

Navigating tropical landscapes; understanding how frugivore traits affect movement patterns and seed dispersal dynamics.



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“People must feel that the natural world is important and valuable and beautiful and wonderful and an amazement and a pleasure.” – Sir David Attenborough

General Abstract

Tropical forests, recognised as some of the most biologically diverse ecosystems on Earth, play a pivotal role in providing essential natural ecosystem services that impact millions of people globally. Despite their ecological significance, these vital habitats face increasing threats due to human activities, with only a fraction currently under protection. The need to understand the implications of human-induced modifications, such as fragmentation, on these ecosystems is paramount for their long-term viability. This research focuses on the complex behaviour of frugivorous birds within the context of tropical landscapes. Frugivores, acting as crucial agents in forest regeneration through seed dispersal, play key roles in understanding the ecological repercussions of habitat alterations. By investigating their movement patterns, dietary preferences, and interaction networks, this study aims to contribute vital insights into the understanding of the complex behaviours exhibited by tropical frugivores in relation to their ever-changing environments.

Chapter 2 begins with a global review of frugivorous animal tracking studies. This review not only establishes a baseline for future studies but also identifies taxonomic and geographic gaps in our current understanding. The findings reveal intriguing connections between morphological and environmental traits, shedding light on the factors influencing seed dispersal distances. *Chapter 3* investigates the movement ecology of four large-bodied frugivorous bird species in Central Panama. The study uncovers diverse species-specific movement strategies influenced by traits and seasonality. The individualised movement patterns demonstrate the variability in movement strategies amongst similar species and offer ideas of how large-bodied frugivores can shape local seed dispersal dynamics. *Chapter 4* explores the dietary composition and interaction networks of avian frugivores in Central Panama. The study showcases the adaptability and different roles of frugivorous avian species in shaping the local environment. The findings offer valuable insights into the intricate dynamics of frugivore networks, emphasising their role in maintaining ecosystem balance and resilience, even in the face of anthropogenic influences.

Declaration of Authorship

I, Adam Fell, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate I have acknowledged the nature and extent of work carried out in collaboration with others.

Signed: 

Date: 19/12/2023

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Impact of COVID-19

The outbreak of Covid-19 impacted the progression of my PhD research, introducing a series of challenges to the completion of the PhD thesis. The pandemic significantly affected and shortened planned fieldwork seasons. The initial deployment of GPS tags in early 2020 was disrupted by the need to evacuate Panama and return to the UK for quarantine. This unforeseen disruption restricted the intended data collection and disrupted the continuity of the study and prevented us from returning to the field until 2022.

The unanticipated multiple global lockdowns made it impossible to retrieve the data that was being recorded on tracking devices in the field and resulted in the loss of some data. The inability to begin exploratory analyses on the movement patterns of tagged individuals became a consequential setback. The planned fieldwork season in Jan – April 2021 was prevented, forcing an adjustment of the thesis timeline. It was possible to return to the field in January 2022, 20-months after the original data collection began. This return, however, required an accelerated pace to compensate for the lost time, essentially compressing three fieldwork seasons into one. The challenges extended beyond fieldwork; the nature of tracking data meant that analysis was contingent on data retrieval and waiting for adequate data to accumulate, which is especially crucial for exploring seasonal aspects of bird movements. Thus, data processing and analysis was significantly delayed allowing for time to accumulate sufficient tracking data.

The profound impacts of the Covid-19 disruptions underscore the resilience required in the face of unforeseen challenges in scientific research. This thesis, shaped by these extraordinary circumstances, stands as a testament to my adaptability and perseverance in the pursuit of ecological understanding, even amidst global crises.

Chapter 1: General Introduction

1. Introduction

1.1 Threats to tropical forests

Tropical forests are the most diverse and species rich biomes on earth (Gentry, 1992). Although these systems only occupy 7% of the earth's land surface, over two thirds of all terrestrial biodiversity reside in tropical forests (Laurance, 1999; Gardner et al, 2009). These ecosystems are vital for maintaining global biodiversity, and providing essential natural ecosystem services that ensure areas are habitable for millions of people worldwide. Tropical forests maintain rivers and watersheds, stabilise soils, control climates, and act as carbon sinks (Laurance, 1999; Bonan, 2008; Edwards et al, 2014). Despite the high value of tropical forests, only 10% of the tropical forest biome is currently under protection (Schmitt et al, 2009), and the long-term viability of these protected areas may be threatened by adjacent human activity (Wittemyer et al, 2008).

Deforestation is considered the main threat to biodiversity loss within the tropics (Bradshaw et al, 2009). Habitat loss, fragmentation and changes in land use have reduced much of the global tropical forest from large continuous tracts of vegetation to complex human-modified tropical landscapes (HMTLs) (Gardner et al, 2009). HMTLs are comprised of isolated fragments of primary forest and secondary forest embedded in a matrix, typically composed of agricultural land and urban areas (Tabarelli et al, 2010). It is estimated that global primary tropical forest cover has been reduced to less than 30% of its original extent (Chazdon, 2014), with 4.1 million hectares of tropical forest cover lost in 2022 alone (Pro et al, 2023). An estimated 195 million hectares of tropical forest has been lost between 1990 – 2015 (FAO, 2016; Keenan et al, 2015). The expansion of HMTLs through the process of forest fragmentation and habitat loss is a severe threat to biodiversity and can impact species through the alteration of various biological and evolutionary processes (Saunders et al, 1991; Fahrig, 2003; Fischer & Lindenmayer, 2006). For example, changes in spatial structure of forests at the landscape scale result in changes to community assemblages of plants and animals within the isolated patches. This in turn can cause a number of cascading effects on ecological processes such as pollination, predator-prey interactions, and seed dispersal (Ferraz et al, 2014)

As the global human population increases, the demand for food will also increase, driving agricultural intensification and expansion (Hurt et al, 2011). Isolated forest patches are most at risk from clearance for agriculture intensification as areas outside continuous forests are the first to be utilised (Skole & Tucker, 1993; Tilman et al, 2001; Tscharntke et al, 2005). Tropical nations have some of the highest population growth rates globally, which tends to correlate with annual rates of deforestation (Laurance, 1999). It is estimated that by 2050, half of the world's population will live in the tropics (Edelman et

al, 2014; Lewis et al, 2015; Barlow et al, 2018). Thus, continued habitat fragmentation and land use change over the coming decades, accompanied by increasing climate change effects, could ultimately drive mass species extinctions of tropical forest species (Laurance & Useche, 2009).

Understanding the effects of fragmentation necessitates a thorough understanding of how animals navigate altered landscapes, with a particular emphasis on frugivores given their pivotal role in seed dispersal and landscape regeneration. Landscape connectivity, defined as the ease with which the landscape facilitates movement across various features such as habitat corridors (Taylor et al, 1993; Collinge, 2009), is crucial for mitigating the impacts of fragmentation on wildlife populations (Stouffer & Bierregaard, 1995; Martensen et al, 2012; Mayhew et al, 2019). Focusing on frugivores, whose movements are integral to maintaining connectivity across HMTLs, is essential for combating future fragmentation effects. Their behaviour, especially in terms of movement and dispersal, is critical in fragmented landscapes, influencing seed dispersal patterns and thus playing a significant role in forest regeneration and biodiversity maintenance. Frugivore movements can be categorised into three types: Local movements involve daily activities within their home range, such as traveling between feeding sites and nesting areas. Migratory movements are longer-distance travels, often seasonal, driven by changes in food availability due to fruiting phenology (Powell & Bjork, 1995). Dispersal movements, typically undertaken by younger individuals seeking new territories, are essential for establishing new populations or recolonising areas where species have gone locally extinct (Morales et al, 2010). Understanding these movement patterns among frugivores is vital for devising effective conservation strategies that enhance landscape connectivity and support the ecological roles of frugivores in HMTLs.

1.2 Birds as a model study species and bird communities in HMTLs

Birds serve as an ideal study species for the effects of anthropogenic disturbance because they are one of the best described taxa over recent years and have a plethora of species-specific functional trait datasets available (Vanderwalle et al, 2010). In tropical forests birds have been the focus of numerous comprehensive studies, particularly in understanding their complex diets and interactions, and breeding behaviours, all of which helps to lay the foundations of any future research (Bregman et al, 2014). Birds also provide critical ecosystem services that are essential for the succession and survival of tropical forest habitats, such as seed dispersal (Sethi & Howe, 2009; Anderson et al, 2011). The diverse foraging guilds represented among avian species further enhance their suitability as study subjects among tropical forests, offering insights into various ecological roles and responses to environmental changes (Gray et al, 2007). Furthermore, their mobility ensures they are able to connect different landscape components and mediate the resilience of forests to anthropogenic change by the long-distance dispersal of early successional plant species (Şekercioğlu, 2006; Bregman et al, 2014; de la Peña-Domene et al, 2014).

Many studies describe the presence and abundance of bird species in different land-uses but fail to explain why it is that a certain species can persist where another may not (Lindell et al, 2004; Carrara et al, 2015; Pavlacky et al, 2015; Wolfe et al, 2015). Currently, very little is known about how birds disperse in undisturbed habitats let alone in fragmented landscapes and the diverse habitats that compose HMTLs. The answer likely lies in how animals use their spatial environment and their capacity to move among forest fragments to meet dietary, roosting, and reproduction needs, while avoiding predation (Tucker et al, 2018). To understand the differences in bird communities, species are often split up into groups depending on their dependency on different forest types: forest specialists regularly use mature, continuous forest, in contrast forest generalists use a range of forest habitats, e.g. primary, secondary, and degraded forests. Certain characteristics have been linked to the likelihood of bird species using agricultural land, these include body mass, dependency on forest interior vs forest canopy/edge, feeding guild (insectivores/ frugivores/ granivores/ omnivores) and specialisation of foraging strategies.

Harris & Reed (2002) suggested that specialists, forest interior, and non-migratory species are more likely to be behaviourally inhibited in crossing open areas compared to generalist, forest canopy, and migratory species. A number of studies support this by suggesting that organisms that inhabit less frequently disturbed areas are more likely to be specialised and demonstrate a narrower range of environmental tolerance to change (Soto-Saravia et al, 2021). This suggests that more specialised species, which are likely to be more sedentary species, are more prone to extinction following fragmentation (Şekercioğlu, 2007, Rivas-Salvador & Reif, 2023). However, a long-term study from the Biological Dynamics of Forest Fragments Project in Brazil found that bird species that were more mobile pre-fragmentation were the species most at risk of extinction after fragmentation (Van Houtan et al, 2007), while sedentary birds were “pre-adapted” to confined fragments. Such studies illustrate how traits, and therefore specialisation, shape species response to land use changes along multiple different axes. For example, it is not necessarily how mobile a species is in undisturbed habitats, but the change in mobility in response to fragmentation that may determine persistence in fragmented habitats.

With loss of primary forests, it is possible that many forest species can persist in secondary forest, buffering them from extinction (Wright & Muller-Landau, 2006; Banks-leite et al, 2010). This claim is supported by evidence that secondary forests can either promote recolonization of isolated primary patches or function as habitat for forest-specialist species (Stouffer & Bierregaard, 1995b; Pardini et al, 2005). A recent study by Karp et al, (2019), described the bird communities in remnant forests of Costa Rica as “indistinguishable” to those found in the protected areas and reserves. This suggests that most bird species are able to adapt to disturbance within working landscapes, and that there is little change in the number of species persisting in totally deforested sites compared to nearby forest (Karp et al,

2019.). However, there were shifts in species abundance with increases in generalist species and decreases in forest specialists. Other studies conclude that species richness and composition in tropical secondary forest differs from primary forests, and that secondary forests should be regarded as suitable habitat only for a limited subset of forest species (Barlow et al, 2007; Gardner et al, 2007; Laurance, 2007). This latter contention is supported by analyses showing that the ability of bird species to use secondary habitats in the tropics does not reduce their risk of becoming extinct from deforestation (Harris & Pimm, 2004). Ultimately, shifts in bird assemblages from forested landscapes to HMTLs are not easy to describe and bird species composition is the synergistic result of both intrinsic species traits and landscape configuration, which determines the presence or absence of a specific species found in these fragments (Vidal et al, 2019). There remains little consensus on which landscape factors are truly important for predicting species assemblages succeeding fragmentation.

Studies in temperate forest regions show a strong positive relationship between species richness and forest area size. This pattern is less defined in tropical regions and further factors have been suggested to have a greater impact on species presence (Estrada et al, 1997; Graham & Blake, 2001). For example, in secondary forests, patch age can have a greater impact on bird capture rates than factors such as the distance to continuous forest or extent of continuous forest present (Stouffer et al, 2006; Prugh et al, 2008). Some species' persistence even increased with an increasing distance from extensive forest, potentially because species become isolated in the patch and cannot disperse to other forest areas as distances are too large (Şekercioğlu et al, 2007). This is surprising considering we generally expect larger and more connected habitats to provide a greater range of resources, including food, shelter, and breeding sites, which we expect to support a diverse composition of species. The composition of the intervening matrix habitat can also be a strong predictor of species persistence in patches and sensitivity to patch size and isolation (Prugh et al, 2008), where species may be able to persist in small fragments when the intervening matrix is more hospitable (e.g. pastures with standing trees and living fences). Many studies find that many species can occupy heterogeneous landscapes, and opportunistically use and even persist in the inter-patch habitat matrix (Vandermeer & Carvajal, 2001; Bender & Fahrig, 2005; Driscoll, 2005; Debinski, 2006; Revilla & Wiegand, 2008).

Further studies on HMTLs and bird assemblages are needed to improve our understanding of how bird communities and ecosystems processes are changing in relation to tropical deforestation. Studies of the animal communities present in forests and degraded landscapes provide valuable information about which species are restricted to undisturbed forests and which can persist in fragmented landscapes (Graham & Blake, 2001; Moura et al, 2013; Bradfer-Lawrence et al, 2018). However, the processes that determine species presence are not evident in these studies, and more detailed descriptions of bird movement are needed to understand how they use and move among different habitats across the landscape.

1.3 Ecosystem processes and bird communities in HTMLs

In temperate zones, up to 40% of plant species rely on animals for dispersal, whereas in Neotropical forests up to 90% of the woody plant species are adapted for animal consumption and dispersal (Howe & Smallwood, 1982). Therefore, ecosystem services provided by animals, such as seed dispersal, are vital for forest regeneration and stability on previously deforested and fragmented lands, especially in tropical forests. This is particularly true in landscapes where land conversion is only temporary, and agricultural land is later abandoned and left to regenerate (Sloan et al, 2016). Secondary forests regenerating on abandoned farmland comprise more than half of the world's extant tropical forest cover (FAO, 2016) and tend to support less diverse communities of many taxa than primary forests (Gibson et al, 2011). Although, as secondary forests age, they become more structurally complex and accumulate species, and the community composition of most taxa become increasingly similar to that of old growth forests over time (Dent & Wright, 2009), suggesting that regenerating forests may help to mitigate loss of undisturbed forest.

Changes in the plant community composition of secondary forests are likely to impact animal species composition and vice versa. For animals, species-level responses to disturbance are often predicted by life history and functional traits (Newbold et al, 2013; Pigot et al, 2020). In turn, these traits are linked with specific ecosystem processes that species provide, for birds these include seed dispersal, control of insect herbivores and pollination (Moran et al, 2004). The majority of plant species found in the tropics require animals to help disperse their seeds (Wunderle Jr, 1997) and different frugivorous species have evolved to consume and disperse different plants. For example, the tropical tree genus *Virola* or wild nutmegs have relatively large seeds (> 2cm diameter) and so many animal species are unable to consume these seeds. Birds with large gape widths, such as toucans (genus *Ramphastos*), are specialist dispersers for this genus (Moreira et al, 2017). Thus, if birds with large gape widths (like toucans) become locally extinct in a forest fragment, then tree species with large seeds will no longer be dispersed across these landscapes and could eventually lead to depleted seed bank composition in regenerating forests (Holbrook & Loiselle, 2009).

Life history and morphological traits determine the dispersal ability of avian frugivores (Newbold et al, 2013). For example, larger bodied bird species can disperse further than smaller bird species (Wotton & Kelly, 2012), and so larger bird species tend to be less affected by habitat fragmentation as they can move among fragments. Habitat specialisation is also key and more specialised species are more sensitive to disturbance (Devictor et al, 2008). A number of studies that have predicted species- and site-specific responses using traits, find that long-lived, large, non-migratory and frugivorous or insectivorous birds are more likely to be at risk from local scale deforestation and reductions in patch size, whereas short-lived, small and migratory habitat generalists tend to be less affected by habitat loss

(Newbold et al, 2013; Pavlacky et al, 2015; Bregman et al, 2016; Hatfield et al, 2018; Bovo et al, 2018; Tobias & Pigot, 2019).

Understanding how landscape dynamics can alter frugivore behaviour and interactions is integral to predict the long-term conservation value of HMTLs and secondary forests. We focus on frugivorous birds specifically, because their diverse requirements and number of functional groups can often lead to species-specific responses to habitat disturbances (Frishkoff & Karp, 2019). Movement behaviour of frugivorous birds dictate their interactions with the plant community and influence seed dispersal patterns (Cortes & Uriarte, 2013; Sasal & Morales, 2013). Birds, with their ability to cover extensive foraging ranges, play a crucial role in connecting different landscape components, mediating the resilience of forests to landscape changes (Mueller et al, 2014). Understanding how the movement behaviour of frugivorous birds responds to habitat fragmentation is essential. Numerous studies conclude that larger-bodied frugivores are able to travel further distances therefore contribute to maintaining genetic connectivity among fragmented landscapes (Mueller et al, 2014; Naniwadekar et al, 2019). In addition to movement behaviour, the diet of frugivorous birds plays a pivotal role in seed dispersal dynamics. Different bird species have evolved to consume and disperse specific plants, creating complex ecological interactions. For instance, the gape width of birds influences the size of seeds they can ingest, making larger-bodied birds specialised dispersers for certain plant species (Rehling et al, 2021). This suggests that changes in the composition of frugivorous bird communities among landscapes can have cascading effects on seed dispersal in regenerating forests (Garcia & Martinez, 2012; Anderson et al, 2021).

1.4 Radio-tracking to understand animal behaviour

Radio tracking studies can provide us with an unequivocal understanding of animal movement. These studies improve our knowledge of the ecology of many species and provide much-needed insight into how behaviour changes over space and time. Previous tracking studies of frugivorous birds largely focused on describing the movement within undisturbed tropical forests, and studies have described home range characteristics and dispersal distance of species in undisturbed habitats (Lindsey et al, 1991; Poonswad & Tsuji, 1994; Holbrook et al, 2002). This kind of baseline natural history information is vital for conservation and informs our understanding of forest dynamics and foraging and breeding behaviours (Holbrook, 2011). For more mobile species, it is essential to understand their ability to move among habitats patches and the scale of their movements because conservation actions implemented at one location within the home range may have little impact if other geographically distant sites are further disturbed are ultimately still affected by conditions elsewhere even if they are geographically distant (Runge et al, 2014; Chibesa et al, 2017).

There are fewer tracking studies in tropical forests compared to other habitats (i.e. oceanic birds, savannah herbivores). Dense vegetation and complex landscape structure limit tracking efforts and interferes with the telemetry equipment (Dussault et al, 1999; Kays et al, 2011). However, recent developments in biologging technology have made tracking studies in tropical forests more feasible. Novel GPS tags can record high-resolution movement trajectories while on-board sensors integrate remote sensing data with environment measurements (Wikelski et al, 2007; Cagnacci et al, 2010; Brown et al, 2013; Wilmers et al, 2015). High-resolution movement data can also record brief but important social behaviours between animals, such as competition or predation events (Kays et al, 2015). Accelerometers can also be used in conjunction with GPS units to reveal more detailed behavioural patterns (Brown et al, 2013; Hammond et al, 2016; Williams et al, 2017). On-board sensor technology provides environmental data, such as the humidity, temperature, and light intensity, of the habitats that the animal occupies, which can help us to understand why some species may be better suited to certain environments than others (Hooker et al, 2007; Dodge et al, 2013). The recent rapid development of tracking technology has meant that studies can now directly address questions about the movement and behaviour of species and how they interact with their environments (Avgar et al, 2013; Katzner & Arlettaz, 2020). Additionally, the development of solar powered tags, remote downloading capabilities and kinetic energy harvesting has enabled “lifetime” studies that track individuals over long timeframes, potentially lifetimes, and has improved our ability to track more species in more remote habitats (Hart et al, 2020; Gregersen et al, 2023).

The use of high-resolution animal tracking in habitat loss and fragmentation studies can be used to infer and understand how species move across human-modified landscapes, and how animals use different landscape components. For example, by identifying activity budgets, foraging sites, and breeding sites (Graham, 2001; Gillies et al, 2011). Using GPS tags, Chibesa et al (2017) found that Trumpeter Hornbills spent a large proportion of time in urban residential gardens but seem to avoid cultivated land. These studies will provide a greater understanding of how animals interact with changes in landscape structure and the conservation implications that may come from continued fragmentation of their habitats.

Accelerometry data can be used to infer energy expenditure and understand how species see the landscape relative to the energetic costs of using it (Wilson et al, 2012). This has been used in tropical ecology and deforestation research to explore how animals move among fragments, riparian corridors, and isolated trees (Gillies et al, 2008; Salinas-Melgoza et al, 2013; Mueller et al, 2014; Şekercioğlu et al, 2015). By determining if there are any significant changes in species behaviour in relation to changes in landscape dynamics, we can start to understand how fragmented tropical landscapes are able to sustain and support long-term viable species populations. If the conversion of tropical forests to agricultural lands and plantations has profound negative effects on animal behaviour, then these species

may not be able to persist long-term in these agricultural habitats, which defines conservation implications for various species and habitats.

1.5 Integrating movement ecology with diet to predict seed dispersal

GPS tracking devices can not only collect data on a specific individual, but also on the environment where it travels and lives. A few detailed studies have illustrated how tracking, not only birds, but a variety of frugivorous taxa, can be used to obtain information related to ecosystem services and seed dispersal (Holbrook, 2011; Lenz et al, 2011). For example, Kays et al (2011) tracked Keel-billed and Chesnut-mandibled Toucans in Panama and found that birds moved further in the mornings after feeding and that they have the potential to disperse *Virola* seeds up to 1km away from the parent tree. While Naniwadekar et al (2019) found that hornbills in Northern India have the potential to move seeds over 13km from the parent tree. To effectively estimate seed dispersal distances is highly complex and involves estimating where seeds are deposited based on animals' diets, movements, and gut retention time. In combination these three pieces of information can estimate seed dispersal shadows. Several studies have calculated gut retention times of seeds and fruits for large-bodied frugivorous species (Holbrook & Smith, 2000; Kays et al, 2011; Mueller et al, 2014) and paired with analysis of the movement behaviour for that gut retention time period to estimate the "dispersal kernel". This is the probability distribution of the seed dispersal distance (Cousens et al, 2008; Kays et al, 2011).

Telemetry data is used to understand the direction and distance an animal moves over different time scales from minutes to months (Cagnacci et al, 2010). The higher the resolution of this data, the more precise movement tracks can be plotted and, in theory, the more precise the seed dispersal kernel will be. When movement data resolution is not high enough, tracks can still be estimated through the process of dead reckoning (Bidder et al, 2015). Sparsely collected GPS locations can be joined up by integrating data from remote sensors, such as an animal's speed, heading, and changes in depth or altitude. The development of higher resolution remote sensors has also helped improved models for dispersal kernels by taking into consideration spatial patterns of animal movement and feeding behaviours (Kays et al, 2011). These incorporate further complex information to determine how far a seed may be dispersed, such as time of feeding and aggregation of seeds around sleeping roosts (Russo et al, 2006).

Remote sensing equipment can be used to describe exact foraging events. Accelerometer tags have recently been used to analyse specific movements and behaviours in many animal species (Shepard et al, 2008; Wilson et al, 2008). Certain behaviours are related to specific isolated movements that can be detected with accelerometers, such as toucan feeding that is associated with a sudden head toss backwards. If accelerometers are placed either on the bird head or beak and recorded at a high enough frequency, then these behaviours can be recorded to identify fruit ingestion events. The location of fruit ingestion can then be paired with gut retention time and GPS tracking to estimate more precisely the

potential deposition sites. Intermandibular Angle Sensors (*IMASEN*) may also be of potential use for identifying frugivore foraging; these sensors have previously been used to assess when penguins catch prey whilst diving (Wilson et al, 2002). These magnetic sensors are placed on either side of the beak and measure the width of beak opening, which relates to prey type, size and identifies a successful foraging event.

1.6 Metabarcoding and frugivorous interaction networks

Seed dispersal shapes spatial structure of plant populations and the species compositions of plant communities (Jansen et al, 2008). Therefore, documenting seed dispersal patterns is the first step in understanding plant community ecology and allows us to identify how changes in the landscape, such as deforestation, can affect plant species colonisation and persistence in the landscape. Given that tropical forests hold > 90% zoochorous trees species (Howe & Smallwood, 1982), it is essential to first understand the common interactions between animal frugivores or seed dispersers and their food plants. This can be achieved by describing the composition of frugivore diets through DNA metabarcoding of faeces.

Integrating frugivore diet composition, derived from DNA metabarcode data, with tracking studies provides a powerful approach to unravel the complex interplay between frugivorous species and their environment, particularly in the context of seed dispersal (Meyer et al, 2022). Metabarcoding involves the extraction and sequencing of DNA from frugivore faecal samples, allowing for the identification of endocarp-derived genetic material (Moorhouse-Gann et al, 2018). This genetic fingerprinting elucidates the specific tree species whose fruits were consumed, establishing a direct link between frugivore foraging behaviours and seed dispersal. By concurrently conducting tracking studies, researchers can correlate the dietary information obtained through metabarcoding with the actual trajectories of individual animals (Evens et al, 2020; Martinez-Fonseca et al, 2022). This integration enables an understanding of how frugivores navigate and utilise the landscape as well as the plant species that they consume and eat, providing insights into the potential distances over which seeds of specific species may be dispersed.

The description of frugivore diets enables us to understand the diversity of species consumed and so distinguishes between generalist and specialist diets. This precision is crucial for delineating frugivorous networks and enabling us to identify key dispersers for specific tree species and uncover patterns of dietary specialisation. The approach goes beyond a mere inventory of consumed fruits, offering a deeper understanding of the ecological relationships between frugivores and the plant species with which they interact. Specialist frugivores exhibit a heightened dependency on specific plant, therefore playing a crucial role in maintaining the reproduction and distribution of those specific species (Schleuning et al, 2011; Watson, 2013). Whereas generalist frugivores exhibit a broad range of dietary

preferences across various plant species and therefore play a versatile role in the ecosystem by interacting with a wide array of plants, showcasing adaptability and flexibility in their foraging behaviours (Carlo & Morales, 2016; Palacio et al, 2016). Furthermore, identification of connector and keystone species in frugivory networks offers invaluable insights into the complex dynamics of seed dispersal. Keystone species, with their disproportionate impact on community structure, regulate plant abundance and distribution, contributing significantly to overall ecosystem stability (Escribano-Avila et al, 2018; Santos et al, 2022). Simultaneously, connector species can enhance network connectivity and facilitate the flow of seeds, which in turn can promote gene flow among fragmented habitats (Olesen et al, 2007).

Understanding the impact of non-native plant species on frugivory networks is imperative for comprehending the broader ecological consequences of environmental changes (Rojas et al, 2019; Fricke & Svenning, 2020). Non-native plants can alter the spatial and temporal distribution of fruit resources, and may disrupt established frugivory networks, affecting seed dispersal patterns and subsequently influencing plant population dynamics (da Silva & Pizo, 2020; Costa et al, 2022). Recognising the interactions between frugivores and non-native plants becomes essential in mitigating potential ecological disruptions and fostering the resilience of frugivory networks in the face of changing landscapes. This integrated methodology contributes to predicting the adaptability of frugivorous communities in response to environmental changes. By linking genetic data on seed sources with the spatial dynamics of frugivore movements, researchers gain valuable insights into the adaptability of these species to modified landscapes. This information is vital for assessing the potential impacts on seed dispersal patterns and, consequently, the dynamics of plant populations in human-modified tropical landscapes.

