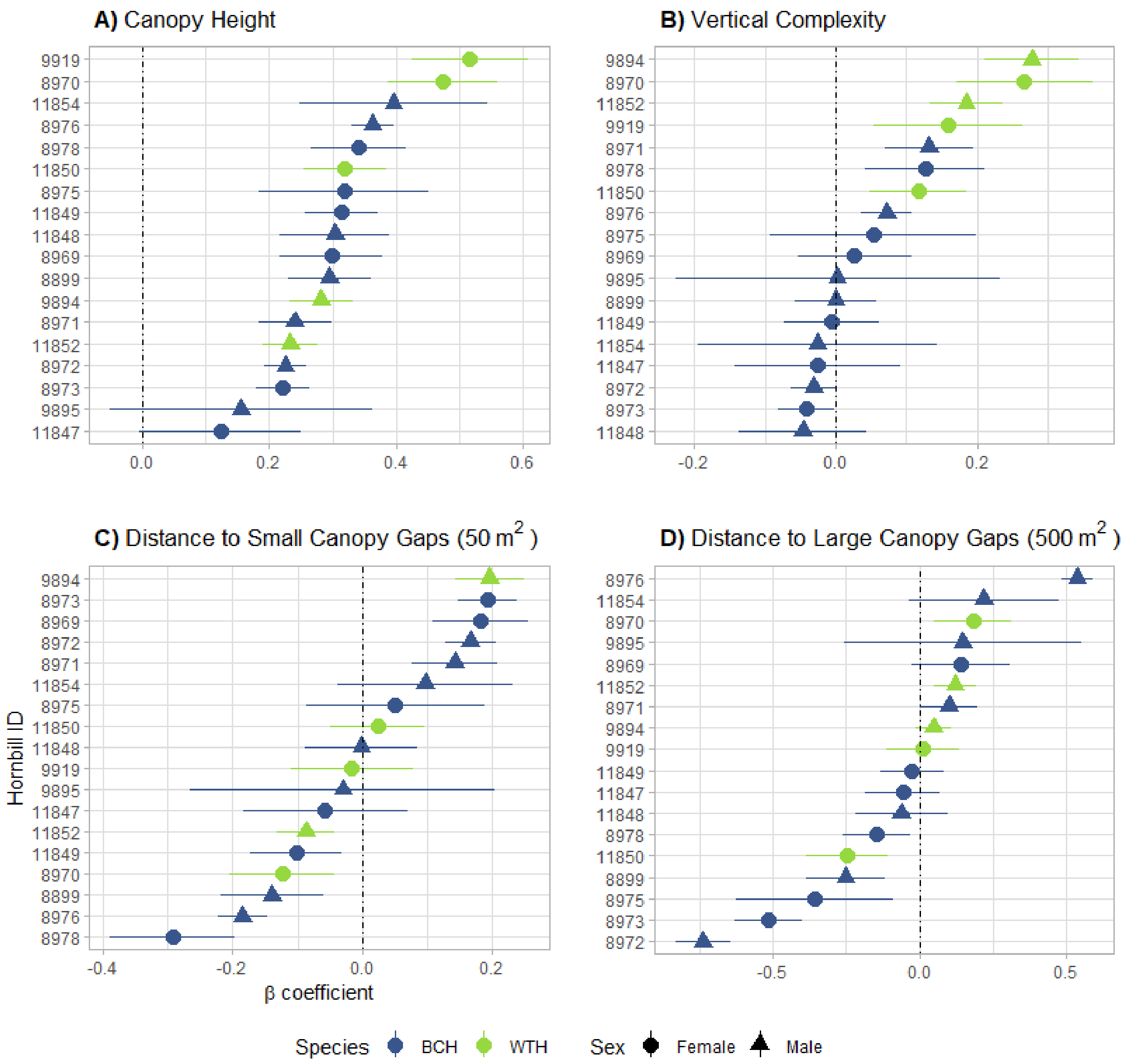

A) Canopy Height
9919
8970
11854
8976
8978
11850
8975
11849
11848
8969
8899
9894
8971
11852
8972
8973
9895
11847
0.0
0.2
0.4
0.6
B) Vertical Complexity
9894
8970
11852
9919
8971
8978
11850
8976
8975
8969
9895
8899
11849
11854
11847
8972
8973
11848
-0.2
0.0
0.2
C) Distance to Small Canopy Gaps (50 m^2)
9894
8973
8969
8972
8971
11854
8975
11850
11848
9919
9895
11847
11852
11849
8970
8899
8976
8978
-0.4
-0.2
0.0
0.2
D) Distance to Large Canopy Gaps (500 m^2)
8976
11854
8970
9895
8969
11852
8971
9894
9919
11849
11847
11848
8978
11850
8899
8975
8973
8972
-0.5
0.0
0.5
Hornbill ID
β coefficient
Species
BCH
WTH
Sex
Female
Male

Figure 2.3: Population-level selection coefficients for swamp habitat (β) with respect to ambient temperature, based on generalized linear mixed-effects models fit to each of four temperature bins per species. Points and bars represent estimates and 95% confidence intervals, respectively. The dotted line at y=0 represents no selection. BCH = black-casqued hornbill, WTH = white-thighed hornbill.

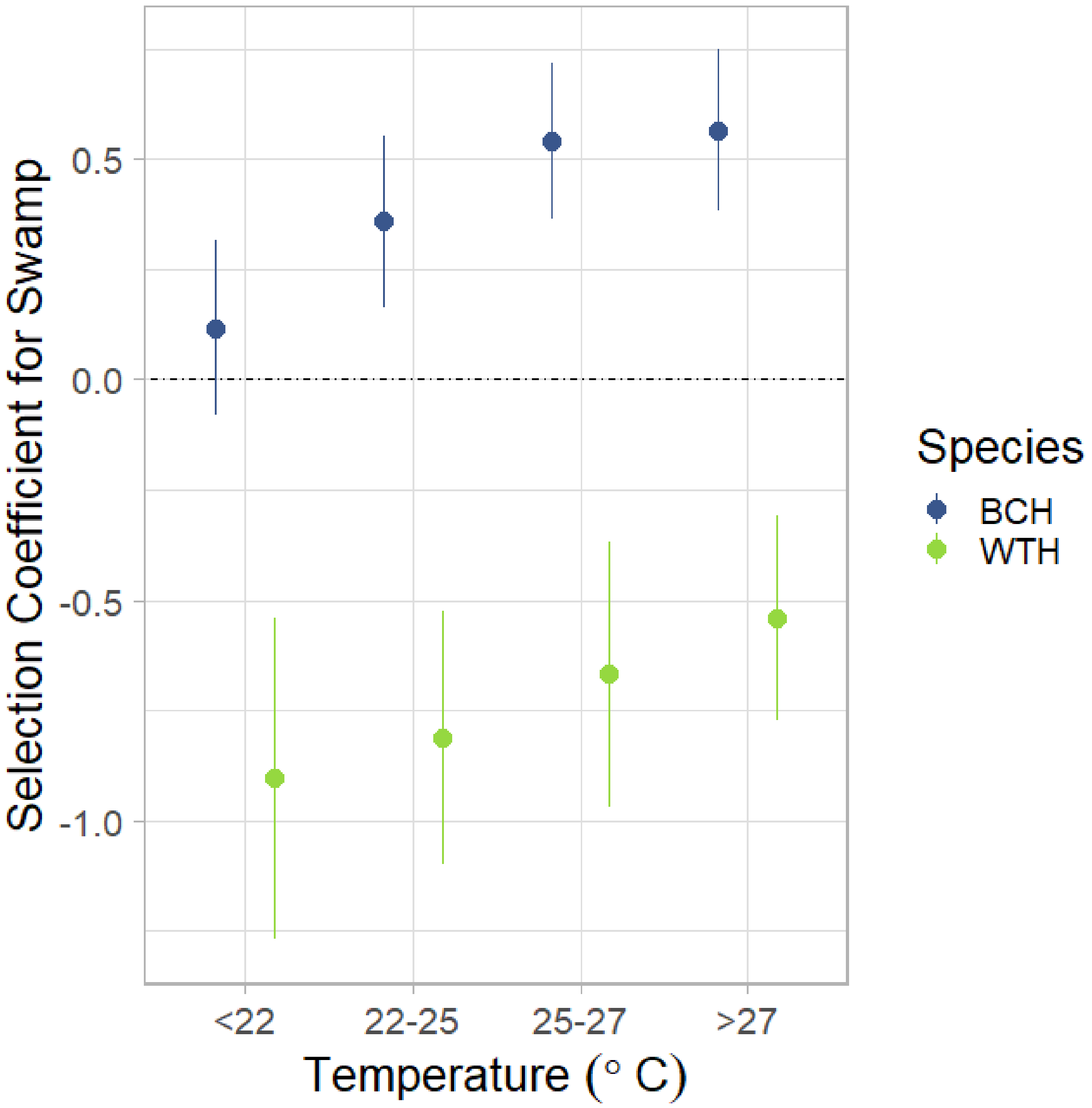


Figure 2.4: GPS locations of a **A)** male white-thighed hornbill (ID: 9894), and **B)** male black-casqued hornbill (ID: 8972), for June 2023 overlain on a map of canopy height (1 m resolution) with swamp habitats delimited in gray. The maps show both hornbills' preference for the tallest trees of the landscape, the white-thighed's avoidance of a swamp, and the black-casqued's regular use of a swamp. The extensive area of low canopy height (blue color) in panel B is an inselberg, and because the home range of 8972 is associated with the inselberg, this hornbill's iSSA revealed a preference for habitats near large canopy gaps.

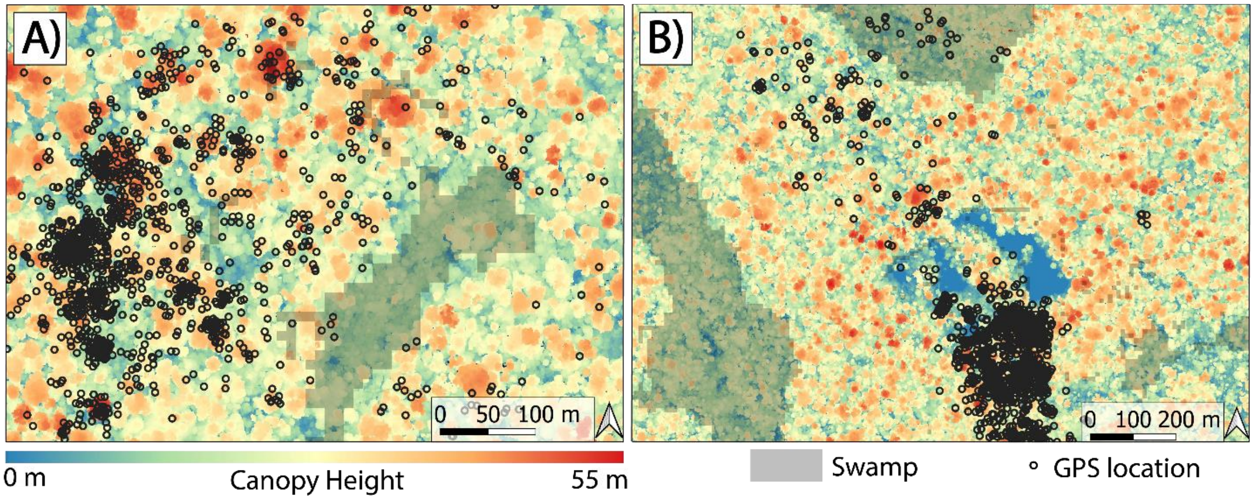
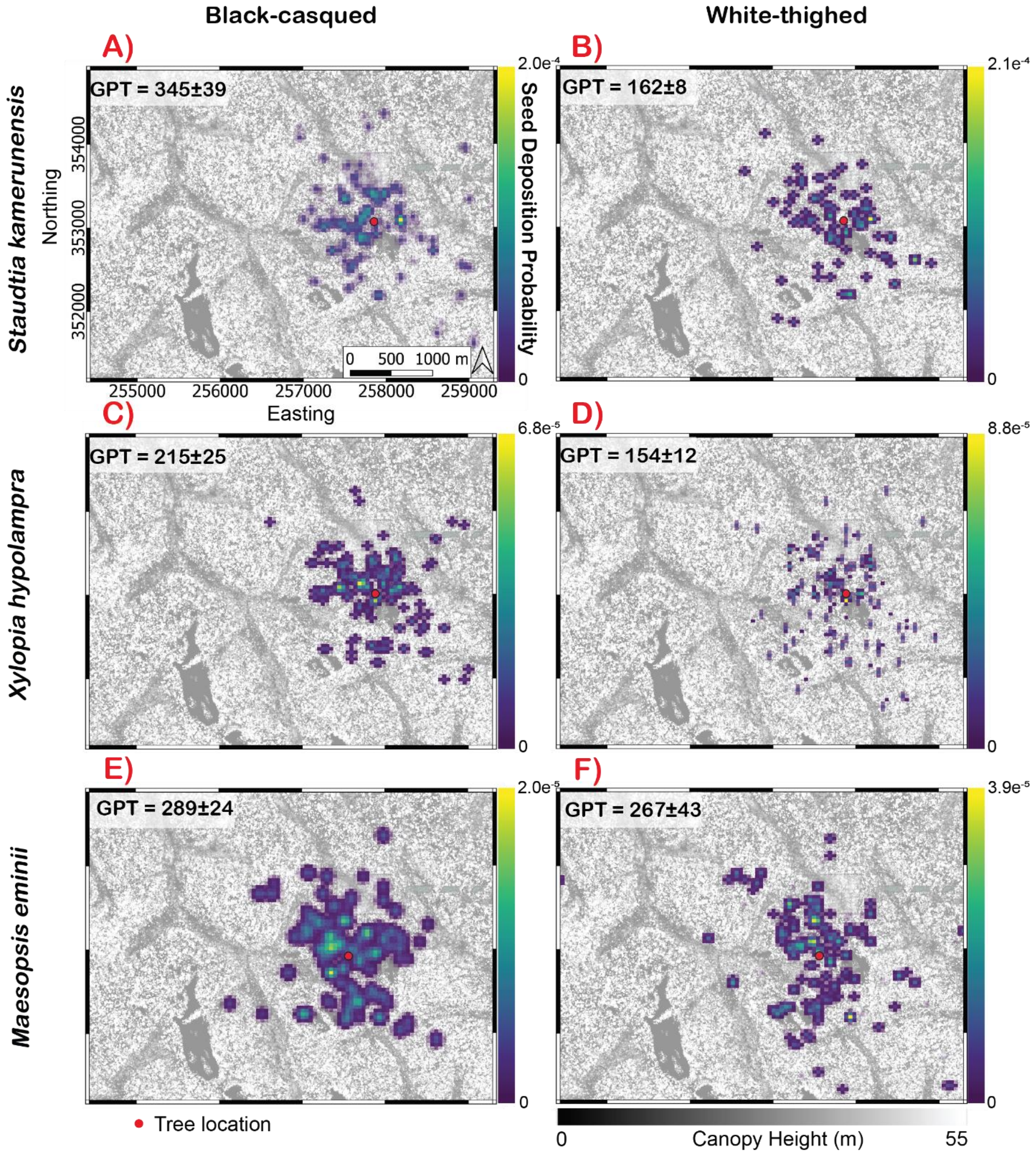


Figure 2.5: Comparing patterns of seed dispersal between black-casqued **(A, C, E)** and white-thighed hornbill **(B, D, F)**. Each seed dispersal simulation is based on a redistribution kernel that incorporates step lengths, turning angles, and habitat selection of the respective hornbill species. Each simulation originated at the crown of a fruiting tree on the study site (represented by red points); combinations of hornbills and trees include *S. kamerunensis* **(A, B)**, *X. hypolampra* **(C, D)**, and *M. eminii* **(E, F)**. Resulting patterns of seed dispersal are based on a gamma distribution of gut passage time along the length of 100 hornbill movement simulations. All seed deposition maps are plotted over a 1 m canopy height map modified to enhance visual clarity. GPT = Gut passage time, in minutes, ± standard error.


Black-casqued
White-thighed
A)
B)
C)
D)
E)
F)
Staudtia kamerunensis
Xylopia hypolampra
Maesopsis eminii
GPT = 345±39
GPT = 162±8
GPT = 215±25
GPT = 154±12
GPT = 289±24
GPT = 267±43
Northing
352000
353000
354000
Easting
255000
256000
257000
258000
259000
0 500 1000 m
Seed Deposition Probability
2.0e-4
2.1e-4
6.8e-5
8.8e-5
2.0e-5
3.9e-5
0
Tree location
0
Canopy Height (m)
55

SUPPLEMENTARY MATERIAL: Supporting tables and figures for Chapter 2

Table S2.1: Covariates included in model selection for integrated Step Selection Analysis

Covariate	**Definition**	**Units**	**Spatial resolution**
Canopy Height	Height of first LiDAR return (scaled and centered)	Meters	10 m
Vertical Complexity Index	A fixed normalization of the entropy function, based on the 3D point cloud (scaled and centered)	Unitless	10 m
Distance to gap 50 m^2	Distance to gap of minimum size 50 m^2, 5 m height threshold (scaled and centered)	Meters	10 m
Distance to gap 500 m^2	Distance to gap of minimum size 500 m^2, 5 m height threshold (scaled and centered)	Meters	10 m
Swamp	Habitat class defined as swamp, all other classes (*terra firme* forest, inselberg) taking on zero	Unitless (binary)	10 m
Temperature:Swamp	Interaction between ambient temperature (scaled and centered) and habitat class defined as swamp	NA	10 m
log(Step length + 1)	Distance between two successive GPS locations + 1 m—to account for step lengths of 0—and log-transformed	Meters	NA
cos(Turn angle)	Cosine of the angle between two successive GPS locations	Radians	NA
Step ID	Stratum consisting of a selected step (n=1) and randomly generated steps (n=10)	NA	NA

Table S2.2: Pearson's correlation coefficient for each pairing of covariates included in habitat selection models

	CanopyHeight10m	VCI	dist2gap50	dist2gap500	Swamp
CanopyHeight10m	1	0.472887	0.223225	0.124654	-0.24559
VCI	0.472887	1	0.179814	0.179794	-0.21498
dist2gap50	0.223225	0.179814	1	0.200184	-0.04672
dist2gap500	0.124654	0.179794	0.200184	1	0.000122
Swamp	-0.24559	-0.21498	-0.04672	0.000122	1

Table S2.3: Predictors of black-casqued hornbill activity—measured using Overall Dynamic Body Acceleration—ranked using AICc. The models shown are limited to those that contribute to a cumulative weight of 99%. ***k*** = number of parameters; **log(ʃ)** = log-likelihood; **AIC$_c$**= Akaike Information Criterion corrected for small sample size; $\boldsymbol{\Delta_i}$ **=** difference in AIC$_c$ units between model *i* and the top model; $\boldsymbol{w_i}$ = weight of model *i*; $\sum_{i=1}^{n} w_i$ = cumulative weight up to and including model *i*.

Model	***k***	**log(ʃ)**	**AIC$_c$**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$	$\sum_{i=1}^{n} w_i$
Temp + Swamp	5	1829.194	-3648.39	0	0.968117	0.968117
Temp+ Swamp + dist2gap50	6	1825.983	-3639.96	8.423388	0.014349	0.982466
Temp	4	1823.742	-3639.48	8.904432	0.011281	0.993747

Table S2.4: Predictors of white-thighed hornbill activity—measured using Overall Dynamic Body Acceleration—ranked using AICc. The models shown are limited to those that contribute to a cumulative weight of 99%. ***k*** = number of parameters; **log(ʆ)** = log-likelihood; **AIC**$_c$= Akaike Information Criterion corrected for small sample size; $\boldsymbol{\Delta_i}$ **=** difference in AIC$_c$ units between model *i* and the top model; ***w***$_i$ = weight of model *i*; $\sum_{i=1}^{n} w_i$ = cumulative weight up to and including model *i*.

Model	***k***	**log(ʆ)**	**AIC**$_c$	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$	$\sum_{i=1}^{n} w_i$
Temp	4	-458.593	925.188	0	0.92302	0.92302
Temp + VCI	5	-460.669	931.3419	6.153862	0.042552	0.965572
Temp + dist2gap500	5	-461.902	933.8091	8.621047	0.012393	0.977965
Temp + Swamp	5	-462.003	934.0114	8.82332	0.011201	0.989166
Temp+ Canopy Height	5	-463.134	936.2721	11.08402	0.003617	0.992783

Figure S2.1: Sampling period of all 21 hornbills tracked over the course of this study, where each point represents a single day of tracking. BCH = Black-casqued hornbill; WTH = white-thighed hornbill.

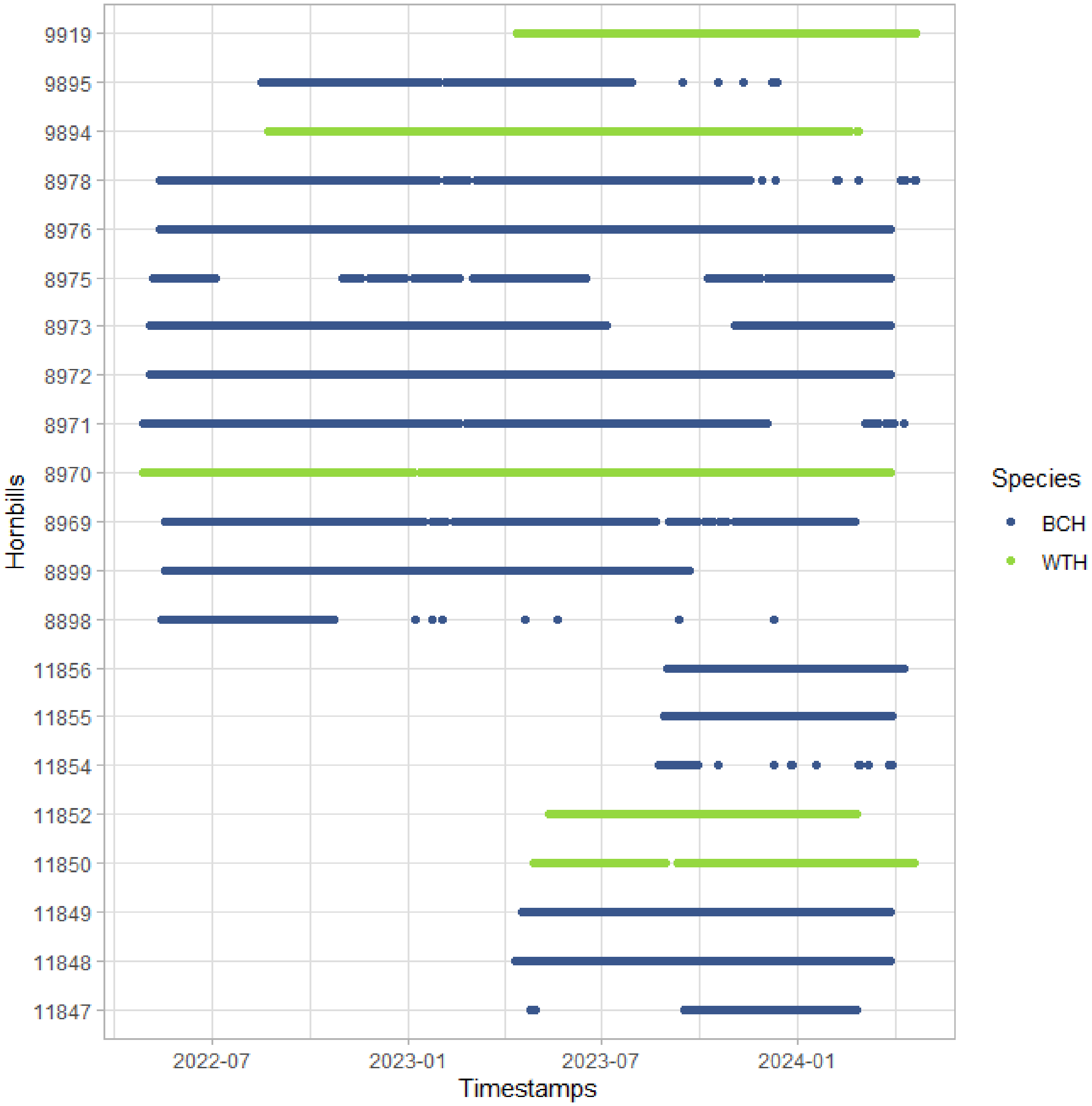


Figure S2.2: Teflon harness removed from a recaptured white-thighed hornbill.

Assessment: We recaptured a male white-thighed hornbill on August 17th, 2021, 15 days after its initial capture. To our knowledge, it is the only hornbill ever to be captured a second time in Cameroon. This event provided an opportunity to assess the impact of the Teflon harness on the bird's body. After removing the harness, we noted rougher skin patches underneath the Teflon ribbon straps compared to the rest of bird's body, but no injuries. We found evidence of the bird attempting to remove the harness at the center attachment point over the breast; both shoulder straps were worn nearly to detachment. The trammel line reinforcing the interior of the harness was undamaged and may have prevented the bird from removing the harness completely. After this assessment, we began to shape the Neoprene patch over the breast so that it aligned completely with the Teflon straps and provided less surface area for the bird to manipulate with its bill.

Figure S2.3: Hornbill selection for habitat variables at 10 m resolution, based on 10 random steps, including **A)** Canopy height, **B)** Vertical complexity, **C)** Distance to small canopy gaps (50 m^2), **D)** Distance to large canopy gaps (500 m^2), **E)** Swamp habitat, and **F)** The interaction between swamp selection and ambient temperature. Covariates included in the habitat selection-free movement kernel of iSSAs include **G)** Step length and **H)** Turn angle. Points represent coefficients and lines represent 95% confidence interval for each individual hornbill in the study. (BCH = Black-casqued hornbill, WTH = White-thighed hornbill). The dotted line at x=0 in each plot represents no selection. Note that the range of values in the x and y axes differs for each plot.

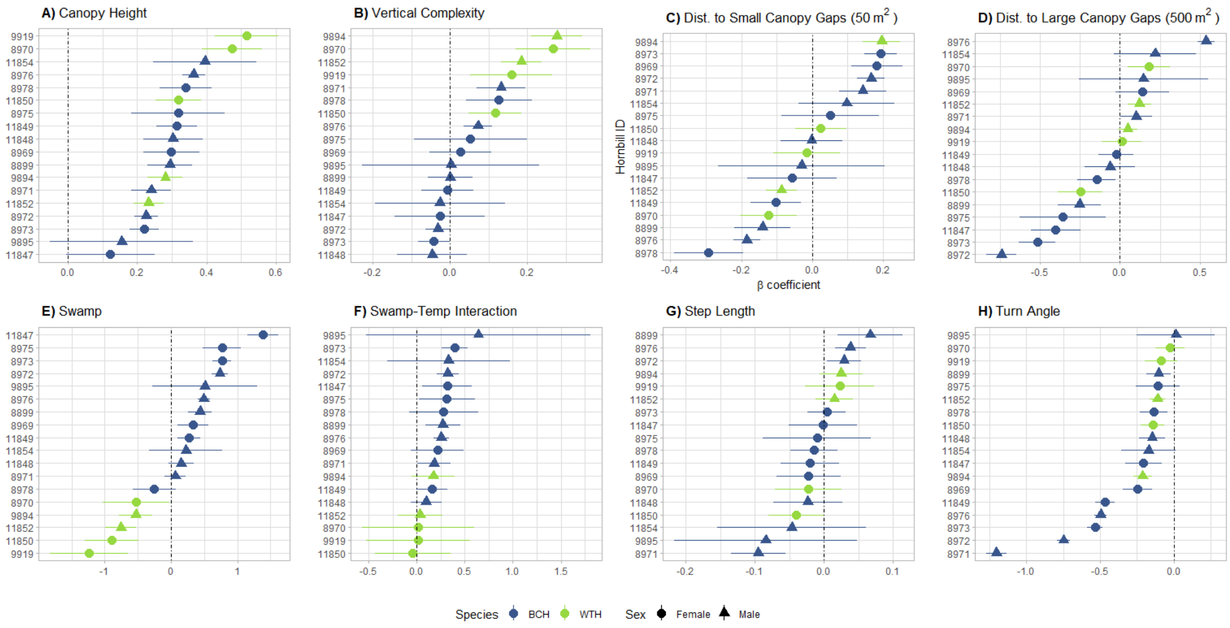


Figure S2.4: Hornbill selection for habitat variables at 10 m resolution, based on 100 random steps, including **A)** Canopy height, **B)** Vertical complexity, **C)** Distance to small canopy gaps (50 m^2), **D)** Distance to large canopy gaps (500 m^2), **E)** Swamp habitat, and **F)** The interaction between swamp selection and ambient temperature. Covariates included in the habitat selection-free movement kernel of iSSAs include **G)** Step length and **H)** Turn angle. Points represent coefficients and lines represent 95% confidence interval for each individual hornbill in the study. (BCH = Black-casqued hornbill, WTH = White-thighed hornbill). The dotted line at x=0 in each plot represents no selection. Note that the range of values in the x and y axes differs for each plot.

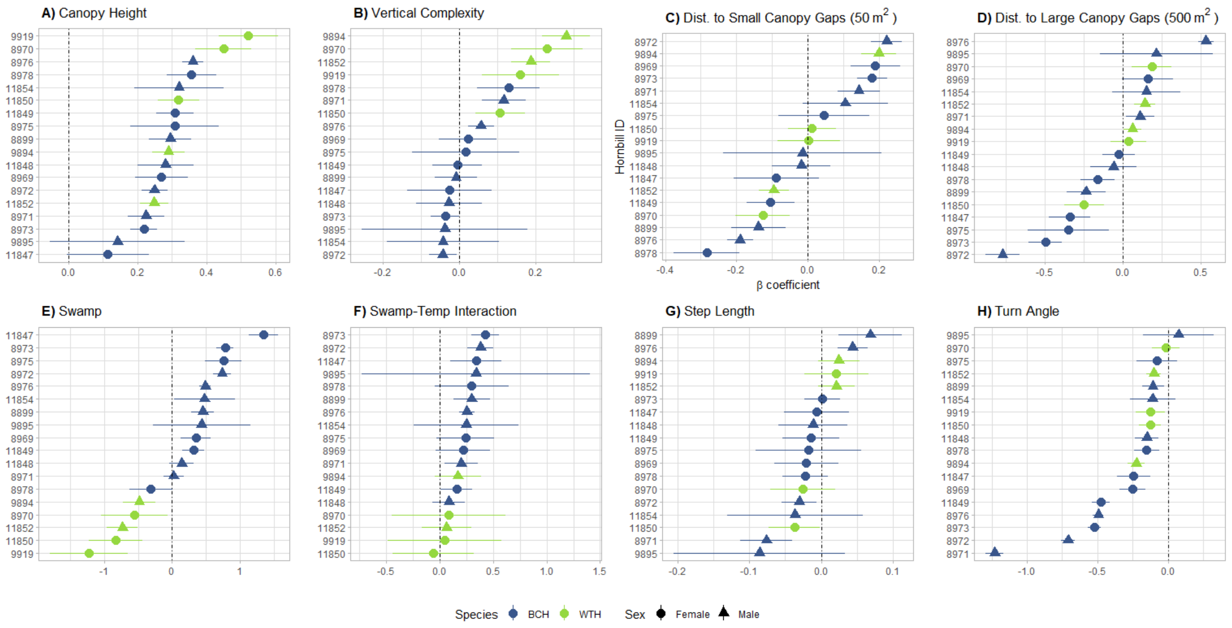


Figure S2.5: Predicted ODBA with respect to temperature for **A)** Black-casqued and **B)** White-thighed hornbill based. Smoothed trendlines are based on a generalized linear mixed-effects model that treats individual hornbill ID as a random effect, with 95% confidence intervals based on predictions conditioned on the fixed effects.

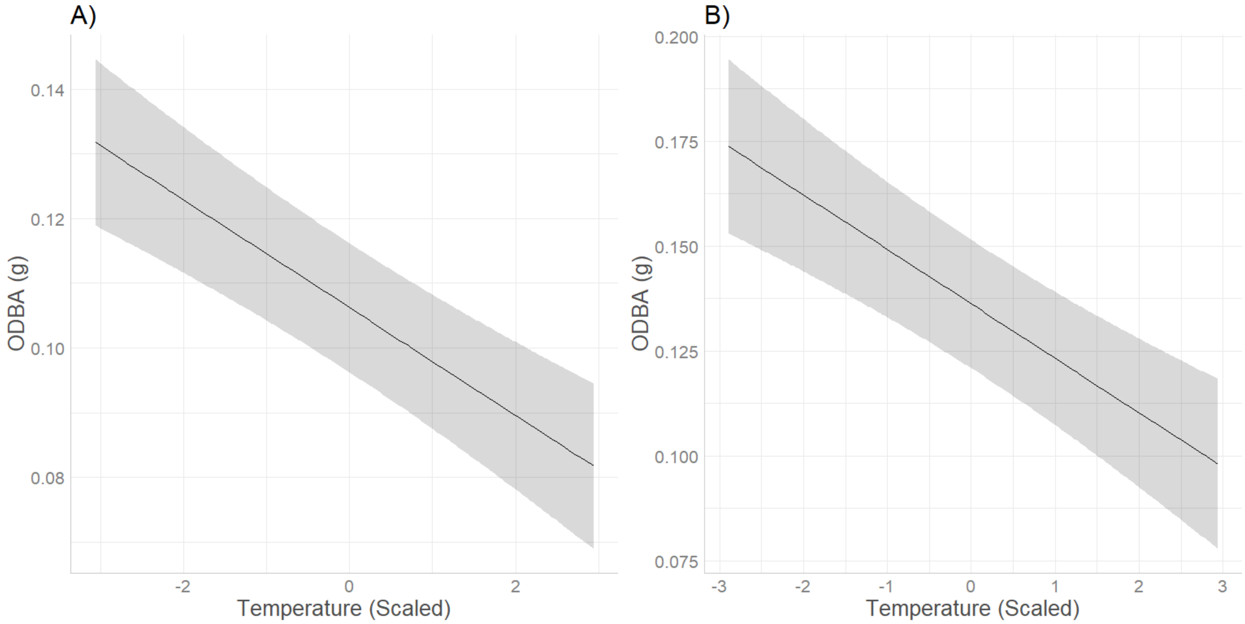


Figure S2.6: Predicted ODBA with respect to swamp habitat for black-casqued hornbill. Estimates and 95% confidence intervals are based on a generalized linear mixed effects model that treats individual hornbill ID as a random effect.

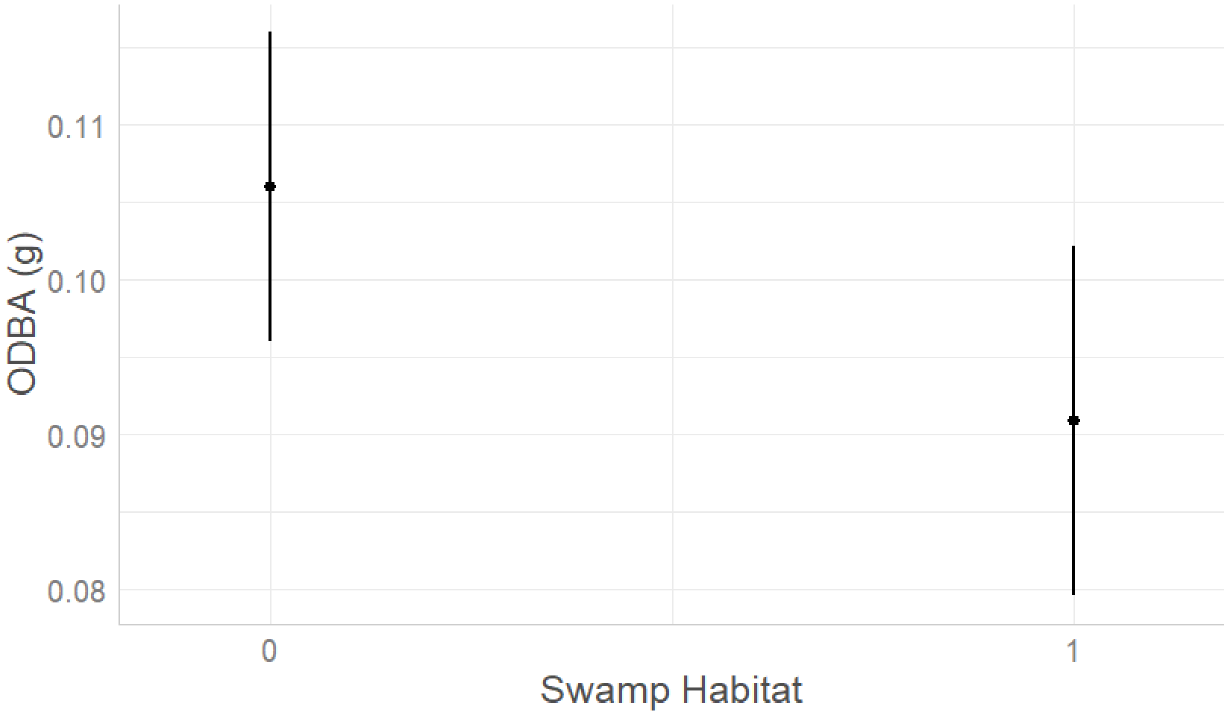


Figure S2.7: Density plots comparing the distributions of covariates at simulated hornbill locations used in seed dispersal models based on (**A, C, E**) white-thighed and (**B, D, F**) black-casqued hornbill movements. "Used" and "available" locations represent the ends of observed and randomly generated movement steps, respectively. As in used-habitat calibration plots, note that the lines for "used" habitat fall within the distribution of lines for 100 simulated predictions.

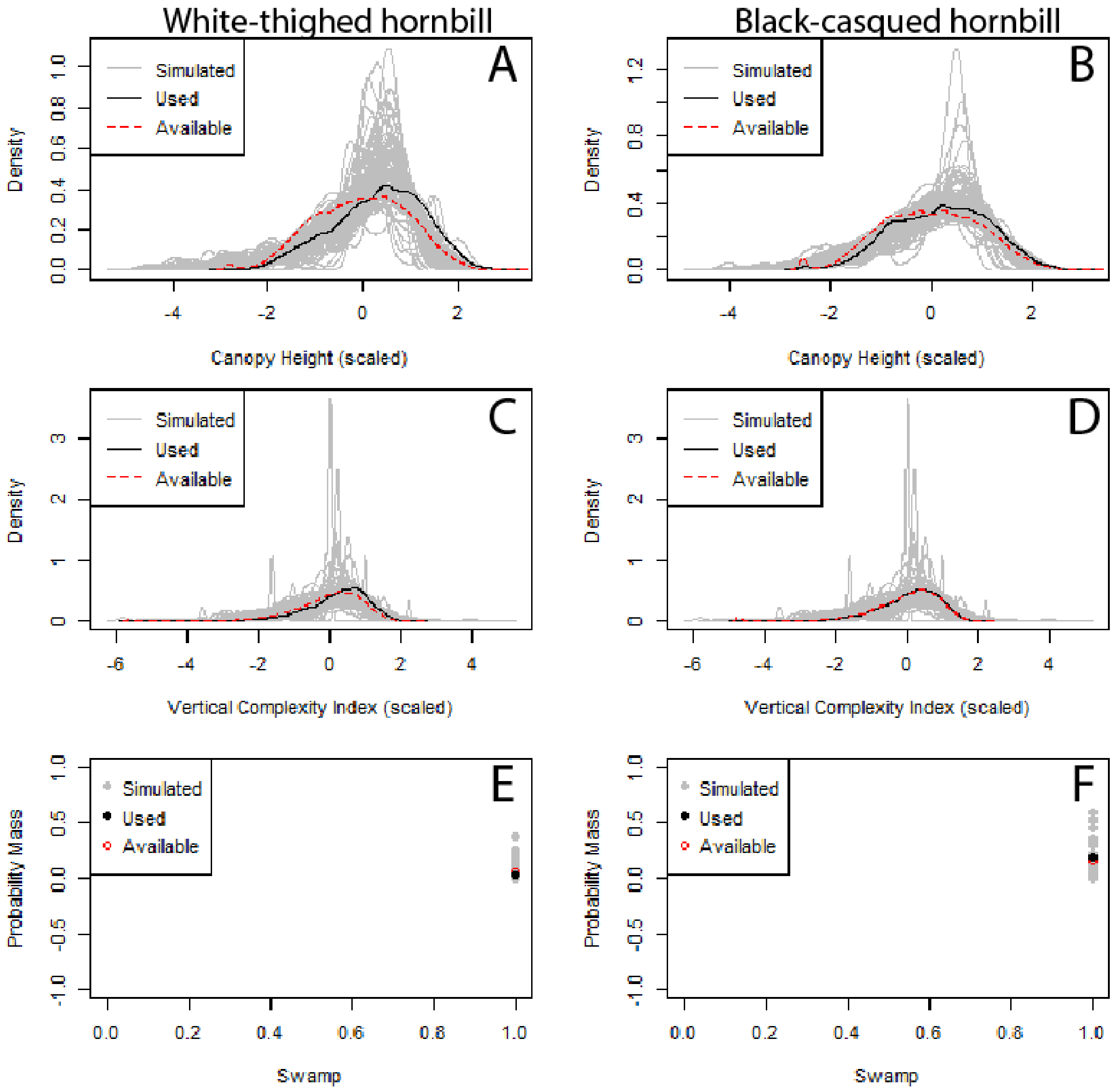
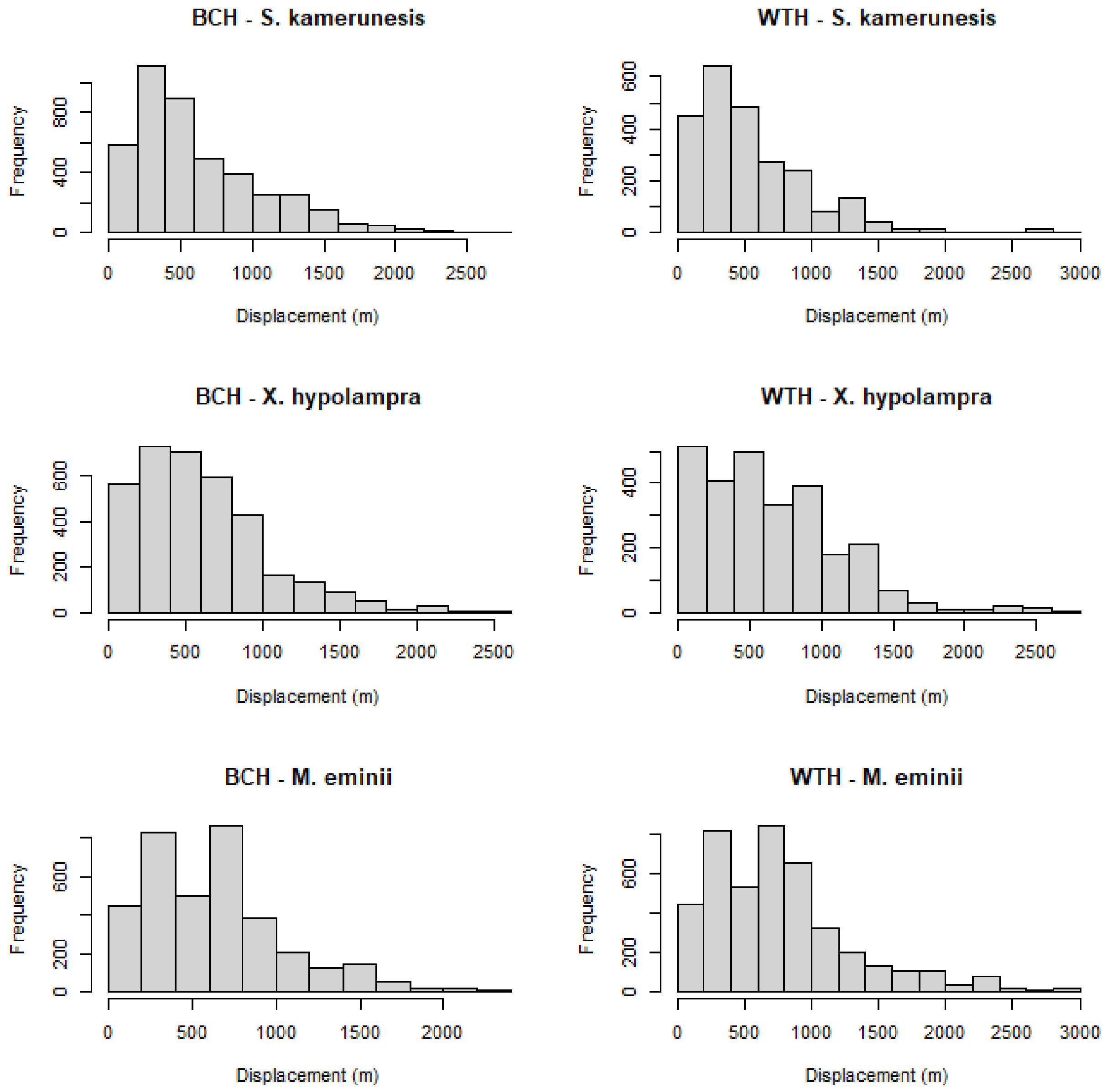


Figure S2.8: Histograms representing displacement distances based on simulated seed dispersal events. Hornbill-tree pairings match those shown in Figure 5 (BCH = Black-casqued hornbill; WTH = White-thighed hornbill).



CHAPTER 3

Upscaled LiDAR metrics reveal habitat structural preferences of hammer-headed bats (*Hypsignathus monstrosus*) in a Central African rainforest

This manuscript is in preparation as Russo, N.J., J.M. Takuo, V. Tegebong, M. LeBreton, M. Dean, A. Ferraz, N. Barbier, M. Wikelski, E.M. Ordway, S. Saatchi, and T.B. Smith. Upscaled LiDAR metrics reveal habitat structural preferences of hammer-headed bats (*Hypsignathus monstrosus*) in a Central African rainforest.

ABSTRACT

Animals with key ecological roles, such as seed-dispersing fruit bats, rely to varying degrees on habitat structure to indicate the locations of rewards and risks. To understand how variation in vegetation structure influences fruit bat selection throughout the diel cycle, we related movement steps of hammer-headed bats (*Hypsignathus monstrosus*) to attributes of canopy height, vertical and horizontal structure, and habitat type in a mature rainforest of southern Cameroon. Vegetation structural metrics were measured with UAV-LiDAR at 10 m resolution for a 25 km^2 study area. Because bats frequently moved outside the study area, we also characterized vegetation height and horizontal complexity over the full extent of bat movement trajectories by upscaling UAV-LiDAR measurements using primarily GEDI spaceborne lidar data. Hammer-headed bats preferred areas of intermediate canopy height close to large canopy gaps (≥500 m) and preferred *Raphia*-dominated swamp habitats. Individual bats varied in selection for vertical vegetation complexity, distance to smaller canopy gaps (≥50 m) and plant volume density of intermediate vegetation strata. We also found that hammer-headed bats prefer swamp habitats, intermediate canopy height, and areas closer to canopy gaps over the full extent of movement trajectories, using upscaled LiDAR metrics. These behaviors indicate a potential preference for

open airspace during foraging or moving among resources, and for dense swamp vegetation during roosting and foraging periods. In addition, most bats made regular long flights of up to 17.7 km shortly after sunset and before sunrise, and mostly limited their movements to three or fewer destinations throughout the tracking period. These results highlight the importance of integrating remote sensing and animal tracking data to understand habitat selection of a species whose movements influence viral spillover risk and spatial patterns of seed dispersal.

INTRODUCTION

Animal movements are underexplored in tropical habitats, with critical consequences for ecosystem functioning and viral spillover. Fruit bats (Pteropodidae) are important long-distance seed dispersers (Van Toor *et al.* 2019) and viral reservoirs of tropical ecosystems (Plowright *et al.* 2021). For example, a single colony of straw-colored fruit bats (*Eidolon helvum*) in Ghana can disperse hundreds of thousands of seeds in one night, and up to 95 km—among the longest distances of any known disperser (Van Toor *et al.* 2019). Beyond the economic value this ecosystem service provides for tropical reforestation, seed dispersal by bats ultimately influences the genetic diversity and species composition of rainforest tree communities (Nathan & Muller-Landau 2000; Jeltsch *et al.* 2013). Understanding the movements of fruit bats is also important in disease transmission. Many bat species have an unusually high virus tolerance and may, consequently, act as viral reservoirs. Changes in bat behavior and resource selection—especially those that lead bats to come into contact with humans—are thought to heighten the possibility of viral spillover (Plowright *et al.* 2021; Eby *et al.* 2023).

Animals value landscapes according to the distribution of resources and risk. Resources include foraging, resting, and nesting areas, while risks include predation and thermal stress (Wittemyer *et al.* 2019). Vegetation structure can indicate the locations of resources and influence route use (Davies & Asner 2014; Abrahms *et al.* 2021). Three-dimensional vegetation structure has been shown to shape bat communities, with some species specialized for denser vegetation and others preferring open airspace for foraging (Blakey *et al.* 2017). Vegetation can sometimes hinder maneuverability by obstructing bats' flight paths (Froidevaux *et al.* 2016). Characterizing 3D vegetation structure at fine scales (sub-meter resolution) is possible with terrestrial, drone-mounted, and airborne Light Detection and Ranging (LiDAR; Lines *et al.* 2022). This capability enables ecologists to quantify the 3D space use of arboreal and aerial animals (Hermans *et al.* 2023). However, animals may move across seasonal home ranges that exceed extents that can be surveyed by high-resolution LiDAR. Spaceborne LiDAR, including the recent Global Ecosystem Dynamics Investigation (GEDI) mission, addresses this problem by collecting 3D vegetation structure data at a near-global extent (Dubayah *et al.* 2020), albeit with gaps in spatial coverage. Spaceborne LiDAR is crucial for understanding how animals evaluate landscapes throughout migrations, dispersal, and nomadic movements.

It is advisable for movement ecology research to keep pace with advances in remote sensing, which now enable the characterization of 3D vegetation structure at broad spatial extents (Neumann *et al.* 2015). Some species of fruit bats fly dozens of kilometers per night (Van Toor *et al.* 2019), encountering a variety of habitats as they commute among resources. Well-studied species display advanced spatial memory of fruiting trees and roosting sites (Toledo *et al.* 2020; Harten *et al.* 2024); in fact, the Egyptian fruit bat (*Rousettus aegyptiacus*) creates new routes among these resources using cognitive map-based navigation (Toledo *et al.* 2020). Disentangling the role of landscape features in predicting bat movement behavior will help guide conservation decisions and predict disease spread (Eby *et al.* 2023). Continued research linking animal movement to remotely sensed landscape features can address how animals move in relation to landscape features, and how their movements influence vegetation structure through seed dispersal and nutrient transport (Russo *et al.* 2023).

Hammer-headed bats (*Hypsignathus monstrosus*) are a lekking species that can be found in mature rainforests, rural settlements, and urban areas in Central and West Africa, and they are the largest fruit bat species of continental Africa (Kingdon 2015; Schloesing *et al.* 2023). This species has been observed migrating along the Congo River, and its short-distance movements have been tracked previously at a lek in the Republic of Congo (Olson *et al.* 2019; Schloesing *et al.* 2023). Still, next to nothing is known about longer-distance movements of hammer-headed bats, which are important viral reservoirs (Leroy *et al.* 2009). A GPS tracking study revealed that hammer-headed bats prefer agricultural areas in a managed forest-agricultural landscape, and typically move along waterways (Schloesing *et al.* 2023). Because hammer-headed bats often vocalize in large canopy gaps and roost in dense vegetation, we expected 3D vegetation structure to influence their habitat selection in a mature tropical lowland rainforest.

We aimed to reveal the attributes of 3D vegetation structure that influence hammer-headed bat movements. Specifically, we explored 1) Individual-level selection for 3D vegetation structure and time-dependent selection for habitat types at high spatial resolution (10 m), 2) Population-level selection for vegetation structure at coarser spatial resolution (30 m) and across the full extent of bat movement trajectories, and 3) Nightly movement distances and recursions to locations of high use.

METHODS

Study site

All field research took place within the Bouamir Research Site (hereafter, “Bouamir”), a 25 km^2 study area near the center of the Dja Faunal Reserve in southern Cameroon (3°11’ N, 12°48’ E). The site comprises mainly *terra firme* forest, *Raphia* palm-dominated swamps, and grass-covered peaks called inselbergs. A drone-mounted lidar survey for the entire study site was completed in March 2022, providing metrics of 3D vegetation structure based on a point cloud with an average density of 300 points · m^{-2} (Reddy *et al.* 2024; **Fig. 3.1A**).

Bat capture and tracking

We captured bats using mist nets (38 mm gauge) placed in the canopy in front of known roosts within Bouamir and captured five bats each in Aug. 2022 and Aug.-Sep. 2023 (n=10 total bats). We constructed and operated canopy mist nets following Russo et al. (2024a) from sunset until sunrise. We tagged seven males and three females with a solar-powered 15 g GPS tag containing an accelerometer (e-obs; e-obs.de). Tags were glued to a lightweight “cape” (Olson *et al.* 2019) fastened around the neck using a 0.9525 cm (3/8”) strap (BioThane) secured with a plastic snap rivet. Tags collected a GPS location every thirty minutes from 17:00-7:00 local time. We downloaded GPS data manually from each tag throughout the tracking period using an e-obs BaseStation with a 10-element Yagi antenna. We retrieved 3-15 nights of data from nine bats (**Fig. S3.1**) and used GPS data from these individuals for analyses. All capture and tracking methods were approved by Cameroon’s Ministry of Scientific Research and Innovation and Ministry of Wildlife and Protected Areas, and the University of California, Los Angeles Animal Research Committee, under protocol #2019-037-01.

Habitat selection at site level (25 km^2)

We quantified habitat selection of each bat based on seven structural metrics measured with LiDAR within the Bouamir Research Site (**Fig. 3.1A;** descriptions in **Table S3.1**) and included an interaction between hours after sunset and use of swamp habitat. After an initial period of data exploration, it appeared that most of the bats preferred areas with intermediate canopy height relative to available habitat, so we chose to include a quadratic term for canopy height that would capture this nonlinear relationship. We included only habitat categories for swamps and non-swamps because many of the bats moved among swamps and forests and some bats rarely or never encountered inselbergs. Swamp habitat was defined using a Convolutional Neural Network applied to a cloud-free Sentinel-2 image (Brodrick *et al.* 2019). We quantified selection for each habitat feature using an integrated Step Selection Analysis (iSSA) that included the log-transformed step lengths and cosine of the turn angles as predictors in the selection-free movement kernel (Avgar *et al.* 2016). This approach compares bat movement "steps"—the straight-line distance between successive GPS locations—to 10 randomly generated steps based on the observed distribution of step lengths and turn angles (Thurfjell *et al.* 2014). We scaled and centered each continuous covariate before inclusion in analyses. We determined the direction and magnitude of selection for each covariate based on selection coefficient estimates from the iSSA. All iSSA models were fit using the "fit_issf" function in the "amt" R package (version 0.2.1.0; Signer *et al.* 2019). To determine the influence of canopy height on habitat selection for each bat, we calculated the Relative Selection Strength (RSS) for each value of canopy height relative to the mean canopy height of habitat selected by the bats, while holding all other covariates constant (Avgar *et al.* 2017). This metric enabled us to characterize a nonlinear relationship between canopy height and habitat selection for each bat.

Finally, we used a generalized linear mixed effects model (GLMM) to estimate population-level selection for each covariate, using the "glmmTMB" R package (version 1.1.7; Muff *et al.* 2020; Brooks *et al.* 2023). This model included all covariates from the iSSAs as fixed effects and treated individual bat IDs as a random effect.

Habitat selection at the landscape level

Because the UAV-LiDAR metrics at 10 m spatial resolution only covered the extent of Bouamir (25 km^2), and most of the bats flew beyond the site at some point during the tracking period (**Fig. 3.1B**), we generated metrics of vegetation structure for a 300 km buffer around the Dja Faunal Reserve (~494,000 km^2), which covers the full extent of bat movement trajectories. These metrics included canopy height, which we characterized by upscaling UAV-LiDAR canopy height measurements in a machine learning framework, and two derivatives of the model (height heterogeneity and location of canopy gaps). We used the vegetation relative height 95th percentile (RH 95) metric from Global Ecosystem Dynamics Investigation (GEDI) Level 2A (L2A) data as our target variable for creating an upscaled, wall-to-wall map of canopy height (Belgiu & Drăgu 2016; Dubayah *et al.* 2020). The GEDI data extended across the 494,000 km^2 study area and were collected from 2019 to 2022. To calibrate the RH 95 measurements, we systematically tested combinations of GEDI filters through six different algorithm setting groups, each of which determines how waveforms are interpreted (Hofton & Blair 2019). Our objective was to identify the settings that fit closest to the reference UAV-LiDAR data. Under this calibration approach for RH 95, we identified the optimal settings as the fifth algorithm setting group with quality flag filter equal to 1 and sensitivity filter ranging from 0.98 to 1. To further ensure data quality, we manually removed erroneous data that were not filtered out through this method but were detectable through visual inspection. We constructed the training dataset using the GEDI RH 95 values as the target variable for a Random Forest model, with Landsat 8 bands 2-7 and NIRv (near-infrared reflectance strictly from vegetation), Copernicus Digital Elevation Model (DEM), Copernicus DEM-derived slope and aspect, ALOS PALSAR-2 (HH and HV), and Sentinel-1 (VV and VH) serving as the input variables (n = 14 bands). We generated a canopy height map for the region because unlike available products, our procedure was specific to southern Cameroon and provided complete coverage of the 494,000 km^2 study area (Potapov *et al.* 2021; Lang *et al.* 2023).

We derived canopy height heterogeneity by aggregating canopy height values to 100 m and 1000 m resolution and calculating the standard deviation for each pixel. We also characterized canopy gaps at the landscape-level using the “getForestGaps” function from the “ForestGapR” R package (Silva *et al.* 2019). Unlike at the site level, landscape-level canopy gaps were characterized as areas devoid of vegetation greater than 15 m from the ground. This definition increased the sensitivity of our methods to detect canopy gaps. We included an upper area threshold of 500 Ha for canopy gaps to include large villages but avoid including river surface area as canopy gaps. We generated a raster representing distance to nearest canopy gap in meters using the “distance” function in the “terra” R package (version 1.7-39; Hijmans *et al.* 2024). We included the terms for swamp and the interaction between swamp habitat selection and time since sunset in the landscape-extent model. These were the only two terms included at the same resolution and extent in both the site- and landscape-extent models. We also included log-transformed step length and cosine-transformed turn angle in the landscape-extent model. We conducted a population-level iSSA using a GLMM containing all landscape-level covariates (**Fig. 3.1B**), using the same methods described in the section “Habitat selection at the site level (25 km^2)”.

Movement behavior

Fruit bats are known to repeatedly visit resources with directed movements (Toledo *et al.* 2020; Schloesing *et al.* 2023), known as “recursions” (Berger-Tal & Bar-David 2015). To characterize recursive movements of each bat to areas of high use, we quantified the number of recursions to a 100 m radius around each GPS location using the “getRecursions” function in the "recurse" R package (version 1.1.2; Bracis *et al.* 2018). We used a *k*-means clustering algorithm to identify up to three centroids of recursions throughout each bat's movement trajectory, representing the 75th percentile of recursions or greater (Valletta *et al.* 2017).

Because some of the bats appeared to commute to 1-3 locations after sunset and remain within a small radius at those locations, we were also interested in how step lengths varied with time since sunset. We explored this relationship using a generalized additive mixed model (GAMM) with a smoothed term for hours after sunset, implemented in the "mgcViz" R package (version 0.1.11; Fasiolo *et al.* 2023). We also summarized both the distances between each bat's successive GPS locations and distances from the capture location (Maximum Net Squared Displacement) using the "adehabitatLT" package (version 0.3.27; Calenge 2019). All analyses were conducted using R version 4.3.1 (R Core Team 2023).

RESULTS

Habitat selection at the site level (25 km^2)

The quadratic term for canopy height strongly predicted habitat selection for seven of the nine bats, indicating a nonlinear relationship between canopy height and habitat selection. Examining the Relative Selection Strength across the range of scaled canopy height values revealed that these seven bats move preferentially among habitats with intermediate canopy height (**Fig. 3.2**). This nonlinear relationship was also significant at the population level (GLMM: $p<0.001$; **Table 3.1**).

Four of the nine bats preferred areas closer to canopy gaps of at least 50 m^2 (**Fig. 3.3C**), and seven bats preferred areas closer to large canopy gaps (500 m^2 or larger; **Fig. 3.3D**). At the population level, hammer-headed fruit bats preferentially selected habitats closer to large canopy gaps (GLMM: $p=0.001$; **Table 3.1**), but not small canopy gaps. We did not detect a significant influence of Leaf Area Index (**Fig. 3.3A**), Vertical Complexity Index (**Fig. 3.3B**), or Plant Volume Density at heights of 10-15 (**Fig. 3.3E**) or 15-20 m (**Fig. 3.3F**) on bat habitat selection at the population level (**Table 3.1**). Still, individual bats varied in their preference for these four structural attributes, displaying both positive and negative selection (**Fig. 3.3**). We also found that bats preferentially selected swamp habitats relative to *terra firme* forest and inselbergs (GLMM: $p<0.001$; **Table 3.1**), and that this preference did not vary throughout the night (GLMM: $p=0.369$; **Table 3.1**).

Habitat selection at the landscape level

At the population level, hammer-headed bats selected for intermediate canopy height at a coarser spatial resolution (30 m) and at the full extent of movement trajectories (GLMM: $p<0.001$; **Table 3.2; Fig. 3.2B**). Bats also selected areas closer to canopy gaps at the coarser spatial resolution and greater extent (GLMM: $p<0.001$; **Table 3.2; Fig. 4**). At 100 m spatial resolution, bats selected for areas of greater canopy height heterogeneity (GLMM: $p=0.019$; **Table 3.2**) but selected for lower canopy height heterogeneity at 1000 m resolution (GLMM: $p<0.001$; **Table 3.2**). At the landscape extent, bats preferred swamp habitats relative to other habitat types (GLMM: $p<0.001$; **Table 3.2; Fig. 3.4**), and this preference did not vary with time since sunset (GLMM: $p=0.279$; **Table 3.2**).

Movement behavior

For each bat, we used *k*-means clustering to identify 1-3 sites with recursive movements in 75th percentile (**Fig. 3.4**), indicating locations of high probability of use. Recursive movements to high-use locations varied among bats but ranged from 8 to 63 visits. All bats displaced at least 3 km from their capture location (**Fig. S3.2**). The longest movement distance recorded was 17.7 km, and this displacement occurred within 30 min between successive GPS locations (**Figs. 3.4;**

S3) During this flight, a female bat (ID:10232) left the protected Dja Faunal Reserve and entered a human-settled landscape (**Fig. 3.1B**). We detected a nonlinear relationship between step lengths and hours after sunset (GAMM: $R^2=0.067$; $p<0.001$), with many individuals moving the greatest distances shortly after sunset and again before sunrise (**Fig. S3.4**).

DISCUSSION

In this study, we showed how hammer-headed bats select habitats with respect to 3D vegetation structure. At the population level, bats preferred areas of intermediate canopy height and areas close to large canopy gaps. This relationship was evident at both site-level (25 km^2) and landscape-level (i.e., entire movement trajectory) extents. However, individual variation in selection for other features of 3D vegetation structure—including vertical complexity, plant volume density, and distance to smaller canopy gaps—indicated that variation in both vertical and horizontal vegetation structure is important for supporting a population's foraging and roosting behaviors.