1.7 Synthesis

Frugivorous birds in HMTLs play a pivotal role in mitigating the impacts of habitat fragmentation by functionally connecting habitat patches and facilitating seed dispersal. To unlock their contribution, a fundamental understanding of the movement behaviours of these birds is essential, especially in the context of landscape alterations. Movement ecology studies serve as a key tool in unravelling the spatial dynamics and behaviours of frugivorous birds and can identify foraging, roosting, and breeding behaviours. This knowledge holds significant conservation implications and can help guide strategies for habitat preservation and restoration to optimise seed dispersal by frugivorous birds. The integration of movement ecology with dietary composition enables us to predict seed dispersal. Leveraging novel technologies in animal tracking and metabarcoding, we can identify how frugivorous animals contribute to seed dispersal across tropical landscapes, describe frugivory interaction networks and provide deeper insights into ecosystem services. This thesis begins by summarising our current knowledge of

frugivorous tracking studies, how researchers use GPS data to understand seed dispersal distances and the potential knowledge gaps that need to be assessed. It then specifically describes the movement behaviours of four, large-bodied frugivorous birds in Central Panama in relation to their body sizes, foraging strategies and responses to seasonal changes. Lastly, it unravels the complex network structure between frugivorous birds and their food plant. It identifies specific traits of species that have a disproportionate effect on the network and assesses the potential impacts that non-native plants species may impose on the frugivory network structure

1.8 Study site and data collection

A comprehensive systematic review was undertaken for *Chapter 2*, focusing on global frugivorous tracking studies, and encompassing literature available up to April 2022. A literature search was conducted using Web of Knowledge and Google Scholar search engines using the key words: (animal_move* OR gps_track* OR gps_tag* OR gps_loc* OR radio_trans* OR radio_tele* OR radio_track* OR radio_tag) AND (seed_dispers* OR frugiv*). The literature was then screened for the following criteria: 1) full-text and peer-reviewed article in English or suitable for online translation, 2) Article presents data from radio transmitters or GPS tags attached to a predominately frugivorous animal or directly to a food resource (i.e. seed or fruit).

The fieldwork for *Chapters 3 & 4* was conducted in Gamboa, a small village on the banks of the Chagres River in Central Panama, situated in between two protected forests: Soberania National Park and Forest Protector Arraijan (Figure 1A; -79.69707, 9.11624). The local forest is a mixture of secondary (20-80 years old) and old-growth lowland moist forest. Gamboa is composed of residential areas with small patches of forest, standing trees and gardens with many non-native ornamental and cultivated species. Panama has a tropical climate with a mean annual temperature of 28 °C and a unimodal precipitation regime of an average rainfall of 2226mm, with the dry season lasting from December – April and the wet season from May – November.

Data collection was undertaken in January – March 2020 and January – March 2022, with the aim of tracking the movements of large frugivores with GPS tags and describing avian frugivore diets using faecal metabarcoding. Birds were captured using nylon mist nets placed in the forest canopy at eight different locations in and around Gamboa (Figure 1B). These locations were chosen to encompass a range of environmental conditions, from residential areas to primary forest edges. Mist nets were opened at dawn and dusk, 05:00 Eastern Standard Time (EST) to 10:30 EST, and 16:00 EST to 18:30 EST. Throughout the operational hours, each net was continuously monitored to ensure that any captured birds did not experience prolonged exposure to extreme temperatures or stress. Large frugivores were then fitted with GPS tracking devices (Keel-billed Toucan, Chesnut-mandibled Toucan, Gray-headed Chachalaca, Red-lored Amazon), and faecal samples were collected from all frugivorous

birds. All handling protocols were approved by both the Animal Welfare and Ethical Review Body (AWERB) at the University of Stirling and the IUCAC of Smithsonian Tropical Research Institute. Our data collection methods were designed to prioritise the welfare of captured birds while obtaining valuable movement data and genetic material.

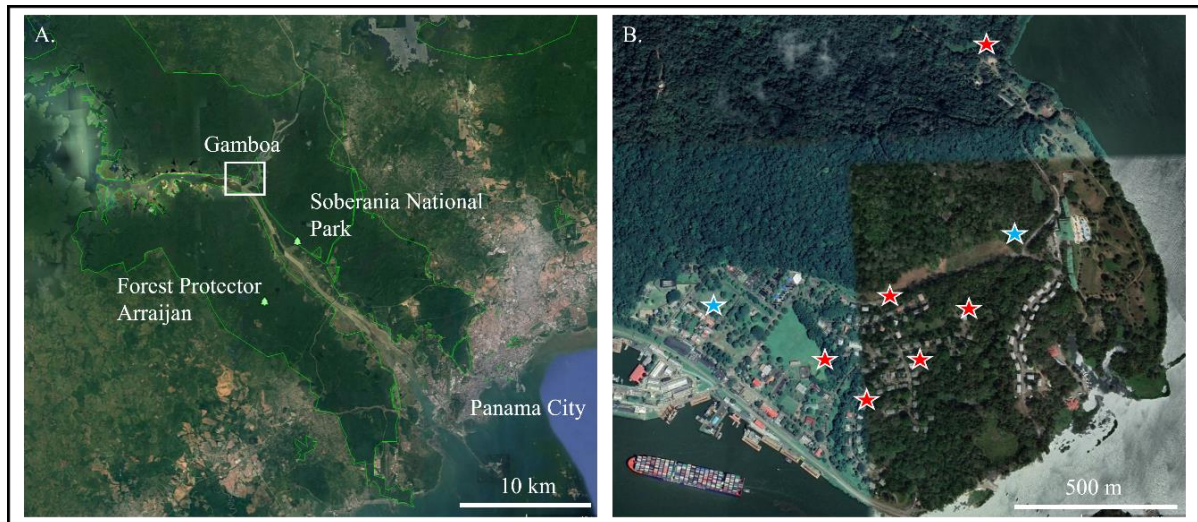


Figure 1A. Map of the location of Gamboa, in relation to Panama City and the two protected forests; Soberania National Park and Forest Protector Arraijan. 1B. The village of Gamboa. Red stars represent locations of mist netting for bird capture and faecal sampling during 2022. Blue stars represent locations of bird capture during 2020.

1.9 Thesis aims

This thesis aims to understand *how frugivore movement patterns and habitat use in human-modified tropical landscapes have consequential effects on seed dispersal, with implications for forest regeneration at the landscape scale in Central Panama*. Specifically, it aims to:

1. Summarise our current understanding of frugivore movement from GPS tracking data with implications for seed dispersal (*Chapter 2*).
2. Describe and compare individual movement behaviours and patterns across four large-bodied frugivorous bird species in a fragmented tropical landscape (*Chapter 3*).
3. Describe the diet compositions and network interactions of frugivorous bird species in a fragmented tropical landscape and discuss the implications for seed dispersal (*Chapter 4*).

Chapter 2: A global systematic review of frugivorous animal tracking studies and the estimation of seed dispersal distances

To assess the current use of animal tracking in frugivory studies and to provide a baseline for future studies, I provide a comprehensive review and synthesis of the existing primary literature of global tracking studies that monitor movement of frugivorous animals. Specifically, I identify studies that estimate dispersal distances and explore how dispersal distances vary with body mass and environmental traits. I show that over the last two decades, there has been a large increase in frugivore tracking studies that determine seed dispersal distances. However, some taxa (e.g. reptiles) and geographic locations (e.g. Africa and Central Asia) are poorly studied. Furthermore, I found that certain morphological and environmental traits can be used to predict seed dispersal distances. I demonstrate that flight ability and increased body mass both significantly increase mean and maximum estimated seed dispersal distances. The results also suggest that protected areas have a positive effect on mean seed dispersal distances when compared to unprotected areas. I anticipate that this review will act as a reference for future frugivore tracking studies, specifically to target current taxonomic and geographic data gaps, and to further explore how seed dispersal relates to key frugivore and fruit traits.

Chapter 3: Understanding the movement ecology of large-bodied avian frugivores in Central Panama.

This chapter examines the movement ecologies of four large-bodied avian frugivore species in Central Panama and challenges the traditional assumption that home range size is primarily related to body mass. I studied four species of frugivores (Keel-billed Toucan, Chesnut-mandibled Toucan, Gray-headed Chachalaca, Red-lored Amazon) and found that species exhibit distinct movement strategies influenced by factors such as wing morphology, foraging, and habitat preferences. Notably, *Amazona* species exhibit the largest home range estimates potentially due to their longevity and ability for sustained flight. Season influenced range distributions, but patterns were complex. Site fidelity varied among species and seasons, indicating complex relationships between ecological factors, resource availability, and breeding activities. The observed patterns of site selection and revisitations emphasise the individualised strategies adopted by each bird rather than species-level patterns. Implications for seed dispersal dynamics are profound, with *Amazona* species potentially contributing to long-distance dispersal due to extensive ranging behaviour. *Ramphastos* species display unique movement patterns, suggesting bursts of high intensity foraging and potential contributions to broad seed dispersion. *Ortalis* species movement was characterised by concentrated foraging in smaller areas, which may create denser seed shadows, impacting local seed dispersal and seedling survival. The findings enhance our

understanding of the intricate relationships between frugivorous bird movement behaviours and seed dispersal processes, offering valuable insights for conservation strategies in tropical landscapes.

Chapter 4: Unravelling the dietary composition and interaction networks of avian frugivores in Central Panama.

Frugivorous avian communities play a crucial role in shaping ecosystem dynamics, particularly in the context of seed dispersal. This chapter provides a comprehensive analysis of avian frugivore dietary preferences, frugivory network structure, and ecosystem resilience. Through the examination of 94 faecal samples from 21 species, I identified 127 plant species, showcasing significant dietary diversity and adaptability. Network analysis revealed complex connections between dietary patterns and morphological traits, which challenged the conventional expectations of body mass predicting the centrality of species in frugivore networks. Instead, an increased rate of frugivory in their diet and a longer tail length resulted in a more central network role. Modularity analysis partitioned the network into separate communities, with keystone species acting as vital connectors to the overall network. I found that, smaller, generalist species played crucial roles, emphasising the complexity of species interactions within the network. I described the contributions of non-native plants to avian diets, revealing unexpected roles and ecological adaptability, such as several non-native plants being highly central in the network, but overall, having no negative effects on the overall network structure (*connectance* & *nestedness*). This study unravels the intricate dynamics of frugivorous avian species, emphasising their adaptability, unexpected species roles, and the dynamic responses to anthropogenic influences. The findings contribute valuable insights into the ecological complexity of frugivore networks and their pivotal role in maintaining ecosystem balance and resilience.

Chapter 5: General discussion

In the discussion section, I explore the implications derived from the exploration of seed dispersal ecology within tropical ecosystems across the three chapters. Beginning with a concise summary of each chapter's main findings, I synthesise the links between the systematic review, movement ecology data, and network interactions. The collective insights explain the differences in frugivorous species' behaviours, ranging from movement patterns to dietary preferences and network roles. The integration of these findings not only refines our understanding of seed dispersal but also uncovers the complexity that challenges the conventional theory emphasising the significance of larger frugivorous birds in seed dispersal dynamics, highlighting the need for more exploration. Moreover, I discuss the practical applications of our results for conservation and ecosystem management, emphasising the identification of keystone species, the role of non-native plants, and the interconnectedness of frugivore networks. The discussion extends to opportunities for future research, outlining pathways to upscale local data to broader landscape scales. By presenting a holistic perspective, this section contributes to the ongoing

discourse on tropical ecology and seed dispersal dynamics, providing a foundation for future investigations aimed at preserving biodiversity and ecological resilience in the face of global environmental changes.

Chapter 2: A global systematic review of frugivorous animal tracking studies and the estimation of seed dispersal distances

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AF & DD conceived the study; AF, TS, BD & DD designed analysis; AF led the writing of the text. All authors contributed critically to draft versions prior to publication. Two anonymous reviewers commented on an earlier draft version during the revision process.

2.1 Abstract

Seed dispersal is one of the most important ecosystem functions globally. It shapes plant populations, enhances forest succession, and has multiple, indirect benefits for humans, yet it is one of the most threatened processes in plant regeneration, worldwide. Seed dispersal distances are determined by the diets, seed retention times and movements of frugivorous animals. Hence, understanding how we can most effectively describe frugivore movement and behaviour with rapidly developing animal tracking technology is key to quantifying seed dispersal. To assess the current use of animal tracking in frugivory studies and to provide a baseline for future studies, we provide a comprehensive review and synthesis on the existing primary literature of global tracking studies that monitor movement of frugivorous animals. Specifically, we identify studies that estimate dispersal distances and how they vary with body mass and environmental traits. We show that over the last two decades there has been a large increase in frugivore tracking studies that determine seed dispersal distances. However, some taxa (e.g. reptiles) and geographic locations (e.g. Africa and Central Asia) are poorly studied. Furthermore, we found that certain morphological and environmental traits can be used to predict seed dispersal distances. We demonstrate that flight ability and increased body mass both significantly increase estimated seed dispersal mean and maximum distances. Our results also suggest that protected areas have a positive effect on mean seed dispersal distances when compared to unprotected areas. We anticipate that this review will act as a reference for future frugivore tracking studies, specifically to target current taxonomic and geographic data gaps, and to further explore how seed dispersal relates to key frugivore and fruit traits.

2.2 Introduction

Seed dispersal is one of the most important ecosystem functions globally (Aslan et al, 2013). Seed dispersal plays a pivotal role in shaping plant populations by facilitating regeneration through the movement of seeds and subsequent plant recruitment. Additionally, gene flow is influenced by the movement of alleles driven by seed dispersal, further contributing to local population dynamics and genetic diversity. (Jansen et al, 2008; Jordano, et al, 2011). Humans indirectly benefit from this global service through the seed dispersal of valuable timber species, and edible and medicinal plants (Wenny et al, 2016), yet seed dispersal is one of the most threatened processes in plant regeneration, worldwide (Neuschulz et al, 2016). Habitat loss and fragmentation are the main threats to seed dispersal as they restrict the movement and natural behaviour of local seed dispersers (Mahoney et al, 2018; Browne and Karubian, 2018). Accurate measurement of seed dispersal distances is essential to fully understand the effect of habitat loss on critical ecosystem functions.

Over half of woody plant species globally, and up to 90% of tropical tree species, require animals to disperse their seeds (Howe & Smallwood, 1982). Animal-mediated seed (or diaspore) dispersal can take

many forms, including endozoochory (carried within an animal), epizoochory (attached to the outside of a disperser), and synzoochory (intentionally carried, mostly in the mouth). The way seeds are transported can often help predict the fate of the seed (Nascimento et al, 2020), but the decisions that animals make relating to movements before, during and after interacting with fruit ultimately drive the dynamics of animal dispersed plant populations (Morales et al, 2013). These decisions are shaped by landscape composition, animal traits, diet preferences and behaviours (Baguette & Van Dyck, 2007). Even decisions that are not directly related to foraging, e.g., use of leks, latrines or roosting, can incidentally impact the deposition of seeds through altered movement paths (Sasal & Morales, 2013).

Recent studies call for animal movement and behaviour to be better integrated with seed dispersal studies to enable researchers to fully understand the processes that determine seed rain (Côtés & Uriarte, 2013; Borah & Beckman, 2022) and to advance a mechanistic understanding of animal-mediated seed dispersal. For example, interdisciplinary collaborations linking plant demography and movement ecology could use animal tracking studies to determine the precise location of seed deposition and to describe the dispersal potential of different frugivorous animal species (Borah & Beckman, 2022; Dent & Estrada-Villegas, 2021).

Since the early 1990s, researchers have used tracking technology to study frugivore movement. Animal movement studies have increased exponentially in the last two decades due to the continued advancement of animal tracking and biologging technology (Kays et al, 2015; Williams et al, 2020; Nathan et al, 2022). Recent GPS miniaturisation has enabled tracking studies to focus on smaller animals, while previous tracking was constrained to larger species to meet tag size requirements (Wild et al, 2022). In addition, the development of solar powered tags and remote downloading has enabled long-term studies and allowed researchers to track more species in more remote habitats (Bridge et al, 2011; Flack et al, 2016). Such developments make understanding seed dispersal through the lens of movement ecology more accessible and plausible, and increasingly, studies have used tracking data to infer seed dispersal effectiveness (Holbrook & Smith, 2000; Kays et al, 2011; Hirsch et al, 2012; Rehm et al, 2019). Most commonly, studies infer the movement of seeds using distances travelled during seed retention time (the time the seed is retained by a frugivore, i.e. often the time taken for seeds to move through the gut). Simulated GPS tracks are predicted for the species-specific seed retention time using the fitted distributions of actual animal movement, which can then be used to fit seed dispersal kernels (Nathan & Muller-Landau, 2000).

Seed dispersal is defined by 1) frugivore diet, 2) seed retention time and 3) movement behaviour (Morales et al, 2013; Morales & Lopez, 2022). Frugivore diets can be described by targeted observations or faecal analysis. Observational studies identify frugivore-plant interactions directly and are a low-cost method, but they can be subject to observer errors and bias, and require significant field

effort (Matthews et al, 2020). Analysis of faecal samples can be a more efficient and accurate method for describing diet. Novel DNA metabarcoding techniques recover a short sequence of DNA that is characterised as a unique species identifier (Kress et al, 2015). This method can be used to identify plant species present in frugivore feces and functions with minimal fragmented plant material, which is typical of faecal matter due to degradation through digestion (Gonzalez-Varo et al, 2014). This method requires a dedicated DNA barcoding sequence dataset of local plants for reference, so that the sequences can be matched, which can be prohibitive especially in highly diverse systems (Galimberti et al, 2016). Nonetheless, metabarcoding provides a highly effective new method for describing frugivore-plant interactions for multiple species.

Describing seed retention time is complex and involves detailed observation and identification of ingestion and deposition events. This is challenging and typically requires knowledge of the foraging behaviour of the species, which often comes from hours of observational studies (Sorensen, 1981; Schleuning et al, 2011; Plein et al, 2013). Traditionally, seed retention time has been measured by direct or video observations of feeding and deposition events, either in the wild or in captive trials. However, recent advances in tracking technology have enabled development of small tags that can be ingested by larger frugivores (Beirne et al, 2019), and high-resolution tracking tags that can identify certain behaviours through small changes in body position and movements (Wild et al, 2022). For example, accelerometers can measure small yet significant changes in an animal's posture to determine specific movements (Shepard et al, 2008). By pairing these with detailed observation, patterns in the acceleration data can be matched with specific behaviours, such as consumption or defecation events (Fehlmann et al, 2017).

Frugivores often have complex movement patterns but, when broken down into trajectories and integrated with seed retention times, these offer a basis for predicting the likely deposition sites of seeds (Morales et al, 2013). Frugivore movement can be measured using structured observations (Morales et al, 2013; Ramos et al, 2020), or by tracking animals with GPS or radio tracking devices (Kays et al, 2011; Abedi-Lartey et al, 2016; Rehm et al, 2019; Martin-Velez et al, 2022). Structured observations refer to a systematic and organised approach to studying and recording animal movement patterns in a controlled and consistent manner, usually by selecting vantage points and positions to observe animals and by making detailed drawings of movement patterns on cells of printed maps (e.g. Ramos et al, 2020). Movement paths from tracking devices describe in more detail where an animal has travelled and, for frugivorous animals, these can be used to predict where seeds are deposited. These paths are constructed using movement models such as random walks, correlated/biased random walks, and Levy walks, which use the probability distributions of movement lengths and turning angles (Reynolds, 2010; Michelot & Blackwell, 2019). Once a movement path is generated, seed shadows can be produced to determine the probability of deposition at specific distances. Seed shadows are made up of 1) Distance

of seed from source, 2) Distribution and density of dispersed seeds, 3) Number of overlapping, conspecific seed shadows (Cortes & Uriarte, 2013). Many seed shadow models use a single lognormal distribution to calculate dispersal kernels, which may not be sufficient to correctly identify spatially aggregated seed deposition patterns that are common for vertebrate seed dispersers (Russo et al, 2006). However, these models are improved by considering an animal's behavioural response to different environmental stimuli and their ability to handle potential biases within the movement data, such as spatial and temporal autocorrelation (Morales & Lopez, 2022).

The movement patterns of frugivorous animals are determined by species traits, landscape context and fruit resources. Species morphological traits define a species' functional role within an ecosystem and can impact the provisioning of ecological services. For example, large-bodied avian frugivores are recognised as important dispersers due to the large number of seeds they disperse and their ability to disperse a diverse range of seed sizes, including large seeded species (Wotton & Kelly, 2012; Galetti et al, 2013; Naniwadekar et al, 2019). Bird species gape width determines diet breadth, and species with larger gape widths tend to have a more heterogeneous diet and interact with more fruiting plants (Wheelwright, 1985; Kitamura, 2011; Naniwadekar et al, 2019). Flying species are also key seed dispersers as they typically disperse seeds over longer distances and can functionally connect habitat patches in fragmented landscapes and exploit resources unavailable to terrestrial vertebrates (Lundberg & Moberg, 2003; Şekercioğlu, 2006; Borah & Beckman, 2022). The relative importance of different frugivore guilds in seed dispersal networks varies with biogeographic region and habitat (Dent & Estrada-Villegas, 2021; Garcia-Rodriguez et al, 2022; Tsunamoto et al, 2020). Birds tend to be generalist and opportunistic feeders, whilst mammals, especially larger bodied species, can have more specialised roles and are highly important for the dispersal of larger seeds (Ong et al, 2022). Understanding how morphological traits of frugivores are linked to seed dispersal potential is a critical step in understanding the link between animal and plant communities and can help to disentangle how changes in landscape structure affect colonisation, persistence, and recovery of animal and plant communities.

An interdisciplinary approach that integrates animal movement and plant ecology is needed to better understand animal mediated seed dispersal, (Dent & Estrada-Villegas, 2021; Borah & Beckman, 2022). Here we provide a comprehensive review and synthesis of the existing primary literature of global tracking studies that monitor movement of frugivorous animals, assess the current use of animal tracking in frugivory studies and provide a baseline for future studies. We identify studies that explicitly estimate dispersal distances (using estimations of habitat range, gut retention times and foraging behaviour) and assess how dispersal distances vary with animal body mass and the following environmental variables, biome, human footprint index and the presence of a protected area.

Specifically, we provide a review of all published literature that presents frugivorous animal tracking data and summarise species, location and methods used across studies. We then use the global review to assess: (i) If certain regions or taxa are over- or under-represented in terms of frugivore tracking studies, (ii) How the methods used to track frugivorous animals have changed over time (iii) How environmental variables and animal species traits (volant, body mass) shape seed dispersal distances among distinct frugivore taxa.

2.3 Methods

2.3.1 Dataset collation & screening process

A literature search was conducted using Web of Knowledge and Google Scholar search engines between May and July 2020 using the key words: (animal_move* OR gps_track* OR gps_tag* OR gps_loc* OR radio_trans* OR radio_tele* OR radio_track* OR radio_tag) AND (seed_dispers* OR frugiv*). This search string generated 240 studies, of which 34 were omitted as they were data files from Figshare or Movebank data repositories (<https://www.datarepository.movebank.org/>), not published studies. The remaining literature was then screened for the following criteria: 1) full-text and peer-reviewed article in English or suitable for online translation, 2) Article presents data from radio transmitters or GPS tags attached to a predominately frugivorous animal or directly to a food resource (i.e. seed or fruit). One publication, Tamura and Hayashi (2008) could not be included as we were unable to translate the uploaded, scanned document through an online translator. We defined a frugivore following Terborgh (1986) and Fleming et al (1987) as an animal whose diet consists of at least 50% fleshy fruits (Wilman *et al*, 2014). This included some largely herbivorous and omnivorous species where seeds and fruits comprised over 50% of their diet during particular seasons or life stages (i.e., pregnancy, migration, etc. Bairlein, 2002; Bodmer & Ward, 2006; Carnicer et al, 2009)

If more than one study used the same dataset, the earliest study was selected for inclusion in the review. Of the 206 studies screened, 109 met the criteria to be retained. Twelve of these studies used transmitters attached to food resources rather than frugivores directly and were retained as the information could be used to calculate seed dispersal distances. Additional articles were found in the literature cited by these articles, which had not been obtained through the previous search. This resulted in a further 39 studies that met the scientific criteria. Finally, we found a further 14 studies during a search in April 2022 using the same previous search string to incorporate studies published between the first search and the completion of the review. All studies were then screened to identify only the studies that calculated seed dispersal distances from monitoring frugivore movements through biologging techniques. A total of 162 peer-reviewed research studies were included in the review, and 67 of these were identified as studies that estimated seed dispersal distances. No date restrictions were applied to the search, thus the

earliest study included in the review was published in 1978 and the most recent in 2022. Thus, two sets of studies were used to address the study aims: 1. All 162 studies were used to investigate how frugivore tracking studies are distributed globally and how tracking methods have changed over time (aims i and ii); and 2. A subset of 67 studies were used to investigate seed dispersal distances (aim iii).

2.3.2 Data extraction

For each study, data were extracted that detailed: 1) year of study, 2) tracking method, 3) overall purpose of study, 4) country of study, 5) habitat type, 6) taxonomic group and 7) species tracked (see *Supplementary table 13*). Quantitative information including the number of individuals tracked, the average number of tracking days and the average number of location points collected per individual tag were also collated. This information was calculated from tracking summary results only when the total number of location points and deployment days were stated. Some articles did not provide sufficient information for these metrics to be calculated, and these studies were omitted from further analyses. Tracking method included either radio transmitters (VHF), GPS or resource tracking with attached radio/GPS tags. Frugivore species data included taxonomic group at a species level, the number of species studied and the number of individuals per species per study.

The mean number of tag days was calculated for each study where data were provided. This was the mean number of days reported per study where data were collected across all tracked individuals per species. The mean number of tracking locations per species per study was also calculated when this information was provided. Mean and maximum seed dispersal distances were stated in 45 and 56 publications, respectively. When publications presented estimates for different sized seeds, different seed species or different seasons, we took an average across the different estimates as there was too much variability among studies to sub-divide data into different seed sizes, season, or different sexes etc.

To explore what factors influenced dispersal distance, we extracted frugivore body mass and environmental variables from each study to be used as predictors for our models. Estimates of mean species body mass (g) for birds and mammals were extracted from Wilman et al (2014). To investigate the allometric relationship between body mass and seed retention time (SRT) of the animal species within our studies, we additionally extracted seed type, seed size and SRT (minutes) from the studies that reported the required information. SRT information was extracted from a total of 42 studies and included 59 unique animal species. This information was reported differently for all studies and the SRT values were averaged across multiple seed types and sizes for an individual animal species in an individual study (*Supplementary figure 1*). We categorised species as either *volant* (i.e., capable of flying) or *nonvolant*. This is functionally informative, because in our data set a large proportion of the

mammals studied were bat species, while birds included some flightless species such as cassowaries and emus.

To assign studies to protected areas, we used the UNEP-WCMC and IUCN Protected Planet: World Database on Protected Areas and World Database on Other Effective Area-based Conservation Measures (UNEP-WCMC and IUCN, 2023). The geographic coordinates for studies were either extracted from data presented in the publication (138 studies) or derived from Google Earth based on locations mentioned in the publication methodologies (24 studies). We used the *wdpar* package (v1.3.7; Hanson Jo, 2022) in R to compare study locations to the Protected Areas map (UNEP-WCMC and IUCN, 2023). The study was defined as being undertaken in a protected area if the animal was recorded within a protected area (i.e., national park or reserve) at any point during the study. The creation date of each protected area was compared with the study date to ensure that these overlapped before assigning protective status. Each study site was categorised by biome using the *readOGR* function in the *rgdal* R package (v1.6-2; Bivand et al, 2022); these data were derived from Ecoregion Snapshots: Descriptive Abstracts of the Terrestrial Ecoregions of the World. 2021, developed by One Earth and RESOLVE. Version 2021 (www.oneearth.org). The global distribution of studies was mapped. Temperate climates are described as being $> 35^{\circ}$ or $< -35^{\circ}$ N and tropical climates between 23.4° and -23.4° N. For each of the studies that had geographic location data, the Human Footprint Index (HFI) value was extracted from Venter et al (2016) using the *extract* function in the *raster* R package (v3.6-3; Hijmans et al, 2022). The coordinates used were the same as those used to assign protected status. HFI was used to identify the impact of human activity and landscape modification on seed dispersal. Two studies, Weir & Corlett (2007), and Wotton & Kelly (2012), were omitted from the seed dispersal analysis as there was no HFI data available for these locations. The HFI values extracted here use data from 2009 and do not align exactly with the dates of our studies estimating seed dispersal distances (ranging from 1987-2022), but we use these values as a broad-scale indicator of human disturbance.

2.3.3 Data analysis

2.3.3.1 Quality and quantity of tracking data

A total of 162 peer-reviewed studies were included in this review, from which 107 were used to assess data quality and quantity. Twenty-two studies were omitted because they tracked taxa with insufficient sample sizes for analysis (reptile = six studies & fish = two studies) or seed/ fruit resources (14 studies). Resource tracking studies were omitted from this part of the analysis as this method of tracking is limited by study design and results were not comparable to the use of GPS and radio transmitters. A further 33 studies were omitted as the publications failed to report the required information, i.e., individual tag performance and information was not recorded or available.

To calculate the mean number of tag days, 84 studies representing 130 individual species were used (see *Supplementary table 2*). To calculate mean tag locations, 81 studies representing 117 individual species were used (see *Supplementary table 3*). Generalised linear models (GLMs), with a gamma distribution and log-link function, were fitted to assess the effect of taxa (bird or mammal) or tracking method (GPS or radio tracking) on the number of tagging days and number of tagging locations recorded. Models with and without interaction terms were compared using Akaike Information Criterion (AIC) values, and the model with the lowest AIC was selected.