Bats preferred *Raphia* palm-dominated swamps to other habitat types at both site- and landscape-level extents. Black-casqued hornbills (*Ceratogymna atrata*) exhibit a similar behavior at the Bouamir Research Site (Russo *et al.* 2024b); *Raphia* swamps likely provide a cool location for a day roost and dense vegetation that may conceal bats from predators. Still, we did not detect a population-level signal of selection for plant volume density of mid-story vegetation strata. Swamp habitats occur throughout Cameroon's rainforest zone and may be a necessary landscape feature for hammer-headed bat populations. Indeed, hammer-headed bats in the Republic of Congo preferred areas near watercourses, which could also indicate a preference for foraging or roosting in wetlands (Schloesing *et al.* 2023). Figs (*Ficus* spp.) are an important component of fruit bat diets that occur frequently along Central African waterways (Gautier-Hion & Michaloud 1989).

The preference of several individuals to move among areas close to large canopy gaps may also reflect the selection of trees that produce abundant fruits with small seeds. *Musanga cecropioides* is one of the preferred species in the hammer-headed bat's diet (Schloesing *et al.* 2023), and it typically grows in disturbed and early successional areas, with some mature trees persisting in mature rainforest (Zebaze *et al.* 2022). Although we did not determine which other species might be consumed by hammer-headed bats in the area, small-seeded tree species like *M. cecropioides* are typically efficient colonizers of disturbed habitats (Howe & Smallwood 1982) and large canopy gaps such as inselbergs. Our results show that individual bats vary widely in their preference for other attributes of 3D vegetation structure, which may influence their roles as seed dispersers. Individual animals exhibit "personalities", or behavioral types, that reflect different preferences in space use and have been hypothesized to influence spatial patterns of seed dispersal (Spiegel *et al.* 2017; Zwolak & Sih 2020; Stuber *et al.* 2022). Such individual variation indicates the importance of landscape heterogeneity in supporting animal populations and their ecological roles, which can influence landscape heterogeneity in turn through seed dispersal (Russo *et al.* 2023). Although fragmentation can limit many large-bodied frugivores from dispersing seeds among forest patches, smaller frugivores like bats may play a key role in reforestation and recovery of aboveground carbon stocks by frequenting villages and canopy gaps (Bello *et al.* 2024).

Canopy height heterogeneity is a measurement of horizontal complexity in vegetation structure. At the landscape extent, bats selected areas of greater heterogeneity at the 100 m scale and lower heterogeneity at the 1000 m scale. Swamps, inselbergs, and the research camp where all bats were captured typically had high height heterogeneity at the 100 m scale. At the 1000 m scale, horizontal variation in vegetation structure was high in a region to the south of where bats were captured, marked by a high concentration of inselbergs. Accordingly, the 1000 m scale may not be relevant to the scale of home range selection by many of the bats. The positive population-level selection for canopy height heterogeneity at the 100 m scale may reflect a preference for transitional areas between forest and swamp or forest and inselberg.

Very few studies report animal movement data from the Central African tropics, and these studies are mainly from a limited number of taxa and intensively studied locations (Kays *et al.* 2022). Compounding this issue is the difficulty of tracking bats over multiple seasons due to limitations in battery life (Teague O'Mara *et al.* 2014). Hammer-headed bats are thought to migrate long distances, but tracking technology has not yet revealed the nature of these events. During the short period we tracked hammer-headed bats (3-15 nights), we recorded displacements up to 17.7 km from roosting locations. These distances were greater than those reported from other studies of this species over a similar time period, but unlike these previous studies (Olson *et al.* 2019; Schloesing *et al.* 2023), individuals in our study were not tagged at leks. Future tracking studies that capture seasonal variation in hammer-headed bat movement, including migrations, would be invaluable for characterizing this species' behaviors and their consequences for ecosystem functioning and disease transmission.

Nightly movements of hammer-headed bats were relatively predictable, with repeated visits, or recursions, to one to three locations over the duration of the tracking period. Although these locations were sometimes several kilometers apart, bats frequently exhibited directed movements, with long movement steps and turn angles near zero. Bats typically undertook these long, directed flights shortly after leaving the roost at sunset. These observations provide further evidence of fruit bats' advanced spatial memory. The Egyptian fruit bat, a related species, has been shown to possess a "cognitive map" of roosts and fruiting trees and develop shortcuts among these locations in an arid environment (Toledo *et al.* 2020). In more complex environments, such as tropical rainforests, spatial memory is thought to be less useful for animal movement due to the costs of processing information (Fagan *et al.* 2013). Hammer-headed bats might overcome this problem by moving among easily distinguishable landscape features, such as inselbergs, which create large canopy gaps. Longer-term tracking studies would reveal how bats navigate and find new resources when fruits are depleted at repeatedly visited trees.

Although battery life still limits long-term studies of fruit bat movements, an important step towards understanding seasonal variation in fruit bat habitat selection is to characterize both vertical and horizontal vegetation structure at spatial extents that cover the full range of their movements. We addressed this challenge by upscaling canopy height, gap, and heterogeneity metrics from a 25 km^2 UAV-LiDAR study area to a 494,000 km^2 study area covering most of southern Cameroon and neighboring regions. Hammer-headed fruit bats forage in open spaces, roost in dense vegetation, and commute long distances across landscapes containing forests, wetlands, inselbergs, waterways, villages, agriculture, and other anthropogenic features (Schloesing *et al.* 2023). NASA's GEDI mission enabled us to characterize 3D structure at a broader extent than what is possible with UAV-LiDAR alone (Dubayah *et al.* 2020). Still, UAV-LiDAR surveys characterize 3D vegetation structure at much higher spatial resolution (Boucher *et al.* 2023), so it is advantageous to investigate habitat selection with both UAV-LiDAR and spaceborne LiDAR, as we showed in this study.

Conclusions

Tropical forests are hotspots for biodiversity, due in part to their high structural complexity (Ehbrecht *et al.* 2021). Tropical humid forests exhibit high structural complexity in both vertical and horizontal dimensions, and our study showed that hammer-headed bats require a wide variety of vegetation cover types, including open space near canopy gaps, swamp habitats, and forests of intermediate height. In human-settled areas, hammer-headed bats move primarily among agricultural areas and waterways, likely driven by the need to find fruits (Schloesing *et al.* 2023). Understanding how hammer-headed bats move among foraging and roosting sites in mature rainforest habitat can lend insight into the habitat requirements necessary to promote their role as seed dispersers and limit the risk of viral spillover events.

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TABLES AND FIGURES

Table 3.1 Estimated effects of environmental and behavioral covariates on bat habitat selection at the Bouamir Site extent (25 km^2), from a generalized linear mixed effects model (GLMM) that treats individual bat ID as a random effect. The number of asterisks (*) after a coefficient estimate correspond to significance at the level of 0.05, 0.01, and 0.001, respectively. PVD = Plant Volume Density.

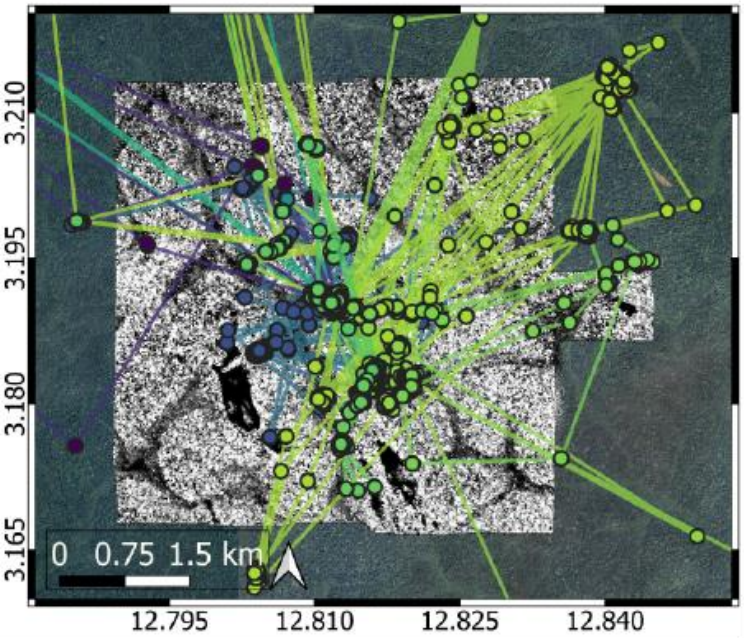
Covariate	**Estimate (SE)**	**p-Value**
Canopy Height	0.097248 (0.069760)	0.16331
Canopy Height^2	-0.208750 (0.046693)	7.80e-06 ***
Vertical Complexity Index	-0.029917 (0.058727)	0.61045
Leaf Area Index	-0.01175	0.762192
Distance to gap 50 m^2	-0.18008	0.12523
Distance to gap 500 m^2	-0.29549	0.002515**
PVD 10-15 m	0.002663	0.95379
PVD 15-20 m	0.038824	0.246195
Swamp	0.847766	3.96e-08***
Hour after sunset:Swamp	0.009779	0.368722
log(Step Length)	0.106827	5.96e-10***
cos(Turn Angle)	-0.51521	1.13e-05***

Table 3.2 Estimated effects of environmental and behavioral covariates on bat habitat selection at the landscape extent, from a generalized linear mixed effects model (GLMM) that treats individual bat ID as a random effect. The number of asterisks (*) after a coefficient estimate correspond to significance at the level of 0.05, 0.01, and 0.001, respectively.

Covariate	**Estimate (SE)**	**p-Value**
Canopy Height	-0.16152	0.067684
Canopy Height^2	-0.13631	3.76e-09***
Distance to gap, threshold 15 m	-0.20026	9.35e-07***
Canopy heterogeneity (100 m)	0.148429	0.019564*
Canopy heterogeneity (1000 m)	-0.28654	1.29e-05***
Swamp	0.50916	0.000303***
Hour after sunset:Swamp	0.010785	0.279466
log(Step Length)	0.046192	0.000115***
cos(Turn Angle)	-0.57647	2.11e-08***

Figure 3.1: Movement trajectories of all bats tracked at the Bouamir Research Site and a depiction of the two spatial extents of habitat selection analyses. **A)** Attributes of 3D vegetation structure measured at 10 m were limited to Bouamir. **B)** We used upscaled 3D vegetation structure metrics to quantify habitat selection at the full scale of bat movement tracks. Many of the bats flew nightly distances of several kilometers, and one bat crossed the boundary of the Dja Faunal Reserve. The inset photo shows a hammer-headed bat carrying a 15 g e-obs tag.

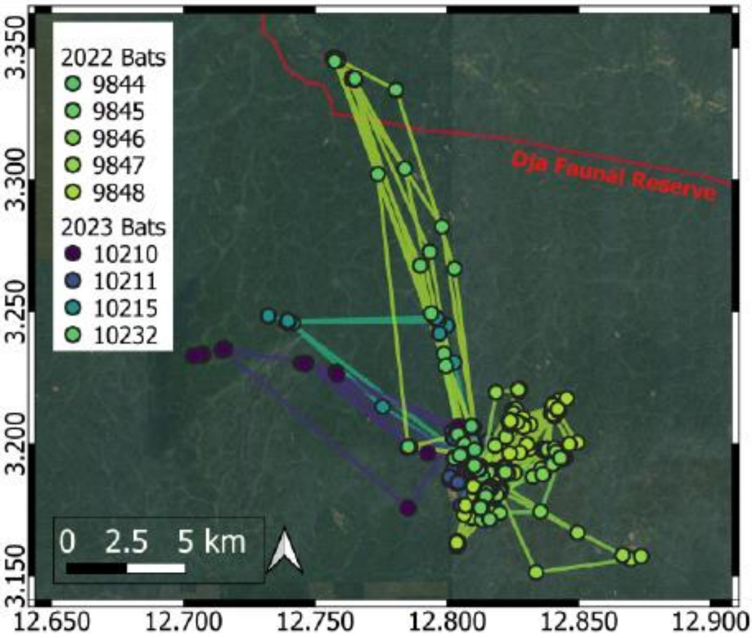
A) Site Level (25 km²)



Covariates

- Canopy Height (10 m)
- Canopy Height² (10 m)
- Vertical Complexity (10 m)
- Leaf Area Index (10 m)
- Distance to gap ≥50 m²
- Distance to gap ≥500 m²
- Plant Volume Density
  - 10-15 m (10 m)
  - 15-20 m (10 m)
- Swamp (10 m)
- Hour after sunset:Swamp

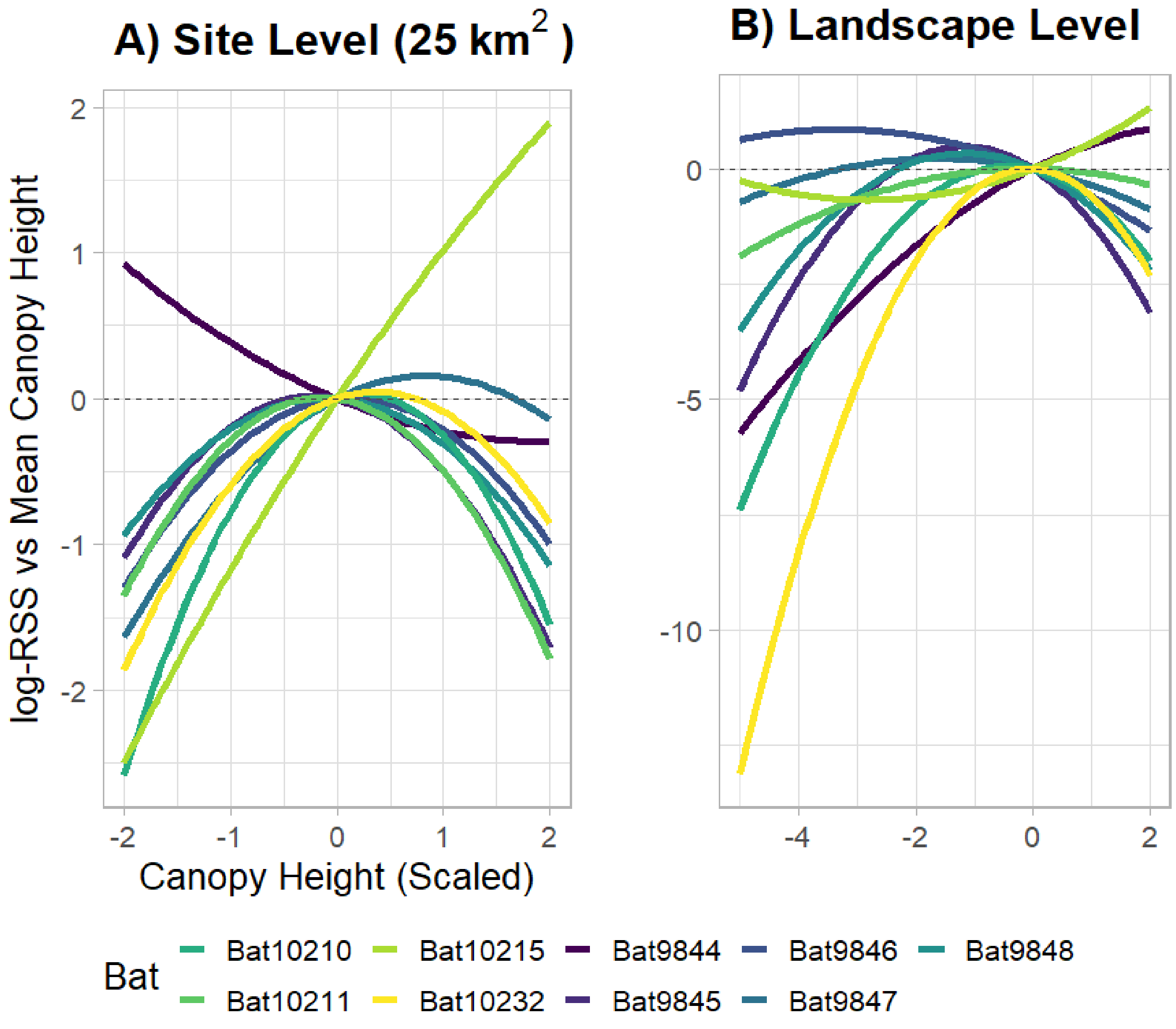
B) Landscape Level (Full Movement Tracks)

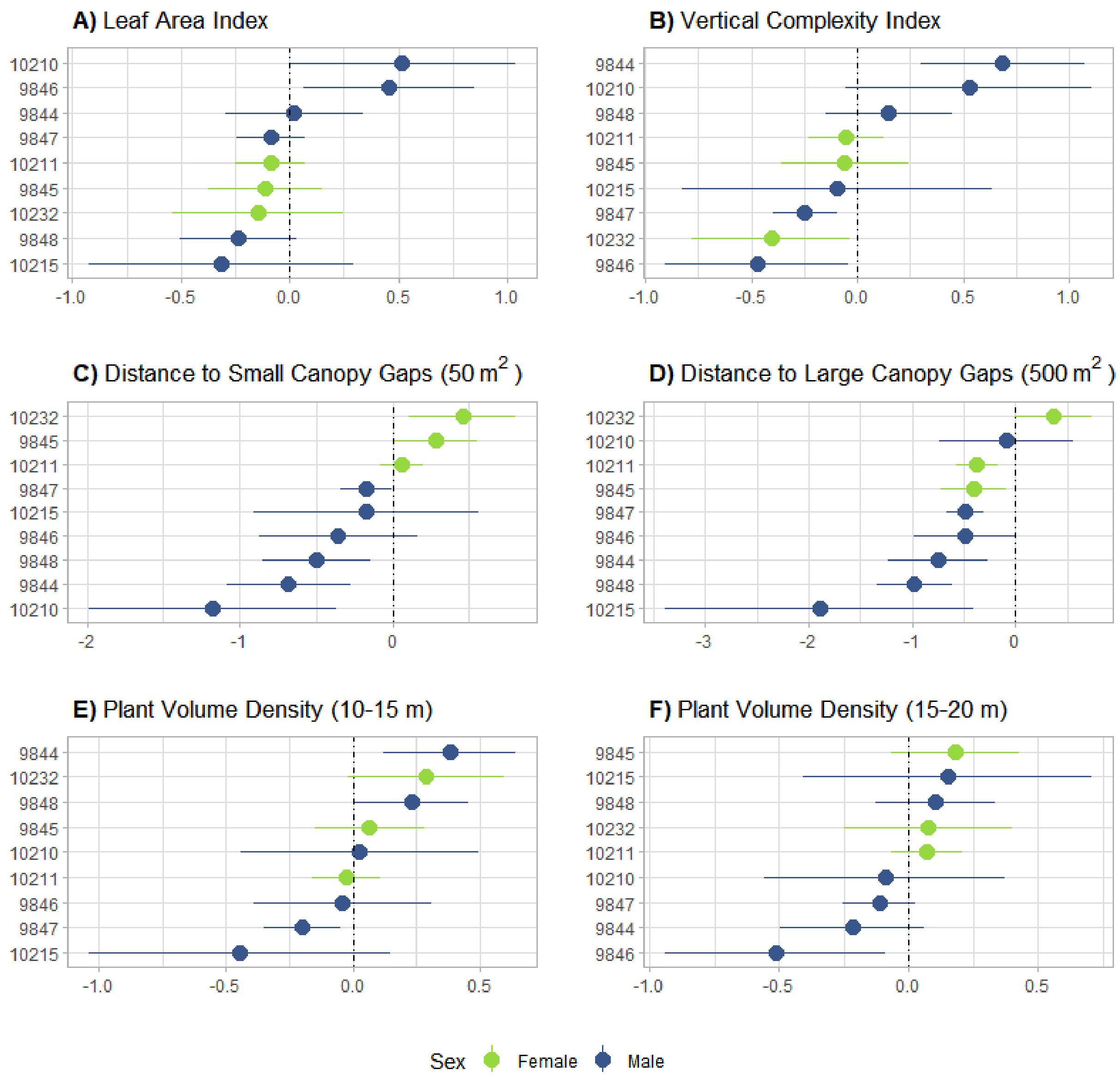


Covariates

- Canopy Height (30 m)
- Canopy Height² (30 m)
- Distance to gap (30 m)
- Canopy Heterogeneity
  - (100 m)
  - (1000 m)
- Swamp (10 m)
- Hour after sunset:Swamp

Figure 3.2: Relative Selection Strength (RSS) for each value of canopy height relative to the mean (indicated by the dashed line at y=0). Each line represents an individual bat, and negative selection for a canopy height value relative to the mean is indicated where the line takes on values less than y=0, and positive selection is indicated where the lines take on values greater than y=0. Note that the plots were generated using a different model structure, and that the limits of both axes differ between the plots.





A) Leaf Area Index

B) Vertical Complexity Index

C) Distance to Small Canopy Gaps (50 m^2)

D) Distance to Large Canopy Gaps (500 m^2)

E) Plant Volume Density (10-15 m)

F) Plant Volume Density (15-20 m)

Figure 3.3: Selection coefficients and 95% confidence intervals (CI) for each linear environmental predictor of bat movements within Bouamir Research Site (25 km^2), including **A)** Leaf Area Index, **B)** Vertical Complexity Index, **C)** Distance to small (50 m^2 or greater) and **D)** large (500 m^2 or greater) canopy gaps, and **E)** Plant Volume Density at a height of 10-15 and **F)** 15-20 m. 95% CIs that do not overlap x=0 indicate a significant effect of the covariate on bat habitat selection. Each bat is represented in the y-axes. Note that the order of bats differs for each plot.

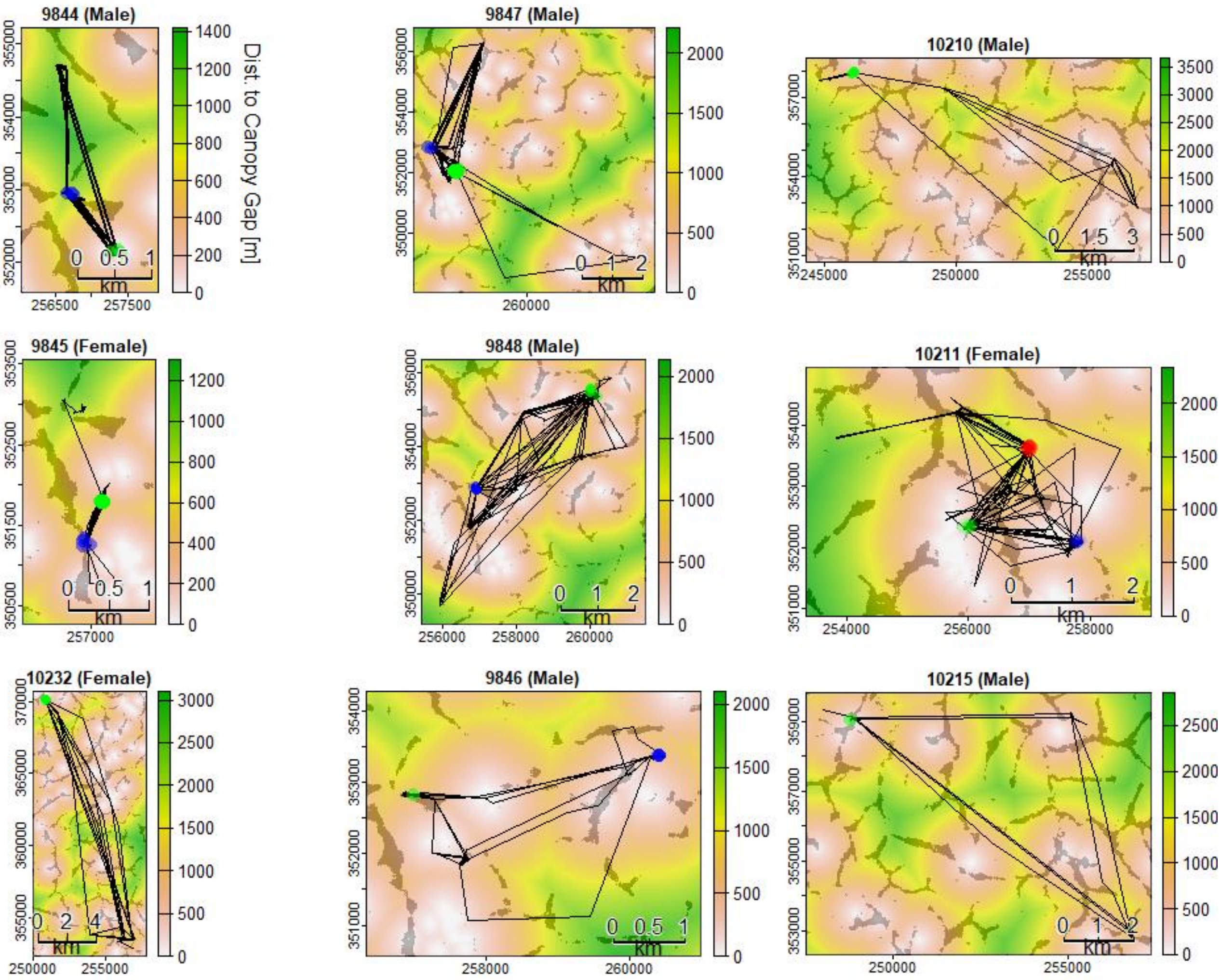


Figure 3.4: Movement trajectories of each bat plotted over distance to canopy gap (15 m threshold) and the distribution of swamp habitats (gray polygons). Clusters of green, blue, and red points represent areas with the greatest revisitation rates (75th percentile or greater).

SUPPLEMENTARY MATERIAL: Supporting figures and tables for Chapter 3

Table S3.1: Descriptions of covariates included in model selection for integrated Step Selection Analyses

Covariate	**Definition**	**Spatial resolution**	**Spatial Extent**
Canopy Height	Height of first lidar return	10 m	Bouamir Site
Canopy Height (Upscaled)	Height of 95th percentile of first lidar returns, with gaps interpolated using Machine Learning	30 m	Landscape
Vertical Complexity Index	A fixed normalization of the entropy function, based on the 3D point cloud	10 m	Bouamir Site
Leaf Area Index	Density of vegetation material, calculated from the 3D point cloud as the sum of leaf area density profiles at 5 m intervals throughout the vertical column	10 m	Local
Distance to gap ≥50 m^2	Distance to gap of minimum size 50 m^2, 5 m height threshold	10 m	Bouamir Site
Distance to gap ≥500 m^2	Distance to gap of minimum size 500 m^2, 5 m height threshold	10 m	Bouamir Site
Distance to gap, 15 m threshold	Distance to canopy gaps of 15 m threshold, and with area not exceeding 10,000 m^2	30 m	Landscape
Plant Volume Density (10-15 m)	Volume of plant area (wood and foliage) 10-15 m above the ground	10 m	Bouamir Site
Plant Volume Density (15-20 m)	Volume of plant area (wood and foliage) 15-20 m above the ground	10 m	Bouamir Site
Canopy Heterogeneity (100m)	Standard deviation of "Canopy Height Upscaled", aggregated to 100 m	100 m	Landscape
Canopy Heterogeneity (1000m)	Standard deviation of "Canopy Height Upscaled", aggregated to 1000 m	1000 m	Landscape
Swamp	Habitat class defined as swamp, all other classes (*terra firme* forest, inselberg) taking on zero	10 m	Bouamir Site/ Landscape
Hour:Swamp	Interaction between hour of the day and habitat class defined as swamp, all other classes (*terra firme* forest, inselberg) taking on zero	10 m	Bouamir Site/ Landscape
Step length	Distance between two successive GPS locations	NA	Bouamir Site/ Landscape

Turn angle	Angle between two successive GPS locations	NA	Bouamir Site/ Landscape
Step ID	Stratum consisting of a selected step (n=1) and randomly generated steps (n=10)	NA	Local/ Landscape

Figure S3.1: Sample periods of bats tracked in **A)** 2022 and **B)** 2023.

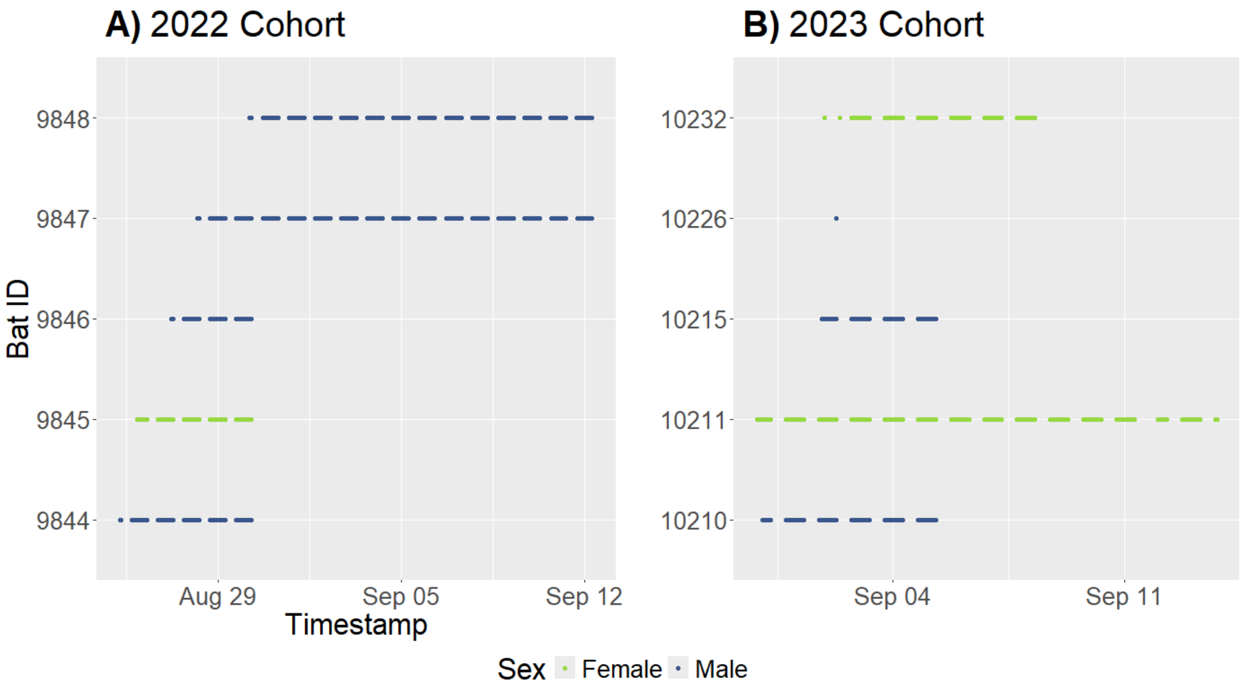


Figure S3.2: Maximum Net Squared Displacement of each bat throughout its tracking period relative to the starting location, which in most cases (except ID:9845) was near the bat’s regular roosting location.

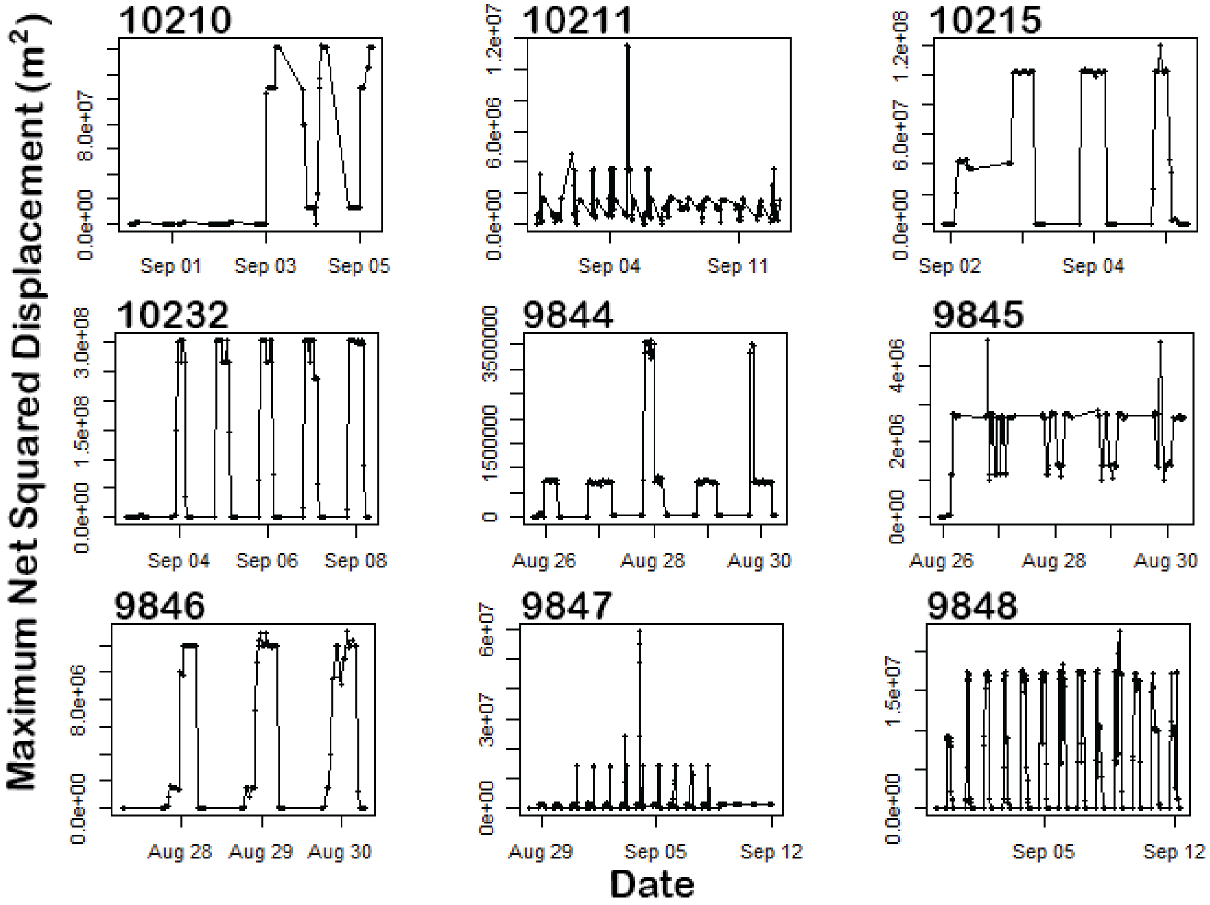


Figure S3.3: Distances between successive relocations for the full tracking period of all bats (n=9), with a constant sampling interval of 30 mins.

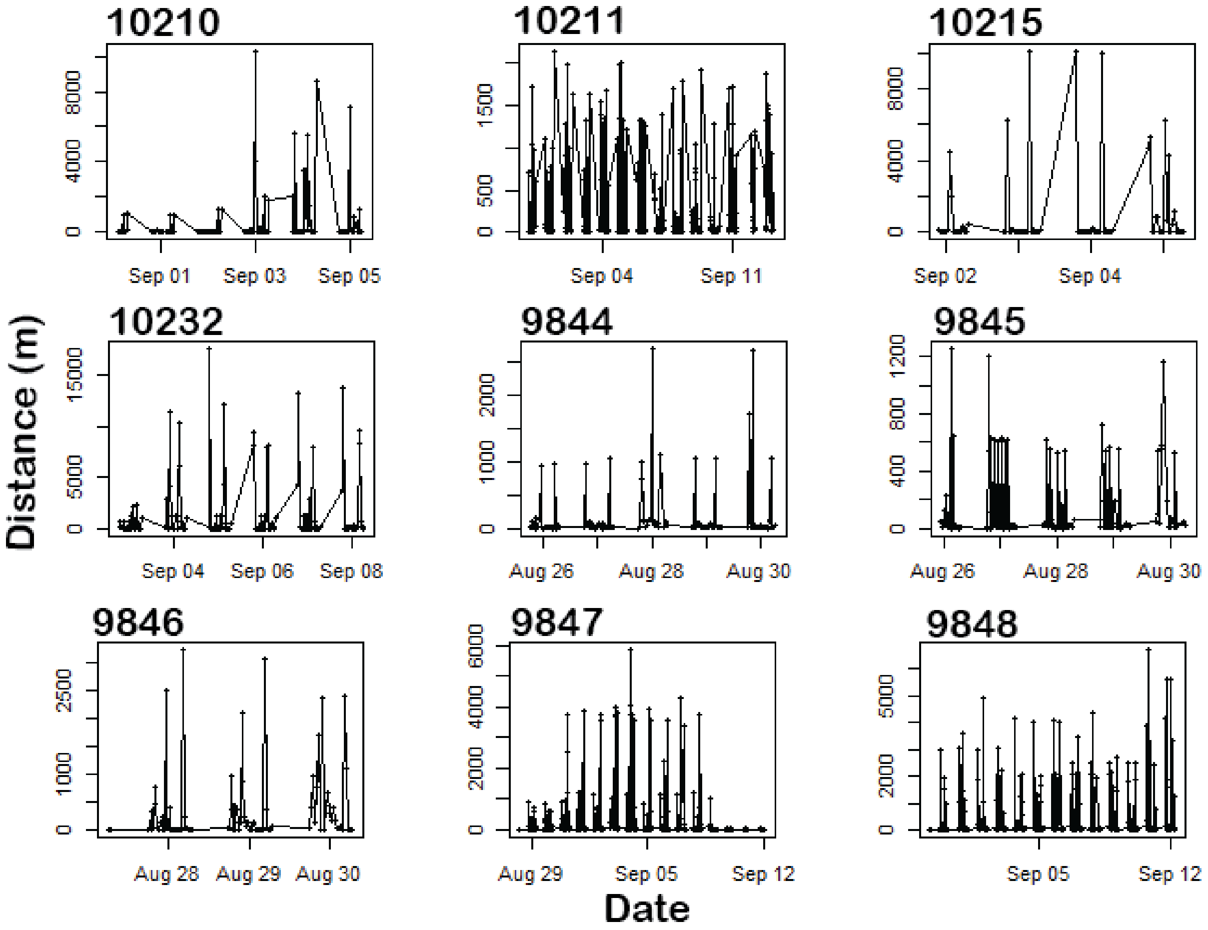
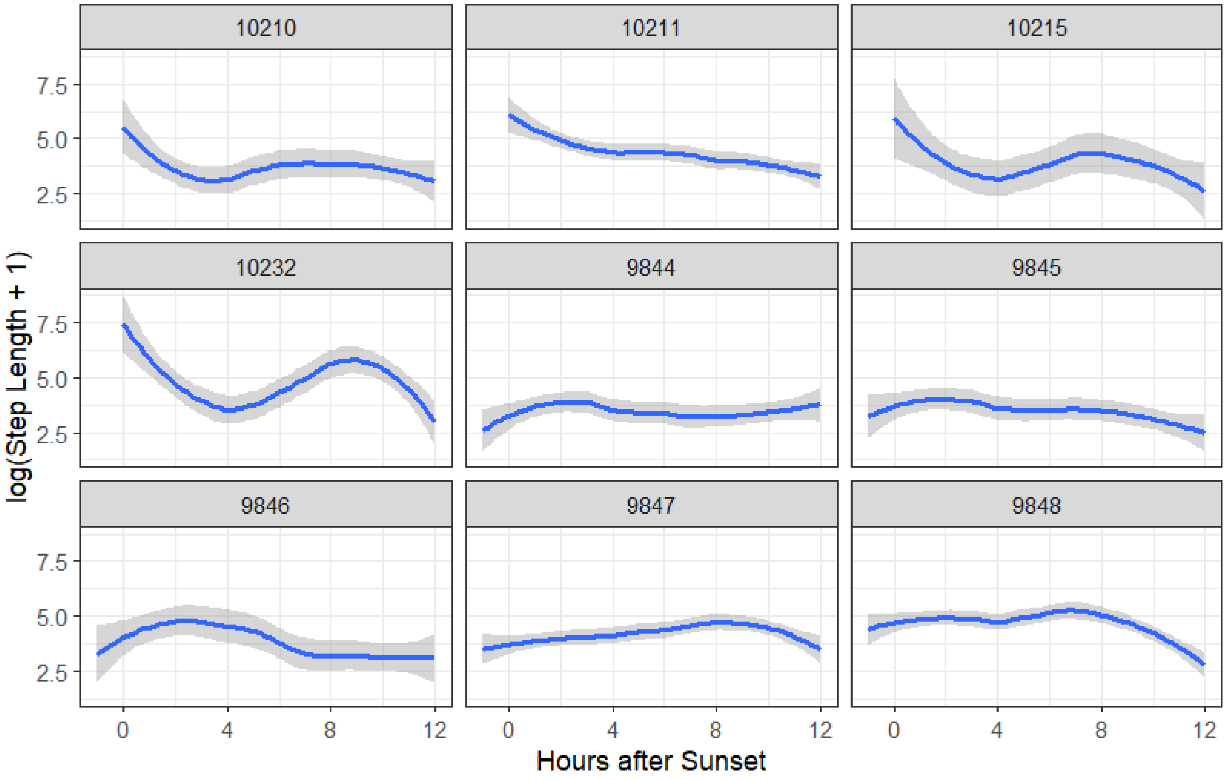


Figure S3.4: Smoothed relationship between step lengths (log transformed) and hours after sunset for each individual bat (n=9), with 95% Confidence Interval.



CHAPTER 4

Long-distance movements and behavioral variation of hornbills diversify seed dispersal patterns

This manuscript is in preparation for publication as Russo, N.J. *et al.* Long-distance movements and behavioral variation of hornbills diversify seed dispersal patterns.

ABSTRACT

The diversity of animal movements and the ecological processes they engender are an often-overlooked aspect of biological diversity. Tropical rainforests harbor the greatest biological diversity on the planet, but the movements of tropical animals are not well known compared to those of higher latitudes. Movements of tropical frugivores are crucial for seed dispersal in rainforests, where up to 90% of trees rely on animals to disperse their seeds. In this study, we GPS-tracked and quantified the movements of 29 African hornbills during two time periods (2009-2012 and 2022-2024) and simulated seed dispersal patterns based on 1) seasonal variation in habitat selection and 2) diversity of movement personalities, or "syndromes." Black-casqued (*Ceratogymna atrata*) and white-thighed (*Bycanistes albotibialis*) hornbills clustered into three movement syndromes based on movement distances and home range use. Seed dispersal scenarios involving hornbills from all three movement syndromes yielded the greatest diversity in both distances and directions of seed dispersal routes. In scenarios based on hornbill habitat selection during Cameroon's major dry season, when fruits are scarce, the mean seed dispersal distance and standard deviation were greater than in the minor rainy, minor dry, and major rainy seasons. Variation in directions of seed dispersal routes was greatest in the major dry and minor rainy seasons. We also found that daily movement distances of white-thighed, but not black-casqued hornbills were greater during periods of lowest fruit availability, as indicated by a ground survey of 26 tree species dispersed by hornbills. For each month, at least one tree species bore ripe fruit, and hornbills undertook movements that enabled seeds to disperse greater than 8000 m. These results suggest that behavioral diversity in hornbill movements enables trees to disperse their seeds across various distances and directions throughout the year. Considering rainforest restoration in the Congo Basin, these results show that while some hornbills are more itinerant in their flight patterns, other hornbills remain within a limited home range year-round, and hornbills of all movement syndromes contribute to a diverse seed rain in regenerating rainforests.

INTRODUCTION

Animals act as "mobile links" among ecosystems by dispersing nutrients, pathogens, seeds, and other propagules (Lundberg & Moberg 2003; Jeltsch *et al.* 2013; Bauer & Hoye 2014). There is a paucity of animal movement data in the Congo Basin (Kays *et al.* 2022), yet this ecoregion is considered one of the most important in the world for sequestering and storing carbon (Dargie *et al.* 2017; Berzaghi *et al.* 2019). Most of the carbon-rich tree species in African rainforests are dispersed by animals (Poulsen *et al.* 2013; Osuri *et al.* 2016), so the future of global carbon stocks will depend heavily on the fate of seed-dispersing animals. In addition, seed dispersers shape the distribution and genetic diversity of economically valuable tree species (Van Toor *et al.* 2019; Rogers *et al.* 2021). Recent advances in remote sensing and animal tracking facilitate detailed research on habitat selection by seed dispersers and resulting effects on ecosystems (Russo *et al.* 2023), making it timely to investigate diversity in movement behavior for animals with key ecological roles.

Individual variation in animal movement impacts ecological processes (Shaw 2020; Graf *et al.* 2024), but it is still not well-established as a component of biodiversity in itself. Animals differ from each other in movement behavior in ways that lead to recognizable movement "syndromes", such as migrants, nomads and central place-foragers (Abrahms *et al.* 2017). This concept is built on the long recognition of behavioral syndromes, such as bold versus shy individuals, in shaping population dynamics and ecological processes (Sih *et al.* 2004, 2012). Additional movement syndromes can be detected by considering different timescales or components of animal movement tracks (Kays *et al.* 2023). Individuals within populations can exhibit different movement syndromes and spatial personalities (Abrahms *et al.* 2017; Stuber *et al.* 2022), and shift movement patterns throughout their lifetime (Hertel *et al.* 2020; Aikens *et al.* 2024). Diversity in movement behavior may reflect evolutionary diversification in behavioral traits (Ruegg *et al.* 2014), or adaptation to global change (Tucker *et al.* 2018b). Standardizing metrics for movement behavioral diversity is important for broad-scale biodiversity monitoring and assessing the impacts of animal movement on ecological processes (Kissling *et al.* 2018).

Seed dispersal depends on animal movement, so this mechanistic process is likely shaped by movement diversity. Seed dispersal research centered on animal movements has progressed from initial studies on dispersal distance (Murray 1988) to spatial patterns of dispersal (Nathan & Muller-Landau 2000; Russo *et al.* 2006, 2024b; Nield *et al.* 2020). Combining movement and habitat selection models is important for modeling spatial patterns of seed dispersal because animals may move differently depending on temporal and spatial contexts (Kleyheeg *et al.* 2017). Long-distance seed dispersal is important for tree species because it increases the genetic diversity of populations (Jordano 2017) and helps ensure that seeds avoid pathogens and predators (Janzen 1970). Directionality is also an important aspect of seed dispersal; seeds that disperse far must also arrive in areas suitable for germination (Schupp *et al.* 2010; Carlo *et al.* 2013). Several components of the seed dispersal process can influence where seeds are deposited, including gut passage times of seeds (Abraham *et al.* 2021) and habitat selection of frugivores (Wenny & Levey 1998; Russo *et al.* 2006; Cortes & Uriarte 2013). Studies focusing on the movement behavior of seed dispersers have found that animals can disperse seeds among habitat fragments (Mueller *et al.* 2014; Nield *et al.* 2020) and aid in ecosystem recovery (Dent & Estrada-Villegas 2021). Nearly all zoochorous trees are dispersed by more than one species of frugivore, and the roles of different frugivores often complement each other in the "total dispersal kernel" of the tree species (Nathan 2007). Less explored is how movement behavioral variation within species contributes to spatial patterns of seed dispersal (Lenz *et al.* 2011; Zwolak & Sih 2020; Graf *et al.* 2024).

Advances in remote sensing have revealed how landscape structure influences animal movements and how animals influence landscape structure in turn through their ecological roles (Russo *et al.* 2023). Light detection and ranging (LiDAR) is a valuable tool for characterizing landscape structure, and the Global Ecosystem Dynamics Investigation (GEDI) spaceborne LiDAR has enabled measurements of 3D vegetation structure throughout temperate and tropical latitudes at moderate spatial resolution (30 m; Dubayah *et al.* 2020; Potapov *et al.* 2021). Scaling up from local to regional research on the feedback between vegetation structure and animal behavior requires integrating LiDAR data from multiple scales, including terrestrial, UAV, airborne, and spaceborne LiDAR (Russo *et al.* 2023; 2024c). Both vertical and horizontal vegetation structure can influence animal habitat selection, especially for arboreal animals that move through 3D environments (Gámez & Harris 2022). Characterizing 3D space use sheds light on how animals find fruits and where they are likely to disperse seeds.

Rainforests are experiencing a decline in fruit availability, with consequences for frugivore populations (Bush *et al.* 2020). Whether this is a broader pattern of Congo Basin rainforests is difficult to discern without long-term fruit production and phenology data, which are rare or nonexistent for much of the region (Whitney & Smith 1998; Bush *et al.* 2020). Frugivores are thought to track fruit availability during food-lean periods of the year (Whitney & Smith 1998; Boyle *et al.* 2011); the ephemerality of fruiting events may lead to adaptations in movement behavior among seasons and years. Capturing the relationship between frugivore movements and the spatial distribution of fruiting tree crowns is difficult without remote sensing. Although high-resolution spatial imagery for tropical regions is available through commercial small satellites (Csillik *et al.* 2020), fruits are still difficult to detect from above a tree crown, and persistent cloud cover of tropical regions would hamper seasonal comparisons of fruit production. Consequently, coordination between remote sensing and ground-based data acquisition is necessary to research biological diversity in tropical rainforests (Turner *et al.* 2003; Turner 2014).

Periods of fruit scarcity in tropical rainforests affect the distribution of frugivores (Boyle *et al.* 2011; García *et al.* 2011). During Cameroon's major dry season, when fruits are less abundant, white-thighed hornbill (*Bycanistes albotibialis*) populations decrease twelvefold and black-casqued hornbills (*Ceratogymna atrata*) decrease fourfold in the region's largest protected area (Whitney & Smith 1998). Hornbills are the largest seed-dispersing birds of Congo Basin rainforests, and these two species undertake long-distance movements during food-lean periods (Holbrook *et al.* 2002; Chasar *et al.* 2014). Previous tracking studies of hornbills, based on radio telemetry (Holbrook *et al.* 2002) and ARGOS daily GPS locations (Chasar *et al.* 2014) showed variation among individuals in seasonal distance traveled and habitats encountered, albeit with limited sample sizes for the two species. In addition, the temporal resolution of these studies was too coarse for broad-scale seed dispersal modeling, given the gut passage times of seeds (Holbrook & Smith 2000).

Our objectives were to: 1) quantify seasonal differences in habitat selection by black-casqued and white-thighed hornbill in Cameroon, 2) quantify differences in hornbill movement behavior in relation to fruit availability, 3) simulate seed dispersal patterns arising from hornbill movement behavior and seasonal habitat selection, and 4) investigate how diversity in hornbill movement behavior affects the distances and directions of seed dispersal events.

METHODS

Study Site

At 526,000 Ha, the Dja Faunal Reserve is the largest protected area in Cameroon. This study took place in two phases in the Dja Reserve and villages north of the protected area, Bifolone and Kompia. The carbon-rich and biodiverse rainforest of the Dja Reserve has never been logged, but illegal hunting persists at the edges and near trails within the Reserve. Research in the Dja Reserve occurred within the Bouamir Research Site, a study area near the center (3°11′N, 12°48′E). The Bouamir Site (hereafter, “Bouamir”) is notable for its high density of grass-covered rocky outcrops called inselbergs (nine within 25 km^2). The primary habitat types of Bouamir are *terra firme* forest and swamps dominated by *Raphia* palms (Whitney *et al.* 1998). The Dja Reserve is bounded in the North, South, and West by the Dja River (Holbrook & Smith 2000). In the villages of Bifolone and Kompia, secondary forests, agricultural areas, and roads are also present. Southern Cameroon experiences two rainy and two dry seasons per year (Whitney & Smith 1998).

Hornbill capture and tracking

We used GPS tracking to characterize the seasonal movements of black-casqued and white-thighed hornbills. From 2009-2012, five white-thighed and three black-casqued hornbills were tagged in the villages of Bifolone and Kompia and tracked with GPS tags that recorded one GPS fix every 12-24 hours (Chasar *et al.* 2014). White-thighed hornbills were tagged with 22 g tags (Model PTT-100, Microwave Technology Inc., Columbia, MD, USA), and black-casqued with 30 g tags (Model 30GPS, North Star Science and Technology LLC, King George, VA, USA). From 2022-2024, we tagged an additional 16 black-casqued and five white-thighed hornbills with solar-powered 27 g (n=18) or 25 g tags (n=3) manufactured by e-obs (e-obs.de). We captured all birds from both projects (n=29) using pulley-mounted canopy mist nets (Russo *et al.* 2024a). All GPS tags were placed on the dorsum and held in place with a "backpack" harness made from 1.12 cm (0.44") tubular Teflon ribbon (Bally Ribbon Mills; Kenward 2001). Harnesses on birds tagged in 2022 and beyond also contained 36.29 kg (80 lb.) strength nylon trammel line (Avinet) to reinforce the interior (Russo *et al.* 2024b).

Habitat selection covariates

An unoccupied aerial vehicle (UAV) LiDAR survey of the entire Bouamir Research Site was completed in March 2023 with a Dji Zenmuse L1 waveform scanner, with an average point cloud density of 300 points $\cdot$ m^{-2} (Reddy *et al.* 2024). Because most of the hornbills flew far beyond the limits of the LiDAR survey (36 km^2), we used a machine learning framework to upscale drone LiDAR metrics to a landscape-level study area encompassing a 300 km buffer around the Dja Faunal Reserve (~494,000 km^2). These metrics included canopy height, canopy height heterogeneity, and distance to the nearest canopy gap. Canopy gaps were identified as areas with no vegetation above 15 m, with an upper threshold of 500 m^2, using the "getForestGaps" function from the "ForestGapR" R package (Silva *et al.* 2019). We calculated canopy height heterogeneity as the standard deviation of measurements at 100 m and 1 km resolution. The UAV-LiDAR metrics served as reference data, to which we compared spaceborne LiDAR data from the Global Ecosystem Dynamics Investigation (GEDI; Dubayah *et al.* 2020). Due to the cloudy conditions over Congo Basin rainforests, many GEDI data gaps exist in the region, so we used fourteen bands from four different optical and radar sensors as auxiliary variables to upscale the canopy height, heterogeneity, and gap metrics to the entire study area at 30 m resolution using Random Forest (see Russo et al. 2024c for details). We used this upscaled canopy height map rather than other available products (Potapov *et al.* 2021; Lang *et al.* 2023) because it is region-specific and contains no spatial gaps.

In addition to 3D structural metrics from LiDAR, we characterized habitat type using a Convolutional Neural Network (CNN) applied to a cloud-free Sentinel-2 image of the study area (Brodrick *et al.* 2019). Although this product contained 17 habitat categories, hornbills encountered very few habitat types in all seasons, making cross-season comparisons of habitat selection difficult. For black-casqued hornbills, we narrowed the habitat types to “swamp” and “non-swamp,” where “non-swamp” encompasses *terra firme* forest and inselberg habitat in the Dja Faunal Reserve, and open water, agricultural areas, and roads and villages outside the Dja Reserve. Inselbergs and other bare ground or grass areas are considered large canopy gaps, which are reflected in the “distance to canopy gap” metric. For white-thighed hornbills, we included both swamp and *terra firme* forest as covariates in habitat selection analyses because this species typically avoids swamps (Russo *et al.* 2024b) and all tracked individuals encountered inselberg habitats, thus avoiding the “dummy variable trap” for times of year when the hornbills mostly confined their movements to the protected Dja Faunal Reserve. Given both species’ apparent aversion to roads, we also included distance to the nearest road as a covariate in habitat selection analyses (Chasar *et al.* 2014). We used the Congo Basin roads dataset from Kleinschroth et al. (2019), filtered to include only roads considered "old, open" and "new, open" thus excluding trails and old logging roads. We created a raster representing the distance to the nearest road using the "distance" function in the "terra" R package (version 1.7-39; Hijmans *et al.* 2024).

Quantifying seasonal habitat selection

For each hornbill tracked from 2022-2024 (n=21), we used integrated Step Selection Analyses (iSSAs) to characterize habitat selection in southern Cameroon's four seasons. We delimited the four seasons using a Bayesian estimator of abrupt change, seasonality, and trend (BEAST) applied to total weekly rainfall using the "Rbeast" R package (version 1.0.0, Zhao *et al.* 2019). We also detected seasonal changepoints using the "cpt.means" function in the "changepoint" R package (version 2.2.4; Killick *et al.* 2022) and divided hornbill data based on the weeks identified by the two changepoint methods as seasonal transitions (**Figs. S4.1** and **S4.2**). Rainfall data used in seasonal changepoint analyses were measured using a DAVIS Vantage Pro 2 weather station within the Bouamir Research Site (Deblauwe *et al.* 2023). Further hornbill habitat selection analyses were categorized according to the 1) major dry season (Dec-Mar), minor rainy season (Mar-May), minor dry season (May-Sep), and major rainy season (Sep-Dec).

Each iSSA considered a movement step, or two successive GPS locations, as the unit for habitat selection. Although the tags recorded a GPS location every five minutes when fully charged, we filtered movement steps to two-hour intervals to facilitate seed dispersal modeling—which is based on seed passage times of ~2-6 hours (Holbrook & Smith 2000)—while including as many GPS points as possible. Many tags entered periods of lower battery charge where GPS fix rates decreased to one location per 2 hr. For each observed movement step, the iSSAs generated 100 random steps originating from the same position, and compared values of habitat covariates at “used” and “available” locations in a conditional logistic regression model (Avgar *et al.* 2016). The resulting β estimates represented selection strength for each covariate included in the model. We compared β estimates among the four seasons to identify trends and changes in habitat selection.

Quantifying movement syndromes

We identified “movement syndromes”, or behavioral personalities, of hornbills by including movement metrics in a Principal Component Analysis that revealed the axes of greatest variation among individuals (Abrahms *et al.* 2017; Kays *et al.* 2023). We then clustered individuals according to common movement syndromes using the *k*-means algorithm (Valletta *et al.* 2017). This analysis included all hornbills tracked in both project phases (n=29). We resampled the 2022-2024 hornbill tracks to one location per day, which matched the fix rate of the 2009-2012 data more closely. The movement metrics included in the PCA were 1) maximum net squared displacement (MNSD); 2) mean squared displacement (MSD), 3) home range area, measured as the minimum convex polygon (MCP); 4) intensity of home range use; 5) mean residence time (RT) in a radius of 100 m around each point in the movement track; 6) straightness of movement track; 7) sinuosity of movement track; and 8) turn angle correlation (TAC). We calculated all metrics at the scale of the entire movement track using the “amt,” “adehabitatHR,” or “adehabitatLT” R packages (Calenge 2019; Signer *et al.* 2019).

Hornbill movements in relation to fruit availability

We used data from a ground-based phenology study (2022-2023) to characterize the fruiting periods of 26 hornbill-dispersed species—representing roughly half the diet of both species (Whitney *et al.* 1998)—and to quantify fruit availability at the Bouamir Research Site throughout hornbill tracking. Phenology monitoring was performed monthly for 297 individual trees, with phases described according to fruiting and flowering phenology. Each tree on the site was scored according to the number of crown portions (0-4) containing ripe fruits. To create a monthly Fruit Availability Index for hornbill-dispersed tree species, we summed the number of crown portions on the study site containing fruits. We scaled and centered each hornbill's mean daily movement distance per month and related this metric to the monthly Fruit Availability Index using a generalized linear mixed effects model (GLMM) implemented in the "lme4" R package (version 1.1.34; Bates *et al.* 2015). We fit a separate model to black-casqued and white-thighed hornbills, with individual hornbill ID as a random effect.

Modeling seed dispersal

We used a seed dispersal simulator developed by Russo *et al.* (2024b) to predict seed dispersal patterns arising from hornbill seed dispersal and compare patterns among the four seasons. For each season, we generated 200 simulations of 16-hour hornbill movement paths originating from a single location north of the Dja Faunal Reserve (264895.5 E, 391898.5 N), with a movement step duration of 2 hours. The 200 simulations comprised 10 movement paths each for 20 of the 21 hornbills tracked from 2022-24. Data for two individual hornbills contained too few GPS points to fit an iSSA for each season (IDs: 8898, 11854). Interestingly, these individuals—black-casqued hornbills that relocated to nearly the same location west of the Bouamir Research Site—clustered closely based on the PCA. During the minor dry season, when too few GPS points were available for both birds for the iSSA to converge, we simulated an extra 10 trajectories for another male black-casqued hornbill that clustered closely to 8898 and 11854 based on the PCA (ID:8976). We chose one bird for the other three seasons, so that 200 simulations were created for each season. The step duration of each simulation matched that of the iSSA models used to fit the redistribution kernel, a probability density function for the animal's next step (Signer *et al.* 2024). Movement paths were simulated using the "simulate_path" function in the "amt" R package, with "fit_issf" models for each hornbill and a raster stack of covariates serving as inputs, along with a gamma distribution of the bird's step lengths and von Mises distribution of its turn angles (Signer *et al.* 2024). This method ensured that each movement simulation was based on actual hornbills' habitat selection and movement behaviors. We calculated probabilities of seed deposition along each simulated movement track based on a gamma distribution of gut passage times of *Maesopsis eminii* trees estimated from a previous study (Holbrook & Smith 2000).

We also investigated whether diversity in hornbill movement behaviors leads to a greater diversity of seed dispersal strategies available to hornbill-dispersed trees. We predicted seed dispersal patterns in scenarios with 20 of the 21 hornbills and where individuals of only one movement syndrome were present in the landscape. Each scenario was based on habitat selection during Cameroon's major dry season, and the 200 movement track simulations per scenario were divided evenly among individuals assigned to the movement syndrome. To generate 200 simulations for the Syndrome 3 scenario, we needed to simulate an extra four movement paths for one individual. We calculated the weighted mean dispersal distances in each seed dispersal scenario and derived standard deviations from a weighted covariance matrix. We also calculated the weighted circular mean of bearings between simulation starting points and probable seed dispersal locations using the "weighted.mean.circular" function in the "circular" R package (version 0.4-95; Lund *et al.* 2024). We calculated weighted circular standard deviations using the “circ_sd” function in the “windscape” R package (Kling 2024). Standard deviations represent diversity in both distances and directionality of dispersal events.

To investigate the likelihood of seeds dispersing between forest fragments and mature rainforest to degraded areas, we summarized 1) the timing of road crossings by 2022-2024 hornbills throughout the year and 2) the timing of hornbills crossing the boundary of the Dja Faunal Reserve. We used Barrier Behavior Analysis in the “BaBA” R package to characterize hornbill movement behaviors as crossings or “bounce” behaviors, in which the hornbill encountered a road or the Reserve boundary and moved away from it (Xu *et al.* 2021).

RESULTS

Hornbill movements

The maximum displacement a hornbill moved in 24 hours was 26.6 and 30.9 km for a black-casqued (ID:8978) and white-thighed hornbill (ID:9919), respectively. Of the hornbills tagged within the Dja Faunal Reserve (2022-24), 13 of 21 (61.9%) flew at least to the perimeter of the Dja Reserve, and nine left the boundary of the Dja Reserve (42.9%). However, long-distance flights were not universal; five hornbills (23.8%) never flew more than 5 km from where they were captured.

Seasonal habitat selection

Canopy height strongly predicted habitat selection for eight of 13 hornbills with sufficient GPS data (61.5%) during the minor dry seasons, which typically corresponds with the breeding period. This preference was relaxed in the other three seasons; during the major dry seasons, no hornbills preferred taller canopies, and two individuals displayed a preference for shorter canopies (**Fig. 4.1**). In contrast, white-thighed hornbills exhibited little seasonal variation in preference for canopy height. However, the most significant proportion of white-thighed (60%)

showed a significant positive association with taller canopies during the major dry season (**Fig. 4.2**).

Black-casqued hornbills displayed a wide range of preferences for canopy height heterogeneity, which is a measure of horizontal vegetation complexity. Still, most individuals (64.3%-92.3%) preferred areas of lower height heterogeneity or showed no preference at 100 m and 1 km resolution in all seasons (**Figs. S4.3, S4.5**). Similarly, all white-thighed hornbills preferred areas of lower height heterogeneity at 1 km resolution or showed no preference year-round (**Fig. S4.6)**. However, two individuals preferred areas of greater height heterogeneity at 100 m resolution during the minor dry seasons (**Fig. S4.4**). Individuals of both species appeared to be gap specialists or gap-avoiders, with black-casqued hornbills displaying high consistency among seasons (**Fig. S4.7**). White-thighed hornbills, which typically moved the greatest distances throughout the year, sometimes reversed their preference for canopy gaps—two individuals (IDs:11852, 11850) switched from avoiding canopy gaps during the major dry season to preferring them during the minor rainy season (**Fig. S4.8**). Hornbills encountered different types of large canopy gaps throughout the year, from inselbergs (only within the Dja Faunal Reserve) to villages and other human-impacted areas. One female black-casqued hornbill (ID:11856) preferred areas closer to roads during the major rainy seasons but preferred areas further from roads during the major dry seasons (**Fig. S4.9)**. Except for one individual (ID:9894) that preferred areas closer to roads during the minor rainy seasons, white-thighed hornbills did not exhibit a preference for or aversion towards roads in any season (**Fig. S4.10**).