2.3.3.2 Likelihood of GPS tags being used

A total of 140 studies were used to assess whether the type of tracking method used could be predicted by taxa, body mass of species and year. Resource tracking studies and reptile and fish species were omitted. We fit binomial GLMs to the outcome of studies using GPS tags with taxa (bird or mammal), body mass (g) and year of study (1978 – 2022) as fixed effects. Models with and without interaction terms were compared using Akaike Information Criterion (AIC) values, and the model with the lowest AIC was selected.

2.3.3.3 Drivers of seed dispersal distances

Finally, 67 studies calculated seed dispersal distances. We used 45 of these to assess mean seed dispersal distances and 56 to assess maximum seed dispersal distances. This information came from 61 and 71 individual animal species, respectively, six studies reported median dispersal distances rather than mean. As these were the minority, we decided to remove these from the mean dispersal analysis. A further two studies were removed from both the mean and maximum dispersal analysis as these focused on species during their migrations (Mallard Duck, Red-billed Teal & Egyptian Geese) and the distances estimated did not allow for models to converge. As per previous analysis, studies focussing on fish or reptiles were also omitted because the number of studies were too small.

To assess the effect of body mass and different environmental variables on seed dispersal distances, we fitted GLMs, with a Gamma distribution and log-link function, comparing the predictor variables of body mass, protected areas, volant/non-volant, biome and the study site HFI score. We used volant/non-volant in models rather than taxa due to collinearity between these two variables and because it provides greater functional information about the species than taxa alone. We did not include tracking method because of the limitations inherent to different methods e.g. longer dispersal distances are often identified from GPS tags due to remote download capabilities, while resource tracking is often limited to certain species, in particular small sized mammals. Body mass and HFI were scaled and centred around the means to ensure that they were comparable. To explore the impact of SRT and body mass on dispersal distances we explored the relationship between these two variables by firstly, calculating

the Spearman's rank correlation coefficient to determine correlation and then fitting a linear model (LM) to determine the overall effect of body mass on SRT.

Statistical assumptions for each GLM and LM were validated by visual interpretation of residual diagnostic plots to check for linearity of model-fitted values and their residuals. For each analysis, link functions were tested to determine the best residual distribution model based on AIC comparison and visual analysis of quantile-quantile plots of produced residuals using the *plot.DHARMA()* function in the *DHARMA* package (v0.4.6; Hartig 2022). For the seed dispersal GLMs, a gamma distribution and a log link function allowed for the best model fit. The *dredge* function in the *MuMIn* package (v1.47.1; Barton 2022) was used to assess the optimum variables for each model.

All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2021). A full summary of the different study subsets for each analysis is available in *Supplementary table 12*.

2.4 **Results**

2.4.1 **Literature review**

We reviewed 162 peer-reviewed research studies that used either radio transmitters or GPS tags to record the locations and movements of frugivorous animals. Of these 162 studies, 148 tracked frugivorous animals and 14 tracked seeds or fruits directly (see *Supplementary table 13*). Most of these studies focused on animal ecology and behaviour, and included themes such as *competition*, *behaviour*, *foraging ecology*, *habitat use*, *landscape connectivity*, *migration*, *movement ecology* and/ or *resource selection*, whereas 40 studies focused primarily on *plant ecology*, including *seed dispersal* and *plant recruitment*. The 162 articles identified in our search were published in 70 different journals covering different scientific themes, but principally *animal ecology*, *conservation biology* and *tropical ecology*. The most common journal was *Biotropica*, which published 11% of the studies reviewed here.

The number of studies tracking frugivores increased from the first studies in the late 1970s to a peak of 13 per year in 2016 and 2018 (Fig 1). The earliest studies to use remote tracking techniques for monitoring frugivores were conducted in 1978 (see Heithaus & Fleming, 1978; Morrison, 1978a; Morrison, 1978b), but it was not until 2005 that more than three studies were published per year (Fig 1). The first studies to track frugivores using GPS tags were undertaken in 2008, and both focused on elephants (see Blake et al, 2008; Campos-Arceiz et al, 2008; Fig 1). Since then, the use of GPS tags in frugivore monitoring studies has increased, and from 2017, GPS tracking tags became more commonly used than radio transmitters (Fig 1).

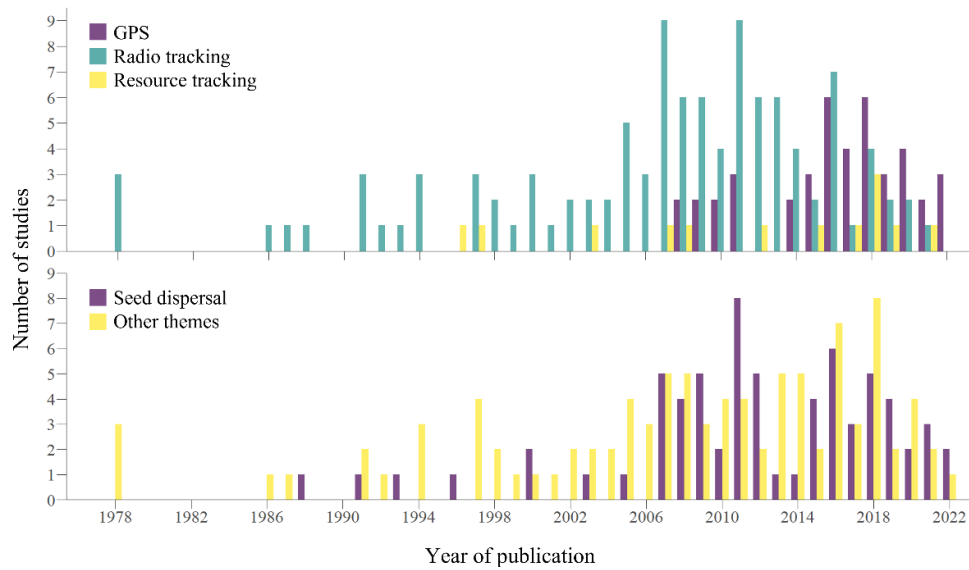


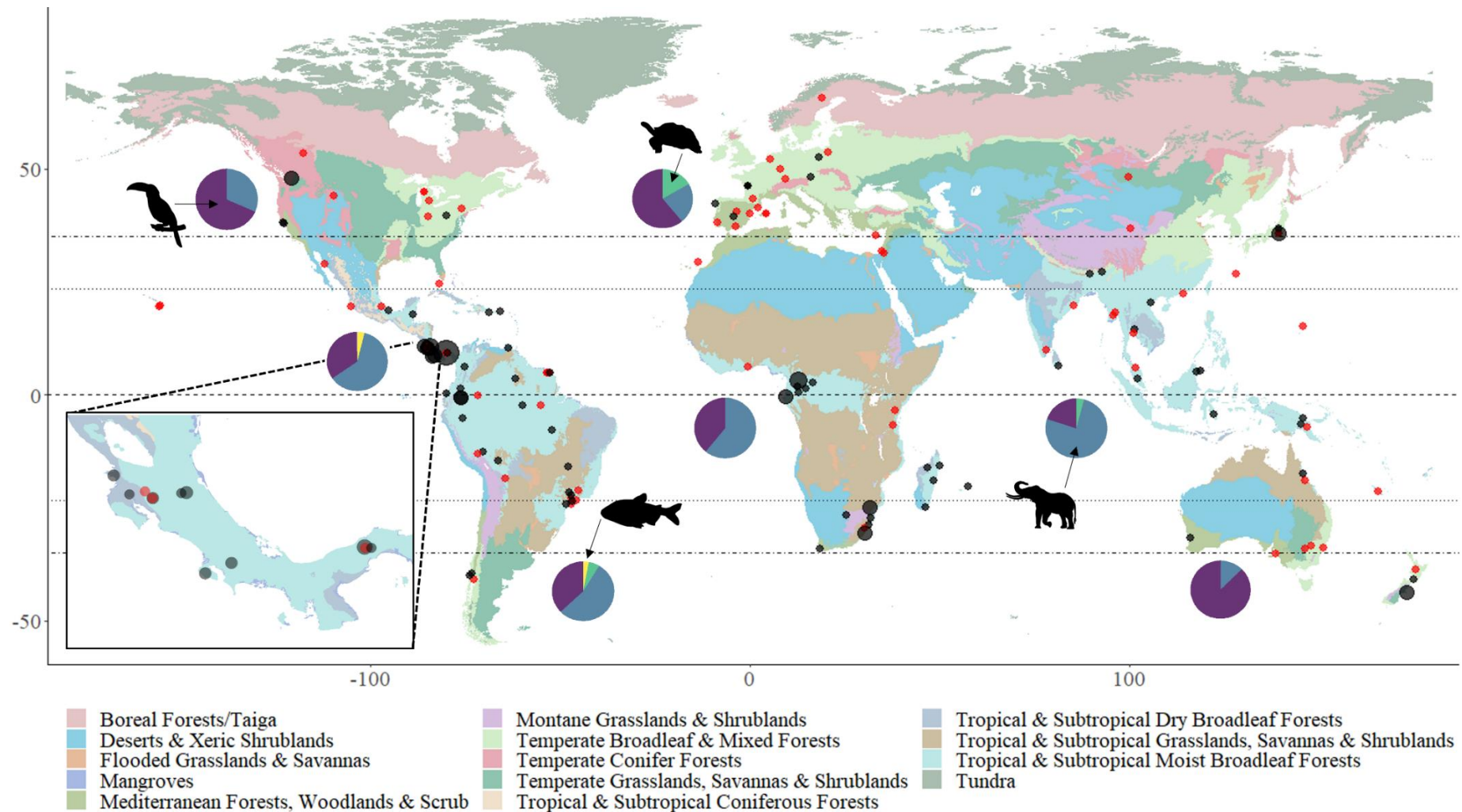
Figure 1. The number of published studies per years that used tracking technology (GPS, radio transmitters, resource tracking) on frugivorous species (a) and the number of published studies per years that either calculated seed dispersal distances or focussed on other themes (b) between 1978 – 2022.

The number of studies that estimate seed dispersal distances from tracking data also increased since the late 1970s to the present (Fig.1); the earliest study was published in 1988 (see Murray, 1988), but not until 2007 were more than two studies published annually (Fig 1). Eight studies were published 1988 - 2006, whilst 59 were published 2007 - 2022 (Fig 1); a 738% increase in the last 16 years compared to the previous 19 years.

2.4.2 Global distribution of tracking studies

Overall, 49 countries across six continents are represented in the 162 studies. Studies were not evenly distributed among countries, and 51 studies were conducted in just four countries: Costa Rica (9% of studies), Brazil (8%), USA (8%) and Panama (6%) (Fig 2). More studies were conducted in tropical and sub-tropical than in temperate regions; this is illustrated in the two most well studied taxonomic groups birds (studies in tropical/sub-tropical regions 64% vs. temperate 36%) and mammals (tropical/sub-tropical regions 83% vs. temperate 17%).

The number of studies conducted within, and outside protected areas varied by region. The percentage of studies conducted within protected areas was highest in Central America and lowest in Europe (Figure 2). This is reflected in the research sites used in Central American studies; nine studies from Panama and 13 studies from Costa Rica were in protected areas. The proportion of studies that addressed the ability of species to disperse seeds also differed among regions. For example, 50% of all tracking studies but only 27% of all seed dispersal, were conducted in the Americas (Figure 2).



1
2 Figure 2. The geographic distribution of 162 frugivore tracking publications undertaken between 1978-2022. Number of studies per location are denoted by
3 point size, with black points denoting studies undertaken inside protected areas, and red outside protected areas. Corresponding pie charts show the proportion
4 of focal taxa represented in studies from each continent (Purple = Bird; Blue = Mammal; Green = Reptile; Yellow = Fish). Map colours represent the 14 biomes
5 taken from *Ecoregion Snapshots: Descriptive Abstracts of the Terrestrial Ecoregions of the World. 2021*. Developed by One Earth and RESOLVE. Version
6 2021 <www.oneearth.org>. Downloaded on [April 2021]

2.4.3 Focal taxa of tracking studies

Across studies, 165 species were tracked in four taxonomic groups: 84 bird species, 75 mammal species, four reptile species and two fish species. Almost half of the mammals (48%) studied were bat or flying fox species. Mammals were the most well studied group (49.4% of studies), followed by birds (45.7%), reptiles (3.7%) and fish (1.2%). Geographically, birds were the target of most tracking studies in Europe (61.1%), North America (68.4%) and Oceania (87.5%), whereas mammals made up most studies in tropical regions across South America (52.9%), Central America (61.5%), Africa (64%) and Asia (75%) (Figure 2). Only 48 species were studied more than once, including 23 birds, 23 mammals and 2 reptiles. The most common frugivores studied were the Seba's short-tailed bat (*Carollia perspicillata*), one of the focal species of six studies, followed by the Eurasian Jay (*Garrulus glandarius*), African bush Elephant (*Loxodonta africana*), Asian Elephant (*Elephas maximus*) and Little Yellow-shouldered Bat (*Sturnira lilium*), all tracked in four studies.

A diverse range of species were studied, which is shown by large ranges in body mass (7.6g – 44000g and 9.4g – 4750000g, for birds and mammals respectively, see *Supplementary table 1*). Body mass proved significant in determining the likelihood of GPS tags being preferred for use in frugivore studies; with every one unit increase in body mass (g), there is an estimated 0.000012 increase in the log-odds of GPS tags being used (estimate $\pm$ std error = 0.000012 ± 0.0000059 , $p = 0.0384$, $df = 195$). However, there was no effect of taxa (estimate $\pm$ std error = 0.5365 ± 0.3577 , $p = 0.1337$, $df = 195$) or an interaction between taxa and body mass (estimate $\pm$ std error = -0.000038 ± 0.000038 , $p = 0.321$, $df = 194$) on the outcome of GPS tags being used (see *Supplementary table 4B*).

For mammals, there was a significant effect of study year on the likelihood of GPS tags being used; with every succeeding year, there was an estimated expected 0.385 increase in the log-odds of GPS tags being used (estimate $\pm$ std error = 0.3849 ± 0.09692 , $p = 0.000072$, $df = 89$; Figure 3). However, body mass had no detectable effect (estimate $\pm$ std error = -0.000079 ± 0.000055 , $p = 0.147$, $df = 89$), nor was there any detectable interaction between year and body mass (estimate $\pm$ std error = 0.0000027 ± 0.0000018 , $p = 0.125$, $df = 89$, see *Supplementary table 6B*). For birds, there was no detectable effect of year on the outcome of GPS tags being used (estimate $\pm$ std error = -0.03877 ± 0.1432 , $p = 0.78666$, $df = 101$). However, body mass (estimate $\pm$ std error = -0.03935 ± 0.01125 , $p = 0.00072$, $df = 101$), and an interaction between body mass and year (estimate $\pm$ std error = 0.00146 ± 0.000412 , $p = 0.000408$, $df = 101$; Figure 3) was significant in predicting the outcome of GPS tags being used (see *Supplementary table 5B*).

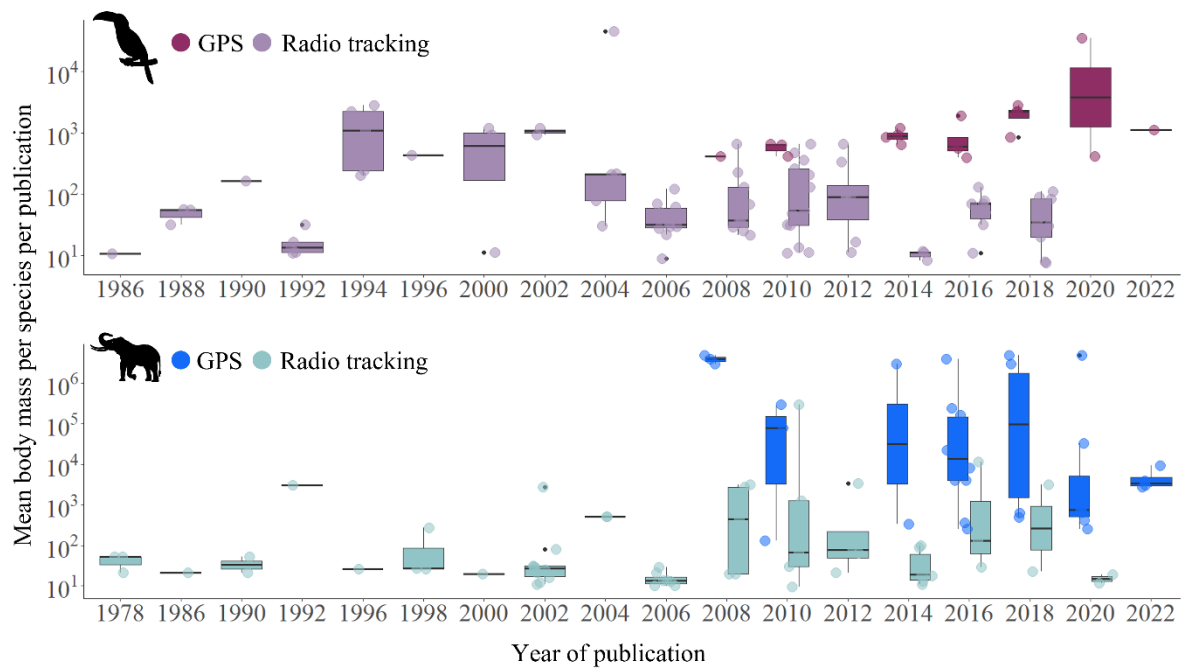


Figure 3. The mean body mass of species tagged, with either GPS tags or radio transmitters, per study during 1978-2022, for frugivorous birds, and frugivorous mammals.

2.4.4 Quality and quantity of data collected

Among all studies analysed, 107 studies used radio transmitters, 42 used GPS and 14 studies tracked resources using radio transmitters and/or GPS tags (i.e. attached to seeds/fruits rather than individuals). One study used both radio and GPS tags to follow animals (Campos-Arceiz et al, 2012; Asian tapirs). The mean number of tags deployed per species per study was 17.48 ± 1.67 , the median 10, the range 1-172 and $n = 206$. A total of 115 out of 148 animal tracking studies reported information necessary to calculate deployment successes. Of these, 49 studies (33.1%) recorded tag failure (tag loss, battery failure, insufficient data for analysis etc), whereas 66 studies reported a 100% tag success rate. The average tag success rate across all studies was 86.2%. The tag success rate may be lower than reported as the remaining 33 studies did not clearly state whether the figures reported were the number of tags deployed or the number successfully returned and used in analysis.

Generalised linear models indicated that tracking method was a significant predictor of the duration of tags and the number of locations recorded per study (Fig 4). Studies using radio tags recorded fewer days (estimate $\pm$ std. error = -1.79 ± 0.49 , $p < 0.001$; Fig. 4A, see *Supplementary table 7B*), and locations (estimate $\pm$ std. error = -2.01 ± 0.48 , $p < 0.001$; Fig. 4B, see *Supplementary table 8B*), than GPS tags. Neither taxa nor an interaction effect between taxa and tracking method influenced duration of deployment, but there was an interaction effect between these two for the number of locations collected (estimate $\pm$ std. error = -1.58 ± 0.67 , $p < 0.05$; Fig. 4B).

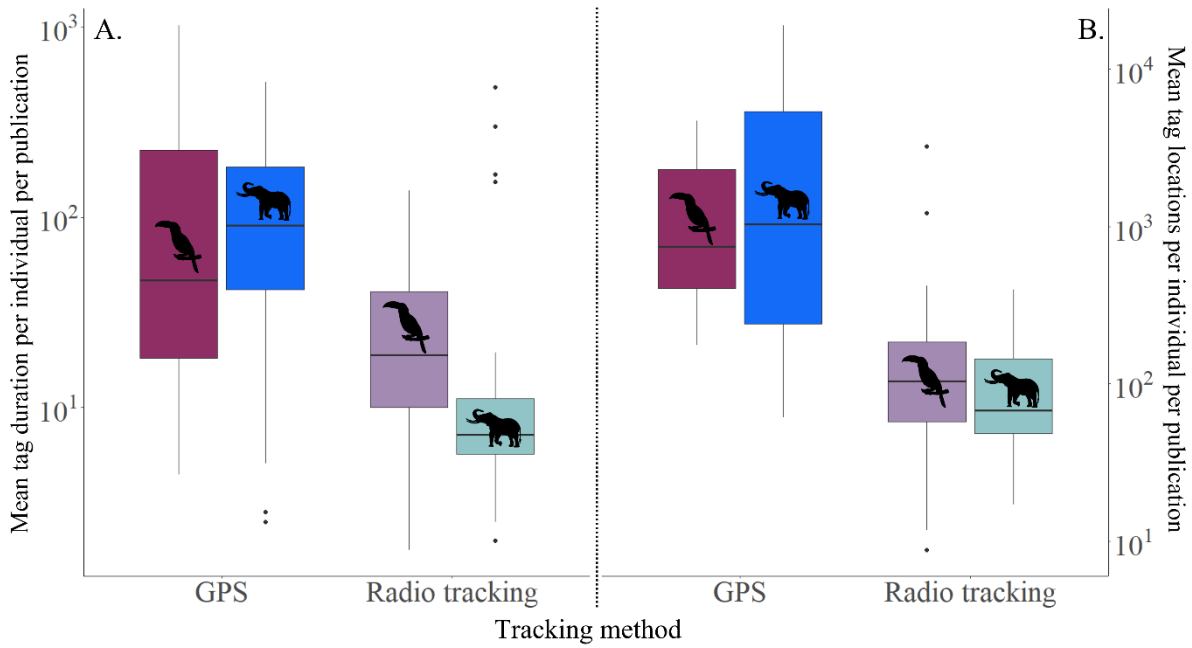


Figure 4. A comparison between tracking method (GPS & radio transmitters) and animal taxa (bird and mammal) with respect to A. The mean number of tagging days and B. The mean number of total location points collected per individual species per study.

2.4.5 *Drivers of seed dispersal distances*

Mean and maximum dispersal distance increased significantly with species body mass (mean dispersal estimate $\pm$ std. error = $0.67\text{m} \pm 0.21\text{m}$, $p = 0.00245$; maximum dispersal estimate $\pm$ std. error = $0.78\text{m} \pm 0.28\text{m}$, $p = 0.0071$; Fig. 5a and 5b). Volant species (bats, flying foxes and flying birds) had significantly higher mean seed dispersal distances than nonvolant species (mean dispersal estimate $\pm$ std. error = $0.95\text{m} \pm 0.45\text{m}$, $p = 0.0384$; Fig. 5a). Volant species also had marginally significant higher maximum seed dispersal distances than nonvolant species (maximum dispersal estimate $\pm$ std. error = $1.02\text{m} \pm 0.6\text{m}$, $p = 0.094$; Fig. 5b). Maximum dispersal distances also increased significantly with an interaction between body mass and volant species (maximum dispersal estimate $\pm$ std. error = $2322.85\text{m} \pm 726.28\text{m}$, $p = 0.002$; Fig. 5b). The studies that were undertaken in protected areas also showed a significantly higher mean seed dispersal distance than those that were not in protected areas (mean dispersal estimate $\pm$ std. error = $1.29\text{m} \pm 0.43\text{m}$, $p = 0.0037$; Fig. 5a), but these were not significant for maximum seed dispersal distances (maximum dispersal estimate $\pm$ std. error = $0.243\text{m} \pm 0.63\text{m}$, $p = 0.7$). Additionally, HFI was not significant for mean or maximum dispersal models and was not included in subsequent models (mean dispersal estimate $\pm$ std. error = $0.07\text{m} \pm 0.22\text{m}$, $p = 0.7$; maximum dispersal estimate $\pm$ std. error = $0.09\text{m} \pm 0.32\text{m}$, $p = 0.8$). Lastly, species with a larger body mass had a significantly longer seed retention time than smaller sized species, with SRT increasing by 30 seconds for every additional kilogram in body mass (Spearman's $\rho = 0.789$, $p = 9.52\text{e-}15$, $n = 64$; mean seed

retention time estimate $\pm$ std. error = 0.00054mins $\pm$ 0.0001mins, $p = 1.57e-6$; *Supplementary figure 1*)
See *Supplementary tables 9C, 10C and 11* for full model outputs.

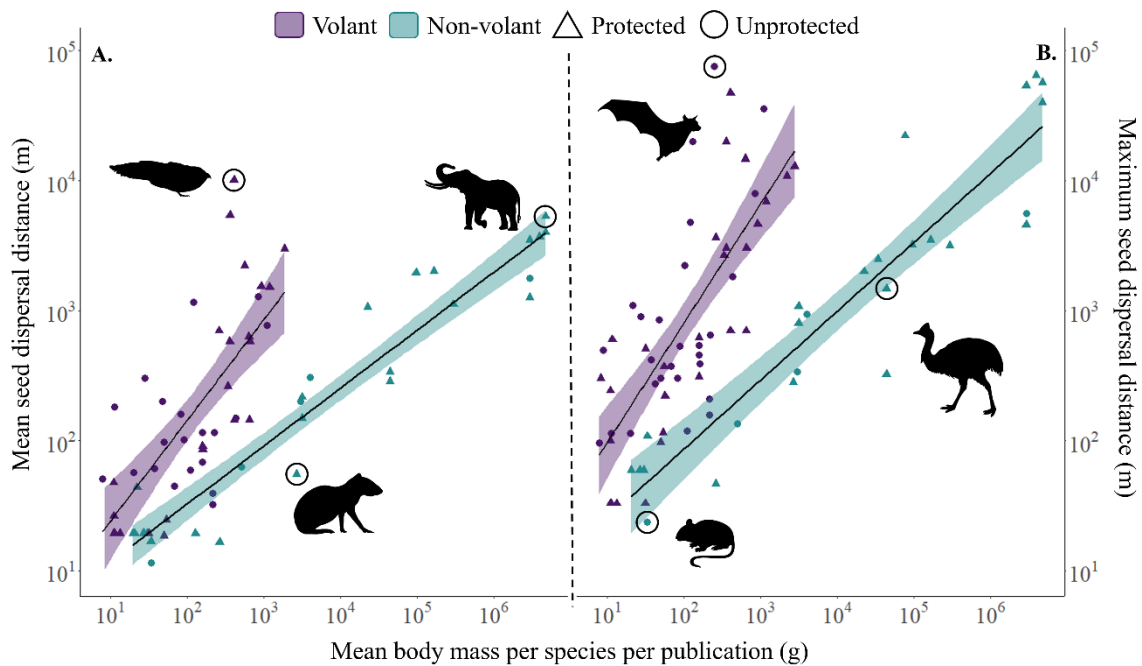


Figure 5. The estimated A. mean and B. maximum seed dispersal distances of bird and mammal species in relation to their body mass. Regression lines for volant/non-volant species are denoted by colour and show standard errors with a 95% confidence interval. Point shape denotes whether the study was conducted in a protected area or not. Images indicate the species for the closest circled point and from left to right indicate Oilbird (*Steatornis caripensis*), Central American Agouti (*Dasyprocta punctata*), African forest Elephant (*Loxodonta cyclotis*), Large Japanese Field Mouse (*Apodemus speciosus*), Straw-coloured Fruit Bat (*Eidolon helvum*) and Southern Cassowary (*Casuarius casuarius*).

2.5 Discussion

2.5.1 Has there been a shift in the number of frugivorous tracking studies?

Seed dispersal and movement ecology are increasingly integrated, and the use of tracking technology to study frugivorous species has significantly increased in the past 17 years, from 33 studies between 1978 – 2004 to 129 studies from 2005 – 2022. The number of studies calculating seed dispersal distances from frugivore movement increased from 8 studies in 1988 – 2006 to 59 studies from 2007 – 2022 (Fig 1).

Radio tracking was the most commonly used tracking method for frugivores up until 2017, but since then, GPS tags have become the most used method. These increases are likely associated with the

advancement in tracking technology, and specifically the reduced costs and increased availability of tags (Kays et al, 2015; Pimm et al, 2015). The smallest commercially available GPS tag in 2006 was 9.5g (*Microwave Telemetry Inc*, 2021) whereas now tags weighing < 3g are commercially available from numerous companies (e-obs GmbH, 2021; TechnoSmart, 2021). In addition, an increasing number of interdisciplinary teams are constructing GPS tags using commercially available components (Allan et al, 2013; Fischer et al, 2018; Paden & Andrews, 2020). These tags tend to be cheaper than traditional tracking devices, potentially increasing the number of research studies that have access to tracking technology. The potential for remote data download, ongoing battery miniaturisation and implementing solar-powered recharge capabilities have enhanced our ability to monitor species across greater distances, in remote locations, and across diverse landscapes, where previous attempts failed (Bouten et al, 2013; Hart et al, 2020; Shimada et al, 2020).

2.5.2 Our current understanding of frugivorous tracking studies

2.5.2.1 Global distribution

Over half (59.3%) of all frugivore tracking studies (162 studies) reviewed here were in tropical regions (between 23.436°N and 23.436°S; Fig 2), a further 14.2% were from the sub-tropics, and 26.5% were from the southern and northern temperate zones. This reflects latitudinal patterns of higher species richness in tropical compared to temperate regions. However, this pattern was not seen in studies that calculated seed dispersal distances (subset of 67 studies), where only 31% of studies were in tropical regions, and does not reflect difference in animal mediated seed dispersal globally; up to 60% of temperate plants rely on animal dispersal compared to 90% of tropical plants (Howe & Smallwood, 1982; Gentry, 1988). This suggests that in the tropics we see a lack of seed dispersal studies using animal movement data, potentially because fieldwork locations and dense forests provide challenges to fieldwork and transmitters (Kays et al, 2011; Monsieurs et al, 2017). However, the uptake of solar powered tags, improvement in battery capacity and remote downloading capabilities may soon rectify this (Byers et al, 2017; Fischer et al, 2018). Our data also suggest that many regions have yet to be explored for the study of frugivore movement, for example Eastern Europe, Central & Northern Africa, Central Asia and much of North America lack tracking studies (Figure 2).

Sites where multiple studies have been conducted tended to be in protected areas and/ or at key field stations. In total, 172 different locations were used for these tracking studies, with almost two thirds (59%) in protected areas, with clustering of multiple studies at long-term research stations (Blanco et al, 2020). This is both a benefit and a limitation; on the one hand, highly studied sites become hotspots for research, with multiple taxa studied in a single location and often with longitudinal datasets (Stouffer, 2020). This provides information on how multiple taxa respond to the same landscape

changes and how patterns may differ amongst species. Alternatively, concentrating multiple studies in a few locations means that we make inferences from a handful of intensely studied sites and lack broader knowledge from diverse locations and landscapes. Most studies we reviewed were in protected areas, but these represent ~17% of terrestrial land surface area (UNEP-WCMC, 2023), suggesting that we need further studies outside parks and reserves as well as comparative studies in protected areas and neighbouring disturbed habitats to effectively survey a representative sample of habitats.

2.5.2.2 *Focal taxa*

Broadly equivalent numbers of studies focused on birds and mammals (74 and 80 respectively). In total, 29% of species were studied more than once, and the most heavily studied species were frugivores that are known to be readily caught and tagged, and those commonly found in research hotspots (Biro, 2013; Rosenthal et al, 2017). These frequently studied species suggest that frugivore tracking studies focus on key long-distance dispersers, including larger-bodied animals that can disperse larger seeds across greater distances (African bush elephant & Asian elephant) and animals that have the ability to fly and connect fragmented landscapes (Little yellow-shouldered bat and Seba's short-tailed bat).

Bats were the most intensely studied group of mammals: a total of 40 studies and half of the mammal studies. The high number of bat studies represents the high diversity of frugivorous bats and their importance in long distance dispersal (Muscarella & Fleming, 2007). However, only four studies calculated seed dispersal distances, potentially due to tag weight limitations. Many bat species are too small to carry tracking devices (O'Mara et al, 2014; van Harten et al, 2019), and those that are not, are often constrained to just a few weeks of data collection because of common tag attachment techniques e.g. surgical glue. Whilst this method is widely used, tags rarely remain attached for longer than 4 weeks (O'Mara et al, 2014), and therefore only provide a limited snapshot of a species movement capabilities. Bats provide important links among forest fragments due to their mobility (Estrada & Coates-Estrada, 2002), and with the advent of smaller tags (Dressler et al, 2016), future studies could better explore their role in seed dispersal.

Four species of reptiles were tracked across these studies including the Yellow-footed Tortoise (*Chelonoidis denticulatus*), Lilford's wall Lizard (*Podarcis lilfordi*), Eyed Lizard (*Timon lepidus*) and Southeast Asian Box Turtle (*Cuora amboinensis*), suggesting that reptiles are currently being underrepresented in biologging studies in terms of their potential role as seed dispersers. This is of particular importance for island habitats where reptiles, predominately lizards and tortoises, often occur disproportionately compared to other species. These habitats are often species-poor in terms of diversity, meaning reptiles become some of the only seed dispersers around (Olesen & Valido, 2003). In particular, giant tortoises are thought to fill traditional megaherbivore roles on islands and are noted

as ecosystem engineers (Blake et al, 2012; Falcon et al, 2020). Therefore, future seed dispersal studies should be encouraged to quantify the role that reptiles play as seed dispersers.

Body mass is clearly instrumental in determining which tracking method is likely to be selected for frugivore studies; globally, 72% of bird species and 55% of mammal species weigh less than 100g (Wilman et al, 2014), which is the minimum body mass for a 5g tag (typical for commercial GPS tags; Altobelli et al, 2022). In our review, the median body mass was 83.4g and 192.8g for birds and mammals, respectively, suggesting that larger animals in general have a significantly increased likelihood of GPS tags being deployed compared to smaller animals, irrelevant of taxa. Whilst radio transmitters can weigh as little as 0.2g (Naef-Daenzer et al, 2005) and offer a low-cost alternative to GPS tags, there are trade-offs with the quality of data collected (Gottwald et al, 2019). Radio telemetry often results in low temporal and spatial resolution due to infrequent location fixes and the required intensive labour in collecting these fixes (Harris et al, 1990; Ryan et al, 2004; Alexander & Maritz, 2015), thus GPS tags are often preferred once an animal passes a minimum size requirement.

Since miniaturisation and technological advances have reduced the size and weight of GPS tracking technology, we would expect frugivores to be tagged with GPS tags more frequently in recent years, but we did not see a clear pattern. For mammals, we found that in later years there was an increased probability of GPS tags being deployed, but body mass did not have a significant effect. We observed the opposite effect with bird species, with increased body mass there was an increased probability of GPS tags being deployed on birds, but an interaction between body mass and years shows a significant effect on the increased probability of GPS tag being deployed for bird species.

The pattern seen here suggests to us that the technological advances made concerning increased storage and remote download capabilities of GPS tags (Kays et al, 2015) have led to the increase of studies focusing on large, frugivorous bird species that have migrational behaviour or extensive home ranges where previous use of radio transmitters would have been ineffective (Hallworth & Marra, 2015; Lenz et al, 2015).

2.5.2.3 Assessing the differences in quality and quantity of data collected through tracking technology

To effectively describe the animal movement and behaviour critical to seed dispersal predictions, we need detailed tracking data. Large time gaps and short study durations can limit inference and may lead to over or underestimating dispersal distances. Both tag duration (*length of time attached to an individual*) and total location points (*number of locations collected per individual tag*) significantly related to the tracking method. Studies using GPS tags captured almost 18 times the number of locations compared to studies using radio tags and were deployed for almost 5 times longer. Increased battery

capacity and solar powered tags enable data collection over many months and possibly years (Silva et al, 2017).

GPS tags are increasingly used to track frugivores; since 2015, 28 studies have used GPS tags compared to just 11 studies during the previous 36 years. This has also allowed for a larger diversity of species to be tracked. Before 2003, the largest frugivore equipped with a tracking device was 3kg. Since then, a further 21 species of frugivore have been tagged, with body mass ranging from 3 - 4750kg. This trend could be linked to the remote download capabilities of GPS tags. Larger animals tend to have larger home ranges (Harestad & Bunnell, 1979) and GPS tags can now be downloaded from many kilometres away or via remote upload to satellites or Wi-Fi (Kays et al, 2015). This is particularly important for migratory animals, where it is often impossible to stay close enough to use radio transmitters (Guilford et al, 2011). With the introduction of remote downloading, GPS tags are preferred because data download is guaranteed after the initial device attachment, without the need to recapture individuals or search for radio transmissions. Additionally, many GPS tags also include the option of onboard accelerometers (Shepard et al, 2008; Brown et al, 2013), which can be used for defining specific behaviours, such as foraging events, that can be incredibly useful when determining seed shadows.

On the other hand, many bird species are still tracked with radio transmitters. Radio transmitters tend to be smaller and can be used on smaller species, but this result may also relate to habitat. Most tropical birds reside within thick vegetation (MacArthur & MacArthur, 1961). GPS tags require low vegetation cover for successful fixes. In dense vegetation, GPS fixes can fail or overestimate movement tracks for up to an additional 28% (DeCesare et al, 2005).

2.5.3 Can body mass and environmental variables be used as predictors for seed dispersal distances?

Frugivore body mass was a key predictor for seed dispersal distance; both mean and maximum seed dispersal distance are positively correlated to body mass in birds and mammals. Larger species tend to have larger foraging areas and range distributions and so carry seeds further from the parental source (Godinez-Alvarez et al, 2020). Flying species also had larger mean distances than non-flying species, suggesting that bird and bat species are key for long distance seed dispersal events (Medellin & Gaona, 1999). This is further strengthened by maximum seed dispersal distances significantly increasing with an interaction between a species body mass and ability to fly. This indicates that an increase in body mass of a volant species has a greater, positive effect on maximum dispersal distance compared to the same increase for a nonvolant species.

Most studies that calculated seed dispersal distances focussed on birds, which are key for seed dispersal due to their mobility and ability to cross matrices and connect habitat patches (Mueller et al, 2014). Additionally, there is large interspecific diversity amongst the functional traits of bird species, which

offers a wider dietary scope and allows them to be relatively flexible to switch to other resources in response to fluctuations in fruit resource availability through seasonal or land use changes (Bender et al, 2017). Amongst the most frequently studied bird species were Eurasian Jay (*Garrulus glandarius*), Clark's Nutcracker (*Nucifraga columbiana*), White-crowned Manakin (*Pseudopipra pipra*) and Swainson's Thrush (*Catharus ustulatus*) – these species have broad, omnivorous diets, ranging from insects to fruit. Birds with generalist diets are key to seed dispersal in fragmented landscapes and tend to move between different habitats and facilitate early forest succession in open areas (Carlo & Morales, 2016; Barros et al, 2019).

Bats species, like birds, can functionally connect fragmented landscapes, and are associated with long-distance seed dispersal (Abedi-Lartey et al, 2016). Although bats are often smaller than birds, the four studies in our review that focused on bats reported dispersal distances that tended to be greater than distances commonly reported for birds of similar body mass (Egyptian Fruit Bat, *Rousettus aegyptiacus* – 132g, Madagascan flying Fox, *Pteropus rufus* – 361g, Orii's flying Fox, *Pteropus dasymallus inopinatus* – 435g, Straw-coloured Fruit Bat, *Eidolon helvum* – 253g), with Straw-coloured fruit bats travelling up to 70km a night (Abedi-Lartey et al, 2016). This is perhaps possible due to their gap crossing abilities, nocturnal activities, plasticity of habitat use, and foraging strategies (Muscarella & Fleming, 2007; Regolin et al, 2020; Lourie et al, 2021). Furthermore, bats can defecate during flight, as opposed to when perched like most birds, which increases the likelihood of seeds being deposited in open areas where pioneer plant species can recruit and initiate forest regeneration (Muscarella & Fleming, 2007; Pena-Domene et al, 2014; Regolin et al, 2020). For instance, *Phyllostomid* bats can disperse seeds of over 300 plant species (Lobova et al, 2009; Voigt et al, 2017) and will regularly commute between foraging areas in natural and degraded landscapes, enabling establishment of early successional plant species (Galindo-Gonzalez et al, 2000; Ripperger et al, 2015). Seed-handling by bats could also increase their effectiveness as long-distance dispersers (Ong et al, 2022), since fruits taken by bats are not limited by mouth/beak gape width, and some bat species carry fruits that exceed their own body mass (Mahandran et al, 2018).

Much like seed-handling, understanding seed retention time (the time between seed ingestion and defaecation) is crucial for the estimation of seed dispersal distances and identifying potential deposition sites of seeds. The duration a seed spends within an individual's digestive system directly influences the distance it will be transported before being deposited (Schupp et al, 2010). However, assessing species seed retention time can often be challenging and complex due to the variability within animal species and across different plant species, and their fruits and seeds (Cortes & Uriarte, 2013). Fruit secondary compounds and ripeness have been found to influence dispersal distances by significantly decreasing or increasing SRT within frugivorous bats, depending on the plant species (Baldwin & Whitehead, 2015; Baldwin et al, 2019). Conducting captive trials is possible, but these can be biased as

the fruits consumed are often not representative of the frugivore's diet and can even be seeds implanted in pulp of cultivated fruits (Holbrook and Loiselle, 2007; Kays *et al*, 2015; Qian *et al*, 2022).

Given these challenges, researchers often need to use a combination of approaches, including controlled experiments, field observations, and modelling, to gain a comprehensive understanding of seed retention time in a particular animal species (Yumoto *et al*, 1999; Cousens *et al*, 2010; Adams *et al*, 2022). Despite these difficulties, obtaining accurate data on seed retention time is crucial for assessing the role of animals in seed dispersal and predicting their ecological impact. Commonly, researchers use allometric scaling of body mass to determine estimates for seed retention time per animal species (Yoshikawa *et al*, 2019). At the species level, we also found a tight relationship between body mass and SRT (*Supplementary figure 1; Supplementary tables 11A and 11B*), however this approach obscures fine-scale variation driven by diet choices and intraspecific variation among frugivores, and we highlight the need for more detailed seed retention information.

Finally, our models also appear to show a trend in mean dispersal distance for those studies undertaken in protected areas. These areas are likely to offer large tracts of undisturbed, continuous habitat enabling frugivores are able to travel long distances unrestricted by inhospitable landscapes such as intensive farmland or urban areas. In our analysis, animals may have moved out of protected areas into surrounding disturbed habitat during the duration of the study. However, our results still support the idea that dispersal distances are longer in areas with more intact habitat and validates previous evidence that seed dispersal services are likely to reduce in areas of landscape change (Wright & Duber, 2001). Furthermore, protected areas ensure frugivore safety through reducing illegal hunting events. This has a direct, positive effect on frugivore abundance and population levels that can increase seed dispersal services (Wright *et al*, 2000; Nunez-Iturri & Howe, 2007; Beckman & Muller-Landau, 2007).

2.5.4 Recommendations

We reiterate the following points from previous reviews (Barron *et al*, 2010; Bodey *et al*, 2018) that it would be beneficial to do the following: standardise terminology, report device type and attachment, and provide all collected data. Many publications are still not following the protocols suggested in these publications, which are vital for future improvements to studies and analysis and will ensure that comprehensive comparisons between studies and species can be undertaken. Reporting the necessary key information can help ensure that standard protocols are followed and therefore improved (Andrews *et al*, 2019).

To improve data management, accessibility, and analysis, we recommend standardising animal tracking terminology when referring to tracking technologies. Currently, multiple words and terms are used synonymously across publications (Cooke *et al*, 2021). We recommend using the terms “GPS tags/

transmitters” and “radio tags/ transmitters” opposed to “units” or “trackers”. Terms such as “radio telemetry” are also used as common synonyms, however this refers to the whole radio tracking system: a radio transmitter, a radio antenna, and a radio receiver. The terms “biologging” and “data loggers” are often used as an umbrella term (Whitford & Klimley, 2019; Cooke et al, 2021), but should be used in conjunction with GPS or radio tags/transmitters so that readers are aware of the technology used. Units would ideally be used to describe the whole device being attached to an animal, which may include accelerometers and/or environmental recording devices.

Studies present multiple different sampling rates and durations, so almost all movement studies are unique. They are often driven by constraints on the number of individual tags that can be deployed, and ultimately rely on the restrictions of capturing animals to tag and the funding of different projects. However, with the improvement and reduced costs of GPS tags, it would be highly beneficial for the community to aim to develop some standard minimum sampling rates and durations to make diverse datasets more compatible (Campbell et al, 2016; Sequeira et al, 2021). Tag failure must also be considered in future studies, and it is critical that studies report all data including tag failures and discrepancies from methods and results.

Finally, to allow reproducibility and future analysis, movement data should be shared in global data repositories. Making data publicly available increases broad and inter-disciplinary collaborations and ensure that data are used most effectively. Data can also be used for further analysis by other scientists from different academic backgrounds and facilitate greater interdisciplinarity between subjects and ensures that data are used to their maximum potential. Repositories can help safeguard fundamental baseline data, which helps drive broader, temporal ecological questions that would not be possible with single or few studies (Tucker et al, 2018; Davidson et al, 2020; Rutz et al, 2020). This is already beginning to happen with data repositories for animal tracking, such as Movebank.org, and through conversations regarding registering all tracking device deployments (Rutz, 2022).

2.5.5 Conclusion

Increases in tracking studies, coupled with the advancement of tracking technology, has led to an exponential increase in seed dispersal studies over the past 17 years, particularly those that estimate seed dispersal distances. This offers a step forward in understanding how changes to landscape structure, e.g., from land-use change, can affect plant colonisation and forest recovery through understanding the movement patterns and behaviours of frugivores through tracking.

We see the next step forward in future seed dispersal studies as straightforward: more studies and repetition. Long-term tracking studies from diverse taxa are necessary to collect movement and behaviour information. Many current tracking studies are limited by battery consumption and tag

memory and are simply capturing a small snapshot of an individual's life and do not consider how temporal changes (e.g., seasons, anomalous years) may affect movement. With longer-duration and finer-scale data, we can begin to understand the drivers of animal movement and the implications for seed dispersal and other ecosystem services in a changing world. Ultimately, seed dispersal distances can successfully inform restoration and conservation projects, but only if estimations are accurate. Only by tracking frugivores can we ensure that this transpires. Through an understanding of seed dispersal, local organisations can manage landscapes to increase the potential of between-patch connectivity to encourage plant regeneration and gene flow.

2.6 Supplementary material

Supplementary table 1. Summary statistics of the mass (g) of taxa tagged with different devices.

	Mean	Median	Min	Max	Se
Birds	1225.9	83.4	7.6	44000.0	648.8
Mammals	175434.2	192.8	9.4	4750000.0	90918.2
GPS	317162.4	1873.0	132.2	4750000.0	161562.2
Radio	3404.0	55.0	7.6	296250.0	27998.2

Supplementary table 2. Summary statistics for the number of days tags were deployed for on different taxa and for different devices.

	Mean	Median	Min	Max	Se
Birds : GPS	181.2	47.1	4.4	1015.7	64.7
Birds : Radio	30.2	18.9	1.8	137.9	4.6
Mammals : GPS	135.8	90.0	2.5	509.0	27.8
Mammals : Radio	34.0	7.2	2.0	480.0	14.1
Birds	73.4	20.0	1.8	1015.7	20.3
Mammals	74.5	10.9	2.0	509.0	15.1
GPS	154.0	75.9	2.5	1015.7	30.5
Radio	32	10.6	1.8	480.0	7.1

Supplementary table 3. Summary statistics for the number of locations collected on different taxa and for different devices.

	Mean	Median	Min	Max	Se
Birds : GPS	1621.1	742.7	176.0	4707.0	396.6
Birds : Radio	216.3	103.7	8.8	3241.9	68.6
Mammals : GPS	4011.5	1032.9	61.0	18995.0	1175.0
Mammals : Radio	109.7	67.4	17.0	395.0	18.4
Birds	562.1	153.8	8.8	4707.0	132.1
Mammals	1835.5	179.4	17.0	18995.0	580.7
GPS	3030.9	972.9	61.0	18995.0	730.2
Radio	176.7	88.4	8.8	3241.9	43.8

Supplementary table 4A and 4B. 4A) AIC scores to determine the best model for predicting tracking method GLM with body mass and taxa as predictors. 4B) Coefficient output table for predicting tracking method GLM with body mass and taxa as predictors.

	Model Formula	AIC scores
Model 1	Tracking method ~ Body mass + Taxa, family = binomial (link="logit")	202.92
Model 2	Tracking method ~ Body mass * Taxa, family = binomial (link="logit")	203.92

<i>Likelihood of GPS tags being used</i>				
	Estimate	Std. Error	z value	Pr(> z)
Intercept	- 1.53	0.25	- 6.01	1.86e-9
Body mass	0.000012	0.000006	2.071	0.038
Mammal	0.54	0.36	1.50	0.13

Supplementary table 5A and 5B. 5A) AIC scores to determine the best model for predicting tracking method GLM with body mass and year as predictors for the subset of bird species. 5B) Coefficient output table for predicting tracking method GLM with body mass, year, and an interaction term as predictors for the subset of bird species.

	Model Formula	AIC scores
Model 1	Tracking method ~ Body mass + Taxa, family = binomial (link="logit")	78.96
Model 2	Tracking method ~ Body mass * Taxa, family = binomial (link="logit")	27.88

<i>Likelihood of GPS tags being used for bird species only</i>				
	Estimate	Std. Error	z value	Pr(> z)
Intercept	-3.78	4.53	-0.84	0.403
Body mass	-0.04	0.011	-3.50	0.0005
Year	-0.04	0.14	-0.27	0.79
Body mass : Year	0.001	0.00004	3.54	0.0004

Supplementary table 6A and 6B. 6A) AIC scores to determine the best model for predicting tracking method GLM with body mass and year as predictors for the subset of mammal species. 6B) Coefficient output table for predicting tracking method GLM with body mass, year, and an interaction term as predictors for the subset of mammal species.

	Model Formula	AIC scores
Model 1	Tracking method ~ Body mass + Taxa, family = binomial (link="logit")	59.15
Model 2	Tracking method ~ Body mass * Taxa, family = binomial (link="logit")	59.88

Likelihood of GPS tags being used for mammal species only

	Estimate	Std. Error	z value	Pr(> z)
Intercept	14.9	3.7	-4.03	0.00006
Body mass	-0.00008	0.00005	-1.45	0.15
Year	0.39	0.1	3.97	7.17e-5
Body mass : Year	0.000003	0.000002	1.53	0.13

Supplementary table 7A and 7B. 7A) AIC scores to determine the best model for predicting the number of tracking days GLM with tracking method and taxa as predictors. 7B) Coefficient output table for predicting the number of tracking days GLM with tracking method, taxa, and an interaction between the two as predictors.

	Model Formula	AIC scores
Model 1	Tracking days~ Tracking method + Taxa, family = Gamma (link="log")	1299.4
Model 2	Tracking days ~ Tracking method * Taxa, family = Gamma (link="log")	1300.6

Predicting the number of tracking days

	Estimate	Std. Error	t value	Pr(> t)
Intercept	5.12	0.42	12.46	<2e-16
Radio tracking	-1.79	0.49	-3.63	0.0004
Mammal	-0.26	0.54	-0.48	0.63
Mammal : Radio tracking	0.38	0.66	0.57	0.57

Supplementary table 8A and 8B. 8A) AIC scores to determine the best model for predicting the number of tracking locations GLM with tracking method and taxa as predictors. 8B) Coefficient output table for predicting the number of tracking locations GLM with tracking method, taxa, and an interaction between the two as predictors.

	Model Formula	AIC scores
Model 1	Locations ~ Tracking method + Taxa, family = Gamma (link="log")	1670.3
Model 2	Locations ~ Tracking method * Taxa, family = Gamma (link="log")	1660.6

<i>Predicting the number of location fixes</i>				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	7.39	0.42	17.65	< 2e-16
Radio tracking	-2.01	0.48	-4.18	5.9e-5
Mammal	0.91	0.55	1.66	0.099
Mammal : Radio tracking	-1.59	0.67	-2.36	0.02

Supplementary table 9A, 9B and 9C. 9A) Model selection output for the best fit model for mean seed dispersal distance GLM with body mass, volant, protected and HFI as predictors. 9B) AIC scores to determine the best model, with or without an interaction, for predicting mean seed dispersal distance GLM with body mass, volant and protected as predictors. 9C) Coefficient output table for mean seed dispersal distance GLM with body mass, volant and protected areas as predictors.

	<i>Dredge</i> – Model selection	AIC scores
Model 1	Mean ~ Body mass + Volant + Protected	1033.1
Model 2	Mean ~ Body mass + Volant + Protected + HFI	1045.4
Model 3	Mean ~ Body mass + Protected	1036.8
Model 4	Mean ~ Body mass + HFI + Protected	1038.7
Model 5	Mean ~ Body mass + Volant	1042.8
Model 6	Mean ~ Body mass + Volant + HFI	1044.0
Model 7	Mean ~ Body mass	1044.7
Model 8	Mean ~ Volant	1045.1

	Model Formula – Mean seed dispersal distance	AIC scores
Model 1	Mean ~ Body mass + Volant + Protected , family = Gamma (link="log")	1032.2
Model 2	Mean ~ Body mass + Volant + Protected , family = Gamma (link="log")	1022.3

<i>Mean seed dispersal distance</i>				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	4.93	0.48	10.31	1.9e-15
Body mass	0.67	0.21	3.15	0.002
Volant	0.95	0.45	2.11	0.04
Protected	1.29	0.43	3.01	0.004

Supplementary table 10A, 10B and 10C. 10A) Model selection output for the best fit model for maximum seed dispersal distance GLM with body mass, volant, protected and HFI as predictors. 10B) AIC scores to determine the best model, with or without an interaction term, for predicting maximum seed dispersal distance GLM with body mass and volant as predictors. 10C) Coefficient output table for maximum seed dispersal distance GLM with body mass, volant and an interaction term as predictors.

	<i>Dredge – Model selection</i>	AIC scores
Model 1	Maximum ~ Body mass + Volant	1500.2
Model 2	Maximum ~ Body mass + Volant + Protected	1502.3
Model 3	Maximum ~ Body mass + Volant + HFI	1502.4
Model 4	Maximum ~ Body mass	1503.1
Model 5	Maximum ~ Body mass + Volant + Protected + HFI	1504.4
Model 6	Maximum	1505.1
Model 7	Maximum ~ Body mass + HFI	1505.3
Model 8	Maximum ~ Body mass + Protected + HFI	1507.3

	Model Formula – Maximum seed dispersal distance	AIC scores
Model 1	Maximum ~ Body mass + Volant, family = Gamma (link="log")	1499.7
Model 2	Maximum ~ Body mass + Volant, family = Gamma (link="log")	1489.9

<i>Maximum seed dispersal distance</i>				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	7.81	0.59	13.29	< 2e-16
Body mass	0.78	0.34	2.27	0.03
Volant	656.32	204.97	3.20	0.003
Body mass : Volant	2322.85	726.28	3.20	0.003

Supplementary table 11A and 11B. 11A) Output for Spearman's rank correlation test between body mass (g) and species average SRT (minutes). 11B) Coefficient output table for the linear model assessing the effect of body mass on the species average SRT.

Spearman's rank correlation test – Body mass & species average seed retention time (SRT)		
S	P-value	Rho
9210.3	9.52e-15	0.79
Alternative hypothesis: true rho is not equal to 0		

<i>Average seed retention time</i>				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	0.022	0.012	1.87	0.07
Body mass	0.00054	0.0001	5.31	1.6e-6

Supplementary table 12. The subset of studies used for each analysis and the reasoning behind the omission of certain studies.

<i>Data analysis</i>	<i>No. of studies used</i>	<i>Reasoning for omission of studies</i>
Global distribution and focal taxon of studies	162	NA
Likelihood of GPS use	140	8 studies focused on fish/reptile species – insufficient sample sizes. 14 studies tracked resources – not comparable to use of GPS or radio transmitters.
Quantity and quality of tracking data	107	8 studies focused on fish/reptile species – insufficient sample sizes. 14 studies tracked resources – not comparable to use of GPS or radio transmitters. 33 studies did not provide required information – i.e. tag performances.
Drivers of seed dispersal distances – Maximum estimate	56	95 studies did not calculate any dispersal distances from tracking data. 6 studies focused on fish/reptile species – insufficient sample sizes. 2 studies focused on species during migration – not comparable. 3 studies did not report maximum dispersal estimates.
Drivers of seed dispersal distances – Mean estimate	45	95 studies did not calculate any dispersal distances from tracking data. 6 studies focused on fish/reptile species – insufficient sample sizes. 2 studies focused on species during migration – not comparable. 8 studies did not report mean dispersal estimates. 6 studies reported median dispersal distances rather than mean.
Seed retention time	42	95 studies did not calculate any dispersal distances from tracking data. 25 studies did not provide seed retention information.

Supplementary table 13. List of 162 frugivore tracking studies included in the review. Information includes Type (if the study only tracked the frugivore or if it also estimated seed dispersal distances), Year of study, Tracking method, Location (the country where the study was carried out in) and Species.