All black-casqued hornbills either preferred or showed no preference for swamp habitats except for the minor dry season, where one individual (ID:8978) appeared to avoid swamps (**Fig. S4.11**). This bird was associated with an inselberg within its minor dry season range, reflected in its preference for habitat near canopy gaps (**Fig. S4.7C)**. All white-thighed hornbills either avoided swamps or showed no preference (**Fig. S4.12**). Except for two hornbills that preferred *terra firme* forest during the minor dry seasons (IDs: 11850, 11852), white-thighed hornbills did not exhibit a preference for *terra firme* forest in any season (**Fig. S4.13**).

Hornbill movement syndromes

Hornbills tracked from 2009-2024 clustered into four behavioral types based on a Principal Component Analysis applied to full-track metrics (**Fig. 4.3**). One male black-casqued hornbill (ID:88009) was the only individual in its cluster, with high movement straightness and maximum net squared displacement. Interestingly, this was the only individual to fly to the southeast of the Dja Faunal Reserve. However, its movement track had several sampling discontinuities, so we focused further analyses only on the other three movement syndromes. The first two principal components explained 61.9% of variation in hornbill movement behavior (**Figs. S4.14-15**). Maximum net squared displacement and mean squared displacement had the greatest quality of representation in the PCA ($\cos^2 = 0.80$ and 0.77, respectively; **Fig. S4.16**). Five white-thighed hornbills clustered into one syndrome with the greatest home range areas and high mean squared displacement (hereafter, Syndrome 1; **Fig. 4.3A**). Although the PCA likely did not capture this feature, all five hornbills in Syndrome 1 undertook long movements northeast of the Dja Reserve, where they began to encounter and avoid larger human settlements (**Fig. S4.17**). Six hornbills clustered into Syndrome 2, displaying some of the straightest long-distance movements (**Fig. 4.3B**). Two of the hornbills also exhibited several "back-and-forth" movements between seasonal home ranges, which typically lasted 7-14 days round-trip. Four of these hornbills flew south of their breeding home range, sometimes beyond the Dja River (**Fig. S4.18**). Syndrome 3 comprised most hornbills (n=17), which either maintained a stable home range year-round or performed occasional, medium-distance movements (**Fig. 4.3C**). Intensity of use was one of the strongest indicators of this movement syndrome (**Fig. S4.14**). Most black-casqued and some white-thighed hornbills used one or a few home ranges intensely (**Fig. S4.19**). Although the two long-distance syndromes (1 and 2) appear to have a persistent heading—i.e., either northeastern or southern nomadic movements, individuals of both syndromes flew to landscapes both north and south of the Dja reserve. In addition, all three syndromes appeared in the older (2009-2012) and newer (2022-2024) cohorts of tracked hornbills. Individuals of both species clustered into Syndromes 2 and 3, and Syndrome 1 comprised only white-thighed hornbills.

Relating movements to fruit availability

Periods of greatest fruit availability corresponded to the minor dry season (~May-Sep.), which is also when hornbills typically breed (**Fig. 4.4A**). However, at least one of the 26 hornbill-dispersed tree species monitored monthly through ground surveys was fruiting in any given month (**Fig. 4.4B**). At the population level, white-thighed hornbills moved significantly greater daily distances during periods of lower fruit availability (GLMM: p=0.0354; **Fig. 4.5A**), while black-casqued hornbills displayed no relationship between movement distance and fruit availability (GLMM: p=0.508; **Fig. 4.5B**).

Seasonal seed dispersal patterns

The greatest weighted mean dispersal distance from seasonal seed dispersal simulations occurred during the dry season scenario (1924 ± 1789 m; **Fig. 4.6A**), followed by the minor rainy season (1670 ± 785 m; **Fig. 4.6B**), minor dry (1308; ± 880 m; **Fig. 4.6C**), and major rainy season scenarios (1089 ± 373 m; **Fig. 4.6D**). The greatest seed displacement from the origin ranged from 8628 m in the minor dry season scenario, when most birds move within a limited home range, to 13888 m in the major dry season scenario, when food is less abundant (**Fig. S4.20**). The weighted standard deviation of dispersal distances in the major dry season scenario (1789 m) was more than twice as great as the standard deviation in any other season, indicating much greater variation in dispersal distances.

The weighted circular mean of seed displacement directions—measured as the absolute angle relative to north—varied among seasons, with most seeds dispersing along a slight southeasterly route in the major dry and minor dry seasons (1.95 ± 0.89 and 1.54 ± 0.69 radians, respectively), a slight northeasterly route during the minor rainy seasons (0.66 ± 0.91 radians), and a stronger southeasterly route during the major rainy season (2.39 ± 0.45 radians). The greatest diversity of dispersal directions occurred during the major dry and minor rainy season scenarios (weighted standard deviation: 0.89 and 0.91 radians, respectively).

Effects of movement diversity on seed dispersal

Because Syndrome 1 birds were more itinerant, the scenario involving seed dispersal by only Syndrome 1 birds yielded the greatest seed dispersal distances (**Figs. 4.7B, 4.8B**). The weighted mean displacement for simulated seed dispersal events by only Syndrome 1 hornbills in the major dry season was 3263 ± 1300 m. Although Syndrome 2 hornbills flew long distances during both rainy seasons, they embarked on few such flights during the major dry seasons, and the weighted mean displacement was, therefore, the shortest, at 737 ± 239 m. Still, some seed dispersal events in this scenario exceeded 10 km (**Figs. 4.7C, 4.8C**). Seeds in the Syndrome 3 scenario never dispersed more than 8000 m, although the weighted mean displacement was greater than in the Syndrome 2 scenario, at 782 ± 321 m (**Figs. 4.7D, 4.8D**). Finally, the scenario that included dispersal events by all 20 hornbills yielded the second-greatest mean displacement (1924 m) and the greatest weighted standard deviation (1789 m). Put another way, the scenario involving seed dispersal by all hornbills yielded the greatest diversity in seed dispersal distances (**Figs. 4.7A, 4.8A**).

The weighted circular mean of seed displacement directions was similar for scenarios involving Syndrome 1 (1.23±0.72 radians) and Syndrome 3 birds only (1.29±0.55 radians). In these three scenarios, seeds are dispersed primarily northeast of the origin and away from a road and village. In the scenario involving dispersal by all hornbills (1.95±0.89 radians), the mean displacement direction was southeast, towards a road. In the scenario involving dispersal only by Syndrome 2 birds, seeds dispersed primarily northwest of the origin (-1.42 ± 0.54). The scenario involving seed dispersal by all birds yielded the greatest diversity of seed dispersal directions, with a weighted circular standard deviation of 0.88 radians.

Of the hornbills tracked from 2022-2024, only four flew within 500 m of a road. Among these individuals, we recorded 206 road encounters, including 98 crossings (47.6%) and 108 "bounces" (52.4%). In addition, we detected 96 instances of a hornbill crossing the boundary of the Dja Faunal Reserve, either to the North, South, or West. These are the only boundaries that either follow or approach the Dja River. Flights across the Dja Faunal Reserve Boundary were more frequent in April and October (n=16 each), two months that flank the breeding season of both hornbill species.

DISCUSSION

The results of this study demonstrate that the movement behavioral diversity of two hornbill species leads to greater diversity in the distances and directions of seed dispersal events in a mosaic of Congo Basin rainforests, swamps, and human-impacted areas. Individuals of both hornbill species exhibit distinct movement syndromes based mainly on the distance of seasonal nomadic movements and intensity of home range use. These movement syndromes—combined with seasonal variation in habitat selection—ensure that hornbill-dispersed trees fruiting during any month of the year can disperse their seeds far from the crown of a parent tree and in any direction.

Seasonal variation in both hornbill species' selection for attributes of 3D vegetation structure highlights how advances in remote sensing improve methods in movement ecology and reveal the need for additional remote sensing products to understand the movements of tropical frugivores. Most hornbills tracked from 2022-2024 preferred areas of greater canopy height during the minor dry seasons, which overlaps with the breeding period, and relaxed this preference in other seasons. We detected this relationship using upscaled GEDI canopy height measurements at 30 m resolution. However, in a different study, we found canopy height to be a stronger year-round predictor at 10 m resolution using only UAV-LiDAR measurements from the Bouamir Research Site (Russo *et al.* 2024b). Higher-resolution remote sensing products for 3D vegetation structure will therefore help identify the most relevant scale of habitat selection by wide-ranging animals in tropical regions.

In addition, we found that white-thighed hornbills fly greater distances when fruits are scarcer at the Bouamir Research Site. This result was based on ground-based phenology surveys of hornbill-dispersed trees for a portion of a 25 km^2 study area, but it has long been thought that African hornbills track fruit abundance over long distances during food-lean seasons (Whitney & Smith 1998; Holbrook & Smith 2000; Chasar *et al.* 2014). Landscape-scale characterizations of fruit abundance are necessary for a greater understanding of how tropical frugivores select habitats; further advances in high-resolution optical and hyperspectral remote sensing may soon point toward a solution (Caillaud *et al.* 2010; Dixon *et al.* 2021). Continued pursuit of remote sensing products to understand distributions of fruiting events may also help explain why some obligate frugivores fly long distances during food-lean periods while others never leave a limited home range (Boyle *et al.* 2011).

The timing of fruiting events can influence spatial patterns of seed dispersal because long-distance movements of seed dispersers are often seasonal (Nathan *et al.* 2008). Although long-distance movements by hornbills are more frequent during the major dry season and its transitional periods, hornbills may still engage in long-distance movements during any time of year. We observed hornbills crossing the boundary of the Dja Reserve every month of the year except August when hornbills are most likely to be nesting (Stauffer & Smith 2004). These results suggest that although hornbills move greater distances when fruits are less abundant, long-distance seed dispersal from mature rainforest to a human-dominated landscape can still occur for trees fruiting during periods of greater overall fruit abundance.

Animal seed dispersal has important consequences for tree species coexistence. In tropical rainforests, rare tree species tend to be less spatially aggregated than in temperate forests, due in part to the latitudinal gradient in animal seed dispersal. Dispersing farther from the parent tree is advantageous for tropical trees because they are more vulnerable to enemies; arbuscular mycorrhizal associations, which are more common in tropical forests, afford less protection against pathogens than ectomycorrhizal associations, which prevail in temperate forests (Wiegand *et al.* 2023). Following seed dispersal, plants must survive the seedling stage and recruitment to adult (Wang & Smith 2002). Diversity in movement behaviors of seed dispersers may play a key role in preventing trees from aggregating in ways that increase seedling mortality (Wiegand *et al.* 2021). Consequently, a greater understanding of the connection between animal movement diversity and spatial patterns of adult trees may help explain the high plant species diversity of tropical rainforests.

Our aim was not to derive population-level generalizations about how hornbills move and disperse seeds; instead, we highlight individual differences among hornbills and how they diversify the seed dispersal routes available to rainforest trees. Hornbills clustered into distinctive movement syndromes based on several movement metrics, with 1) predictable long-distance nomads, 2) individuals with occasional, straighter long-distance movements, and 3) more sedentary individuals that may occasionally undertake medium-distance movements (5-20 km). Only white-thighed hornbills clustered into Syndrome 1, which flew the longest distances along a northeasterly corridor. Although our sample of black-casqued and white-thighed hornbills might be considered representative of the populations—in terms of both relative abundance (Whitney & Smith 1998) and movement syndromes observed—hornbills display a variety of rare behaviors that become apparent with each new GPS track or each passing season. Some of these behaviors, including “streaking” rapidly between seasonal home ranges, are consequential for long-distance seed dispersal, which depends on rare events (Nathan *et al.* 2008).

If not for within-individual and among-individual variation in hornbill behavior, most hornbill-dispersed seeds would likely not disperse more than 1-2 km from the crown. This is because hornbill-dispersed fruits are more abundant during the minor dry season and transitional periods when hornbills are typically more sedentary in a stable home range. Instead, occasional long-distance movements during the period when most tree species are fruiting increases the chances that a greater diversity of tree species disperses its seeds over long distances. This is beneficial from the perspective of both rainforest diversity and landscape recovery. Our seed dispersal models showed that when a geographic region supports individual hornbills from all movement syndromes, trees can disperse their seeds far from the crown and in any direction, any month of the year. Trees benefit from movement diversity because birds with more itinerant movements (e.g., Syndrome 1) disperse seeds over long distances and to new habitats. In contrast, birds with more stable home ranges (e.g., Syndrome 3) disperse seeds over shorter distances but can “cultivate” a smaller area by providing year-round or nearly year-round seed rain from trees that produce fruits at different times. From the perspective of landscape recovery, these results mean that some individuals will disperse seeds far. In contrast, others will continue cultivating a smaller region, contributing seed rain from a wider variety of tree species due to differences in fruiting periods. Moreover, although hornbills rarely crossed roads, they did so in all seasons, meaning that hornbill-dispersed trees can likely disperse their seeds between rainforest fragments no matter their fruiting period.

A closer lens on seed dispersal capabilities of hornbills yields insight into how protected areas in the tropics are established and managed. All hornbills of Syndrome 1 moved long distances along a northeasterly route, and many hornbills of Syndrome 2 and some of Syndrome 3 flew along a southern route outside of the minor dry season, a spatial bias that raises the question of whether some movement syndromes are more imperiled by land use change and hunting than others. The International Convention on Biological Diversity has asserted that 30% of land and ocean should be protected and conserved by 2030 (Hannah *et al.* 2020), and this initiative requires knowledge of the processes that restore ecosystems and generate and maintain biodiversity. Hornbills display a variety of behaviors that suggest they contribute to long-distance dispersal from mature to degraded rainforests. This means that hornbills may be among the most important functional groups when advancing reforestation strategies from initial colonization to late succession. Seed dispersal networks in disturbed tropical landscapes typically begin to break down when the largest mammals are extirpated, because these species require the greatest home range area and are targeted by hunters (Enquist *et al.* 2020). Hornbills in Cameroon are targeted by hunters for the mystical appeal of their heads and casques in international trade (Su *et al.* 2024). Landscape recovery and conservation in the Congo Basin will require strategies that preserve the movements of black-casqued and white-thighed hornbills.

Congo Basin land cover types that can benefit from a greater tempo and diversity of seed rain include recently logged forests and abandoned logging roads (Kleinschroth *et al.* 2019), shade cocoa, and other agroforestry plantations (Ordway *et al.* 2017). Hornbills serve as "mobile links" connecting mature and secondary forests in the region through seed dispersal (Lundberg & Moberg 2003). In addition, tropical trees are economically important as timber and non-timber forest products. The cultural importance of hornbill-dispersed tree species as sources of building materials (e.g., *Raphia monbuttorum* aka Raffia palm), medicine (e.g., *Annickia chlorantha* aka *evuwé*), and fruits (e.g., *Canarium schweinfurthii* aka *sené*; Whitney *et al.* 1998), highlights the irreplaceable role of large frugivorous hornbills in Central African ecosystems. As human activities impact Congo Basin rainforests, a continued relationship between people and the tree species dispersed by hornbills will be crucial for conserving long-distance hornbill movements.

Animal movement data from tropical regions is underrepresented in ecology research (Kays *et al.* 2022), masking a potentially crucial aspect of tropical biodiversity: movement behavior. Long-term animal tracking is necessary to detect trends in animal movement behavior. Seed dispersal by hornbills is vital for tropical tree diversity, resulting in patterns of biological diversity and ecosystem services such as carbon storage (Osuri *et al.* 2016), and production of non-timber forest products. Hornbill movements cover hundreds of kilometers across landscapes undergoing land use changes, including increased small-scale and industrial agriculture (Ordway *et al.* 2017), road construction (Kleinschroth *et al.* 2019), and logging (Antropov *et al.* 2021).

For animals to continue to serve as “mobile links” among tropical forests, greater recognition is needed for movement behavioral diversity and its consequences for maintaining and restoring ecosystems.

ACKNOWLEDGMENTS

We thank several local forest guides in Cameroon for collecting data and sharing their knowledge of the forest with us, including Mbembo Luc, Dando Daniel, Abah Armand, Eloumo “Elgas” Gaston, Obam Lundi, Ngong Antoine, Amiezeh David, Mbengue Moise, Manga Michel, and Biango Felix. We also thank the Republic of Cameroon and the Ministries of Scientific Research and Innovation (MINRESI) and Forestry and Wildlife (MINFOF) for permission to conduct this research and to conservator Oum Njock Gilbert for permissions and matching us with helpful eco-guards, including Mekok Alfred, Doumba “Calao Vert” Olivier, Mevoula Bertrand, and Samuah Harvilange. We thank the Congo Basin Institute and e-obs for logistical support. Finally, we thank Tegueu Prudence, Hongie Mandela, Tekam Antoine, Tegebong Valorian, and Ninying Benedicta for their assistance in tagging and tracking hornbills. We thank Francis Forzi for assistance with canopy netting. This work was funded by a grant from the NASA ROSES program; the NSF Graduate Research Fellowship Program; Walder-Christensen Foundation; Greenville Zoo; Explorers Club; American Philosophical Society; Sigma Xi; Association for Tropical Biology and Conservation; American Ornithological Society; Animal Behavior Society; IDEA Wild; and the UCLA Dept. of Ecology and Evolutionary Biology. We thank Lebienfaiteur Sagang for assistance with data acquisition, and Pierre Ploton for assistance with data processing.

TABLES AND FIGURES

Figure 4.1: Seasonal differences in black-casqued hornbill selection for canopy height (30 m resolution). Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

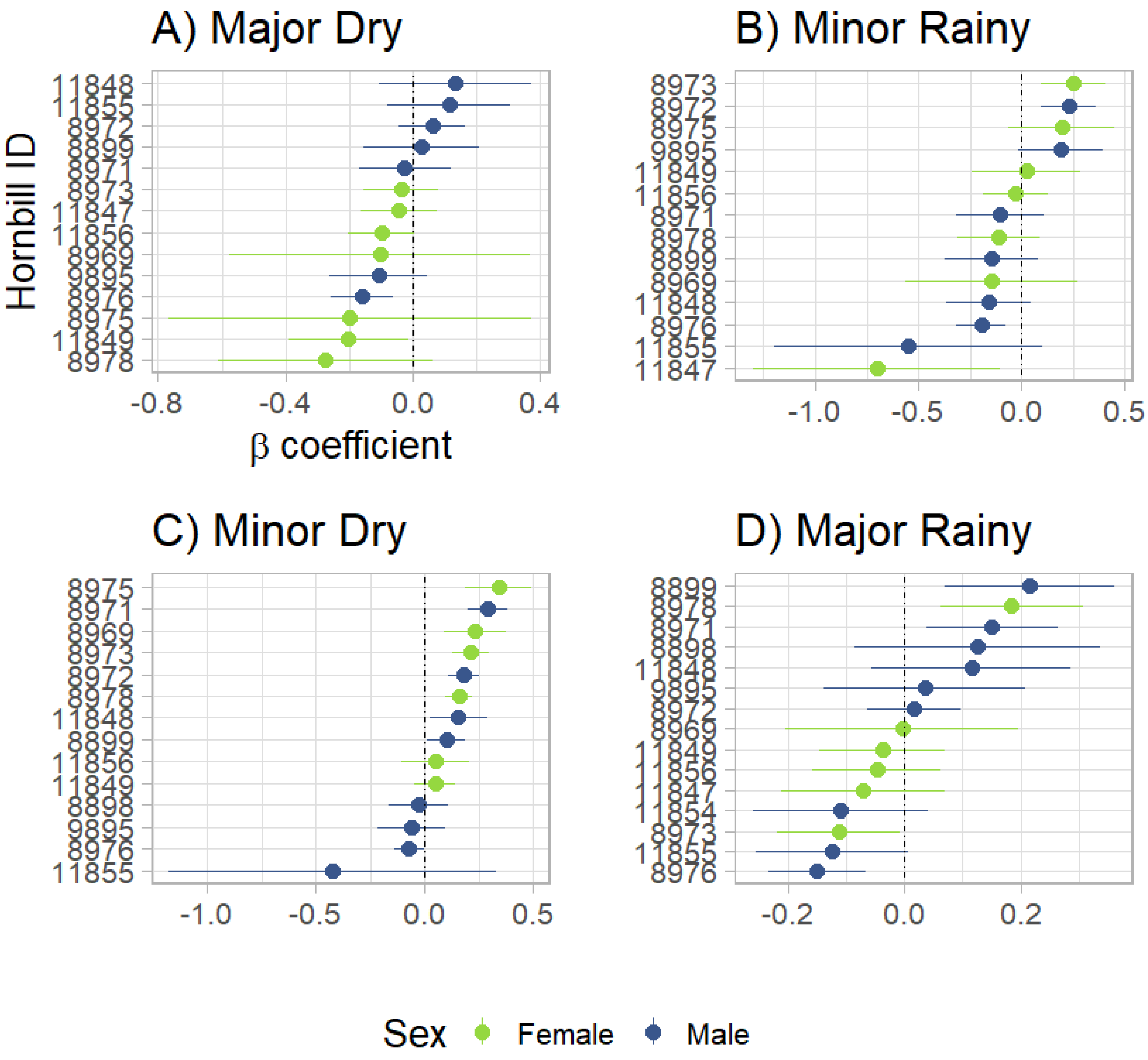


Figure 4.2: Seasonal differences in white-thighed hornbill selection for canopy height (30 m resolution). Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

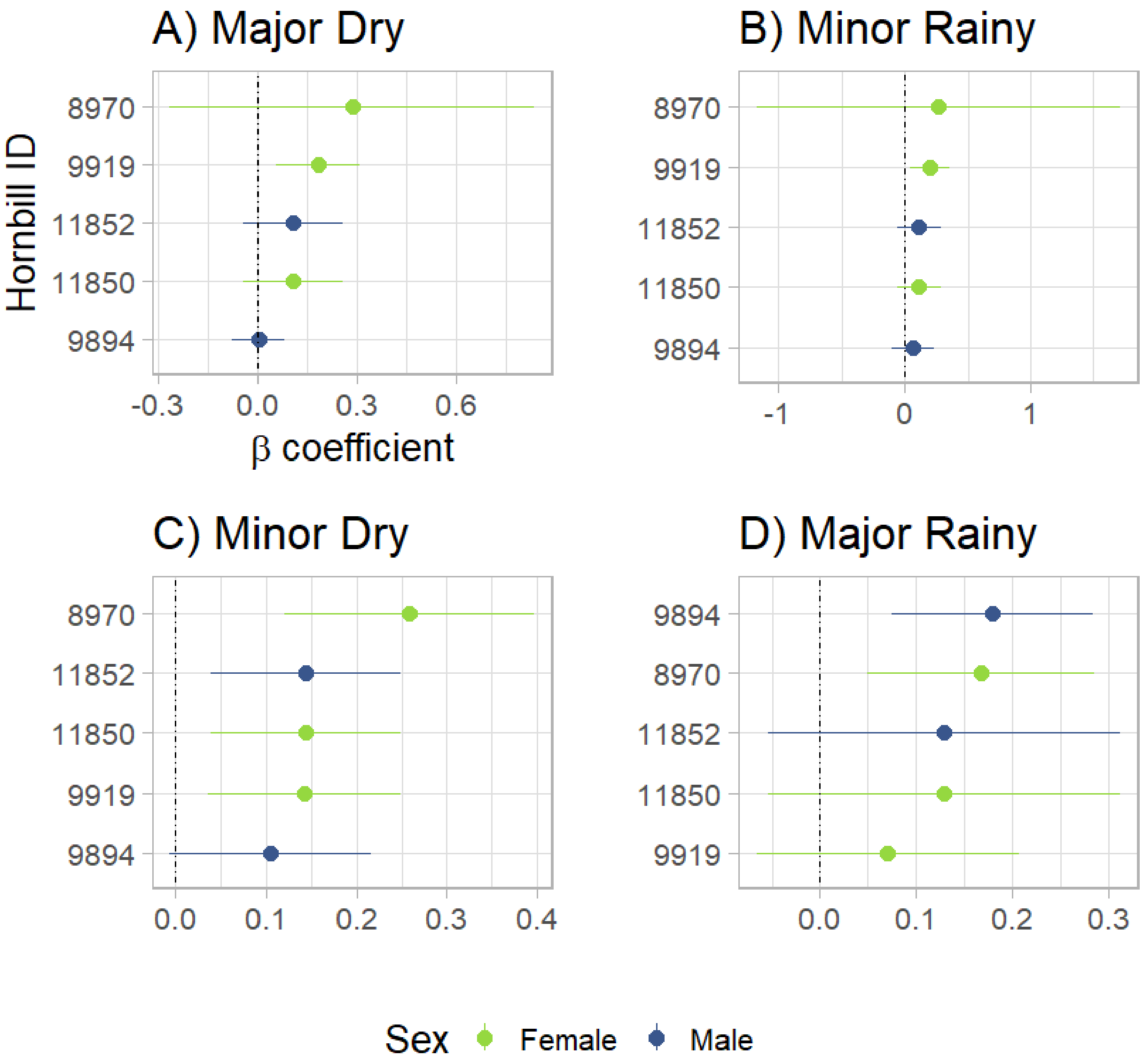


Figure 4.3: Hornbill movement syndromes identified through *k*-means clustering, including **A)** White thighed hornbills that moved the longest distances, and primarily to the northeast (example: 9919); **B)** Other hornbills that moved long distances, but typically along the straightest routes (example: 11856); and **C)** Hornbills with the most stable year-round home ranges (example: 8972).

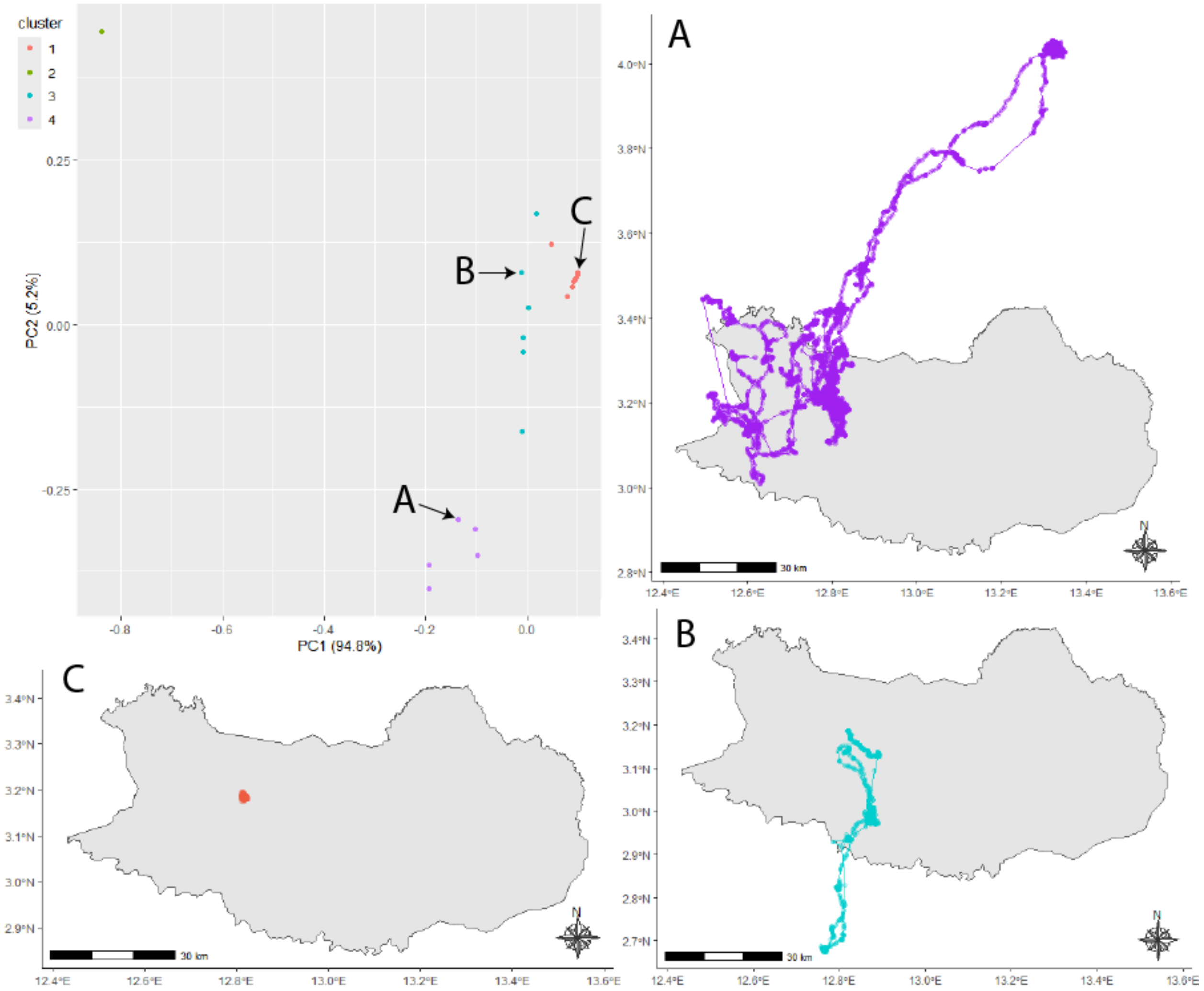


Figure 4.4: Fruit availability within the Bouamir Research Site measured as **A)** the total number of crown portions with ripe fruits per month for hornbill-dispersed trees at the Bouamir Research Site, and **B)** Density of fruiting tree crown portions for 26 hornbill-dispersed tree species whose fruiting phenology was monitored from 2021-2023. The height of each ridge corresponds to the density of fruiting trees for that species.