Study /Reference	Type	Year	Tracking method	Location	Species
1	Track	2002	Radio Tracking	Cameroon	Brown cheeked hornbill
1	Track	2002	Radio Tracking	Cameroon	Black-casqued hornbill
2	Track	2014	GPS	Cameroon	White-thighed hornbill
2	Track	2014	GPS	Cameroon	Black-casqued hornbill
3	Track	2008	GPS	Congo	African bush elephant
3	Track	2008	GPS	Gabon	
4	Track	2011	Radio Tracking	Madagascar	Madagascan rousette
5	Track	2019	GPS	Mauritius	Mauritian flying fox
6	Track	2013	Radio Tracking	South Africa	Wahlberg's epauletted fruit bat
7	Track	2014	Radio Tracking	South Africa	Wahlberg's epauletted fruit bat
7	Track	2014	Radio Tracking	South Africa	Peter's epauletted fruit bat
8	Track	2017	GPS	South Africa	Trumpeter hornbill
9	Track	2016	GPS	Canary Islands	Elenora falcon
10	Track	2019	Resource tracking	Gabon	African bush elephant
11	Track	2012	Radio tracking	Madagascar	Red-ruffed lemur
12	Track	2017	Radio Tracking	Borneo	Binturong
13	Track	2018	GPS	Mongolia	Bar-headed goose
13	Track	2018	GPS	China	
13	Track	2018	GPS	India	
14	Track	2016	Radio Tracking	Cyprus	Egyptian fruit bat
15	Track	1998	Radio Tracking	India	Indian short-nosed fruit bat
16	Track	2018	GPS	Malaysia	Asian elephant
17	Track	2015	GPS	Thailand	Lyle's flying fox
18	Track	1994	Radio Tracking	Thailand	Great hornbill
18	Track	1994	Radio Tracking	Thailand	Brown hornbill
18	Track	1994	Radio Tracking	Thailand	Wreathed hornbill
19	Track	2004	Radio Tracking	Vietnam	Pygmy Loris
20	Track	1997	Resource tracking	Japan	Japanese squirrel
20	Track	1997	Resource tracking	Japan	Field mouse
21	Track	2000	Radio Tracking	Belize	Little yellow-shouldered bat
22	Track	1978	Radio Tracking	Costa Rica	Seba's short-tailed bat
23	Track	1986	Radio Tracking	Costa Rica	Seba's short-tailed bat
24	Track	1994	Radio Tracking	Costa Rica	Resplendent Quetzal
25	Track	1997	Radio Tracking	Costa Rica	<i>Brycon guatemalensis</i>
26	Track	2004	Radio Tracking	Costa Rica	Three-wattled bellbird
27	Track	2011	Radio Tracking	Costa Rica	Blue-throated toucanet

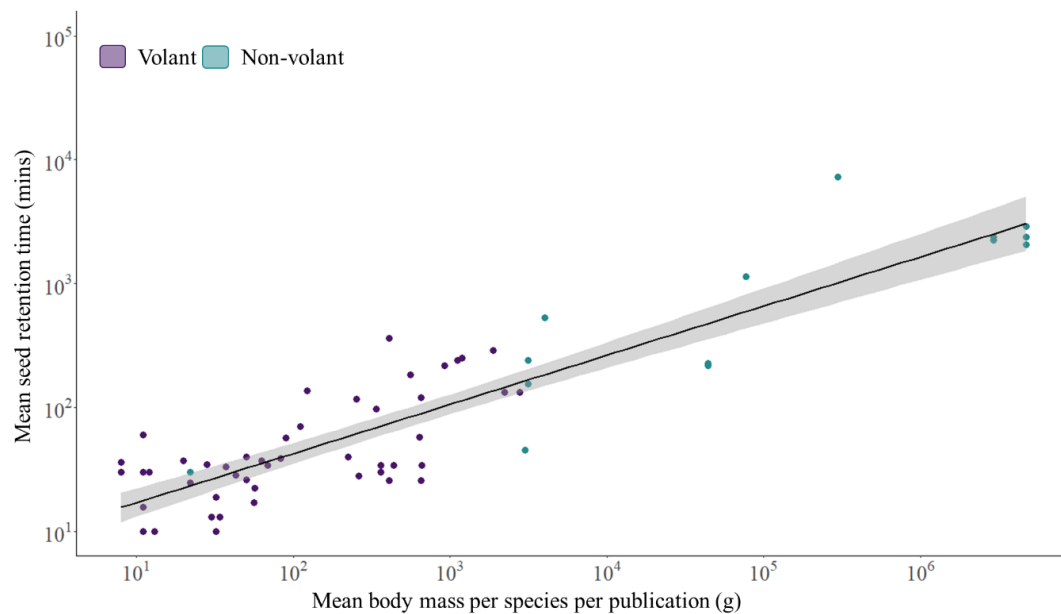
28	Track	2015	Radio Tracking	Costa Rica	Thomas's fruit-eating bat
29	Track	2007	Radio Tracking	Costa Rica	Wood thrush
30	Track	2007	Radio Tracking	Costa Rica	Thomas's fruit-eating bat
31	Track	2010	Radio Tracking	Costa Rica	Commissaris's long-tongued bat
32	Track	2006	Radio Tracking	Costa Rica	Silver-throated tanager
32	Track	2006	Radio Tracking	Costa Rica	Orange-billed nightingale-thrush
32	Track	2006	Radio Tracking	Costa Rica	White-throated thrush
33	Track	1978	Radio Tracking	Panama	Jamaican fruit bat
34	Track	1991	Radio Tracking	Panama	Jamaican fruit bat
35	Track	2005	Radio Tracking	Panama	Spiny rat
36	Track	2006	Radio Tracking	Panama	White-throated round-eared bat
37	Track	2008	Radio Tracking	Panama	Agouti
38	Track	2016	GPS	Panama	White-faced capuchin monkey
38	Track	2016	GPS	Panama	Black-handed spider monkey
39	Track	2006	Radio Tracking	Panama	Chestnut short-tailed bat
40	Track	2018	GPS	France	Roe deer
41	Track	2012	Radio tracking	Menorca	Lilford's wall lizard
42	Track	2011	Radio Tracking	Portugal	Wood mouse
43	Track	2013	Radio Tracking	Sweden	Siberian jay
44	Track	2005	Radio Tracking	USA	Swainson's thrush
44	Track	2005	Radio Tracking	USA	
45	Track	2018	GPS	Canada	Grizzly bear
46	Track	2005	Radio Tracking	Dominican Republic	Hispaniolan parrot
47	Track	1994	Radio Tracking	USA	White-crowned pigeon
48	Track	2014	Radio Tracking	USA	Japanese white eye
49	Track	1998	Radio Tracking	Mexico	Lesser long-nosed bat
50	Track	2001	Radio Tracking	Mexico	Keel-billed toucan
51	Track	2014	Radio Tracking	Mexico	Highland yellow-shouldered bat
52	Track	1978	Radio tracking	Mexico	Jamaican fruit bat
53	Track	2016	Radio Tracking	USA	Cedar waxwing
53	Track	2016	Radio Tracking	USA	American robin
54	Track	2018	Radio Tracking	USA	Swainson's thrush
54	Track	2018	Radio Tracking	USA	Cray catbird
55	Track	2005	Radio tracking	USA	American robin
56	Track	1997	Radio Tracking	Puerto Rico	Red fig-eating bat
57	Track	2009	Radio Tracking	USA	Clarks Nutcracker
58	Track	2010	Radio Tracking	USA	Clarks Nutcracker
59	Track	2016	Radio Tracking	USA	Clarks Nutcracker
60	Track	1997	Radio Tracking	New Zealand	North Island Kaka
61	Track	2008	Radio Tracking	New Zealand	New Zealand pigeon
62	Track	2010	Radio Tracking	New Zealand	North island robin
63	Track	1987	Radio Tracking	Papa New Guinea	Buff-tailed sicklebill
64	Track	2002	Radio Tracking	Papa New Guinea	Lesser bare-backed bat
65	Track	2008	Radio Tracking	Bolivia	Little yellow-shouldered bat
66	Track	2010	Radio Tracking	Bolivia	Red-fronted macaw

67	Track	2003	Radio Tracking	Brazil	Gervais's fruit-eating bat
67	Track	2003	Radio Tracking	Brazil	Striped hair-nosed bat
67	Track	2003	Radio Tracking	Brazil	Silky short-tailed bat
67	Track	2003	Radio Tracking	Brazil	Seba's short-tailed bat
67	Track	2003	Radio Tracking	Brazil	Striped-headed round-eared bat
67	Track	2003	Radio Tracking	Brazil	White-throated round-eared bat
67	Track	2003	Radio Tracking	Brazil	Fringed-lipped bat
67	Track	2003	Radio Tracking	Brazil	Lesser bulldog bat
68	Track	2003	Radio Tracking	Brazil	Agouti
69	Track	2008	Radio Tracking	Brazil	Little yellow-shouldered bat
70	Track	2011	Radio Tracking	Brazil	Black eared opossum
71	Track	2013	Radio Tracking	Brazil	Seba's short-tailed bat
71	Track	2013	Radio Tracking	Brazil	Great fruit-eating bat
72	Track	2014	Radio Tracking	Brazil	Dekeyser's nectar bat
72	Track	2014	Radio Tracking	Brazil	Pallas's long-tongued bat
73	Track	2016	Radio Tracking	Brazil	Pale-breasted thrush
73	Track	2016	Radio Tracking	Brazil	Rufous-bellied thrush
74	Track	2009	Radio Tracking	Brazil	Blue manakin
74	Track	2009	Radio Tracking	Brazil	White-shouldered fire-eye
74	Track	2009	Radio Tracking	Brazil	Rufous-breasted leaftosser
75	Track	2013	Radio tracking	Brazil	White-bearded manakin
76	Track	2013	Radio Tracking	Chile	Austral thrush
77	Track	2016	Radio Tracking	Chile	Monito del monte
78	Track	2017	GPS	Colombia	South American tapir
79	Track	2018	GPS	Colombia	White-footed tamarin
80	Track	2007	Radio Tracking	Ecuador	Chestnut short-tailed bat
80	Track	2007	Radio Tracking	Ecuador	Seba's short-tailed bat
81	Track	1991	Radio tracking	French Guiana	Seba's short-tailed bat
82	Track	2007	Radio tracking	French Guiana	Dwarf little fruit bat
83	Track	1999	Radio Tracking	French Guiana	Bare-tailed woolly opossum
84	Track	2007	Radio Tracking	French Guiana	Dwarf little fruit bat
85	Track	1992	Radio Tracking	French Guiana	White-crowned manakin
85	Track	1992	Radio Tracking	French Guiana	Golden-headed manakin
85	Track	1992	Radio Tracking	French Guiana	White-fronted manakin
85	Track	1992	Radio Tracking	French Guiana	White-bearded manakin
85	Track	1992	Radio Tracking	French Guiana	Thrush-like manakin
86	Track	2018	Radio Tracking	Peru & Ecuador	Shining sunbeam hummingbird
87	Track	2009	GPS	Venezuela	Oilbird
88	Track	2021	Radio tracking	Brazil	Little yellow-shouldered bat
89	Track	2020	GPS	Brazil	White-lipped peccary
90	Track	2020	GPS	Tanzania	Straw-coloured fruit bat
91	Track	2018	GPS	Gabon	African forest elephant
92	Track	2022	GPS	Panama	White-faced capuchin monkey
92	Track	2022	GPS	Panama	Kinkajou
92	Track	2022	GPS	Panama	Coati

92	Track	2022	GPS	Panama	Black-handed spider monkey
93	Track	2021	GPS	Myanmar	Indian flying fox
94	Track	2020	GPS	Australia	Little red flying fox
94	Track	2020	GPS	Australia	Black flying fox
94	Track	2020	GPS	Australia	Grey-headed flying fox
95	Track	2020	Radio tracking	Costa Rica	Pygmy fruit-eating bat
96	Seed	2000	Radio tracking	Cameroon	White-thighed hornbill
96	Seed	2000	Radio tracking	Cameroon	Black-casqued hornbill
97	Seed	2009	GPS	Congo	African forest elephant
98	Seed	2016	GPS	Ghana	Straw-coloured fruit bat
99	Seed	2009	Radio tracking	Kenya	Stripe-cheeked greenbul
99	Seed	2009	Radio tracking	Kenya	Taita thrush
99	Seed	2009	Radio tracking	Kenya	Hartlaub's turaco
100	Seed	2018	Radio tracking	Madagascar	Common brown lemur
101	Seed	2017	GPS	Madagascar	Madagascan flying fox
102	Seed	2011	GPS	South Africa	Trumpeter hornbill
103	Seed	2014	GPS	South Africa	Trumpeter hornbill
104	Seed	2017	GPS	South Africa	African bush elephant
105	Seed	2016	GPS	South Africa	Red-billed teal
105	Seed	2016	GPS	South Africa	Egyptian geese
105	Seed	2016	GPS	South Africa	
106	Seed	2009	Radio tracking	Borneo	Common palm civet
107	Seed	2007	Radio tracking	Hong Kong	Red-whiskered Bulbul
107	Seed	2007	Radio tracking	Hong Kong	Light-vented Bulbul
107	Seed	2007	Radio tracking	Hong Kong	Chinese Hwamei
108	Seed	2019	GPS	India	Wreathed Hornbill
108	Seed	2019	GPS	India	Great Hornbill
109	Seed	2015	GPS	India	Asian elephant
110	Seed	2007	Radio tracking	Israel	Yellow-vented Bulbul
110	Seed	2007	Radio tracking	Israel	Tristram's Grackle
111	Seed	2010	GPS	Israel	Egyptian fruit bat
112	Seed	2009	Radio tracking	Japan	Orii's flying fox
113	Seed	2016	GPS	Japan	Raccoon Dog
114	Seed	2010	GPS	Japan	Asiatic black bear
115	Seed	1996	Resource tracking	Japan	Field mouse
116	Seed	2008	Resource tracking	Japan	Field mouse
116	Seed	2008	Resource tracking	Japan	Japanese squirrel
117	Seed	2011	GPS	Malaysia	Malayan tapir
117	Seed	2011	Radio tracking	Malaysia	Malayan tapir
118	Seed	2008	GPS	Sri Lanka	Asian elephant
118	Seed	2008	GPS	Myanmar	
119	Seed	1988	Radio tracking	Costa Rica	Black-faced solitaire
119	Seed	1988	Radio tracking	Costa Rica	Black and yellow phainoptila
119	Seed	1988	Radio tracking	Costa Rica	Prong-billed barbet
120	Seed	2000	Radio tracking	Costa Rica	Ochre-bellied flycatcher

121	Seed	2015	Radio tracking	Costa Rica	Blue-crowned manakin
121	Seed	2015	Radio tracking	Costa Rica	White-ruffed manakin
122	Seed	2011	GPS	Panama	Keel-billed toucan
122	Seed	2011	GPS	Panama	Chesnut Mandibled toucan
123	Seed	2012	Resource tracking	Panama	Agouti
124	Seed	2018	Resource tracking	Austria	Common pine vole
124	Seed	2018	Resource tracking	Austria	Bank vole
124	Seed	2018	Resource tracking	Austria	Yellow-necked mouse
124	Seed	2018	Resource tracking	Austria	Common dormouse
124	Seed	2018	Resource tracking	Austria	Wood mouse
124	Seed	2018	Resource tracking	Austria	Edible dormouse
125	Seed	2016	GPS	France	Roe deer
125	Seed	2016	GPS	France	Wild Boar
125	Seed	2016	GPS	France	Red Deer
126	Seed	2012	Radio tracking	Germany	Blackbird
127	Seed	2015	GPS	Netherlands	Mallard
128	Seed	2019	GPS	Germany	Mallard
129	Seed	2018	Resource tracking	Poland	European Jay
130	Seed	2012	Radio tracking	Spain	Eyed lizard
131	Seed	2007	Resource tracking	Spain	European Jay
132	Seed	2017	Resource tracking	Spain	European magpie
133	Seed	2015	Resource tracking	Spain	European Jay
134	Seed	2007	Radio tracking	Spain	Liford's wall lizard
135	Seed	2013	Radio tracking	USA	Japanese white eye
135	Seed	2013	Radio tracking	USA	Oma'o
136	Seed	2018	Resource tracking	USA	White-footed mouse
136	Seed	2018	Resource tracking	USA	Chipmunk
136	Seed	2018	Resource tracking	USA	Grey squirrel
137	Seed	2016	Radio tracking	USA	Wood thrush
138	Seed	2011	Radio tracking	Australia	Spiny-cheeked honeyeater
139	Seed	2020	GPS	Australia	Emu
140	Seed	2007	Radio tracking	Australia	Mistletoe bird
141	Seed	2008	Radio tracking	Australia	Painted honeyeater
142	Seed	1991	Radio tracking	Australia	Tooth-billed bowerbird
143	Seed	2005	Radio tracking	Australia	Cassowaries
144	Seed	2018	Radio tracking	New Caledonia	Red-vented bulbul
145	Seed	2012	Radio tracking	New Zealand	Kereru
146	Seed	2003	Resource tracking	Papa New Guinea	Cassowaries
147	Seed	2019	Radio tracking	Saipan	Bridled white eye
147	Seed	2019	Radio tracking	Saipan	Golden white eye
147	Seed	2019	Radio tracking	Saipan	Micronesian starling
147	Seed	2019	Radio tracking	Saipan	Maria Fruit dove
147	Seed	2019	Radio tracking	Saipan	White-throated ground dove
148	Seed	2009	Radio tracking	Brazil	Yellow-footed tortoise
149	Seed	2011	Radio tracking	Brazil	White-crowned manakin

149	Seed	2011	Radio tracking	Brazil	White-fronted manakin
149	Seed	2011	Radio tracking	Brazil	Golden-headed manakin
149	Seed	2011	Radio tracking	Brazil	Thrush-like manakin
149	Seed	2011	Radio tracking	Brazil	White-necked thrush
150	Seed	2019	Radio tracking	Chile	Monito del monte
151	Seed	2012	Radio tracking	Ecuador	Umbrellabird
152	Seed	2016	Radio tracking	Ecuador	White-crowned manakin
153	Seed	2011	Radio tracking	Ecuador	Many-banded aracari
153	Seed	2011	Radio tracking	Ecuador	Channel-billed toucan
153	Seed	2011	Radio tracking	Ecuador	White-throated toucan
154	Seed	1993	Radio tracking	French Guiana	Kinkajou
155	Seed	2008	Radio tracking	Peru	Yellow-footed tortoise
156	Seed	2011	Radio tracking	Peru	Black pacu
157	Seed	2022	Resource tracking	Poland	European Jay
158	Seed	2021	GPS	Gabon	African forest elephant
159	Seed	2021	GPS	Colombia	Oilbird
160	Seed	2022	GPS	Spain	Yellow-legged gull
161	Seed	2020	Radio tracking	Indonesia	Southeast Asian box turtle
162	Seed	2021	Resource tracking	Spain	European magpie



Supplementary figure 1. The mean body mass of volant and non-volant species in relation to their mean seed retention time (SRT). Data extracted from a total of 42 studies that calculated seed dispersal distances and covers 59 different animal species. SRT is an average over multiple seed types for each species for each study. Regression line for all species shows standard error with a 95% confidence interval.

2.7 Reference list for all 162 studies used in this review – Number corresponds to study number in Supplementary Table 13.

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Chapter 3: Understanding the
movement ecology of large-bodied avian
frugivores in Central Panama's tropical
forests

3.1 Abstract

Deforestation poses a significant threat to tropical biodiversity, transforming continuous forests into human-modified tropical landscapes (HMTLs) characterised by isolated fragments embedded in agricultural and urban matrices. As deforestation disrupts spatial structures at the landscape scale, altering community assemblages and impacting ecological processes, understanding animal movement patterns becomes crucial. Frugivorous birds, vital for seed dispersal and forest regeneration, play a pivotal role in shaping tropical forests. Large-bodied frugivores, with their capacity for long-distance movement, are particularly significant indicators of habitat disturbance. Our study focuses on the movement and behaviour of four large-bodied frugivorous bird species in Central Panama. We found significant species-specific differences in the movement behaviour across the species studied. These differences can be determined by morphological traits, foraging strategies and seasonality. This study underscores the necessity of considering species-specific attributes and long-term studies for accurate assessments of large-bodied frugivore movements, providing valuable insights for understanding seed dispersal dynamics and the potential for conservation efforts in the face of ongoing tropical landscape transformations.

3.2 Introduction

Deforestation is considered the main threat to biodiversity within the tropics (Bradshaw et al, 2009). Habitat loss, fragmentation and changes in land use have reduced much of the global tropical forest from large continuous tracts of vegetation to complex human-modified tropical landscapes (HMTLs) (Hansen et al, 2013). It is estimated that primary tropical forest cover has been reduced to less than 30% of its original worldwide extent (Chazdon, 2014), and an estimated 1.2% of total rainforest area is lost each year (Whitmore, 1997; Laurance, 1999). This equates to 195 million hectares of tropical forest lost between 1990 – 2015 (FAO, 2016; Keenan et al, 2015). HMTLs are comprised of isolated fragments of primary forest and secondary forest embedded in a matrix, typically composed of agricultural land and urban areas (Tabarelli et al, 2010). The expansion of HMTLs through the process of forest fragmentation and habitat loss is a severe threat to biodiversity and can impact species through the alteration of various biological and evolutionary processes (Saunders et al, 1991; Fahrig, 2003; Fischer & Lindenmayer, 2006). For example, changes in the spatial structure of forests at the landscape scale result in changes to community assemblages of forest animals through the restriction of their natural movement and isolation within forest patches. This in turn can cause several cascading effects on ecological processes such as seed dispersal, pollination, and predator-prey interactions (Ferraz et al, 2014).

To fully understand how altering animal movement and behaviour can affect large-scale ecological processes, researchers need to first understand the effects that fine-scale movement patterns have at an

individual or group level (Hirsch et al, 2013). By understanding individual movement, we can begin to identify specific ecological drivers of behaviour and what effects these have on broader group dynamics and ecological processes. Thus, understanding the movement ecology of individual animals is crucial in understanding species responses to landscape changes and the effects that these changes will have on broader ecological processes.

Globally, over half of all seed plants are dispersed by animals (Aslan et al, 2013; Rogers et al, 2021). In tropical regions, fruit-eating animals (or frugivores) are responsible for dispersing seeds of most tree species (Muller-Landau & Hardesty, 2005; Galindo-Gonzalez et al, 2000), and their movement and diet shape forest communities. In deforested tropical landscapes, birds and mammals play a critical role carrying seeds across open areas to deposit them in abandoned farmland and regenerating forest (de la Peña-Domene et al, 2014). Seed dispersal by frugivores perfectly illustrates how ecological processes connect animal behaviour to broader ecosystem functions. Large-bodied frugivorous birds are important indicators of habitat disturbance and are vital for the natural regeneration of neotropical forests, as they can move long distances – thus connecting forest fragments - and tend to eat fruits and seeds from a wide range of plant species (Galindo-González et al, 2000; Gray et al, 2007). They help regulate plant communities and diversity and build forest structure through the long dispersal of many plant species (Trolliet et al, 2017; Camargo et al, 2020).

This study focuses on the movement ecology of large frugivorous birds in Central Panama. Panama is home to 675 bird species that inhabit inland areas (*BirdLife International Data Zone*). Of these species, 203 (30%) have a diet consisting of more than 50% fruit and seeds (i.e. frugivorous species; Wilman et al, 2014; McFadden et al, 2022). Large-bodied frugivores are often categorised by having a body mass of 0.1kg or greater (Vidal et al, 2013; Naniwadekar et al, 2019). There are only 69 bird species in the forests of Panama categorised as large frugivores. Gape size tend to correlate with body mass, which positively correlates to distance moved and potential seed dispersal distances (Fell et al, 2023). These species are important dispersers of large-sized seeds and fruits, as their large gape-width enables them to eat a wide range of fruit and seed sizes and they can travel longer distances (Kays et al, 2011; Bradfer-Lawrence et al, 2024). Here, we focus on four of the largest 20 frugivorous bird species in Panamanian forests: Keel-billed Toucan (*Ramphastos sulfuratus*), Chesnut-mandibled Toucan (*Ramphastos swainsonii*), Red-lored Amazona (*Amazona autumnalis*) and Gray-headed Chachalaca (*Ortalis cinereiceps*). While these species share a common frugivorous diet, their distinctive attributes—such as body size, canopy preference, longevity, flight abilities, and dietary preferences—contribute to spatio-temporal variability in their movement patterns and space use. Here we illustrate that these traits must be considered before making generalised comparisons about large-bodied frugivore movements.

Variation in body size among frugivorous birds can have substantial implications for their movement ecology (Lehouck et al, 2009; Wotton & Kelly, 2012). Larger avian species may have distinct foraging ranges and movement patterns compared to smaller species (Spiegel & Nathan, 2007; Lenz et al, 2015). There are no substantial differences in body size among the four study species, but wing morphology and flight capabilities vary considerably. Flight capabilities, often measured using Kipp's distance and wing loading, contribute significantly to the movement strategies of frugivorous birds (Claramunt et al, 2022; Borah & Beckman, 2023). Birds with greater flight capabilities may have broader territories and more flexibility in exploring various parts of their habitat. *Ramphastos* have relatively short and rounded wings, suggesting adaptations for short flights and manoeuvrability within forested habitats. *Amazona* wings are more elongated and pointed compared to the *Ramphastos*, suggesting better aerodynamic efficiency for longer and sustained flights. *Ortalis* wings differ substantially in shape to the three other species and equate to a much smaller wing loading. This suggests that they are generally adapted for short distance, burst flights. Understanding the interplay between flight abilities, habitat structure, and movement patterns can provide insights into the ecological functions that these species provide (Quitián et al, 2019).

Wing morphology may determine the distribution of bird species within the forest structure. For example, *Ortalis* reside on the edges of tropical forests, among thickets and scrub, and are not averse to venturing through degraded landscapes. They will generally inhabit the understory level of neotropical forests (Lopez et al, 2019). The two species of *Ramphastos*, in the family *Ramphastidae*, typically inhabit the canopy level of neotropical forests and are not often seen outside old growth forest (Blake & Loiselle, 2001). The *Amazona* is intermediate between *Ramphastos* and *Ortalis*, in terms of disturbance; they can persist at the canopy level of disturbed landscapes as well old growth forests (Figueira et al, 2015). These differences in vertical stratification and habitat preference can influence their movement behaviours as they navigate between different vegetation layers in search of food resources.

Diet plays a pivotal role in shaping the movement patterns of frugivores, not only due to the preference for specific fruit types, but also the availability and distribution of these resources within a heterogeneous landscape (Kennedy et al, 2010; Schleuning et al, 2011). In the neotropics, resource availability is dictated by seasonal climatic regimes (Schuur, 2003). Fruiting seasons are often sporadic, and many plants fruit at the same time, leading to periods over the year when fruit resources are limited (Levey, 1988; Carlo et al, 2003). In Panama, climate change has reduced the predictability of seasonal patterns further increasing the possibility of extreme precipitation events in the wet season and extreme droughts in the dry season (Feng et al, 2013; Wainwright et al, 2019; Padrón et al, 2020). Both scenarios could negatively affect fruiting phenology of local plant communities. Tropical species are often highly niche

specialised, and so tropical frugivores may be particularly vulnerable in future years as climatic patterns continue to shift (Bender et al, 2019).

Species will likely differ in their ability to respond to changing climatic patterns (Radchuk et al, 2019). For example, *Amazona* tend to be long-lived with the ability to accumulate knowledge and memory over time (Olson et al, 1995; McLean et al, 2022). This may enable them to adapt movement patterns through enhanced navigation skills and improved foraging efficiency (Fagan et al, 2013; John et al, 2016). Longevity could play an important role in mitigating responses to climate change and habitat alterations (Martin & Mouton, 2020; Albaladejo-Robles et al, 2023). As tropical landscapes undergo transformations due to factors such as deforestation, urbanisation, and climate change, exploring how these frugivorous species adjust their movement behaviours can shed light on their adaptability and resilience in the face of environmental disturbances.

Long term monitoring is key to understanding how animal behaviour and movement respond to environmental change. Animal movement is increasingly monitored using tracking devices attached to the individual that record animal locations using radiotelemetry or global positioning systems (GPS; Wikelski et al, 2007; Kays et al, 2015). Traditionally tags were powered with batteries and monitoring time was limited by battery life, but the introduction of solar powered tags has enabled the monitoring of more studies over longer time scales (Byers et al, 2017; Silva et al, 2017; Fischer et al, 2018). Predictions about resource tracking and habitat preference from animal tracking data can help inform conservation policy, and understanding how animal movement patterns change over different periods of their life cycles (breeding vs non-breeding seasons) or seasonal changes e.g wet vs dry seasons, can be key to this process. Home range analysis and habitat preference are a common place to start with movement tracking studies (Bengtsson et al, 2014; Viana et al, 2018; Rosenbaum et al, 2023). Identifying range sizes and movement distances can help inform potential protected areas or movement corridor placements and sizes. However, the use of short-term monitoring studies can misinform these as they do not include sufficient timescales to capture the animal's full range (Jacobson et al, 2023). Since resource availability is correlated with seasonal changes in weather patterns, many species alter their distribution and home range to allow for the fluctuation in seasonal resource availability – whether these be vegetation cover, food, water etc (Ullmann et al, 2018). Different species have different behaviours, which may affect responses to seasonal change. For example, if food resources are scarce during the wet seasons, species may expand their home ranges to enable wider foraging and exploration in search of novel food resources (Warret Rodrigues & Roth, 2023). On the other hand, dispersal restricted species may not be able to expand their ranges, and so reduce movement and limit activity to help reduce energy expenditure (Hou et al, 2020). With long-term monitoring, we can observe these changes and begin building a bigger picture of how species differ in their responses to change, both natural and human induced.

Study aims

Here we provide a comprehensive comparison of the movement ecologies of four large-bodied avian frugivore species in Central Panama. We investigate the typical range distribution of each species, the average distance moved during a day and the smallest distance moved during a 2-hour time step. Furthermore, we investigate the effect of seasonality on space use among species and identify how each species responds to depleted fruit resources during the wet seasons.

Specifically, we hypothesise that:

- I. Due to the similar body size of the species, they will have similar movement patterns and will not differ significantly in movement distances and range.
- II. We propose two alternative hypotheses for the effect of seasonality on space use:
 - a. We anticipate that frugivores will increase range size, and ultimately reduce site fidelity, during the weeks/months of the wet seasons to increase exploratory areas and increase the chance of encountering novel food resources.
 - b. Alternatively, species will reduce energy expenditure during the wet seasons, which will be represented by site fidelity values remaining the same or increasing and/or reductions in averaged overall dynamic body acceleration (ODBA) values in wet compared to the dry season.
- III. Canopy species with larger range sizes will have greater plasticity in responding to environmental changes e.g., in seasonal shifts in climate.

3.3 Methods

3.3.1 Study area

The study was performed in Gamboa, a small village on the banks of the Chagres River in Panama, situated in between two protected forests; Soberania National Park and Forest Protector Arraijan (-79.69707, 9.11624). The local forest is a mixture of secondary forest (20-80 years old) and old-growth lowland moist forest, whilst the village contains gardens, forest patches and open grasslands. Panama has a tropical climate with a mean annual temperature of 28 °C and a unimodal precipitation regime of an average rainfall of 2226 mm, with the dry season lasting from December – April and the wet season from May – November. We used GPS tags to study the movement ecology of four frugivorous bird species: Keel-billed Toucan (*Ramphastos sulfuratus*; three individuals), Chesnut-mandibled Toucan (*Ramphastos swainsonii*; two individuals), Red-lored Amazona (*Amazona autumnalis*; two individuals) and Gray-headed Chachalaca (*Ortalis cinereiceps*; five individuals). Two *Amazonas* individuals were tagged in March 2020, and all other individuals were tagged in January – March 2022. Birds were

captured using mist nets placed in the forest canopies across six different locations. All handling protocols were approved by both the Animal Welfare and Ethical Review Body (AWERB) at the University of Stirling and the IUCAC of Smithsonian Tropical Research Institute.

3.3.2 Data collection

The GPS tags used in this study were manufactured by e-obs GmbH (Grunwald, Germany) and had a rechargeable battery charged via a solar panel. Tracking devices were attached via Teflon strings, like a backpack, to the back of the bird. The tag weight of 10g is below the generally accepted threshold of 3-5% of body weight (our species ranged from 410-650g). Tags for all species except for *Amazona* were programmed to measure GPS locations every two hours during daytime (05:00 – 19:00), with bursts of every 30 mins if the batteries were fully charged. At night, the tags were scheduled to turn off to save battery energy, knowing that after dark, these species would not be active. For *Amazonas*, tags were programmed to measure GPS locations every 30 mins, with bursts of every 10 mins if batteries were fully charged. Along with a GPS module, each tag also measured three-dimensional acceleration (ACC). Since ACC measurements consumed very little energy, the tags were programmed to take ACC measurements of 20 Hz per axis every 10 mins during a 24-hour period. These measurements confirmed little activity during night-time hours. Data was first stored on the device, then remotely downloaded through a radio link once a week to ensure that the device had not fallen off the individual.

Daily, weekly, and monthly precipitation data were acquired from the Smithsonian tropical research institute database. This was recorded on Barro Colorado Island, Panama (9°9'42.36"N, 79°50'15.67"W), approximately 16 km from the tagging sites. The database also identifies the wet and dry season starting dates. Panama has a predictable climate, with a typical dry season beginning in mid-December and ending in mid-April and then an 8-month wet season, with rainfall usually peaking between September and November.

Birds were captured over nine weeks, from January 12 to March 18, using mist nets deployed at six strategically chosen locations around Gamboa (refer to Chapter 4 Figure 1A). Selection criteria for these sites included proximity to abundant food sources, potential roosting and nesting areas, and common flight paths of the target species. The distribution of trapping efforts across these sites was uneven, reflecting a prioritisation of capturing larger frugivores for tracking over comparative analysis among sites. Specifically, one site received 18 days of effort, two sites had 6 days each, and the remaining three sites were visited for 7, 10, and 10 days, respectively.

Nets were operated in two sessions daily, aligning with the peak activity periods of avian frugivores. The first session began at 05:00 *Eastern Standard Time* (EST) and concluded at 10:30 EST, while the second session started at 16:00 EST and ended at 18:30 EST. Continuous monitoring ensured minimal stress and temperature exposure for captured birds, with each net operational for approximately 8 hours per day. Consequently, the total trapping effort across all sites ranged from 48 to 144 hours per site. This approach facilitated efficient capture of targeted species while minimising unnecessary exposure and stress, thereby optimising the data collection process.

3.3.3 Study species

3.3.3.1 Keel-billed Toucan (*Ramphastos sulfuratus*)

The Keel-billed Toucan (*Ramphastos sulfuratus*) is found throughout Central America from Southern Mexico to Northern Colombia. It is currently listed as near-threatened (*BirdLife International, 2021*) due to human activity including habitat loss and hunting. It is the 17th largest primary forest frugivore species in Panama (here we define frugivore as species with diets comprised > 50% fruits and seeds). A Keel-billed Toucan has an average beak width of 33.9cm and an average body mass of 410g (Wilman et al, 2014) Whilst they are a relatively social species and often congregate in groups of 4-12 individuals during the early morning and roosting periods, they are also often seen in pairs or alone. Three individuals were caught and were fitted with GPS tracking devices in January – March 2022.

3.3.3.2 Chesnut-mandibled Toucan (*Ramphastos swainsonii*)

The Chensut-mandibled Toucan (*Ramphastos swainsonii*) was the largest species captured and 10th largest primary forest frugivore in Panama and has an average beak width of 39.9cm and average body mass of 652g (Wilman et al, 2014). The range of this species extends from Mexico to Peru. This species is also classed as near-threatened due to hunting and habitat loss (*BirdLife International, 2016*). Two individuals were caught and were fitted with GPS tracking devices in January – March 2022.

3.3.3.3 Gray-headed Chachalaca (*Ortalis cinereiceps*)

The Gray-headed Chachalaca (*Ortalis cinereiceps*) is found throughout central America from Honduras to Northern Colombia. It is classed as least-concern likely due to its versatility in habitat choice and ability to tolerate disturbed environments (*BirdLife International, 2021*). There is little data available for this species; they have an average beak width of 9.4cm and average body mass of 493g (Wilman et al, 2014). Chachalacas are a large frugivore (the 12th largest in Panama) but they are not canopy species and inhabit mid-layer and forest floor environments, with implications for seed dispersal and the structure of the forest vegetation. They are a social species with distinct territories. In our study area,

there were approximately 10 different groups with group sizes ranging from 8-12 individuals. Five individuals, from distinct family groups, were caught and were fitted with GPS tracking devices in January – March 2022.

3.3.3.4 Red-lored Amazon (*Amazona autumnalis*)

The Red-lored Amazon (*Amazona autumnalis*) is found across central America, ranging from Mexico to Colombia. The species conservation status is of least concern based on IUCN, but population numbers are decreasing (*BirdLife International, 2018*). Red-lored amazons are a large (14th largest in Panama), canopy-dwelling frugivore, and on average has a beak width of 17.1cm and weighs 416g (Wilman et al, 2014). Two individuals were caught and were attached with GPS tracking devices in March 2020.

3.3.4 Data analysis

We tagged 12 individuals from the four species (5 *Ortalis*, 3 *R. sulfuratus*, 2 *R. swainsonii*, 2 *Amazonas*), however one *Ortalis*, one *R. sulfuratus* and one *R. swainsonii* returned locations for < 3 days due to device/harness failure. One *Amazona* (*Amazon_2*) was unable to be recovered after the 18-month delay due to COVID-19 and therefore only provided 7 days of tagging data. This individual was still included in the descriptive movement analysis but removed from all home range analysis. One *R. sulfuratus* (*Ramphastos_1*) and one *Ortalis* (*Ortalis_2*) were omitted from all analysis which included seasonality as they did not yield enough tagging days to cover multiple seasons. The remaining individuals (*Ortalis_1*, *Ortalis_3*, *Ortalis_4*, *Ramphastos_2*, *Ramphastos_3* & *Amazona_1*) were included in all the final analysis (*Supplementary table 1*)

To describe frugivore movement patterns and spatial distribution, we employed Continuous-time Movement Models (CTMM) within the *R* package *CTMM*, capturing the dynamic nature of their trajectories. Utilising Autocorrelated Kernel Density Estimations (AKDE), we estimated individual home ranges, generating smoothed probability density polygons that fit to the spatial distribution of observed locations. The resulting 99% AKDE polygons were calculated to outline areas encompassing 99% of each frugivore's estimated home range, offering a spatial representation of their primary habitat utilisation. Simultaneously, 50% core home range sizes were computed to highlight central regions of activity. We then calculated an average step-length across 2-hour intervals and the minimum daily distance travelled using Euclidean distance.

For one of the *Amazona* individuals, we first had to subset the dataset into three sections before undertaking home range analysis as the individual made long-distance exploratory movements during a 3-month period in 2021 that made calculating home range for the entire survey period impossible. A

weighted average was then taken across the three different home ranges using the *mean* function included in *CTMM*. This segmentation into three means for the *Amazona* individual's home range analysis was necessary due to the constraint of continuous-time movement models, which operate optimally with stationary movement data. Stationarity assumes that the statistical properties of the data remain constant over time (Calabrese et al, 2016). Given the long-distance exploratory movements exhibited during a 3-month period in 2021, applying *CTMM* directly to the entire survey period might violate the stationary assumption. By segmenting the data, each representing a more stationary subset, and subsequently calculating means for each segment, we aimed to create more appropriate conditions for the accurate application of *CTMM*, ensuring a meaningful analysis of the individual's distinct movement patterns across different temporal segments. Weekly and monthly site fidelity were then calculated using the *overlap* function within *CTMM*, for all individuals that had sufficient data to be able to compare at a weekly/monthly level (*all individuals, excluding Amazona_2, Ramphastos_1, Ortalis_2*). Calculated values range from 0-1, with values closer to 1 exhibiting a greater overlap in home ranges and therefore, a greater site fidelity. The lower values show greater range change and potentially more exploratory behaviour.

Overall dynamic body acceleration (ODBA) was extracted from the acceleration data to be used as a proxy for energy expenditure over the study duration. This was averaged over weekly/monthly time periods to see if energy expenditure could be used as a predictor for site fidelity. This would help to corroborate ideas of either increasing energy output to expand range during the limited resource seasons or reduce energy output and home range during these seasons, as predicted by our hypotheses.

Important roosting and foraging sites throughout the different seasons were then identified using the relocation data. We described site reuse using the number of revisits, residency and entrance and exit times, with the *recurse* package (Bracis et al, 2018). As we were interested in broader landscape use, such as foraging areas, the radii used to calculate the relocations was determined based on the number of maximum revisitations, the median step length of the species and the potential location error of the GPS tags. We then performed a cluster analysis of the locations using a minimum threshold for revisitations, which differed between individuals. These highly visited locations were then clumped together using the 'fanny' method in the 'cluster' package (Maechler, 2019) to identify each of the sites. For each site, residence time was calculated using the entrance time, the exit time, and a linear interpolation between both trajectory locations. This enabled us to identify possible uses for each site based on the time of day and length of visit to each of the sites.

3.3.5 Statistical analysis

For all statistical analysis where comparisons are drawn between species, the individual *Ramphastos swainsonii* (*Ramphastos_3*) was grouped with *Ramphastos sulfuratus* due to small sample size of one

individual. This decision is informed by the close taxonomy of the two species and similar functional roles they occupy. We anticipate that this grouping will not unduly influence our results, considering the comparable ecological characteristics and behaviours exhibited by these species. It is noteworthy that a similar approach was adopted by Holbrook (2011), reinforcing the precedent of addressing small sample sizes in closely related species for robust statistical analysis.

We fitted linear mixed models (LMMs) and generalised linear models (GLMs) in R version 4.3.0 to test if seasonal home range could be predicted by rainfall, a rainfall lag and energy expenditure (median ODBA) across the different species. ODBA was standardised for individuals to account for differences within species, then the median was used to account for the skewed distribution of the data. Rainfall was acquired through the Smithsonian tropical research institute database 16 km away from the study site. Total monthly rainfall was used for the monthly models, and total weekly rainfall was used for the weekly models. The rainfall lag consisted of the total rainfall across the previous two weeks before the home ranges were calculated. This was to account for delayed responses to rainfall that might be mediated by environment. To account for repeated observations of the same individual across the study periods, we fitted individual ID as a random effect for *Ortalis* and *Ramphastos* models but not *Amazona* as only one individual had sufficient data for analysis. The models were fitted to both the 99% home range and 50% home range to investigate whether these predictors affected core range use differently to overall range size. We provide the results, P-values, and summary tables for each of the models (*Supplementary tables 2 & 3*).

For the overlap analysis, three seasonal categories were created based on the total rainfall for that month with the dry season including months that had < 100 mm, the intermediate season was between 100 - 300 mm, and the wet season included all months with > 300 mm. The overlap values were then summed, and an overall average was calculated for all potential overlaps between the different seasons. Generalised linear mixed models (GLMMs) were then fitted to assess whether seasonal overlap could be used to predict if site fidelity significantly differed between seasons. The absolute difference in rainfall was used to provide a predictor for the change in rainfall between each overlapping range. Finally, we ran Type III analysis of deviance using Wald chi-square tests on the calculated models to identify differences between specific seasonal overlaps. We provide the results, P-values, and summary tables for each of the models (*Supplementary tables 4 - 8*).

GLMs with either binomial or quasibinomial error structures and a logit link function were constructed to test if there were any differences between the proportion of revisitations to specific sites and whether these differences could be predicted by seasonality and an interaction between site and seasonality. We ran Type III analysis of deviance using Wald chi-square tests on the calculated models to identify if there were differences across specific sites and seasons. Finally, Tukey Post-hoc tests were used to

identify the likelihood of revisitations to specific sites during different seasons. We provide the results, P-values, post-hoc tables and summary tables for each of the models (*Supplementary tables 9 - 25*).

3.4 **Results**

We attached a total of 12 tags across the four species. Three tags failed due to harness attachment, but nine tags yielded a total of 50,717 location fixes and a total of 1,709 animal-days of movement trajectory (*Supplementary table 1*). All tracking data are available online at <http://www.movebank.org>.

3.4.1 **Descriptive movement statistics**

Median daily distances moved varied both between species and within species (Figure 1). *Amazona* had the greatest median daily distance (13.8 km), followed by the *Ramphastos sulfuratus* (2.7 km), *Ramphastos swainsonii* (1.7 km) and then *Ortalis* with the smallest distances (0.6 - 1.3 km). Individuals within *Ramphastos* and *Ortalis* also differed significantly in terms of median daily distance (*Supplementary table 1*).

Median straight-line distance between 2-hour GPS locations differed among species (Figure 1). This ranged from 34.8 - 59.5 m for *Ortalis*, 117 - 199.4 m for the two *Ramphastos* species and 87.1 - 134.8m for the *Amazonas*. There were also considerable differences within the maximum step lengths ranging from 210.3 – 10,042.1 m across all species (*Supplementary table 1*).

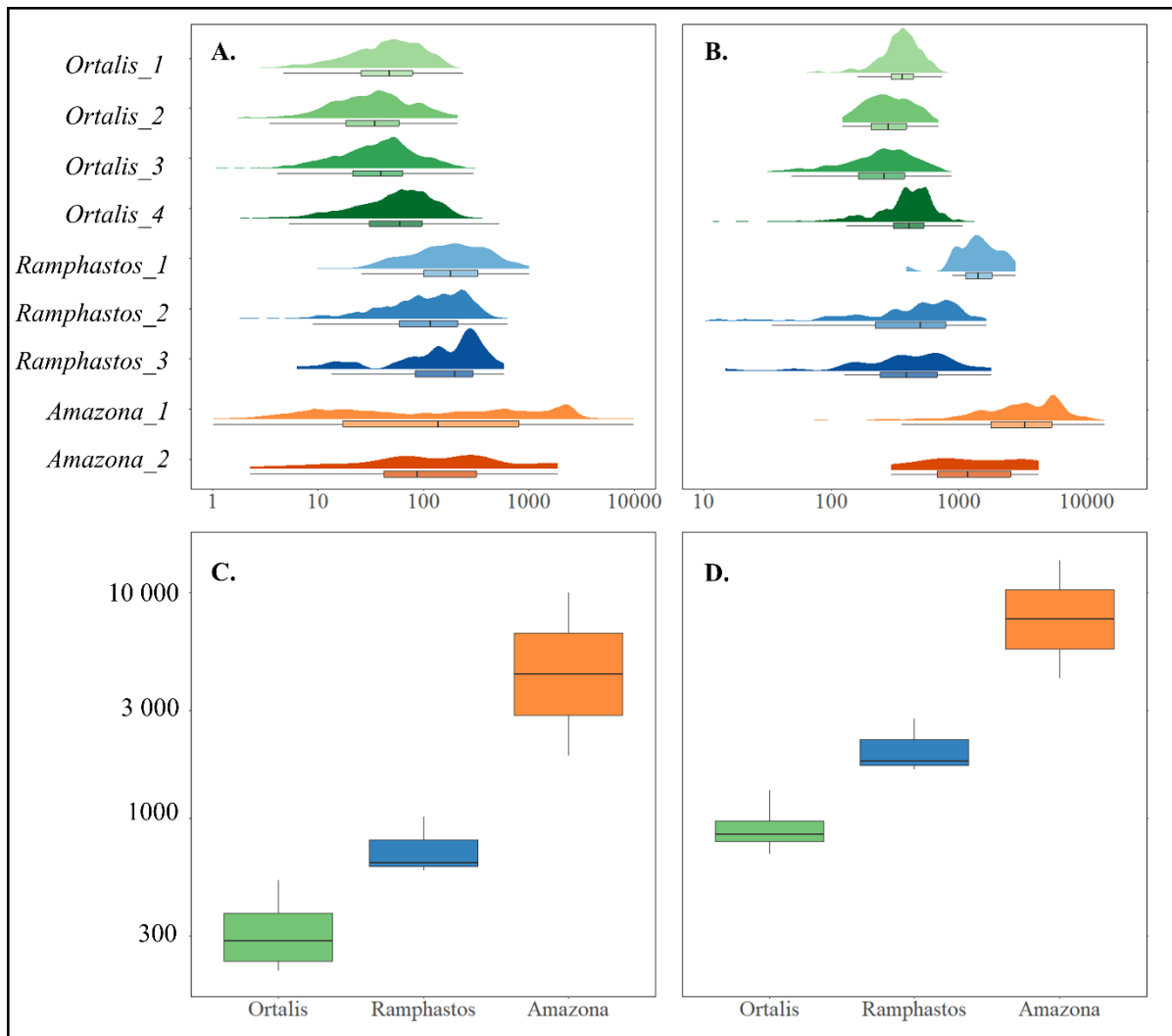


Figure 1A. The distribution of straight-line distances between 2-hour GPS locations (in metres) during the total study duration for all individuals. 1B. The distribution of total daily distances travelled using the straight-line distances between 2-hour GPS locations (in metres) during the total study period for all individuals. 1C. The average, maximum straight-line distance between 2-hour GPS locations (in metres) for the species *Ortalis*, *Ramphastos* and *Amazona*. 1D. The average, maximum daily distances travelled using straight-line distance between 2-hour GPS locations (in metres) for the species *Ortalis*, *Ramphastos* and *Amazona*.

3.4.2 Range distributions

The four species differed significantly in terms of their 99% range sizes (Figure 3 & 4; *Supplementary table 1*). *Amazona* individuals had the largest home ranges (858.4 – 12,548.6 Ha; Figure 4B), and *Ortalis* had the smallest (3.2 – 9.1 Ha; Figure 3 & 4E - F). The two *Ramphastos* species had ranges in between these but did not differ significantly between *Ramphastos* species (*Ramphastos sulfuratus* 24.6 – 114.9 Ha, Figure 4C; *Ramphastos swainsonii* 43.1 Ha, Figure 4D). Figure 3 presents both *Ramphastos* species home range estimates together due to a low samples size of one *Ramphastos swainsonii*. Among species, there was no difference in the percentage of home range used as core use which ranged from 10-15.5% of the total home range. The only exception was for *Amazona_1*, which had a significantly smaller core use range estimate, < 1% of the total home range.

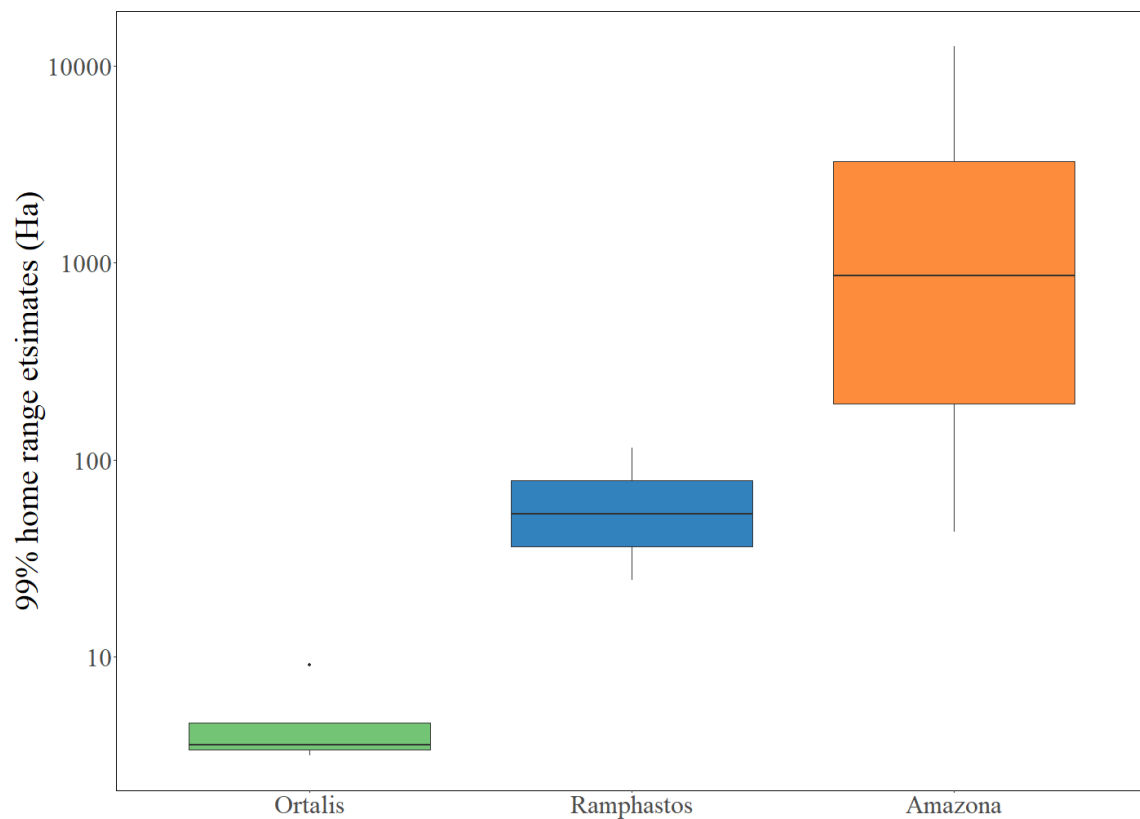


Figure 2. The average 99% home range estimates (Ha) across the species *Ortalis*, *Ramphastos* and *Amazona*.

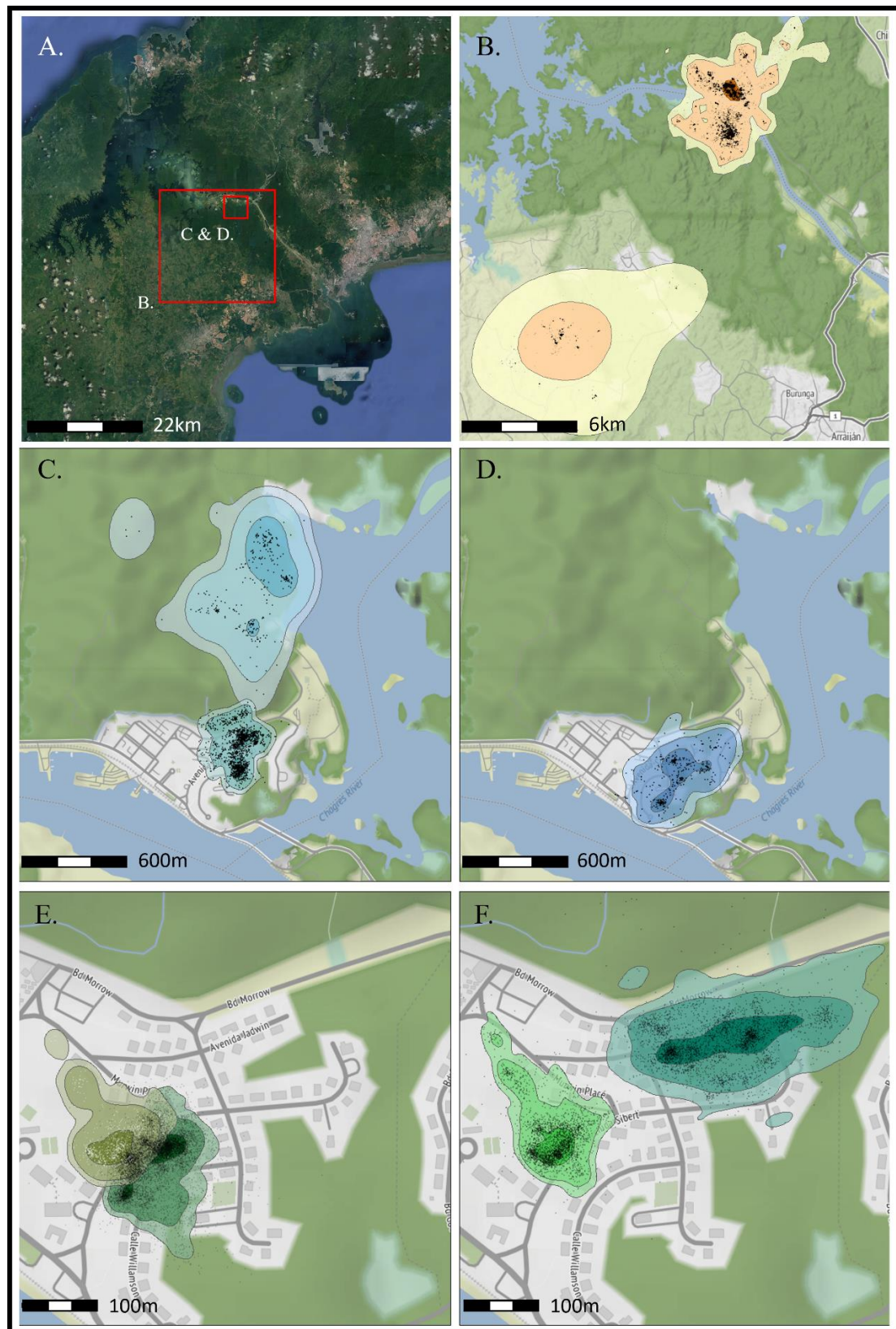


Figure 3A. Map of Panama with the outlines of the areas where the additional figures are located, panels 3E and 3F are close-up maps of the village of Gamboa shown in the bottom of the peninsula in panels 3C and 3D. 3B. Autocorrelated kernel density estimates for *Amazona_1* using all location data, with

polygons representing 50%, 95% and 99% home range estimates. 3C. Autocorrelated kernel density estimates for two *Ramphastos sulfuratus* individuals (*Ramphastos_1* & *Ramphastos_2*) using all location data, with polygons representing 50%, 95% and 99% home range estimates. 3D. Autocorrelated kernel density estimates for *Ramphastos swainsonii* (*Ramphastos_3*) using all location data, with polygons representing 50%, 95% and 99% home range estimates. 3E. Autocorrelated kernel density estimates for two *Ortalis cinereiceps* (*Ortalis_1* and *Ortalis_2*) using all location data, with polygons representing 50%, 95% and 99% home range estimates. 3F. Autocorrelated kernel density estimates for two *Ortalis cinereiceps* (*Ortalis_3* and *Ortalis_4*) using all location data, with polygons representing 50%, 95% and 99% home range estimates.