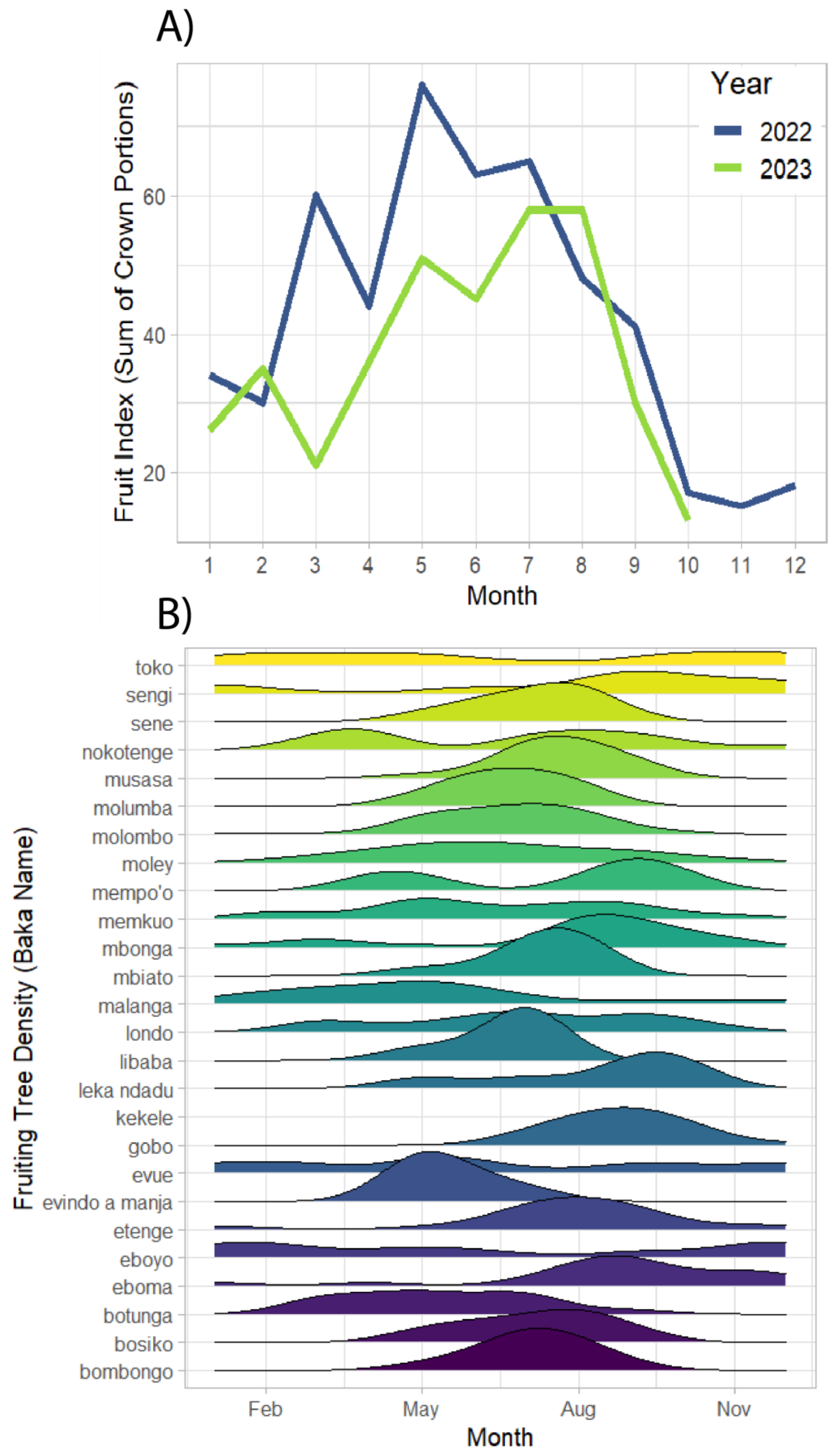

A)
Year
2022
2023
Fruit Index (Sum of Crown Portions)
60
40
20
1
2
3
4
5
6
7
8
9
10
11
12
Month
B)
Fruiting Tree Density (Baka Name)
toko
sengi
sene
nokotenge
musasa
molumba
molombo
moley
mempo'o
memkuo
mbonga
mbiato
malanga
londo
libaba
leka ndadu
kekele
gobo
evue
evindo a manja
etenge
eboyo
eboma
botunga
bosiko
bombongo
Feb
May
Aug
Nov
Month

Figure 4.5: Mean daily distance of hornbills, log-transformed, with respect to month (top) and relationship between mean daily distance traveled by hornbills—summarized for each month and log-transformed—and scaled Fruit Availability Index, measured as the total number of crown portions on the Bouamir Research Site containing fruits consumed by hornbills (bottom) for **A)** White-thighed and **B)** Black-casqued hornbills. The shaded gray region is the 95% confidence interval, calculated using the ggeffects R package from a generalized linear mixed effects model (GLMM).

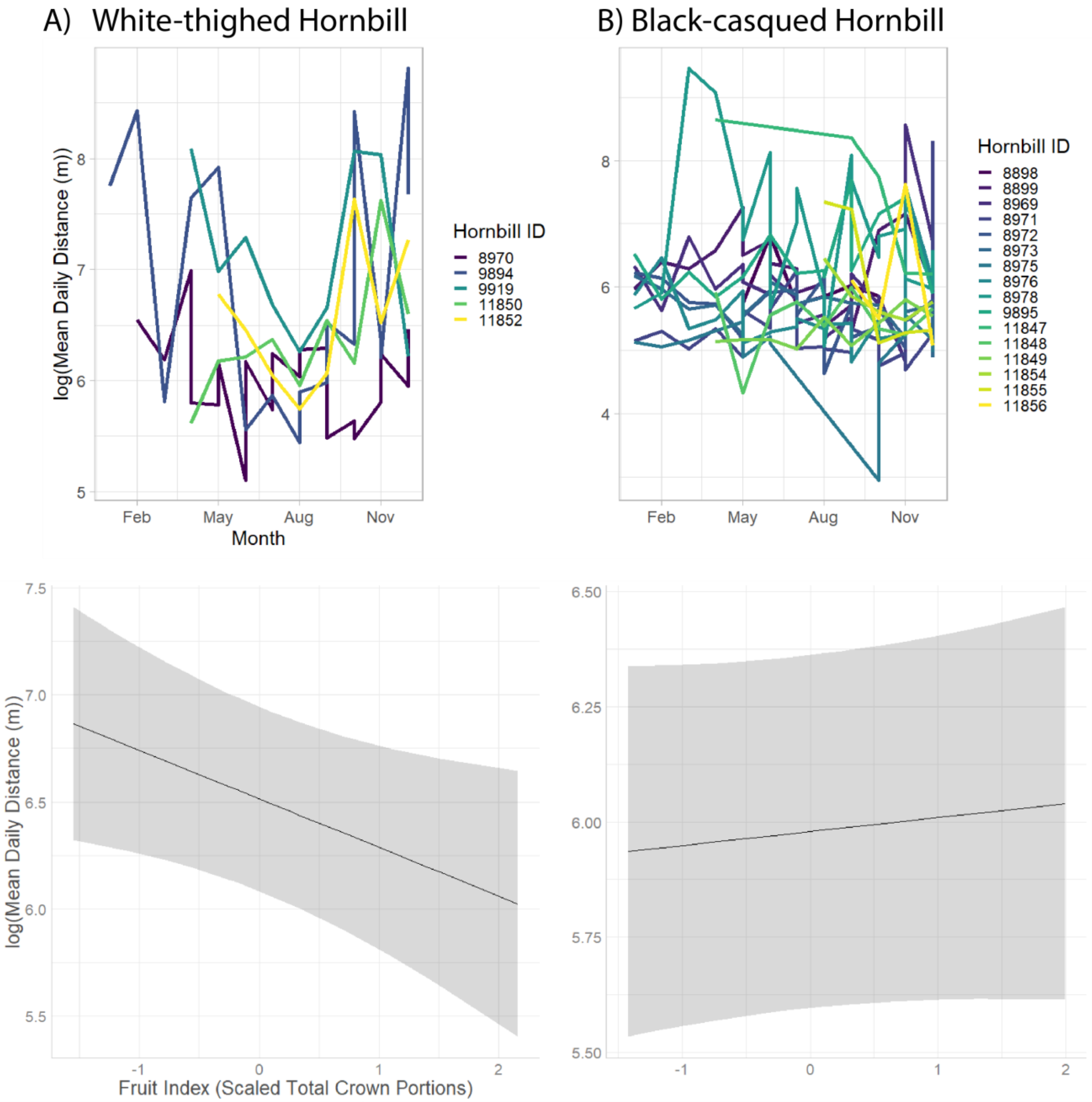

A) White-thighed Hornbill
B) Black-casqued Hornbill
log(Mean Daily Distance (m))
8
7
6
5
Feb
May
Aug
Nov
Month
Hornbill ID
8970
9894
9919
11850
11852
8
6
4
Feb
May
Aug
Nov
Hornbill ID
8898
8899
8969
8971
8972
8973
8975
8976
8978
9895
11847
11848
11849
11854
11855
11856
7.5
7.0
6.5
6.0
5.5
log(Mean Daily Distance (m))
-1
0
1
2
Fruit Index (Scaled Total Crown Portions)
6.50
6.25
6.00
5.75
5.50
-1
0
1
2

Figure 4.6: Seed dispersal simulations based on 20 tracked hornbills, applied separately to the four seasons, including **A)** Major dry (Dec-Mar), **B)** Minor rainy (Mar-May), **C)** Minor dry (May-Oct), and **D)** Major rainy (Oct-Dec). All seed dispersal maps are overlayed on a 30 m map of canopy height. The red point in each map corresponds to the starting location of dispersal simulations.

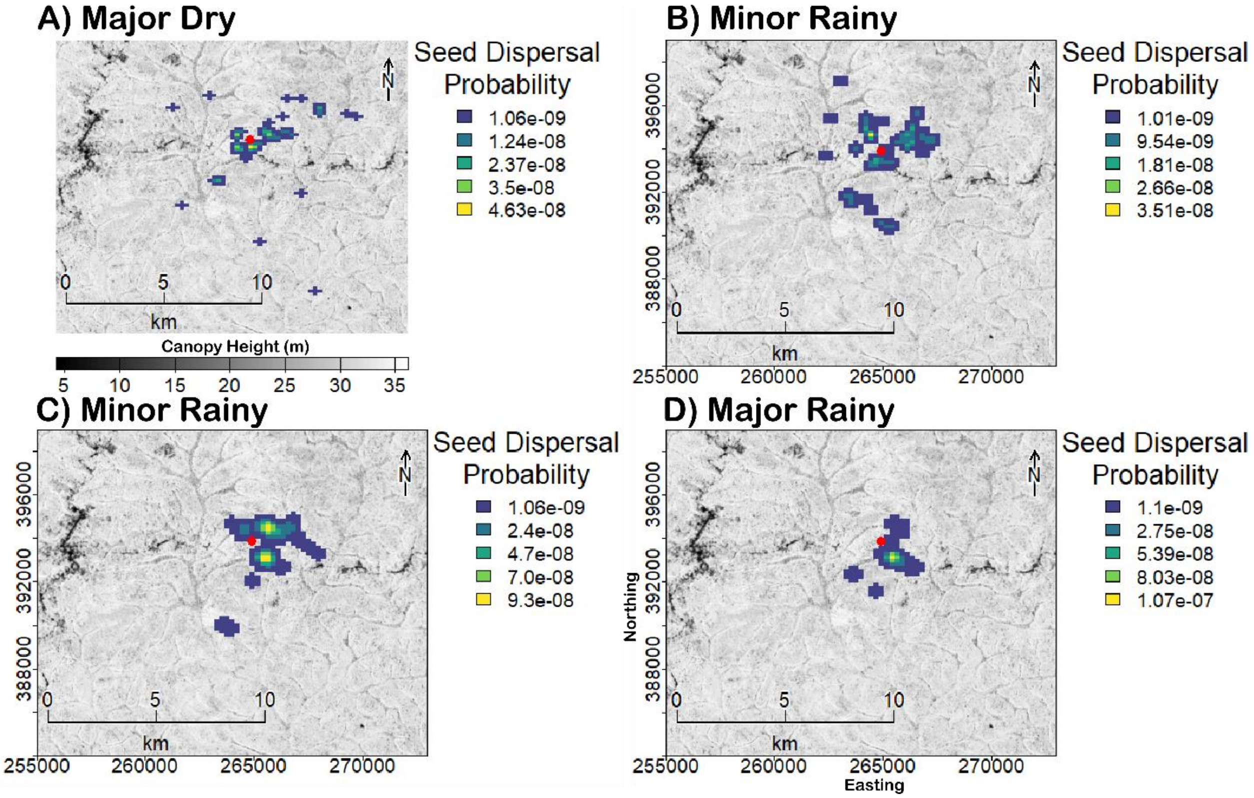


Figure 4.7: Seed dispersal simulations for Cameroon's major dry season (Dec-Mar) based on iSSAs fit to **A)** All tracked hornbills (n=20), **B)** hornbills clustering to Syndrome 1 (n=2); **C)** Syndrome 2 (n=4); and **D)** Syndrome 3 (n=14). All seed dispersal maps are overlayed on a 30 m map of canopy height. The red point in each map corresponds to the starting location of dispersal simulations.

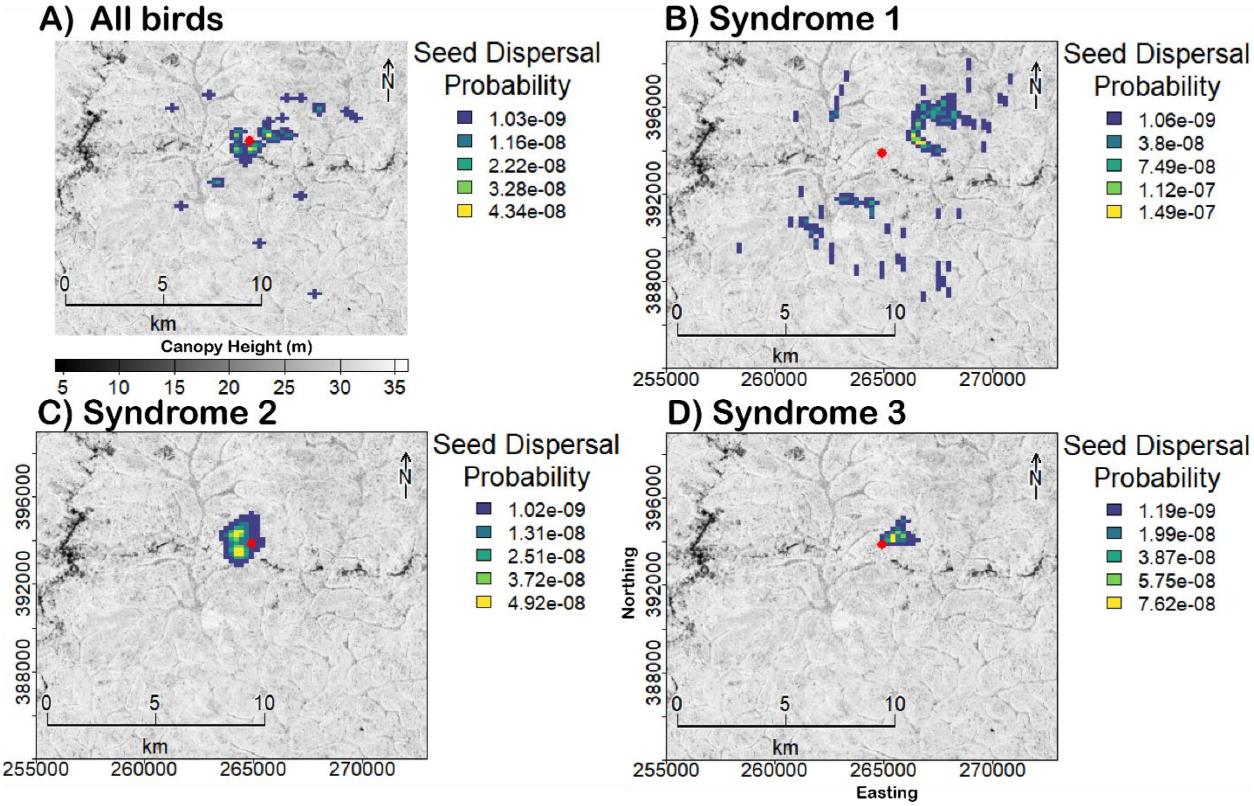
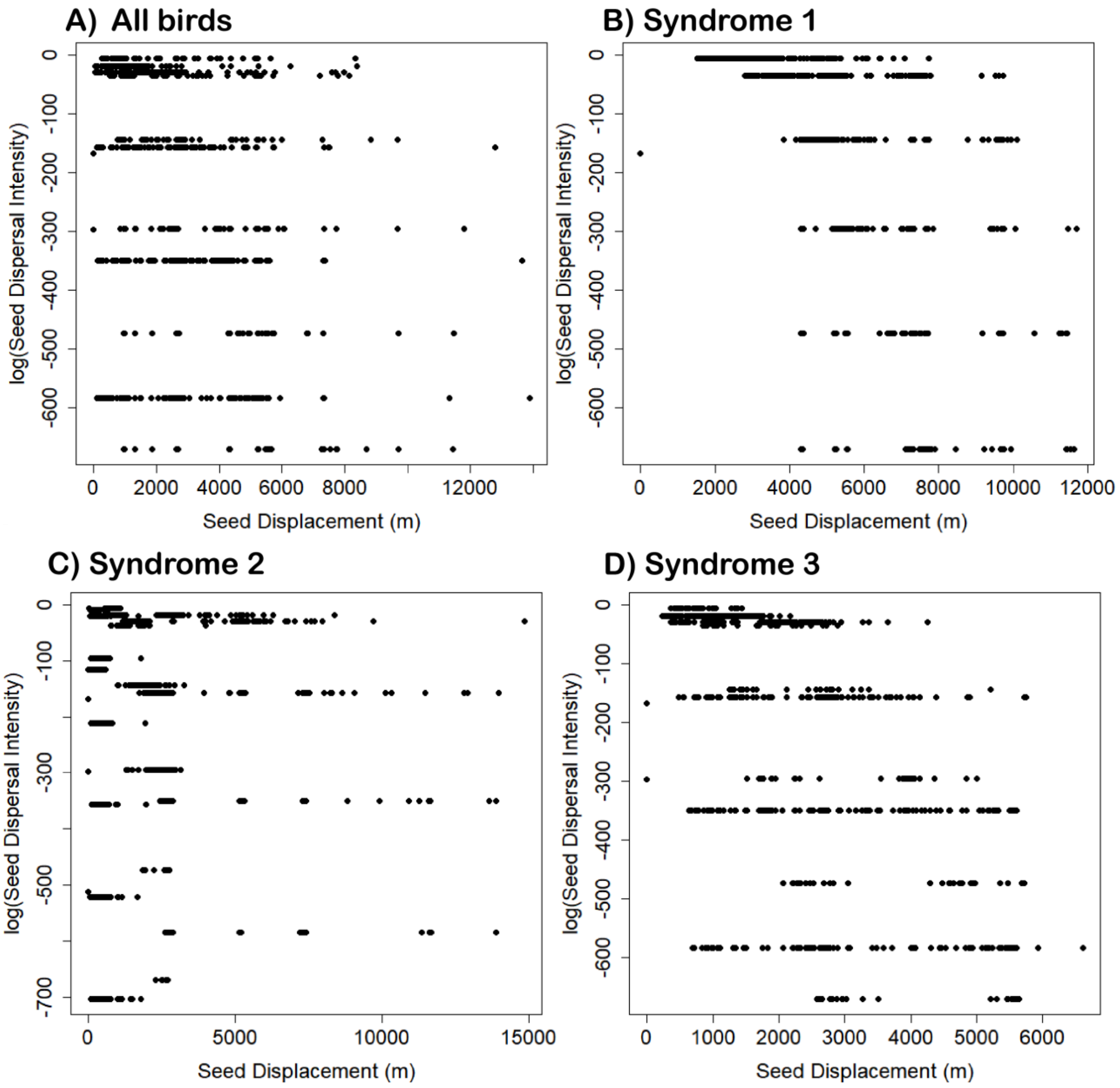


Figure 4.8: Local probability of seed dispersal with distance from the seed origin. This relationship is shown as log-transformed seed dispersal intensity (λ) of Poisson point process seed dispersal models in relation to seed displacement, for scenarios involving **A)** All tracked hornbills, **B)** Dispersal only by hornbills displaying Movement Syndrome 1, **C)** Syndrome 2, and **D)** Syndrome 3.



SUPPLEMENTARY MATERIAL: Supporting figures for Chapter 4

Figure S4.1: Seasonal change points identified using a Bayesian estimator of abrupt change, seasonality, and trend (BEAST) in total weekly rainfall. “Time” on the x-axis is measured as week of the year, for the year 2023. Seasonal changepoints were identified as weeks 12 (major dry-minor rainy), 18 (minor rainy-minor dry), 37 (minor dry-minor rainy), and 48 (major rainy-major dry).

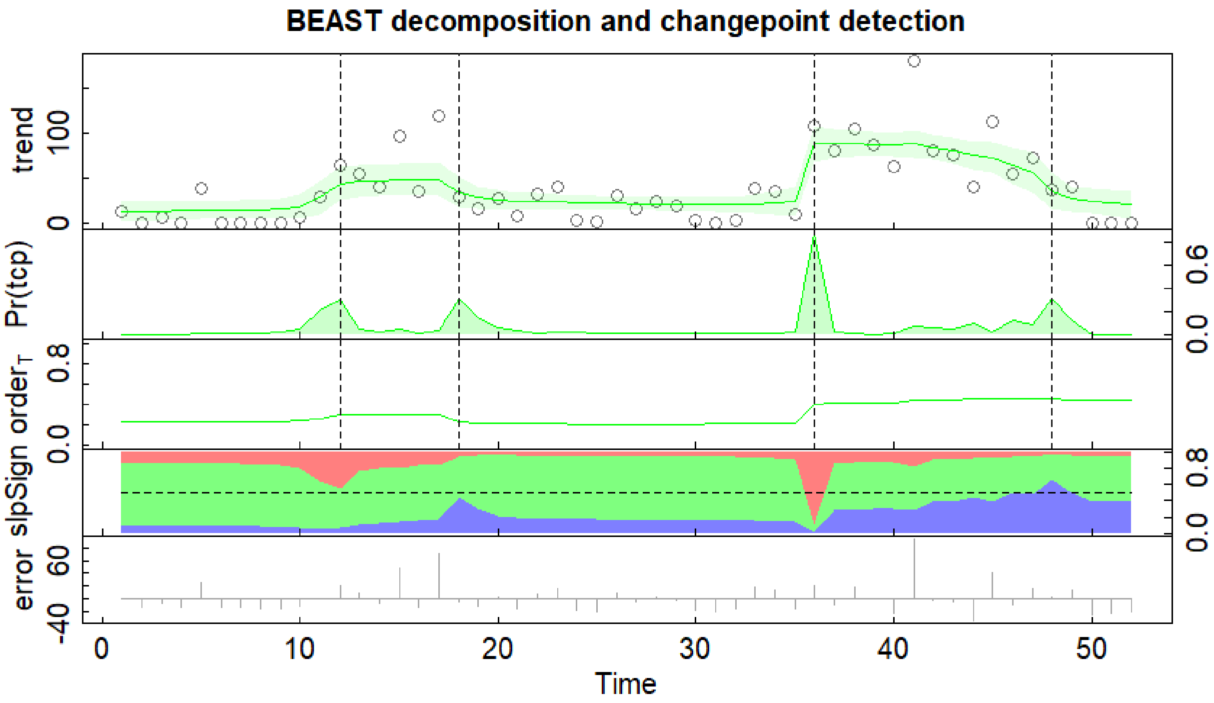


Figure S4.2: Seasonal change points in total weekly rainfall identified using the "cpt.means" function in the "changepoint" R package. "Time" on the x axis is measured as week of the year, for the year 2023. Changepoint weeks were identified as week 10 (major dry-minor rainy); week 18 (beginning of minor dry); week 37 (minor dry-major rainy) and week 48 (major rainy-major dry). The timing of the minor rainy season was the only period without concordance between the BEAST and "cpt.means" methods. We opted to use the seasonal changepoints from the cpt.means method because it resulted in a longer minor rainy season.

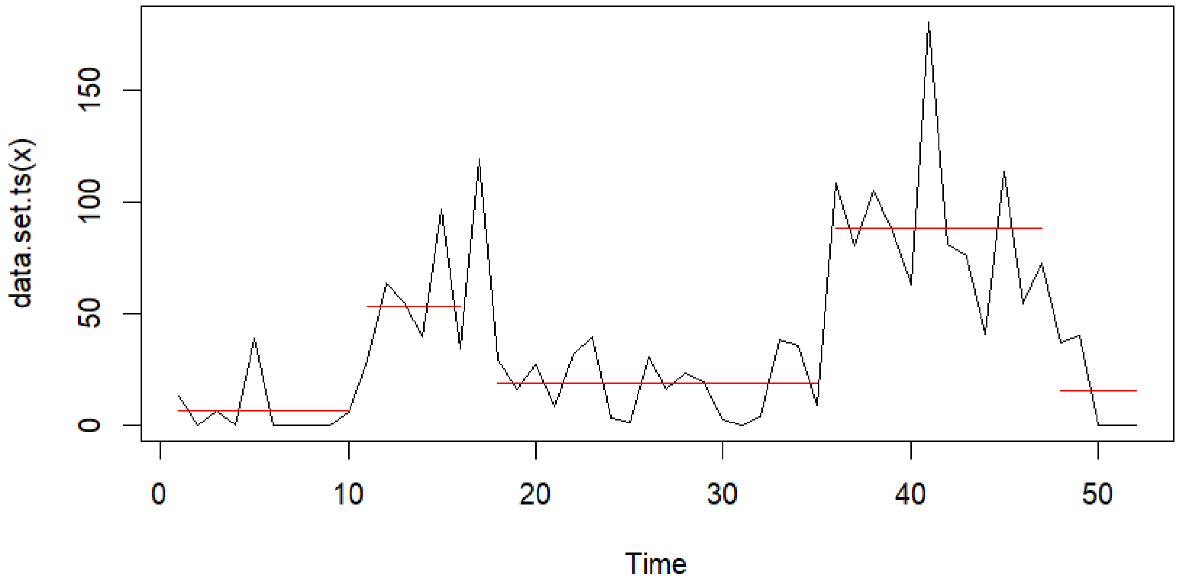


Figure S4.3: Seasonal differences in black-casqued hornbill selection for **canopy height heterogeneity (100 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

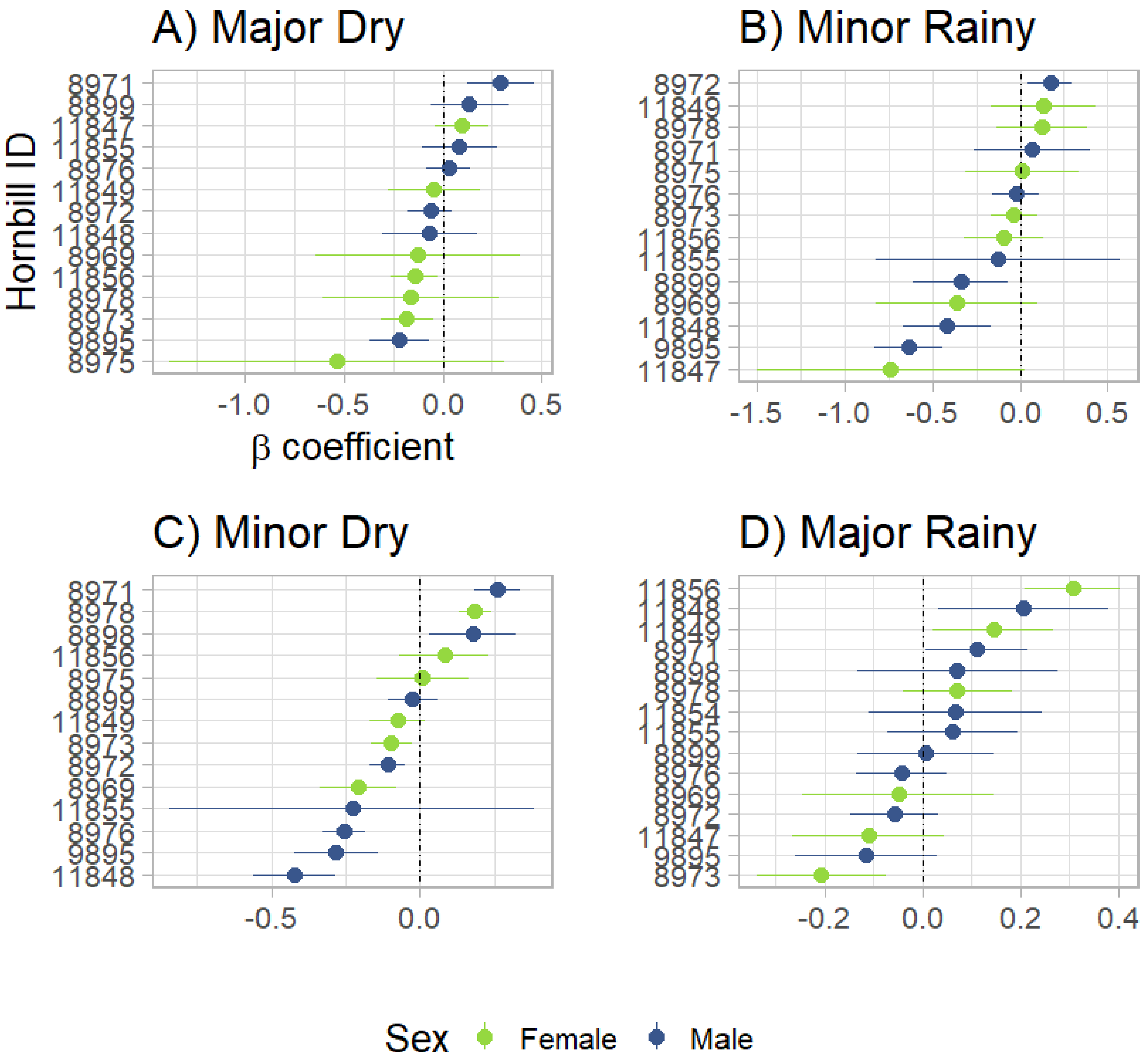


Figure S4.4: Seasonal differences in white-thighed hornbill selection for **canopy height heterogeneity (100 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

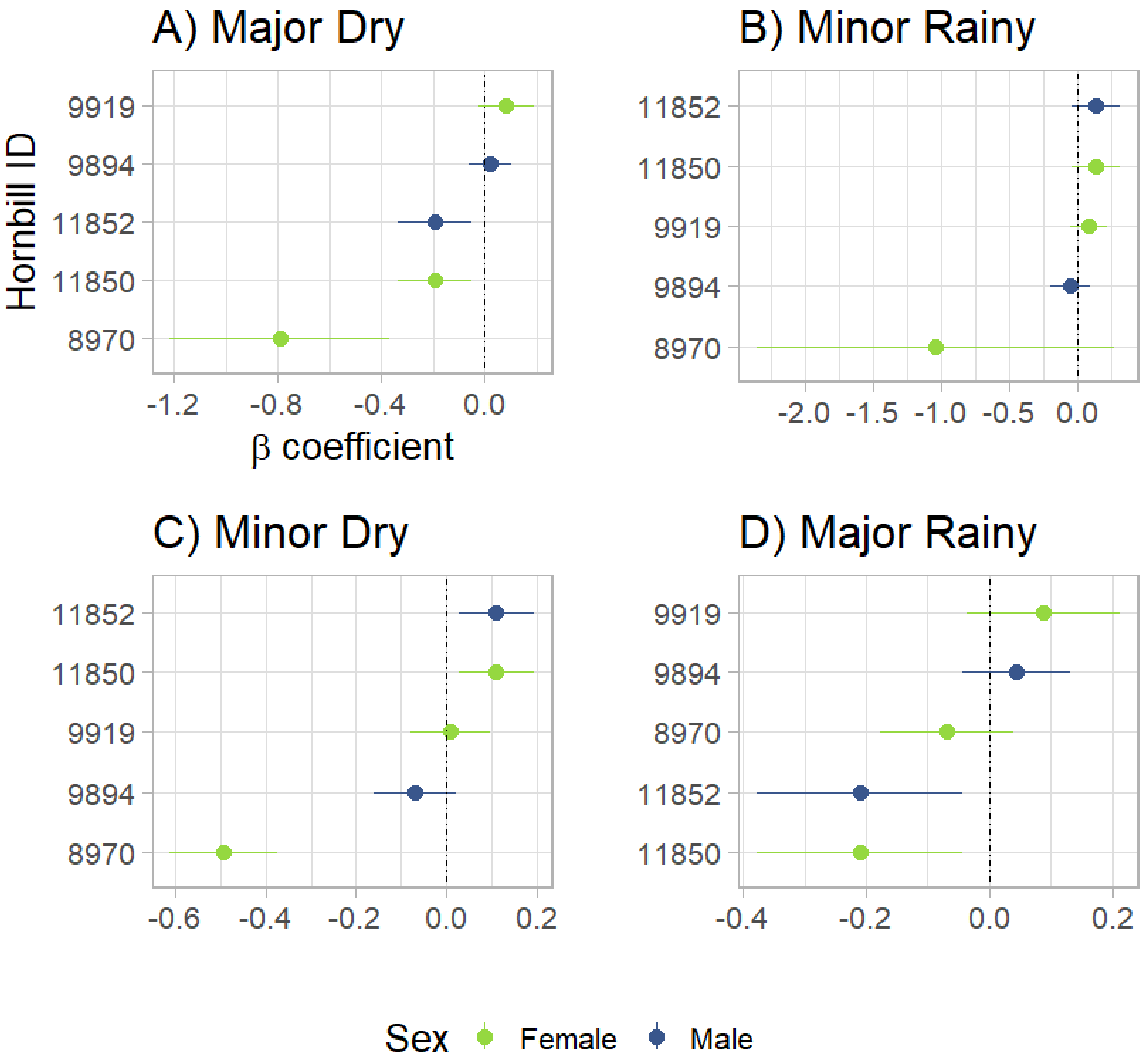


Figure S4.5: Seasonal differences in black-casqued hornbill selection for **canopy height heterogeneity (1000 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