3.4.3 Seasonal influences on range distributions

The following analysis displays the outputs of the home range models using the 99% home range estimates only. The models using the 50% home range estimates revealed comparable results and were therefore not included.

3.4.3.1 Monthly home range model outputs

Monthly home range estimates were stable across seasons for *Ortalis* and *Ramphastos* species, using rainfall and previous weekly rainfall as a measure of seasonal climatic variations. Similarly, energy expenditure (median monthly ODBA) was not associated with changes in these range estimates. However, the *Amazona* home range estimate changed significantly with season, and range size decreased with increasing monthly rainfall (range estimate $\pm$ std. error = -0.016 ± 0.005 , $p < 0.004$; *Supplementary table 7*).

3.4.3.2 Weekly home range model outputs

Weekly home range estimates for *Ortalis* significantly increased with increasing rainfall in the previous two-weeks (range estimate $\pm$ std. error = 0.090 ± 0.045 , $p < 0.005$; *Supplementary table 8*) and with an increase in weekly median energy expenditure (range estimate $\pm$ std. error = 0.518 ± 0.193 , $p < 0.009$; *Supplementary table 8*). There was no effect of seasonality or energy expenditure on *Ramphastos* weekly home ranges (*Supplementary table 9*). *Amazona* weekly range size decreased with an increase in weekly rainfall from the same week (range estimate $\pm$ std. error = -0.006 ± 0.003 , $p < 0.03$; *Supplementary table 10*), and the previous two-weeks (range estimate $\pm$ std. error = -0.008 ± 0.003 , $p < 0.007$; *Supplementary table 10*).

3.4.4 Seasonal influences on weekly site fidelity

All species exhibited significantly different weekly range overlap, i.e., site fidelity, across different seasons (Figure 5). The difference in overlap values between dry-dry and dry-inter was significantly different for *Ortalis* and *Amazona*, however *Ortalis* increased site fidelity whereas *Amazona* decreased it (overlap estimate $\pm$ std. error = 0.102 ± 0.049 , $p = 0.035$; overlap estimate $\pm$ std. error = -0.046 ± 0.015 , $p = 0.002$; *Supplementary table 4A & 4C*). Suggesting that site fidelity is greater in transitional seasons for *Ortalis*, and lower in the transitional seasons for *Amazona*. The only significantly different weekly home range overlaps for *Ramphastos* were between dry-dry and inter-wet season types, where there was a significant decrease in site fidelity (overlap estimate $\pm$ std. error = -0.307 ± 0.134 , $p = 0.022$; *Supplementary table 4B*). Suggesting that site fidelity of *Ramphastos* is lower in the wet seasons.

Seasonal differences in rainfall for *Ortalis* and *Ramphastos* did not lead to significant changes in site fidelity (overlap estimate $\pm$ std. error = 0.0005 ± 0.0003 , $p = 0.112$; overlap estimate $\pm$ std. error = -0.0003 ± 0.0005 , $p = 0.575$; *Supplementary table 5A & 5B*) but did have significant differences for *Amazona* (overlap estimate $\pm$ std. error = $-8.48\text{e-}04 \pm 8.72\text{e-}05$, $p < 2\text{e-}16$; *Supplementary table 5C*). Suggesting that rainfall alone may not be the primary driver of site fidelity for these studied species and site.

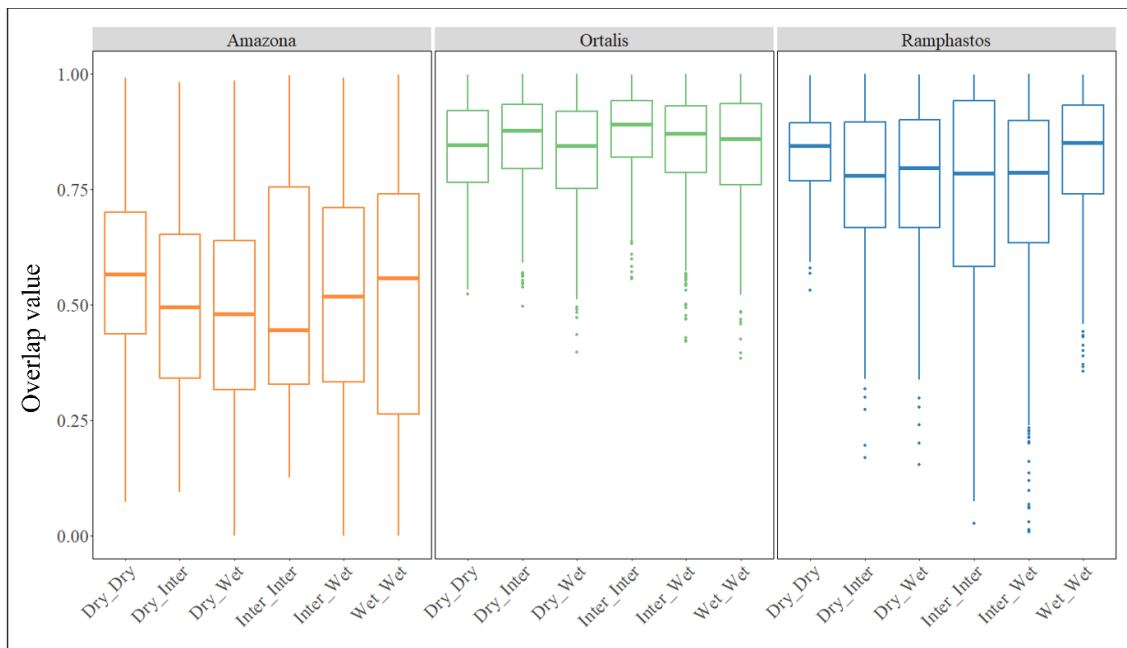


Figure 4. Seasonal overlap per season type for *Amazona* ($n = 1$), *Ortalis* ($n = 3$) & *Ramphastos* ($n = 2$) using weekly overlap values. Calculated values range from 0-1, with values closer to 1 exhibiting a greater overlap in weekly home ranges across different seasons. Values closer to 0 indicate lower overlap in weekly home range use across the different seasons.

3.4.5 Seasonal influence on proportion of revisitations and site identification

The effect of site, seasonality, and an interaction between site and seasonality predicted the proportion of site revisitations at the individual level, but there were no consistent species-level patterns. Figure 6 illustrates a heatmap of revisitations (A) that are used to identify revisited sites based on a predetermined radius (B). The proportion of usage across the different sites is then identified for each month (C) and the total number of daylight and nighttime hours each site is used for (D).

Site identity and the interaction with seasonality significantly affected the proportion of revisitations across different sites for *Ortalis_3*, *Ramphastos_3* and *Amazona_1*, year 2021 (Chi-sq = 17.661, df = 10, $p = 0.061$; *Supplementary table 10*; Chi-sq = 32.03, df = 8, $p = 9.2e-05$; *Supplementary table 17*; Chi-sq = 62.376, df = 12, $p = 8.3e-09$; *Supplementary table 22*). For instance, *Ortalis_3* exhibited a higher likelihood of revisiting site 4 during the dry season (Figure 7A; *Supplementary figure 2B*). In contrast, *Ramphastos_3* was less likely to use site 1 in the dry season and site 4 in the intermediate season (Figure 7E; *Supplementary figure 2E*). *Amazona_1*, in 2021, displayed an increased likelihood of using site 3 during the dry season but decreased use of sites 6 and 7 in the same season (Figure 7K; *Supplementary figure 2G*). This suggests a preference for a particular site during different times of the year, potentially indicating areas of high resources.

Site identity alone significantly affected the proportion of revisits for *Ortalis_4* and *Amazona_1*, year 2020 (Chi-sq = 33.57, df = 6, $p = 8.2e-06$; *Supplementary table 13*; Chi-sq = 19.0, df = 6, $p = 0.004$; *Supplementary table 20*). Neither site, seasonality or an interaction between these variables were able to predict revisitation proportion for *Ortalis_1* and *Ramphastos_2* (*Supplementary table 6 & 15*).

Ortalis_1, *Ortalis_4* and *Amazona_1* (across both years) used particular sites more frequently at night than in the daytime, with total residency hours at certain sites much greater between the hours of 18:00-06:00 (*Ortalis_1* – site 4; *Ortalis_4* – site 4 and site 5; *Amazona_1* – site 1 and site 3 in 2020, site 5 in 2021; Figures 6D & 7D, J & L). Neither of the *Ramphastos* individuals used any of the sites more frequently during nighttime hours (Figure 7F & H). All species showed signs of a preference of usage to particular sites during daylight hours.

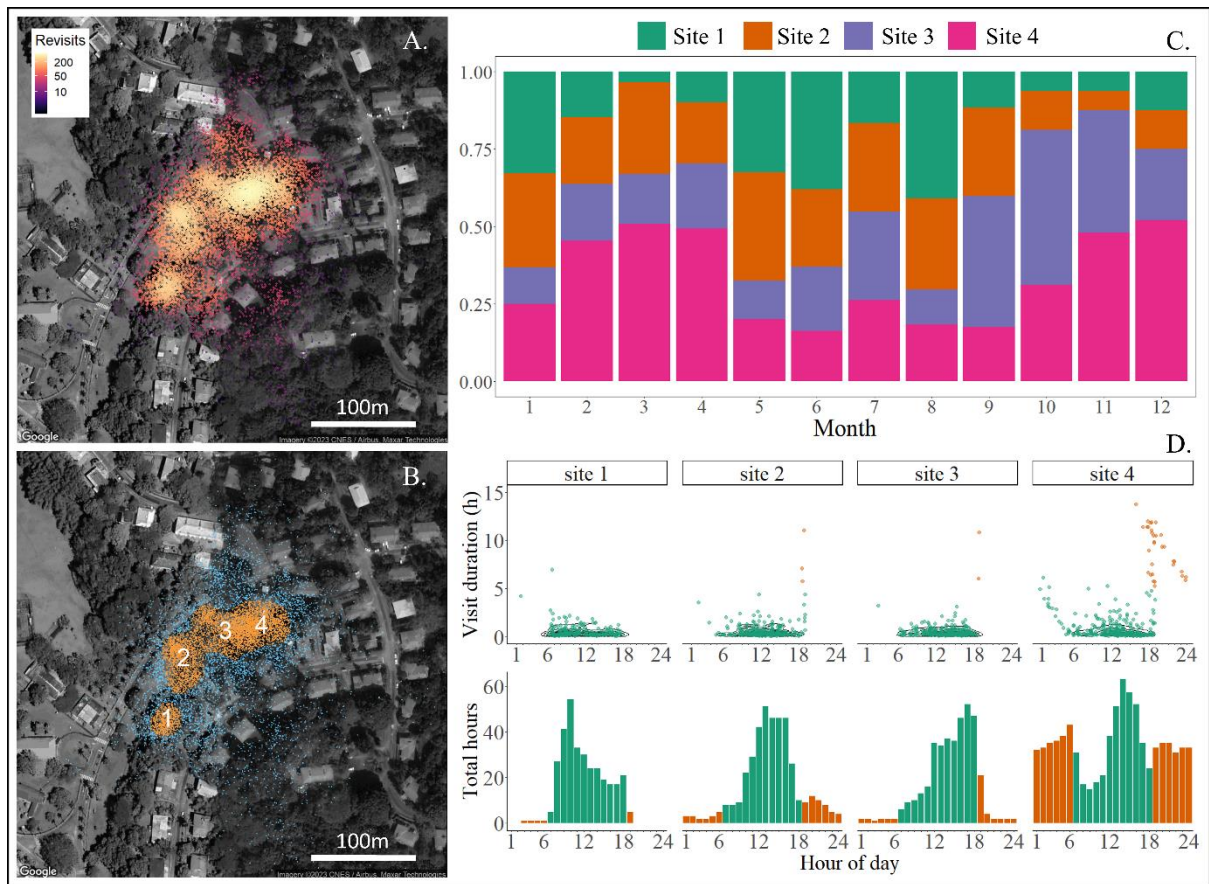


Figure 5. Visualisation of revisitation data for *Ortalis* individual; (A) GPS locations of *Ortalis*_1 revisitation, (B) clustered into 4 separate sites using a radius of 10m and revisit threshold of >150 revisits. (C) Site usage across months represented by proportions. (D) Duration of time spent within each site, with orange representing locations where the individual stayed overnight.



Figure 6. Figures on the left show the site usage across months represented by proportions, figures on the right show the visit durations with respect to the entrance time of the sites and the total time spent at each site with respect to hour of the day. The orange points represent locations where the individual stayed overnight in the site. A & B - *Ortalis_3*, C & D - *Ortalis_4*, E & F - *Ramphastos_3*, G & H - *Ramphastos_2*, I & J - *Amazona_1* (subset by 2020 data) and K & L - *Amazona_1* (subset by 2021 data).

3.5 Discussion

3.5.1 Influence of species traits and life-history on home ranges and movement patterns

Among our four study species of large-bodied frugivores we see distinct movement strategies, suggesting that movement is determined by factors beyond body size. Previous work suggests that there is a general, positive relationship between species body mass and home range size (Carbone et al, 2005; Ottaviani et al, 2006; Sorensen et al, 2020). However, our study suggests that other traits such as wing morphology and species foraging and habitat preferences (e.g., in forest vertical stratification) likely play an important role in shaping their movement behaviours and add complexity to the body mass - home range size relationship (Camargo et al, 2020; Thiel et al, 2021). This insight improves our understanding of the ecological strategies employed by these species and has important implications for their role in seed dispersal dynamics.

Amazona species had the largest home range estimates among the three species studied, followed by *Ramphastos* and then *Ortalis*, which had the smallest home ranges. This pattern aligns with the hypothesis that wing morphology plays a crucial role in determining range size. *Amazona* species have a wing morphology that enables sustained flight (Renton, 2001; Bjork, 2004) and can enable them to explore larger areas with lower energy expenditure compared to *Ortalis* and *Ramphastos*.

Life-history also affects movement and home range size; we propose that longevity potentially influences the extensive home ranges of *Amazona* species. Long-lived species possess greater memory capacities, enabling them to track seasonal variations in resource availability (Munshi-South & Wilkinson, 2006; Baert et al, 2022). This can allow species to remember the locations of key food resources throughout the year, allowing them to make direct movements to these sites and minimise energy expenditure (Bracis et al, 2015; Thorup et al, 2017). This adaptability to changing resource distributions could contribute to their larger home ranges.

The proportion of home range defined for core use, was 10% to 15% across all species. This consistency in core range size suggests a general ecological strategy where specific areas are used for critical activities such as breeding, nesting, roosting, or concentrated foraging, with broader areas used for exploration and wider foraging. However, some seasonal variation in these patterns, and among individuals, illustrates that there is also flexibility in how individuals adjust their core range use in response to environmental changes (Lenz et al, 2015; Stevenson et al, 2017; Smetzer et al, 2021).

Intra-specific differences in range distribution patterns were observed, specifically among the *Ramphastos* and *Ortalis* species, with one individual for each species exhibiting significantly larger home ranges. The study area contains patches of forest, residential areas, gardens, and extensive areas

of forest. Individuals with ranges connected to larger forest patches and areas of extensive undisturbed forest tended to have larger ranges underscoring the importance of habitat accessibility. Access to larger forest fragments or continuous tracts of primary forest appears to encourage greater dispersal of individuals (Dunning et al, 1992; Taylor et al, 1993; Estrada-Carmona et al, 2019). This can be attributed to reduced restrictions or barriers to movement within more extensive habitats.

The *Amazona* species displayed both a significantly larger median and maximum daily distance travelled compared to *Ortalis* and *Ramphastos*. The larger daily distances travelled by *Amazona* species showcases an inclination towards extensive exploration and wide-ranging foraging (Marsden et al, 2000). This aligns with their wing morphology, enabling sustained flight and efficient coverage of larger areas with relatively lower energy expenditure (Sheard et al, 2019; Claramunt et al, 2022), potentially linked to foraging across more diverse habitats and tracking seasonal variations in resource availability. In contrast, the longer median 2-hour step lengths in *Ramphastos* species suggest more focused movements over shorter intervals, potentially reflecting a more targeted exploitation of specific resources within localised areas. *Ortalis* displayed the smallest median step lengths but comparable daily distances to *Ramphastos*. The relatively shorter step lengths suggest that *Ortalis* tends to take more frequent, but shorter, steps during its movements. Considering the preferred habitat of *Ortalis* being the understory, this pattern could be associated with a more meticulous and localised foraging behaviour, where they are actively exploring the immediate surroundings with frequent stops and changes in direction, optimising foraging efforts in a more restricted space (Aben et al, 2012; Habel et al, 2016).

3.5.2 Species-specific home range and site fidelity responses to seasonality

Understanding the seasonal dynamics of range distributions is vital for unravelling the complex movement ecology of frugivorous birds. Short-term tracking studies, while informative, may not fully capture the broader picture of how these species adjust their movements in response to changing environmental conditions. Our study underscores the importance of long-term monitoring and reveals intriguing patterns of seasonal influence on range distributions.

Frugivorous birds often need to adapt their movement patterns to track the availability of food resources, which can fluctuate dramatically with changing seasons (Price, 2004; Maruyama et al, 2013; Mulwa et al, 2013). Central Panama has a highly seasonal climate with a pronounced dry season from December to April and many trees fruit flower during the dry season triggered by peaks in solar irradiance (Wright & Cornejo 1990, Wright & van Schaik 1994; Adler & Kielpinski 2000; Wright & Calderon, 2018). Thus, fruit abundance is high in April/May when the dry season ends, and the wet season starts, and we predict that frugivore range distributions will shift in line with these seasonal variations. However, our findings challenge this assumption given that the monthly range distributions of both *Ortalis* and

Ramphastos species remained relatively stable across seasons. Neither monthly rainfall, previous weekly rainfall, nor energy expenditure emerged as significant predictors of changes in these range estimates. This suggests that, at a monthly scale, these birds maintain consistent movement behaviours irrespective of seasonal variations. In contrast, the *Amazona* individual studied across seasons decreased monthly range size with increasing rainfall. Despite initial exploratory movements during the wet season. This individual ventured far from its original range, but then remained within a confined area during that specific month, emphasising the complexity of seasonal adjustments in movement patterns.

The analysis of weekly rather than monthly range distributions yielded different results. For *Ortalis*, there was a significant increase in range size with an increase in previous two-weeks rainfall and energy expenditure. This suggests that *Ortalis* individuals respond to environmental changes driven by previous climatic patterns, with a lag in their movement behaviour. An increase in energy expenditure also implies that *Ortalis* individuals engage in more extensive movements to expand their ranges, possibly in pursuit of dispersed or newly available fruit resources. The inconsistency across different temporal scales for *Ortalis* highlights the importance of understanding fine-scale variation in movement patterns. In contrast, *Amazona* decreased weekly range size with increasing weekly rainfall and previous two-week rainfall, consistent with monthly range-size results.

More broadly, *Ortalis* and *Amazona* appeared to exhibit opposing responses to seasonal changes in terms of their weekly range distributions. This suggests that they may use different foraging strategies and be tracking different food resources or responding to specific fruiting phenology patterns. In Central Panama, flowering and fruiting of some tree species is triggered by rainfall, while this may inhibit flowering of other species, creating complex dynamics in resource tracking (Fleming, 1979; Kimura et al, 2001; Boyle and Bronstein, 2012).

Site fidelity, the tendency of individuals to revisit or remain in previously occupied areas, is a fundamental aspect of animal behaviour that can be influenced by a variety of ecological factors, including resource availability, reproductive activities, and environmental conditions (Ranc et al, 2020; Papageorgiou et al, 2021; Ramellini et al, 2022). Despite finding no trends in monthly range distributions in relation to seasons, we found significant differences in site fidelity across different seasons for all species.

Ortalis species displayed an increase in site fidelity when transitioning from the dry season to the intermediate season, suggesting that individuals tend to revisit and remain within familiar areas when the environment transitions from a period of lower rainfall (dry season) to a season of increased rainfall (intermediate season). One possible explanation for this increased site fidelity could be tied to resource availability. With the onset of the intermediate season, there may be a flush of fruiting plants or other food resources that encourage individuals to stay within known territories where these resources are

abundant (McLester et al, 2019; Lormée et al, 2021). Alternatively, this increased site fidelity might be related to breeding activities. Which are timed for the start of the wet season, when individuals return to specific locations for nesting or to engage in courtship rituals (Hansbauer et al, 2008). In contrast, both *Ramphastos* and *Amazona* species exhibited decreased site fidelity when transitioning from the dry season to the intermediate or wet season, suggesting that individuals tend to explore new areas more frequently as the environment becomes more conducive to resource availability, potentially linked to fruiting phenology.

Considering the variability in the observed patterns of site fidelity, it is essential to consider the factors that may drive these behaviours. Notably, differences in rainfall did not emerge as a significant predictor of site fidelity for *Ortalis* or *Ramphastos* species. This suggests that other ecological factors may be at play, such as specific resource availability or breeding activities, that were not considered for this specific study.

Site fidelity can be influenced by the distribution and abundance of food resources. Frugivorous birds may return to familiar areas where they have previously found abundant and reliable food sources. The transition from dry to wet seasons, for instance, may lead to changes in fruiting patterns, with some species of plants producing fruit more prolifically during the wet season (Poulin et al, 1992; Mendoza et al, 2017; Dunham et al, 2018). This seasonal variation in food availability could encourage individuals to explore new areas to find the most abundant resources.

Breeding activities can also impact site fidelity. Birds may return to specific locations for nesting, mate attraction, or the protection of their young (Aguilar et al, 2007; DuVal, 2007). It is possible that the observed decrease in site fidelity for *Ramphastos* and *Amazona* during the transition to the wet season is related to breeding behaviours. During this time, individuals may disperse more widely to locate suitable nesting sites or engage in territorial defence and courtship rituals (Martin & Fahrig, 2018). To gain a more comprehensive understanding of the drivers behind seasonal variations in site fidelity, long-term monitoring is crucial. Long-term data collection can reveal patterns that may not be apparent in shorter-term studies and help researchers discern whether these behaviours are consistent across multiple years.

3.5.3 Species and seasonal influences on site selection and revisitations

The proportion of revisitations to specific sites by the frugivorous bird species in our study revealed complex and individual-specific patterns. These findings highlight the ways in which these birds interact with their environment and adapt to changing seasonal conditions. It is important to note that no consistent species-level patterns emerged from our analysis. This lack of uniformity suggests that each species responds uniquely to the interplay of site characteristics and seasonality.

For three individuals (*Ortalis_3*, *Ramphastos_3*, and *Amazona_1* in 2021) the proportion of revisits to specific sites was influenced by both site characteristics and seasonal variations, suggesting that certain sites gained heightened significance for these individuals during specific seasons. This observation implies a tailored response to the environment by each individual bird, wherein particular sites became focal points in accordance with the changing seasons. These patterns highlight the individualised nature of site selection strategies, showcasing that each bird adopts a distinctive approach in navigating its environment. Possible factors contributing to these patterns include the emergence of seasonal foraging hotspots (Kimura et al, 2001), preferences for specific sites during breeding seasons (Berkunsky & Reboreda, 2009; Norton & DuVal, 2023), adaptive responses to environmental changes (Şekercioğlu et al, 2012), and the adoption of individualised strategies by individuals.

In contrast, for *Ortalis_4* and *Amazona_1* (2020) the proportion of revisits was influenced solely by site characteristics. This indicates a consistent preference for specific sites regardless of seasonal changes suggesting that these sites may offer distinct advantages, such as abundant food resources, suitable roosting sites with protection from predators (Conklin & Colwell, 2007; Puehringer-Sturmayr et al, 2023). Revisitation data can also provide insights into preferred site usage patterns. For example, *Ortalis_1*, *Ortalis_4*, and *Amazona_1* tended to use particular sites more frequently during the night, indicating that these sites are likely preferred roosting locations (Bracis et al, 2018). This behaviour could be driven by factors such as shelter from nocturnal predators, suitable roosting structures, or proximity to foraging areas during the day (Naniwadekar et al, 2022).

3.5.4 Implications of movement patterns for seed dispersal

The observed variations in movement patterns among the frugivorous bird species under study have profound implications for seed dispersal dynamics, shedding light on the delicate interactions between ecological strategies and the distribution of seeds in their respective habitats.

The extensive ranging behaviour exhibited by *Amazona* species, marked by significantly larger median and maximum movements, carries important ramifications for seed dispersal. This heightened mobility enhances the potential for long-distance seed dispersal (Tella et al, 2015; Tella et al, 2016), assuming that seeds remain intact through the digestive process. Ranging behaviour is a vital component for determining seed deposition (Stoner et al, 2007) and individuals that travel over larger areas are more likely to deposit seeds at greater distances from the parent trees. This not only contributes to a broader seed distribution but also helps prevent the clustering of seeds beneath perches. By reducing competition among closely packed seedlings and minimizing the risk of disease transmission, this dispersal strategy contributes to the overall health and resilience of the plant community (Fragoso et al, 2003; McConkey & Chivers, 2007; Karubian et al, 2012).

In contrast, the *Ramphastos* species exhibited a unique pattern of movement. While they had the largest median 2-hour step length, indicating occasional bursts of movement, their overall daily distances were lower than those of *Amazona*. This suggests that *Ramphastos* individuals may be less active throughout the day, possibly conserving energy for short bursts of high intensity foraging or movements at particular times of the day. The variable movement strategies within the *Ramphastos* group displayed important intra-specific differences; *Ramphastos_1*, exhibited much larger step lengths and daily distances when compared to its counterparts. This individual inhabited an area of forest with direct connectivity to the primary forest interior. The spatial proximity to critical habitats might provide *Ramphastos_1* with greater resources and foraging opportunities, potentially explaining its heightened activity levels. Another possibility could be that resources are reduced within these habitats. Greater species richness and abundance of other birds in forest habitats may increase competition for resources and increase the need for further travel (Moran & Catterall, 2014). Either way, this increased movement and potential utilisation of larger foraging areas may contribute to a more extensive distribution of seeds. The *Ramphastos*' ability to cover larger distances during foraging increases the likelihood of seed deposition in diverse locations, promoting a broader dispersion of plant species. This not only prevents localised clustering but also establishes connections between fragmented habitats, contributing to the overall resilience and adaptability of plant communities in the broader landscape (Mueller et al, 2014; Gonzalez-Varo et al, 2017; Costa et al, 2022).

Ortalis species, characterised by shorter steps and smaller daily distances, exhibit a preference for smaller, concentrated foraging areas. This behaviour is likely to result in the creation of smaller but denser seed shadows beneath their feeding sites (Kleyheeg et al, 2017). While this can contribute to localised seed dispersal and potentially act as a reservoir, it also has potential implications for seedling survival and competition, as seeds may be concentrated in smaller patches (Comita et al, 2014). Like *Ramphastos_1*, *Ortalis_4* displayed much larger step lengths and daily distances travelled compared to the other *Ortalis* individuals. This suggests that habitat connectivity, regardless of the species involved, can amplify movement, and enhance the potential for seed dispersal across broader areas (Şekercioğlu et al, 2015; Monteiro et al, 2022).

3.5.5 Caveats

One crucial caveat to consider is the relatively small sample sizes of the individuals tracked for each species, which may introduce bias into our interpretations. Small sample sizes can lead to skewed results, limiting the generalisability of our findings. This is particularly relevant when attempting to infer broader ecological patterns or behaviours from a limited dataset. While our study provides valuable insights into the movement patterns and home ranges of these species over an extended timeframe, the inherent limitations of our sample sizes necessitate caution in extrapolating these findings to the entire populations of these species. Further research with larger sample sizes is needed to validate and expand upon our observations, thereby enhancing the robustness and applicability of our conclusions.

However, our findings align closely with those of several previous studies, reinforcing the reliability and validity of our observations. This alignment provides confidence in the robustness of our conclusions regarding the movement behaviours and home range sizes of the frugivorous bird species under investigation.

Kays et al. (2011), whose study was conducted across the same local landscape, reported 95% kernel home ranges of between 19.9 to 88.8 Ha for *Ramphastos spp*, with minimum total distances moved per day ranging from 324 to 4891m. Similarly, Holbrook (2011) found an average home range of 86 Ha for *Ramphastos spp* and Jones (2017) calculated a 95% MCP home range between 10.1 to 166.1 Ha, with a mean of 61.7 ± 18.4 Ha. Our study's median daily distance for the same species was 2700m, and the 99% home range was between 24.6 – 114.9 Ha, demonstrating a remarkable consistency with these earlier studies.

Few studies exist of tracking *Ortalis spp*, but Navarro-López (2020) reported a KDE home range for plain chachalacas (*Ortalis vetula*) between 5 - 24.72 Ha. Our findings for grey-headed chachalacas showed a home range between 3.2 – 9.1 Ha, further supporting and validating our own results.

To our knowledge, there have been no tracking studies of red-lored amazons, however Bjork (2004) documented a MCP home range of 3-151 km² (300-15100 Ha) for mealy parrots (*Amazona farinose*) during the non-breeding season, with some individuals dispersing up to 90km away from their breeding locations for periods of 3-12 weeks before returning. Our results for a comparable *Amazona* species showed a home range of 858.4 – 12,548.6 Ha, with similar non-breeding season dispersal patterns observed in our study.