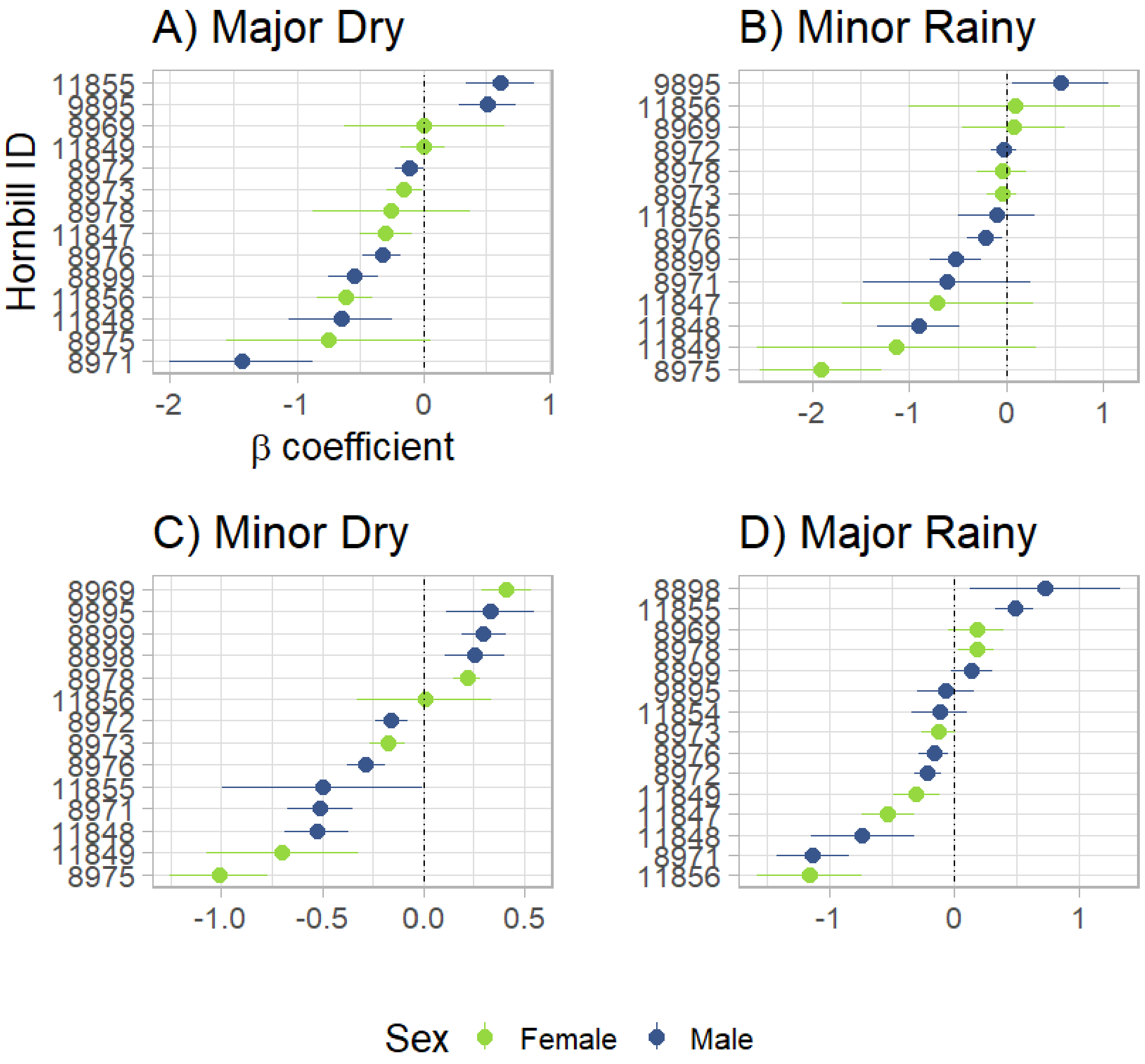


Figure S4.6: Seasonal differences in white-thighed hornbill selection for **canopy height heterogeneity (1000m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

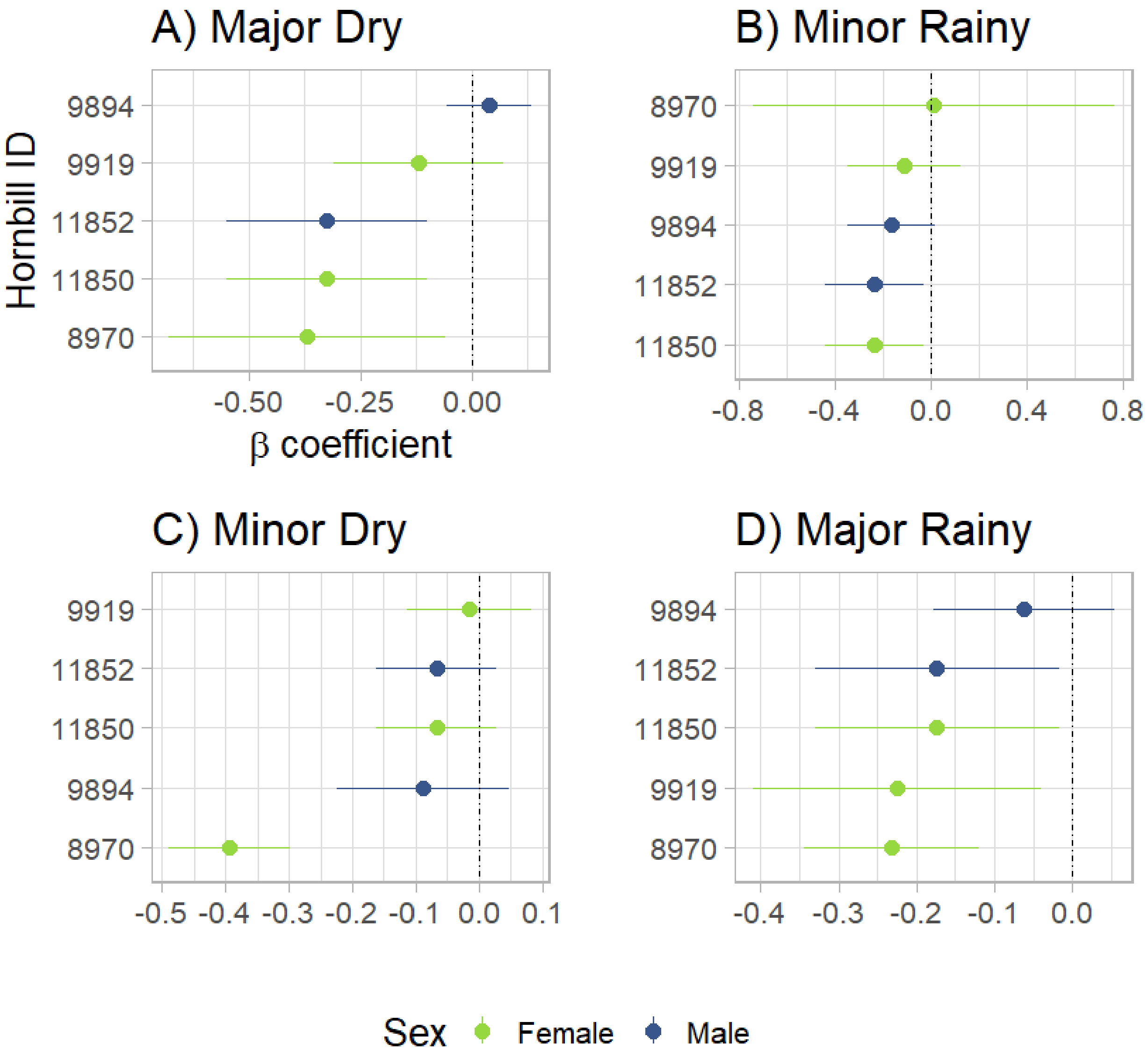


Figure S4.7: Seasonal differences in black-casqued hornbill selection for **distance to nearest canopy gap (30 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

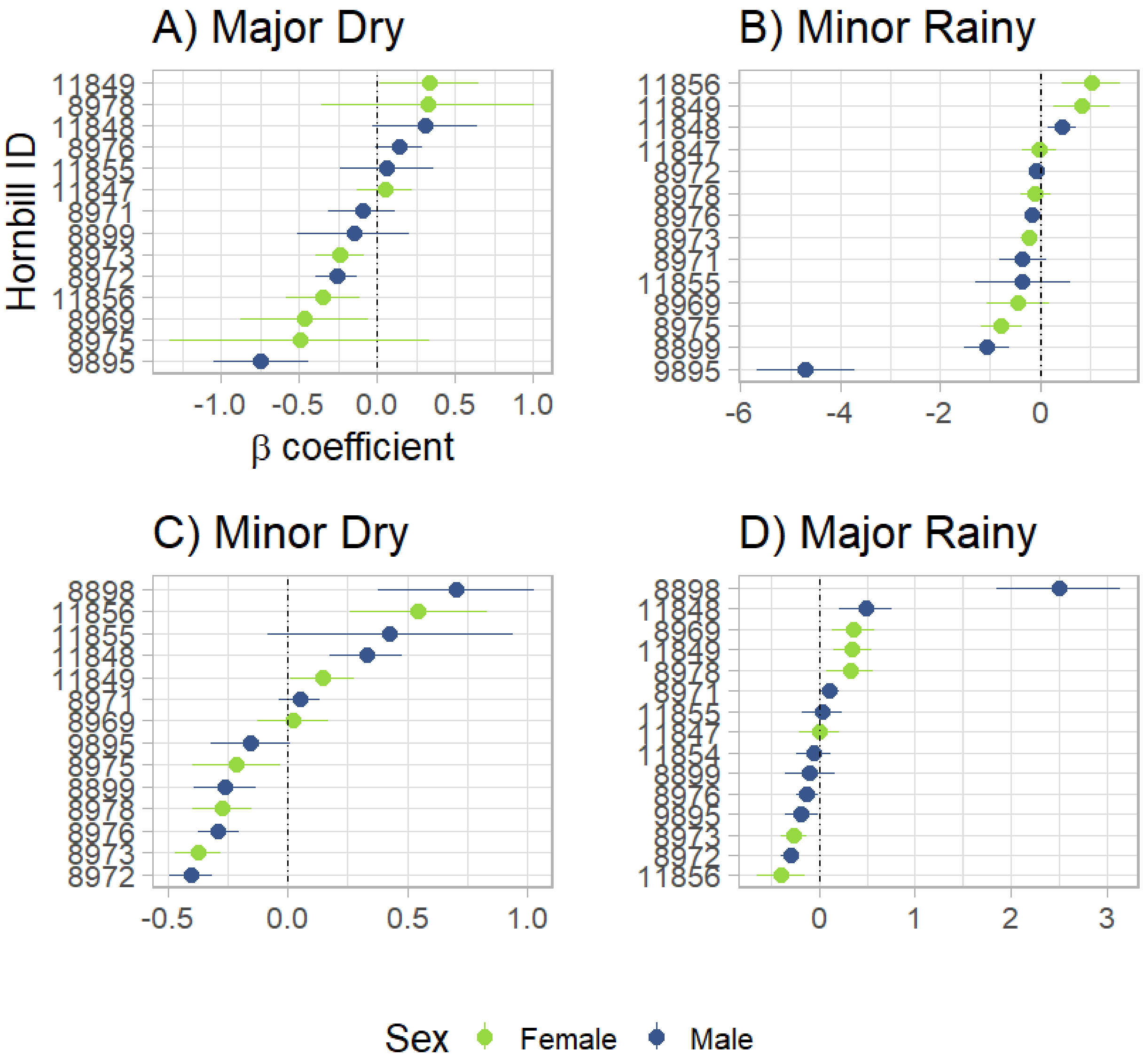


Figure S4.8: Seasonal differences in white-thighed hornbill selection for **distance to nearest canopy gap (30 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

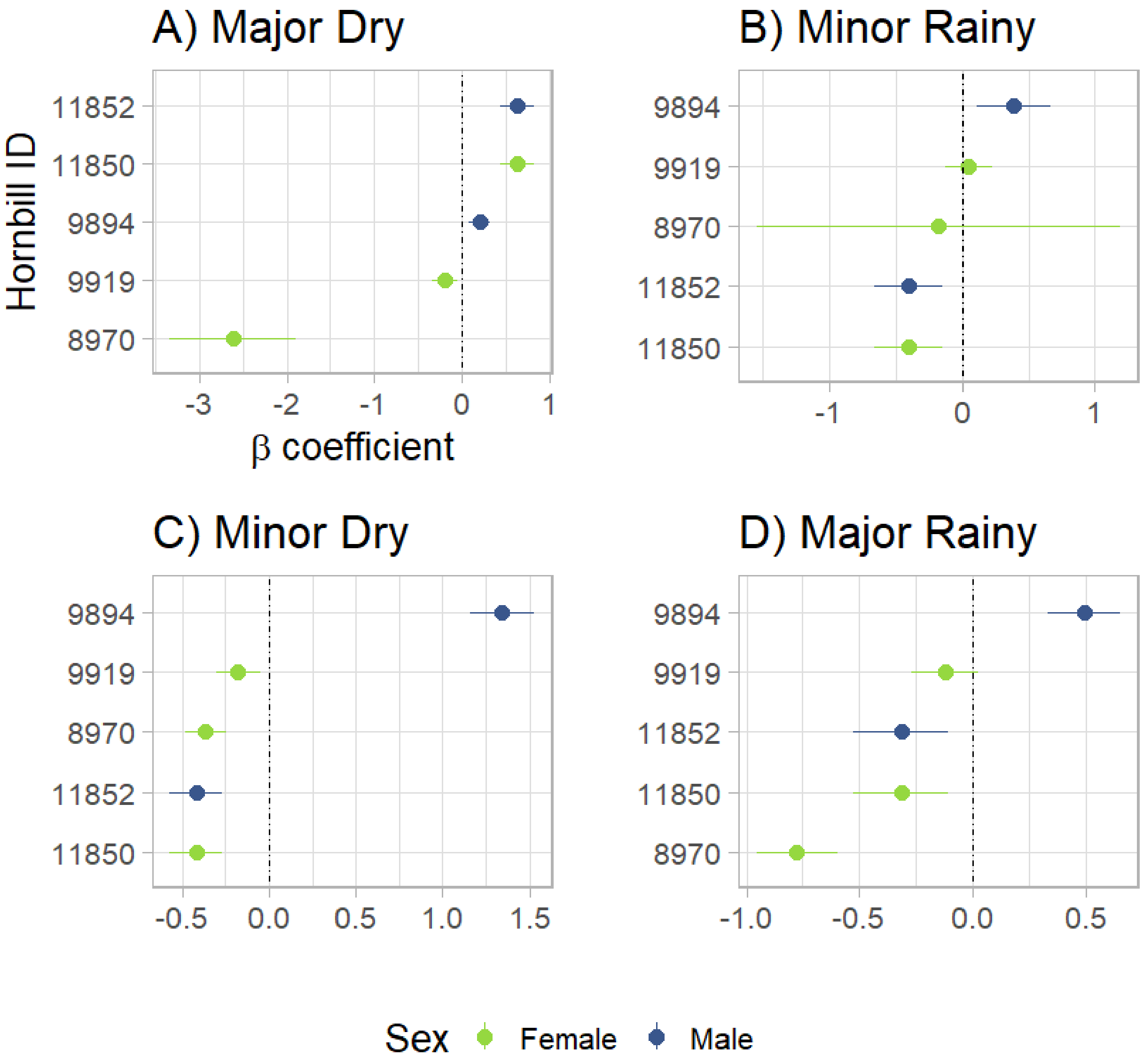


Figure S4.9: Seasonal differences in black-casqued hornbill selection for **distance to nearest road (30 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

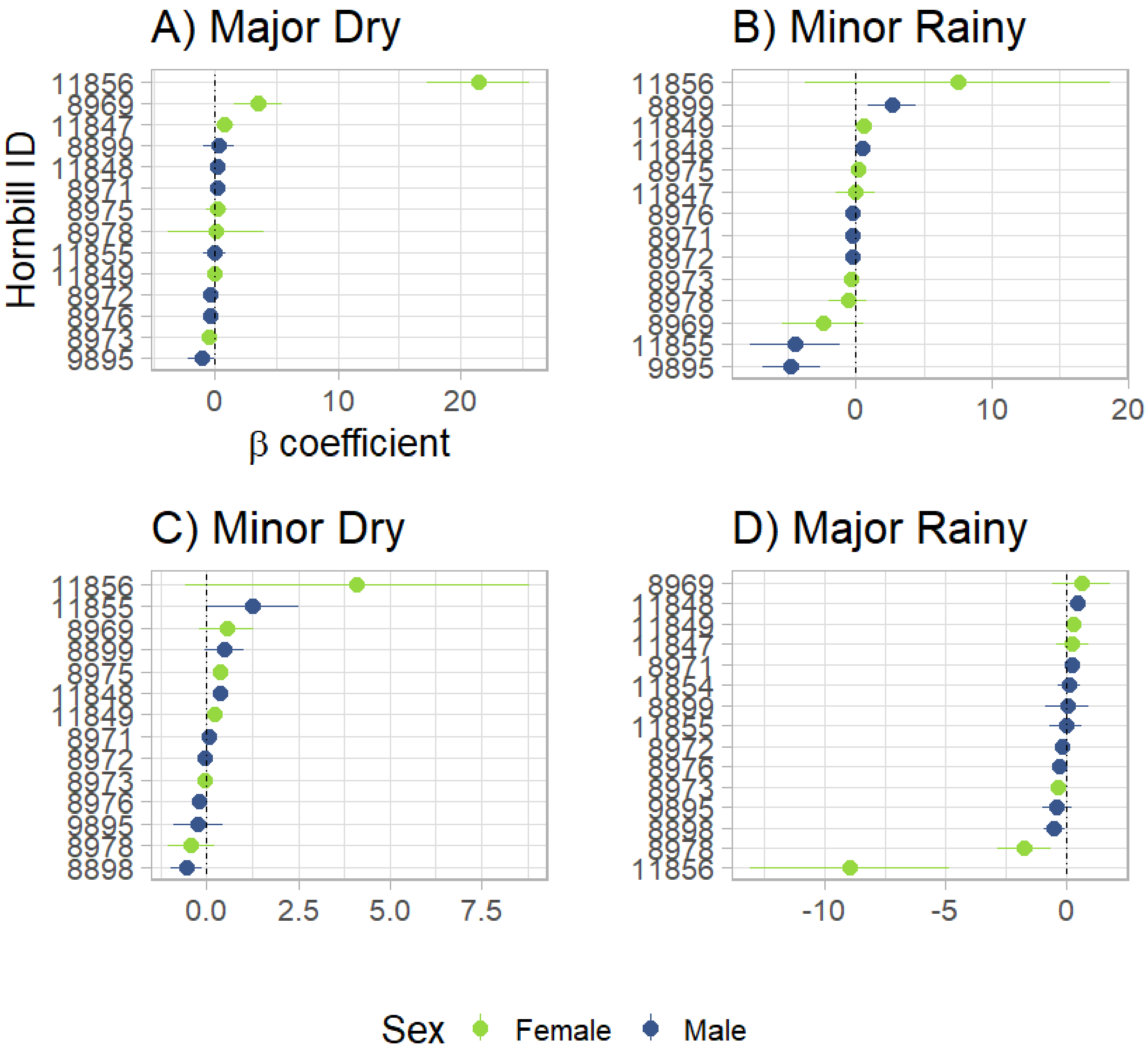


Figure S4.10: Seasonal differences in white-thighed hornbill selection for **distance to nearest road (30 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

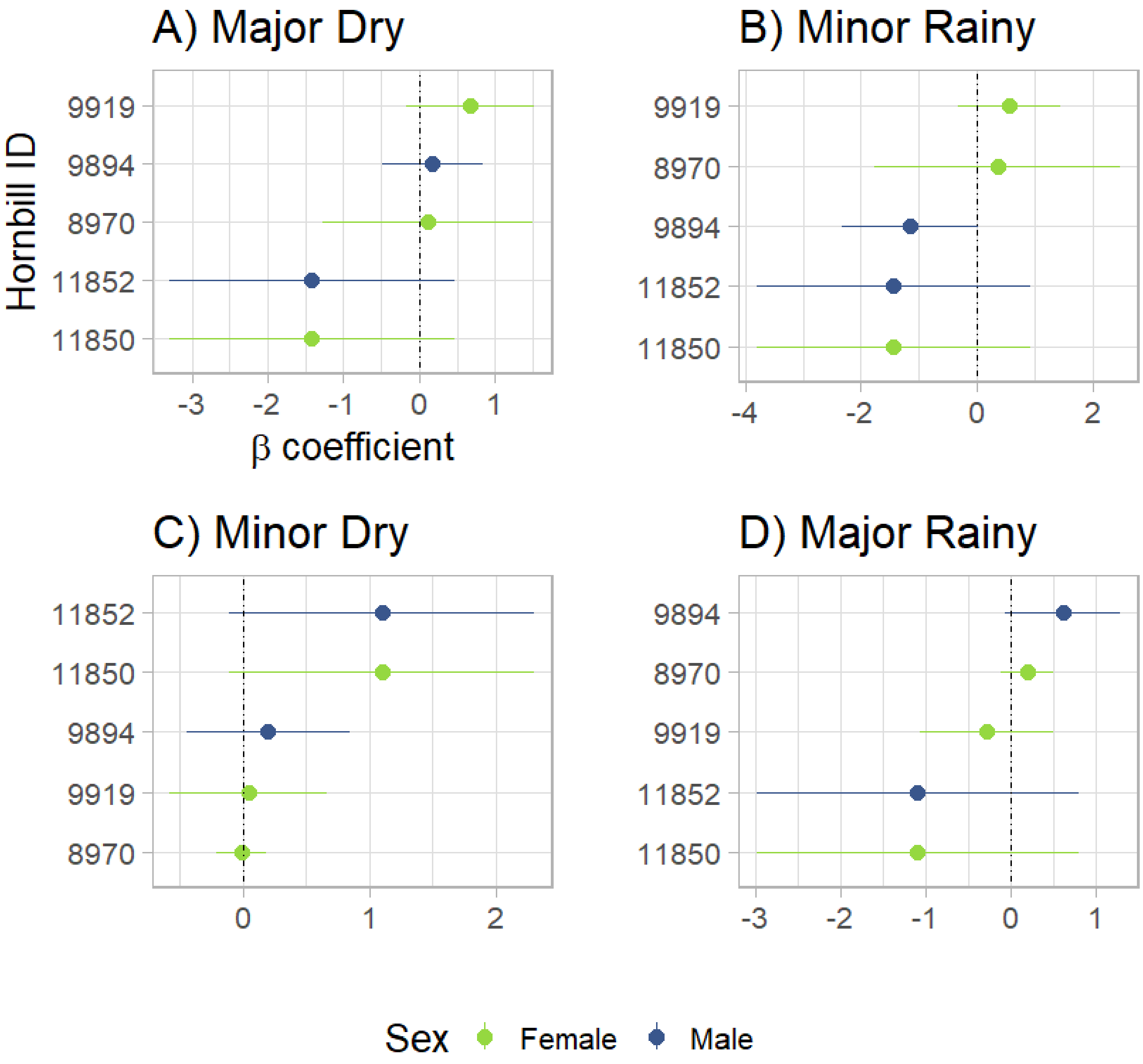


Figure S4.11: Seasonal differences in black-casqued hornbill selection for **swamp habitat (10 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

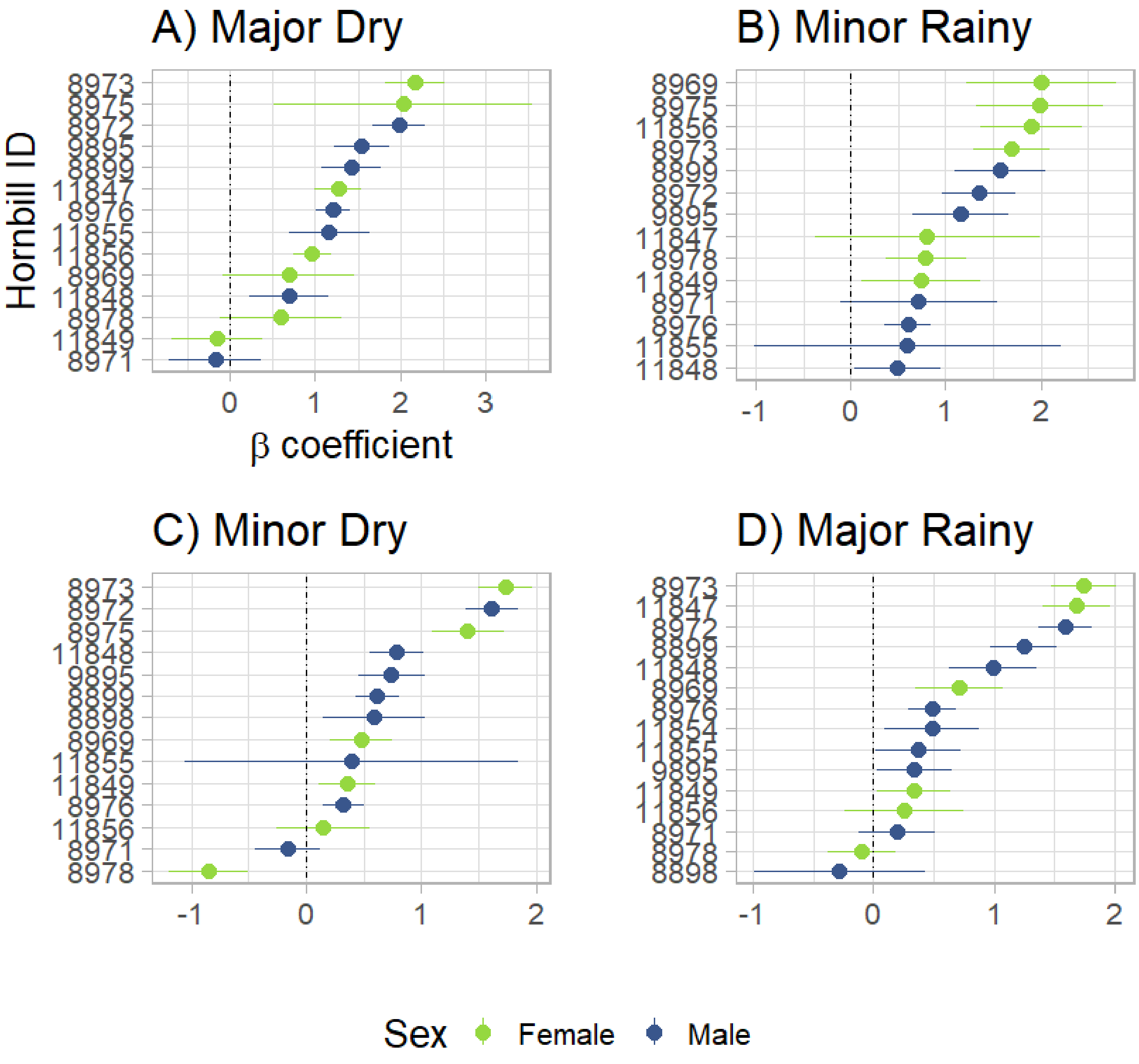


Figure S4.12: Seasonal differences in white-thighed hornbill selection for **swamp habitat (10 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

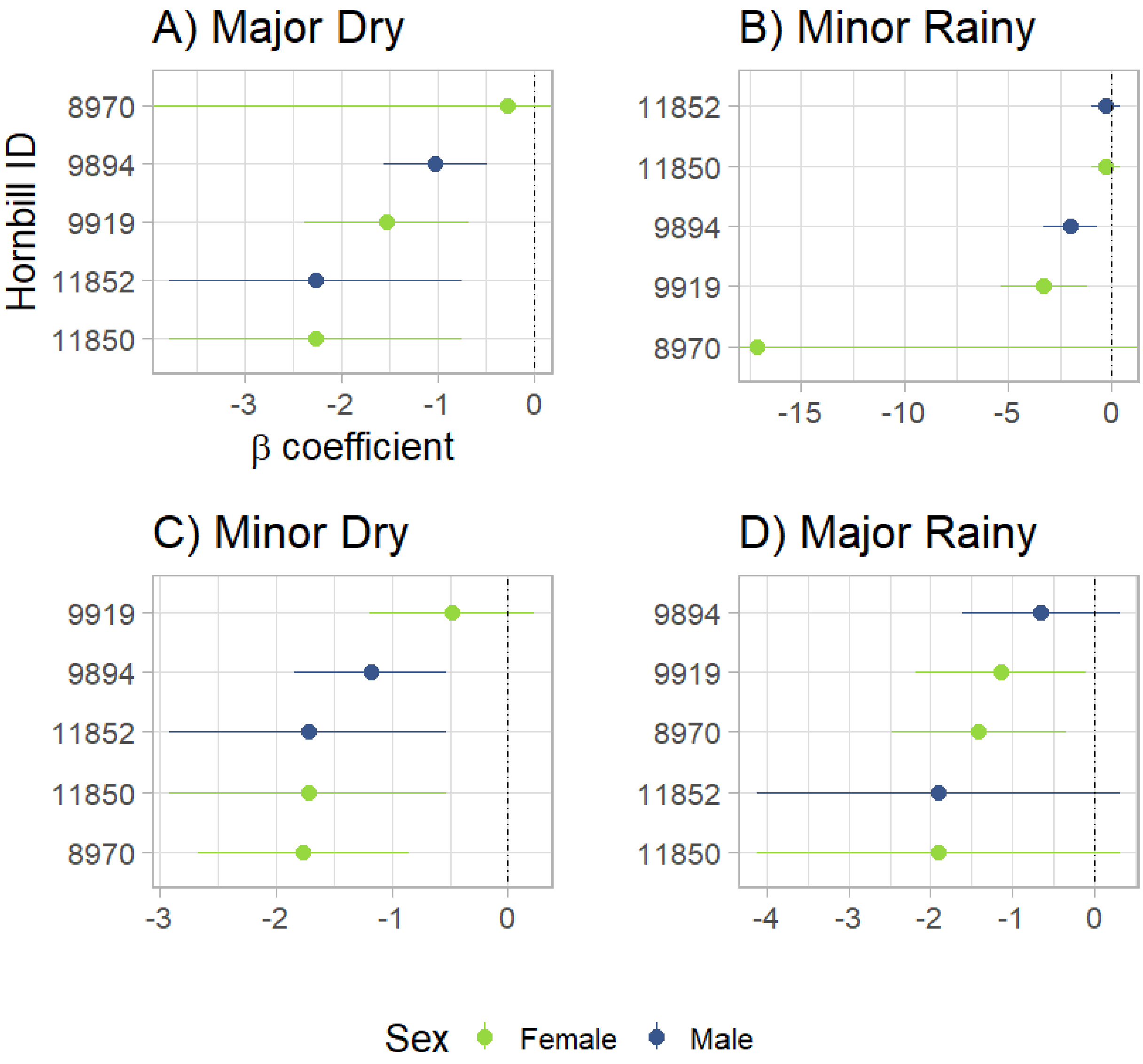


Figure S4.13: Seasonal differences in white-thighed hornbill selection for **forest habitat (10 m resolution)**. Dots and lines represent β coefficients, or selection strength for the variable, and 95% confidence intervals, respectively. The dotted line at β=0 represents no selection. Note that the order of Hornbill IDs in the y axis varies in each plot.

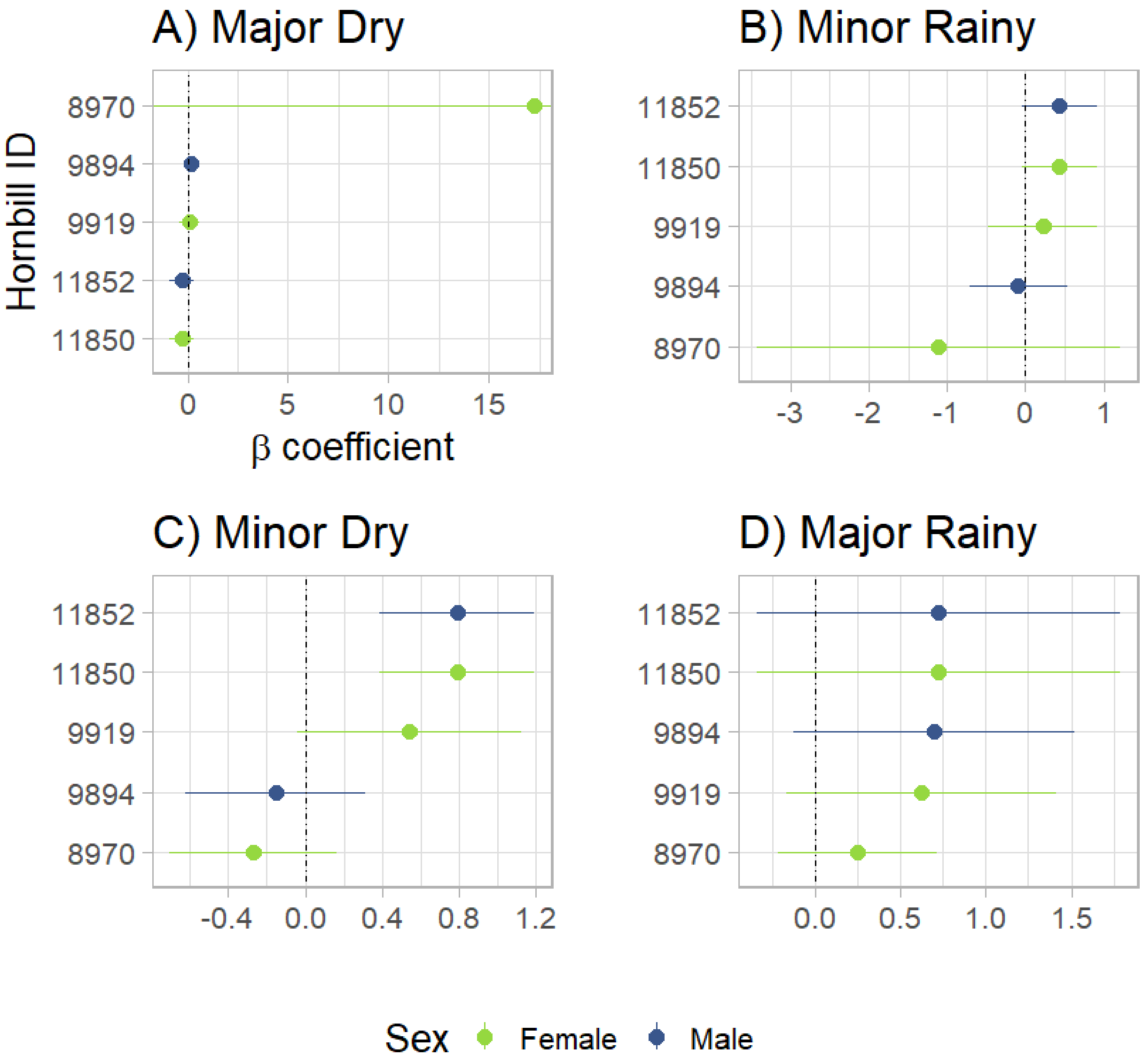


Figure S4.14: Biplot of a Principal Component Analysis (PCA) for movement behavior of 19 black-casqued and 10 white-thighed hornbills, whose points are colored by quality of representation ($\cos^2$). The x- and y-axis represent scores of the first and second principal component, respectively, with each vector representing the magnitude of its loading in each component. MNSD = Maximum net squared displacement; MSD = Mean squared displacement; MCP = minimum convex polygon; RT = residence time; TAC = turn angle correlation.

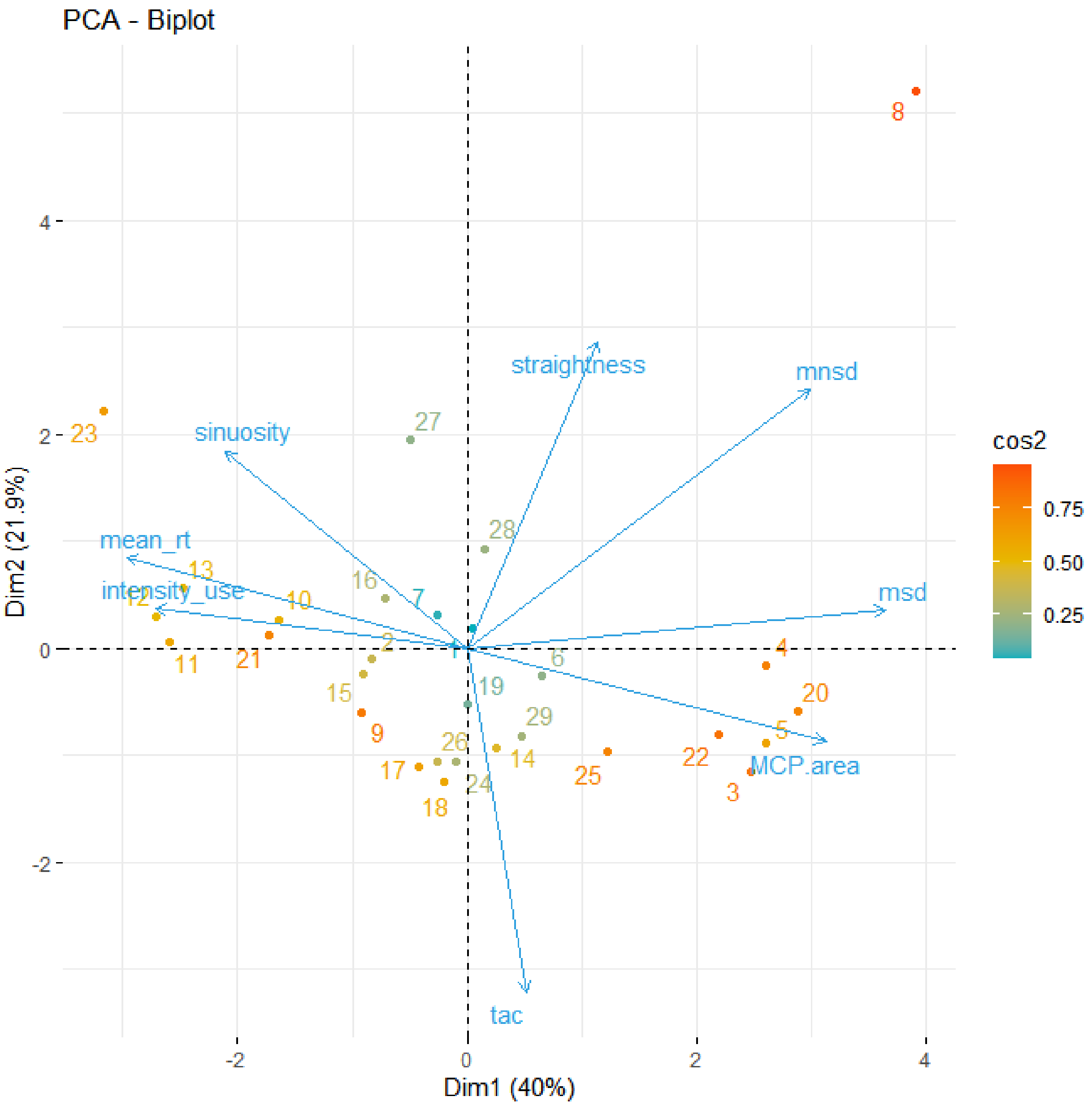


Figure S4.15: Scree plot representing the percentage of explained variance of each principal component (“Dimensions”).

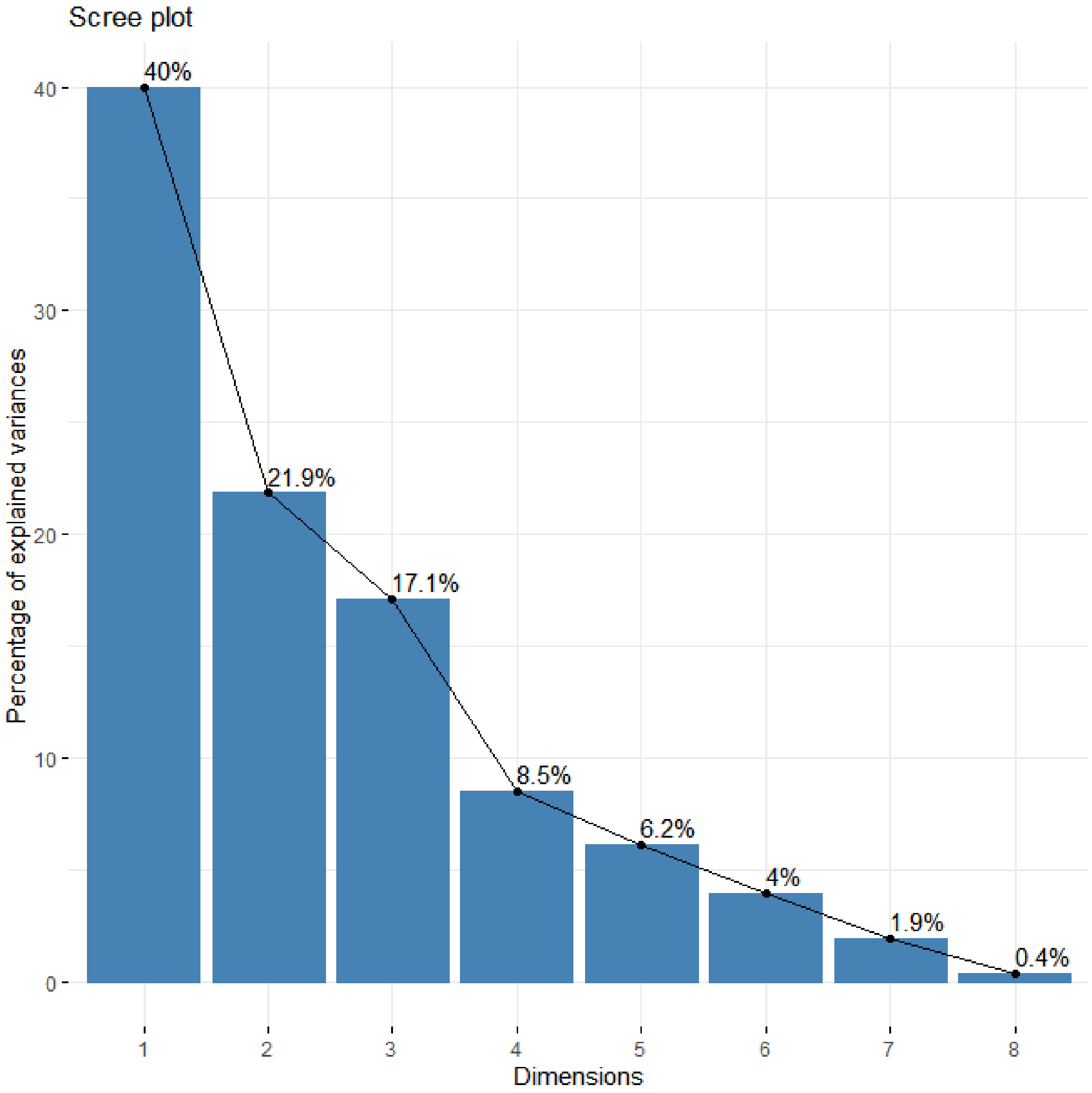


Figure S4.16: Quality of representation of each variable in the PCA, measured as $\cos^2$.

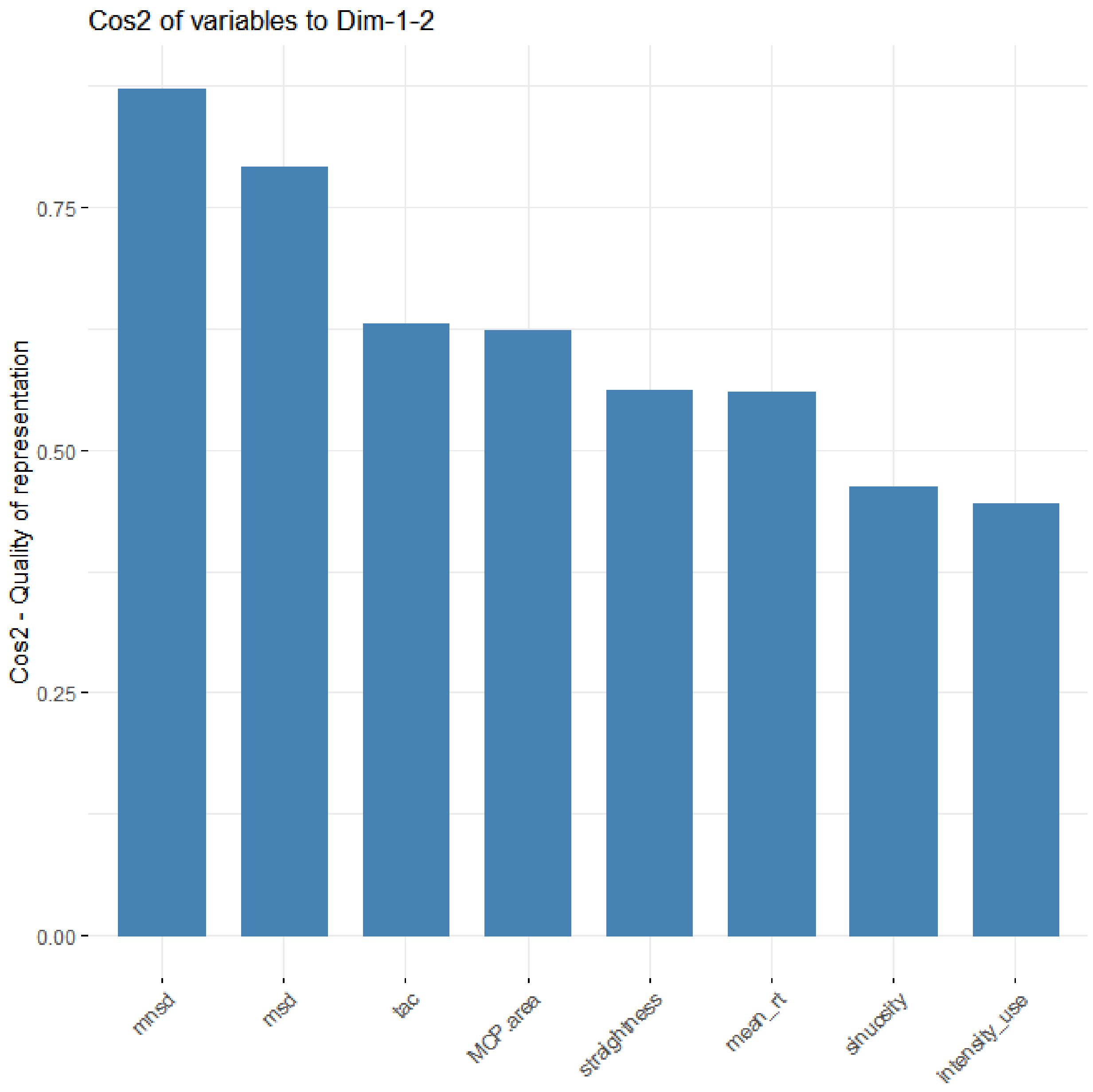


Figure S4.17: Movement tracks of all "Syndrome 1" hornbills, tracked from 2009-2012 or 2022-24. The grey shaded polygon represents the Dja Faunal Reserve.

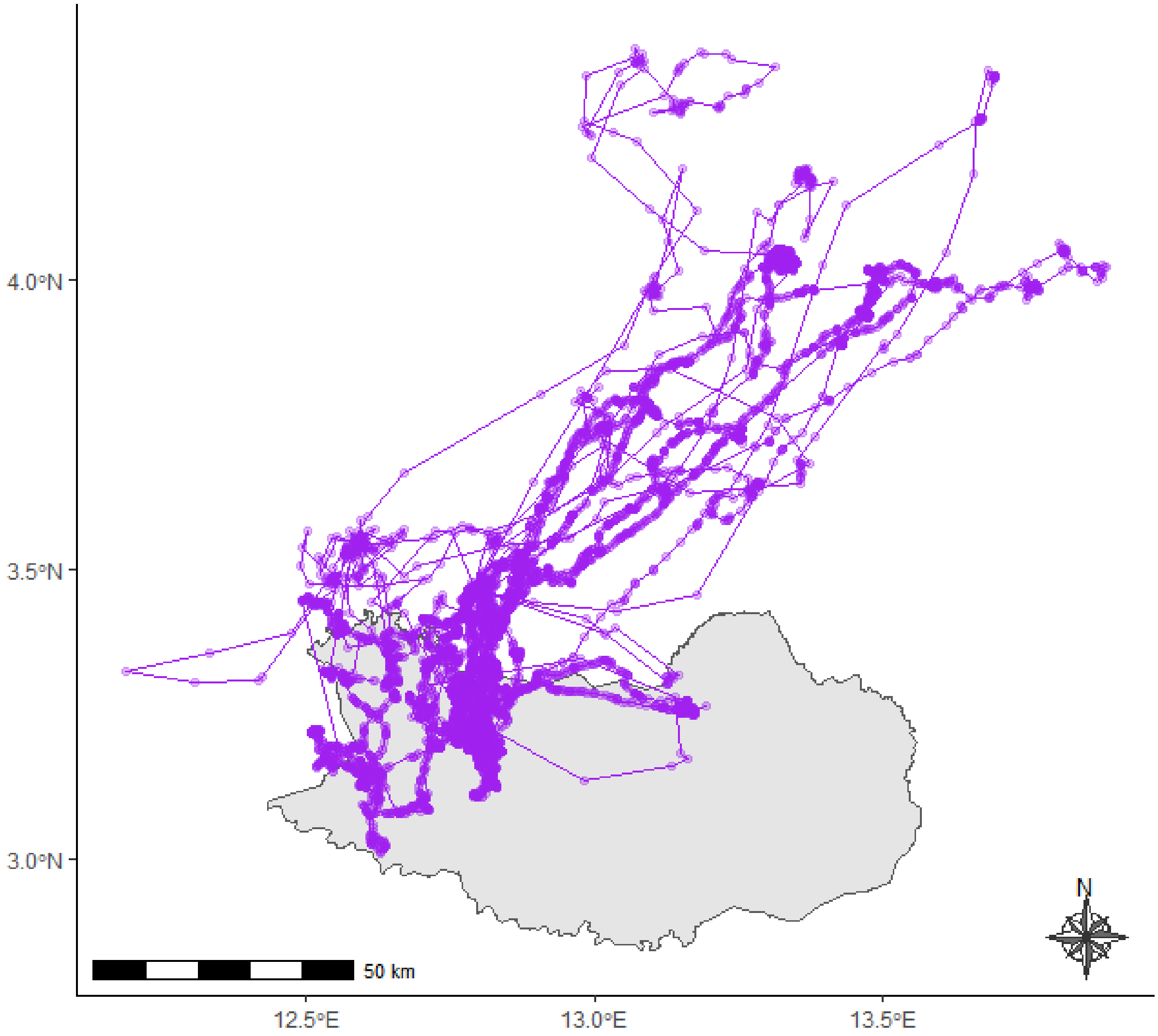


Figure S4.18: Movement tracks of all "Syndrome 2" hornbills, tracked from 2009-2012 or 2022-24. The grey shaded polygon represents the Dja Faunal Reserve.

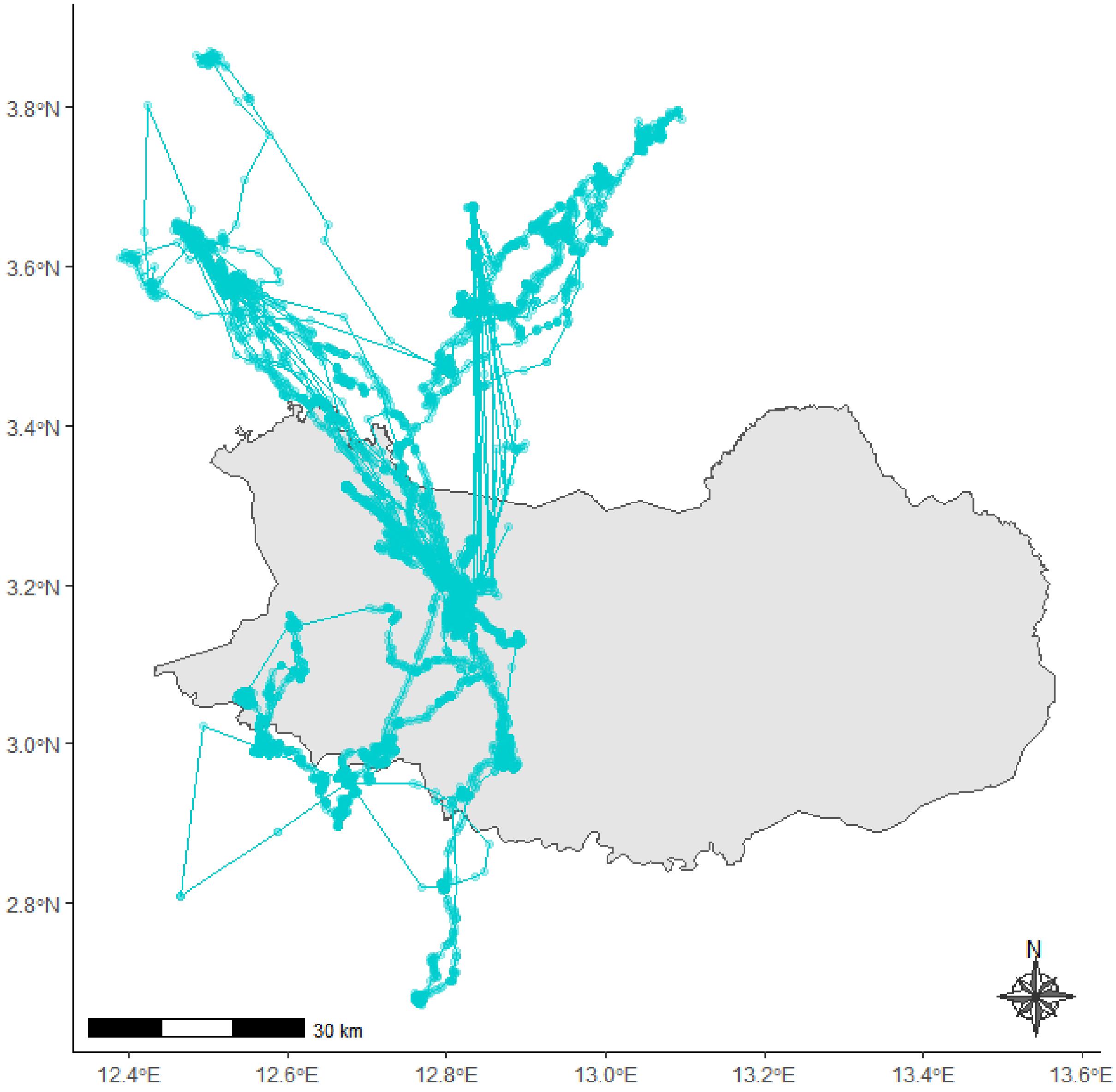


Figure S4.19: Movement tracks of all "Syndrome 3" hornbills, tracked from 2009-2012 or 2022-24. The grey shaded polygon represents the Dja Faunal Reserve.

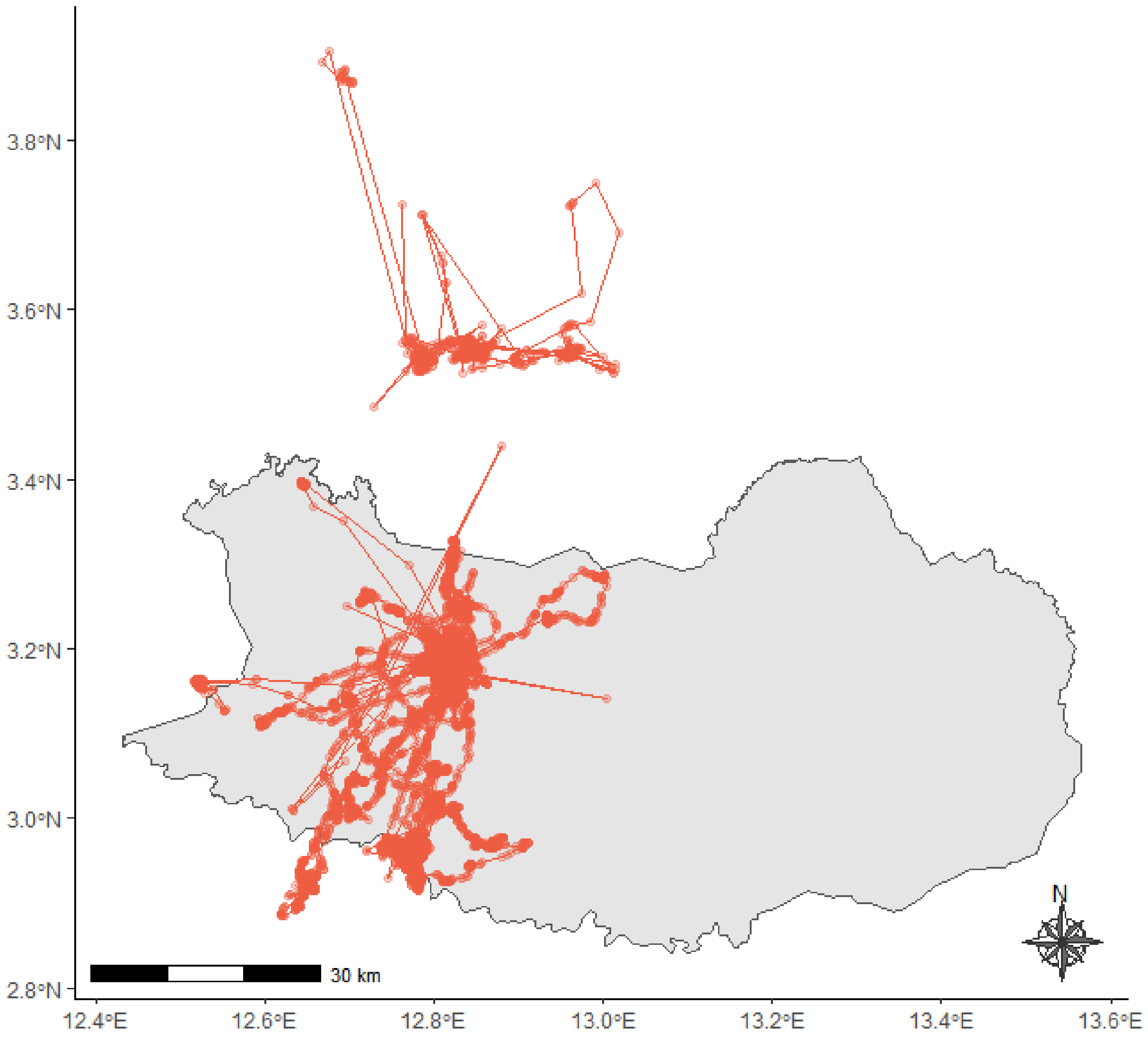
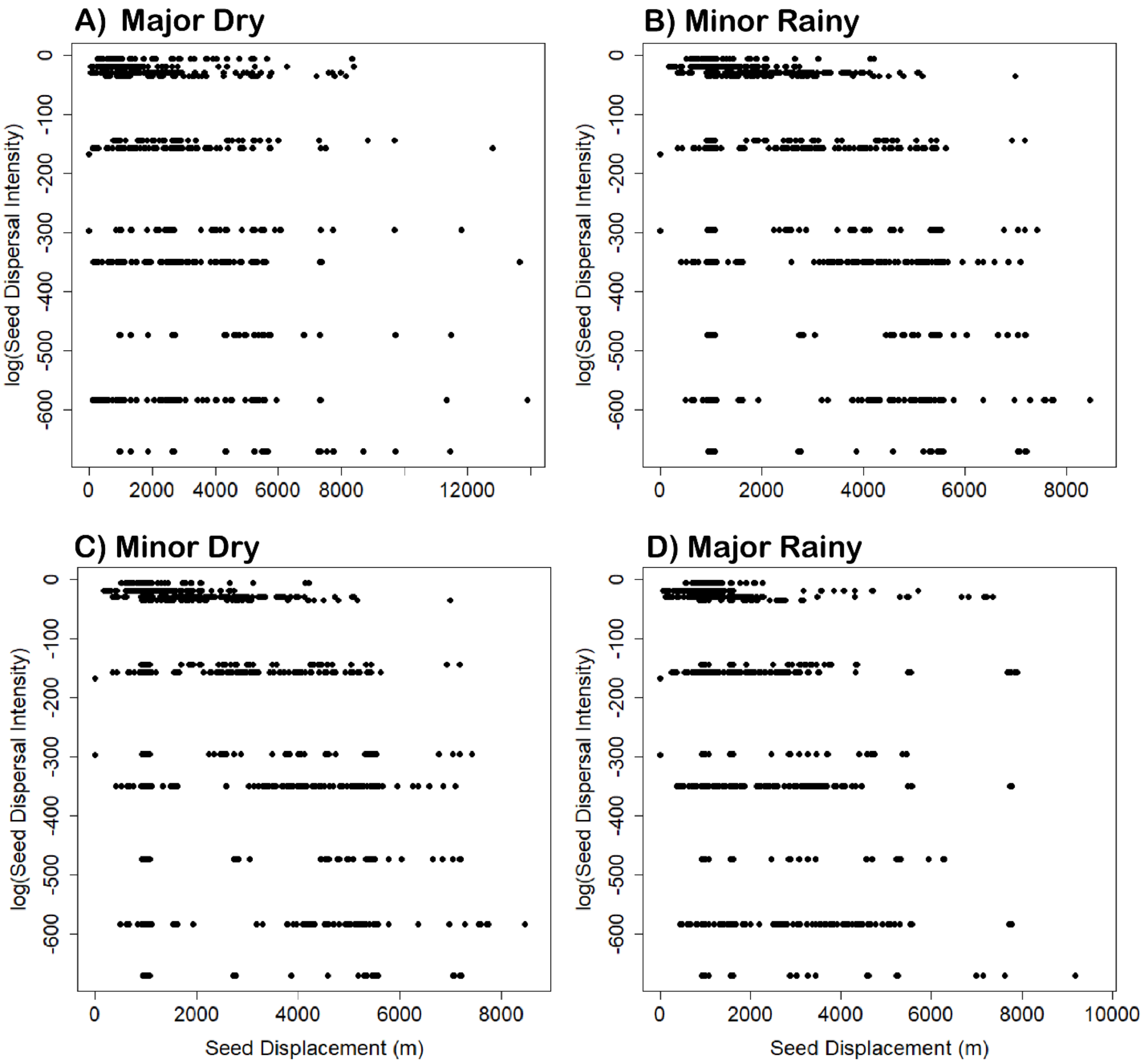


Figure S4.20: Seasonal variation in local probability of seed dispersal with distance from the seed origin. This relationship is shown as log-transformed seed dispersal intensity (λ) of Poisson point process seed dispersal models in relation to seed displacement, for scenarios involving habitat selection by 20 tracked hornbills in **A)** the major dry season, **B)** minor rainy season, **C)** minor dry season, and **D)** major rainy season.



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