These comparisons underscore the reliability of our findings, despite the small sample size of our study. The consistency in home range sizes and movement patterns across various studies suggests that the ecological strategies and behaviours of these species are well-established and not isolated incidents.

One final caveat to consider is the duration of tracking data for *Amazona_1*, which covered two entire years, allowing for stark seasonal differences to emerge. While these differences were evident for this species, it remains to be seen whether similar patterns are present in the other species or if they exhibit distinct seasonal responses. This underscores the necessity of long-term monitoring to comprehensively understand and compare seasonal movement patterns among different bird species.

3.5.6 Conclusion

Our findings challenge the notion that body size alone determines movement behaviour and highlight the importance of considering additional factors such as wing morphology, ecological preferences, and seasonal variation in resources. Despite their similar body sizes, *Amazona*, *Ortalis* and *Ramphastos* species exhibit unique movement patterns and respond differently to seasonality and changing environmental conditions. The ability of these species to adapt and employ varied strategies in response to seasonality and resource availability showcases their resilience to an ever-changing environment. This adaptability is essential for the survival of frugivorous birds in a dynamic and resource-dependent tropical ecosystem. Future research should investigate the specific drivers behind their behaviours, such as resource availability, breeding activities, and habitat fragmentation, to gain a more comprehensive understanding of their role in shaping tropical ecosystems.

In conclusion, our study highlights the temporal flexibility and complexity of movement behaviours among frugivorous birds in response to changing seasonal conditions. While some species exhibit stable monthly range distributions, others show lagged responses to historical weather patterns, emphasising the need for adaptable strategies to track varying food resources. The contrasting responses of different species to seasonality underscore the intricate ecological interactions shaping their movement patterns and emphasise the importance of long-term monitoring in unravelling these patterns. Overall, this study contributes to our broader knowledge of avian frugivore ecology and highlights the importance of considering a holistic approach when studying the movement and behaviour of these bird species in tropical ecosystems. We also show how these divergent movement strategies among frugivorous bird species offer an understanding of their influence on seed dispersal. From promoting broad seed distribution to addressing issues of clustering and competition, the nuanced interplay of movement patterns can help contribute to the overall ecological resilience and diversity of plant communities in their respective habitats.

3.6 Supplementary material

Supplementary table 1. Deployment information for all individuals tracked during the duration of the study. Summary statistics of the median and maximum straight-line distance between 2-hour GPS locations for all individuals and for the median and maximum daily distances travelled using the straight-line distance between 2-hour GPS locations for all individuals. Home range estimates (in hectares, Ha) calculated using Continuous time movement models of all individuals tracked during the duration of the study and the percentage of overall home range used as a core area (50%)

	Tagging statistics			Movement statistics				Home range estimates (Ha)			
Species ID	Tag locations	Deployment dates	Tagging days	Med step length (m)	Max step length (m)	Med daily distance (m)	Max daily distance (m)	99%	95%	50%	Core use %
Ortalis_1	6,224	14/01/2022 – 10/08/2022	209	47.5	240.3	359.6	823.6	3.7	2.2	0.5	12.30%
Ortalis_2	660	14/01/2022 – 19/03/2022	65	34.8	210.4	280.3	693.6	3.2	1.7	0.3	10.90%
Ortalis_3	1,468	14/01/2022 – 09/08/2022	208	40	338.4	259.1	876.5	3.4	1.9	0.3	10.20%
Ortalis_4	1,457	28/01/2022 – 12/08/2022	197	59.5	528.7	408.9	1323.9	9.1	4.5	1.1	12.50%
Ramphastos_1	311	15/01/2022 – 09/02/2022	26	181.8	1010.3	1403.2	2771.2	114.9	57	15	13.10%
Ramphastos_2	813	22/02/2022 – 13/08/2022	173	117	632.6	497.3	1637.5	24.6	15.5	3.3	13.40%
Ramphastos_3	226	05/03/2022 – 09/06/2022	97	199.4	585.3	387.8	1787.6	43.1	26.6	6.7	15.50%
Amazona_1	39,001	17/03/2020 – 13/03/2020	727	134.8	10042.1	3264.8	13883.5	12548.6	4021	102.8	0.80%
Amazona_2	237	14/03/2020 – 20/03/2020	7	87.1	1888.1	1170.7	4182.5	858.4	407.1	85.7	10.00%

Supplementary table 2. Results of the LMM for *Ortalis* and *Ramphastos* monthly 99% home range estimates and their response to monthly rainfall, two-week rainfall lag & median monthly ODBA. Results of the GLM for *Amazona* monthly 99% home range estimates and their response to monthly rainfall, two-week rainfall lag & median monthly ODBA.

<i>Ortalis</i> 99% monthly home range size					
	Estimate	Std. Error	df	t value	Pr(> t)
Intercept	1.34285	0.18943	1.61212	7.089	0.0333
Rainfall lag	0.08919	0.06773	35.26493	1.317	0.1964
Rainfall	-0.05833	0.06867	35.12539	-0.849	0.4014
Median ODBA	0.34872	0.30945	36.73592	1.127	0.2671
(Median ODBA)^2	-0.24191	0.28728	36.78376	-0.842	0.4052
<i>Ramphastos</i> 99% monthly home range size					
Intercept	3.21626	0.29818	0.97261	10.786	0.0625
Rainfall lag	0.06667	0.07972	18.02639	0.836	0.4139
Rainfall	-0.02978	0.07974	18.03971	-0.373	0.7131
Median ODBA	-0.15158	0.3847	18.28986	-0.394	0.6981
(Median ODBA)^2	0.14052	0.38069	18.21455	0.369	0.7163
<i>Amazona</i> 99% monthly home range size					
Intercept	0.147197	0.004363	N/A	33.741	<2e-16
Rainfall lag	-0.007487	0.004862	N/A	-1.540	0.1385
Rainfall	-0.016212	0.00501	N/A	-3.236	0.00396
Median ODBA	0.007823	0.22508	N/A	0.348	0.73162
(Median ODBA)^2	-0.006998	0.22912	N/A	-0.305	0.76304

Supplementary table 3. Results of the LMM for *Ortalis* and *Ramphastos* weekly 99% home range estimates and their response to monthly rainfall, two-week rainfall lag & median monthly ODBA. Results of the GLM for *Amazona* weekly 99% home range estimates and their response to monthly rainfall, two-week rainfall lag & median monthly ODBA.

<i>Ortalis</i> 99% weekly home range size					
	Estimate	Std. Error	df	t value	Pr(> t)
Intercept	1.13306	0.1334	2.91082	8.493	0.00384
Rainfall lag	0.09003	0.04452	142.77778	2.022	0.04503
Rainfall	0.0145	0.04414	141.85157	0.329	0.74294
Median ODBA	0.51816	0.19283	120.18029	2.687	0.00823
(Median ODBA)²	-0.38145	0.17752	139.27928	-2.149	0.03338
<i>Ramphastos</i> 99% weekly home range size					
Intercept	3.46919	0.42773	1.82439	8.111	0.0193
Rainfall lag	-0.04003	0.072	66.2879	-0.556	0.5801
Rainfall	0.04118	0.06929	65.86146	0.594	0.5543
Median ODBA	0.03381	0.17786	65.01682	0.19	0.8498
(Median ODBA)²	0.07814	0.17733	64.99463	0.441	0.6609
<i>Amazona</i> 99% weekly home range size					
Intercept	0.155773	0.002674	N/A	58.252	<2e-16
Rainfall lag	-0.007843	0.002831	N/A	-2.770	0.0066
Rainfall	-0.006412	0.002771	N/A	-2.314	0.0226
Median ODBA	0.019936	0.011847	N/A	1.683	0.0953
(Median ODBA)²	-0.01848	0.01203	N/A	-1.536	0.1275

Supplementary table 4. Results of the GLMM for *Ortalis* and *Ramphastos* weekly seasonal range overlap and the LM for *Amazona* weekly seasonal range overlap and its response to seasonality and the absolute difference in rainfall. Reference level of season type is set to the overlap between two dry seasons.

<i>Ortalis</i> seasonal overlap per season type				
	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.6122	0.1114	14.470	< 2e-16
Rainfall difference	0.0005	0.0003	1.589	0.1122
Dry-Inter	0.1022	0.0486	2.103	0.0354
Dry-Wet	-0.0808	0.0488	-1.654	0.0981
Inter-Inter	0.2485	0.0558	4.448	8.66e-6
Inter-Wet	0.0738	0.0471	1.566	0.1173
Wet-Wet	0.0596	0.0499	1.194	0.2325
<i>Ramphastos</i> seasonal overlap per season type				
Intercept	1.3757	0.1342	10.251	< 2e-16
Rainfall difference	-0.0003	0.0006	-0.560	0.5753
Dry-Inter	-0.2390	0.1399	-1.708	0.0876
Dry-Wet	-0.2036	0.1401	-1.453	0.1462
Inter-Inter	-0.2116	0.1414	-1.497	0.1344
Inter-Wet	-0.3065	0.1339	-2.289	0.0221
Wet-Wet	-0.0002	0.1380	-0.002	0.9987
<i>Amazona</i> seasonal overlap per season type				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	5.83e-01	1.28e-02	45.549	< 2e-16
Rainfall difference	-8.48e-04	8.72e-05	-9.721	< 2e-16
Dry-Inter	-4.55e-02	1.50e-02	-3.047	0.00232
Dry-Wet	-6.37e-02	1.53e-02	-4.16	3.23e-05
Inter-Inter	-2.97e-02	1.59e-02	-1.872	0.06119
Inter-Wet	-4.07e-02	1.44e-02	-2.818	0.00485

Supplementary table 5. Results for the analysis of deviance for *Ortalis* and *Ramphastos* and the analysis of variance for *Amazona* weekly home range overlap and its response to seasonality and the absolute difference in rainfall.

<i>Ortalis</i> seasonal overlap - Analysis of Deviance Table (Type III Wald chisquare tests)			
	Chisq	Df	Pr(>Chisq)
Intercept	209.3858	1	< 2.2e-16
Rainfall difference	2.5236	1	0.1122
Season overlaps	65.4582	5	9.004e-13

<i>Ramphastos</i> seasonal overlap - Analysis of Deviance Table (Type III Wald chisquare tests)			
Intercept	105.0834	1	< 2.2e-16
Rainfall difference	0.3139	1	0.5753
Season overlaps	25.6952	5	0.0001

<i>Amazona</i> seasonal overlap – ANOVA table (Type III tests)				
	Sum sq	Df	F value	Pr(>F)
Intercept	126.75	1	2074.683	< 2.2e-16
Rainfall difference	5.77	1	94.4963	< 2.2e-16
Season overlaps	1.24	5	4.0433	0.001153

Supplementary table 6. Results from the Tukey Post-hoc test to determine which seasonal overlaps significantly differ when predicting *Ortalis* weekly home range.

<i>Ortalis</i> Post-hoc Tukey method						
Contrasts	Odds.ratio	SE	Df	null	z.ratio	p.value
Dry_Dry / Dry_Inter	0.903	0.0439	Inf	1	-2.103	0.2854
Dry_Dry / Dry_Wet	1.084	0.053	Inf	1	1.654	0.5622
Dry_Dry / Inter_Inter	0.78	0.0436	Inf	1	-4.448	0.0001
Dry_Dry / Inter_Wet	0.929	0.0438	Inf	1	-1.566	0.6209
Dry_Dry / Wet_Wet	0.942	0.0471	Inf	1	-1.194	0.84
Dry_Inter / Dry_Wet	1.201	0.0433	Inf	1	5.072	<.0001
Dry_Inter / Inter_Inter	0.864	0.04	Inf	1	-3.157	0.0198
Dry_Inter / Inter_Wet	1.029	0.0358	Inf	1	0.816	0.9648
Dry_Inter / Wet_Wet	1.043	0.0404	Inf	1	1.099	0.882
Dry_Wet / Inter_Inter	0.719	0.0322	Inf	1	-7.361	<.0001
Dry_Wet / Inter_Wet	0.857	0.0274	Inf	1	-4.841	<.0001
Dry_Wet / Wet_Wet	0.869	0.0316	Inf	1	-3.858	0.0016
Inter_Inter / Inter_Wet	1.191	0.0523	Inf	1	3.978	0.001
Inter_Inter / Wet_Wet	1.208	0.0569	Inf	1	4.008	0.0009
Inter_Wet / Wet_Wet	1.014	0.0361	Inf	1	0.398	0.9987

Supplementary table 7. Results from the Tukey Post-hoc test to determine which seasonal overlaps significantly differ when predicting *Ramphastos* weekly home range.

<i>Ramphastos</i> Post-hoc Tukey method						
Contrasts	Odds.ratio	SE	Df	null	z.ratio	p.value
Dry_Dry / Dry_Inter	1.27	0.1778	Inf	1	1.708	0.5263
Dry_Dry / Dry_Wet	1.226	0.1718	Inf	1	1.453	0.6942
Dry_Dry / Inter_Inter	1.236	0.1748	Inf	1	1.497	0.6662
Dry_Dry / Inter_Wet	1.359	0.182	Inf	1	2.289	0.1983
Dry_Dry / Wet_Wet	1	0.1381	Inf	1	0.002	1
Dry_Inter / Dry_Wet	0.965	0.0794	Inf	1	-0.43	0.9981
Dry_Inter / Inter_Inter	0.973	0.083	Inf	1	-0.321	0.9995
Dry_Inter / Inter_Wet	1.07	0.0764	Inf	1	0.945	0.9347
Dry_Inter / Wet_Wet	0.788	0.0624	Inf	1	-3.014	0.031
Dry_Wet / Inter_Inter	1.008	0.0837	Inf	1	0.097	1
Dry_Wet / Inter_Wet	1.108	0.0736	Inf	1	1.55	0.632
Dry_Wet / Wet_Wet	0.816	0.0614	Inf	1	-2.702	0.0748
Inter_Inter / Inter_Wet	1.1	0.0795	Inf	1	1.313	0.7782
Inter_Inter / Wet_Wet	0.809	0.065	Inf	1	-2.634	0.0891
Inter_Wet / Wet_Wet	0.736	0.0472	Inf	1	-4.775	<.0001

Supplementary table 8. Results from the Tukey Post-hoc test to determine which seasonal overlaps significantly differ when predicting *Amazona* weekly home range.

<i>Amazona</i> Post-hoc Tukey method					
Contrasts	Estimate	SE	Df	t.ratio	p.value
Dry_Dry / Dry_Inter	0.04554	0.01495	5879	3.047	0.0281
Dry_Dry / Dry_Wet	0.06373	0.01532	5879	4.16	0.0005
Dry_Dry / Inter_Inter	0.02972	0.01587	5879	1.872	0.4193
Dry_Dry / Inter_Wet	0.04069	0.01444	5879	2.818	0.0548
Dry_Dry / Wet_Wet	0.03751	0.01543	5879	2.43	0.146
Dry_Inter / Dry_Wet	0.01819	0.01073	5879	1.695	0.5349
Dry_Inter / Inter_Inter	-0.01581	0.01202	5879	-1.316	0.7763
Dry_Inter / Inter_Wet	-0.00485	0.00979	5879	-0.496	0.9963
Dry_Inter / Wet_Wet	-0.00803	0.01122	5879	-0.716	0.9801
Dry_Wet / Inter_Inter	-0.034	0.01208	5879	-2.816	0.0551
Dry_Wet / Inter_Wet	-0.02304	0.00953	5879	-2.417	0.1503
Dry_Wet / Wet_Wet	-0.02622	0.01102	5879	-2.379	0.1636
Inter_Inter / Inter_Wet	0.01096	0.01121	5879	0.977	0.9252
Inter_Inter / Wet_Wet	0.00778	0.01248	5879	0.624	0.9893
Inter_Wet / Wet_Wet	-0.00318	0.01025	5879	-0.31	0.9996

Supplementary table 9. Results of the GLM for *Ortalis_1* proportion of revisitations and its response to seasonality and individual sites. Reference level of season type and site is set to dry and site 1.

<i>Ortalis_1</i> seasonal site revisitation				
	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-1.339	0.508	-2.642	0.012
Season_Inter	-0.109	0.610	-0.179	0.859
Season_Wet	0.094	0.631	0.149	0.882
Site_2	0.111	0.706	0.157	0.876
Site_3	-0.247	0.747	-0.331	0.743
Site_4	0.919	0.659	1.394	0.172
Season_Inter:Site_2	0.306	0.839	0.365	0.718
Season_Wet:Site_2	-0.065	0.881	-0.073	0.942
Season_Inter:Site_3	0.623	0.874	0.713	0.480
Season_Wet:Site_3	0.525	0.906	0.579	0.566
Season_Inter:Site_4	-0.355	0.796	-0.446	0.658
Season_Wet:Site_4	-0.669	0.836	-0.800	0.429

Supplementary table 10. Results for the analysis of deviance for *Ortalis_1* proportional revisitation rate and the response to seasonality and specific sites.

<i>Ortalis_1</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	0.162	2	0.922
Site	3.626	3	0.305
Season:Site	2.527	6	0.865

Supplementary table 11. Results of the GLM for *Ortalis_3* proportion of revisitations and its response to seasonality and individual sites. Reference level of season type and site is set to dry and site 1.

<i>Ortalis_3</i> seasonal site revisitations				
	Estimate	Std.Error	Z value	Pr(> z)
(Intercept)	-1.633	0.104	-15.732	< 2e-16
Season_Inter	0.180	0.149	1.209	0.227
Season_Wet	0.093	0.144	0.644	0.519
Site_2	0.114	0.144	0.932	0.351
Site_3	0.439	0.138	3.186	0.001
Site_4	-0.989	0.185	-5.358	8.42e-08
Site_5	0.163	0.143	1.141	0.254
Site_6	0.021	0.146	0.146	0.884
Season_Inter:Site_2	-0.157	0.208	-0.752	0.452
Season_Wet:Site_2	-0.226	0.203	-1.115	0.265
Season_Inter:Site_3	-0.168	0.200	-0.840	0.401
Season_Wet:Site_3	-0.020	0.192	-0.102	0.919
Season_Inter:Site_4	-0.458	0.284	-1.612	0.107
Season_Wet:Site_4	-0.840	0.298	-2.814	0.005
Season_Inter:Site_5	-0.054	0.206	-0.261	0.794
Season_Wet:Site_5	0.094	0.197	0.476	0.634
Season_Inter:Site_6	-0.466	0.219	-2.125	0.034
Season_Wet:Site_6	-0.114	0.205	-0.555	0.579

Supplementary table 12. Results for the analysis of deviance for *Ortalis_3* proportional revisitation rates and the response to seasonality and specific sites.

<i>Ortalis_3</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	1.465	2	0.481
Site	81.863	5	13.42e-16
Season:Site	17.661	10	0.061

Supplementary table 13. Results for *Ortalis_3* of the Tukey Post-hoc test to determine how proportional revisitation rates are predicted by the interactions between specific sites and seasonality.

<i>Ortalis_3</i> Post-hoc Tukey method - seasonal contrasts per site						
Contrasts	Odds ratio	Std.Error	df	null	z.ratio	Pr(> z)
Site 1						
Dry - Inter	0.835	0.124	Inf	1	-1.209	0.446
Dry - Wet	0.911	0.131	Inf	1	-0.644	0.796
Inter - Wet	1.091	0.159	Inf	1	0.597	0.822
Site 2						
Dry - Inter	0.977	0.143	Inf	1	-0.158	0.986
Dry - Wet	1.143	0.163	Inf	1	0.934	0.619
Inter - Wet	1.169	0.174	Inf	1	1.054	0.543
Site 3						
Dry - Inter	0.988	0.132	Inf	1	-0.087	0.996
Dry - Wet	0.929	0.118	Inf	1	-0.578	0.832
Inter - Wet	0.940	0.124	Inf	1	-0.466	0.887
Site 4						
Dry - Inter	1.320	0.319	Inf	1	1.149	0.484
Dry - Wet	2.111	0.552	Inf	1	2.858	0.012
Inter - Wet	1.599	0.453	Inf	1	1.657	0.222
Site 5						
Dry - Inter	0.882	0.126	Inf	1	-0.885	0.650
Dry - Wet	0.830	0.112	Inf	1	-1.383	0.350
Inter - Wet	0.941	0.130	Inf	1	-0.438	0.900
Site 6						
Dry - Inter	1.331	0.214	Inf	1	1.775	0.178
Dry - Wet	1.021	0.149	Inf	1	0.144	0.989
Inter - Wet	0.767	0.124	Inf	1	-1.646	0.227

Supplementary table 14. Results of the GLM for *Ortalis_4* proportion of revisitations and its response to seasonality and individual sites. Reference level of season type and site is set to dry and site 1.

<i>Ortalis_4</i> seasonal site revisitations				
	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-1.900	0.219	-8.650	2.63e-12
Season_Inter	-0.665	0.400	-1.660	0.102
Season_Wet	0.067	0.302	0.222	0.825
Site_2	0.473	0.288	1.641	0.106
Site_3	0.407	0.291	1.401	0.166
Site_4	0.201	0.300	0.671	0.505
Site_5	0.140	0.303	0.463	0.645
Site_6	0.235	0.298	0.787	0.434
Site_7	-1.576	0.485	-3.250	0.002
Season_Inter:Site_2	0.479	0.499	0.953	0.344
Season_Wet:Site_2	-0.180	0.402	-0.447	0.656
Season_Inter:Site_3	0.427	0.505	0.846	0.401
Season_Wet:Site_3	-0.273	0.408	-0.669	0.506
Season_Inter:Site_4	0.844	0.503	1.679	0.098
Season_Wet:Site_4	-0.100	0.416	-0.239	0.812
Season_Inter:Site_5	1.043	0.500	2.085	0.041
Season_Wet:Site_5	-0.006	0.417	-0.014	0.989
Season_Inter:Site_6	0.551	0.511	1.079	0.285
Season_Wet:Site_6	-0.085	0.413	-0.205	0.838
Season_Inter:Site_7	1.766	0.665	2.654	0.010
Season_Wet:Site_7	0.772	0.600	1.287	0.203

Supplementary table 15. Results for the analysis of deviance for *Ortalis_4* proportional revisitation rates and the response to seasonality and specific sites.

<i>Ortalis_4</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	4.160	2	0.125
Site	33.565	6	8.162e-6
Season:Site	12.893	12	0.377

Supplementary table 16. Results of the GLM for *Ramphastos_2* proportion of revisitations and its response to seasonality and individual sites. Reference level of season type and site is set to dry and site 1.

<i>Ramphastos_2</i> seasonal site revisitations				
	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-1.643	0.193	-8.511	1.49e-11
Season_Inter	-0.023	0.272	-0.086	0.932
Season_Wet	-0.111	0.255	-0.434	0.666
Site_2	0.219	0.264	0.830	0.410
Site_3	0.159	0.266	0.599	0.552
Site_4	0.098	0.269	0.363	0.718
Site_5	-0.017	0.274	-0.062	0.951
Site_6	-0.319	0.290	-1.100	0.276
Season_Inter:Site_2	-0.018	0.372	-0.049	0.961
Season_Wet:Site_2	-0.030	0.349	-0.085	0.932
Season_Inter:Site_3	0.056	0.373	0.149	0.882
Season_Wet:Site_3	-0.211	0.357	-0.590	0.558
Season_Inter:Site_4	0.383	0.369	1.037	0.304
Season_Wet:Site_4	0.269	0.349	0.771	0.444
Season_Inter:Site_5	-0.338	0.399	-0.848	0.400
Season_Wet:Site_5	0.217	0.357	0.608	0.546
Season_Inter:Site_6	-0.080	0.412	-0.193	0.848
Season_Wet:Site_6	0.440	0.371	1.185	0.241

Supplementary table 17. Results for the analysis of deviance for *Ramphastos_2* proportional revisitation rates and the response to seasonality and specific sites.

<i>Ramphastos_2</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	0.219	2	0.896
Site	4.595	5	0.467
Season:Site	11.580	10	0.314

Supplementary table 18. Results of the GLM for *Ramphastos_3* proportion of revisitations and its response to seasonality and individual sites. Reference level of season type and site is set to dry and site 1.

<i>Ramphastos_3</i> seasonal site revisitations				
	Estimate	Std.Error	Z value	Pr(> z)
(Intercept)	-2.3026	0.524	-4.391	1.13e-05
Season_Inter	1.433	0.554	2.585	0.010
Season_Wet	0.916	0.574	1.597	0.110
Site_2	0.457	0.684	0.668	0.504
Site_3	1.434	0.620	2.313	0.021
Site_4	0.945	0.644	1.467	0.142
Site_5	1.322	0.624	2.118	0.034
Season_Inter:Site_2	-1.095	0.739	-1.483	0.138
Season_Wet:Site_2	-1.131	0.780	-1.449	0.147
Season_Inter:Site_3	-1.499	0.671	-2.236	0.025
Season_Wet:Site_3	-1.434	0.702	-2.042	0.041
Season_Inter:Site_4	-2.422	0.729	-3.324	0.001
Season_Wet:Site_4	-0.740	0.719	-1.028	0.304
Season_Inter:Site_5	-2.153	0.688	-3.129	0.002
Season_Wet:Site_5	-1.023	0.700	-1.461	0.144

Supplementary table 19. Results for the analysis of deviance for *Ramphastos_3* proportional revisitation rates and the response to seasonality and specific sites.

<i>Ramphastos_3</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	9.844	2	0.007
Site	8.757	4	0.067
Season:Site	32.03	8	9.20e-05

Supplementary table 20. Results for *Ramphastos_3* of the Tukey Post-hoc test to determine how proportional revisitation rates are predicted by the interactions between specific sites and seasonality.

<i>Ramphastos_3</i> Post-hoc Tukey method - seasonal contrasts per site						
Contrasts	Odds ratio	Std.Error	df	null	z.ratio	Pr(> z)
Site 1						
Dry - Inter	0.239	0.132	Inf	1	-2.585	0.026
Dry - Wet	0.400	0.230	Inf	1	-1.597	0.247
Inter - Wet	1.676	0.493	Inf	1	1.755	0.185
Site 2						
Dry - Inter	0.713	0.348	Inf	1	-0.692	0.768
Dry - Wet	1.239	0.655	Inf	1	0.405	0.914
Inter - Wet	1.736	0.631	Inf	1	1.519	0.282
Site_3						
Dry - Inter	1.068	0.403	Inf	1	0.175	0.983
Dry - Wet	1.677	0.678	Inf	1	1.279	0.407
Inter - Wet	1.570	0.464	Inf	1	1.525	0.279
Site 4						
Dry - Inter	2.690	1.273	Inf	1	2.091	0.091
Dry - Wet	0.838	0.363	Inf	1	-0.407	0.913
Inter - Wet	0.312	0.113	Inf	1	-3.202	0.004
Site_5						
Dry - Inter	2.054	0.837	Inf	1	1.767	0.181
Dry - Wet	1.112	0.446	Inf	1	0.265	0.962
Inter - Wet	0.541	0.169	Inf	1	-1.965	0.121

Supplementary table 21. Results of the GLM for *Amazona_1* proportion of revisitations and its response to seasonality and individual sites across the year of 2020. Reference level of season type and site is set to dry and site 1.

<i>Amazona_2020</i> seasonal site revisitations				
	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-1.238	0.407	-3.045	0.004
Season_Inter	-0.642	0.478	-1.343	0.185
Season_Wet	-0.223	0.490	-0.456	0.651
Site_2	-0.581	0.637	-0.913	0.366
Site_3	0.579	0.542	1.070	0.290
Site_4	-1.620	0.853	-1.901	0.063
Site_5	-0.614	0.641	-0.958	0.343
Site_6	-1.620	0.853	-1.901	0.063
Site_7	-1.698	0.876	-1.939	0.058
Season_Inter:Site_2	0.672	0.727	0.925	0.360
Season_Wet:Site_2	0.530	0.747	0.710	0.481
Season_Inter:Site_3	-0.110	0.635	-0.173	0.863
Season_Wet:Site_3	-0.652	0.669	-0.975	0.335
Season_Inter:Site_4	1.758	0.921	1.910	0.062
Season_Wet:Site_4	0.835	0.967	0.864	0.392
Season_Inter:Site_5	0.744	0.730	1.040	0.313
Season_Wet:Site_5	0.634	0.749	0.847	0.401
Season_Inter:Site_6	1.388	0.931	1.491	0.142
Season_Wet:Site_6	0.817	0.968	0.845	0.402
Season_Inter:Site_7	1.619	0.948	1.709	0.094
Season_Wet:Site_7	0.611	1.007	0.607	0.546

Supplementary table 22. Results for the analysis of deviance for *Amazona_1* proportional revisitation rate and the response to seasonality and specific sites across the year of 2020.

<i>Amazona_2020</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	2.179	2	0.320
Site	18.994	6	0.004
Season:Site	14.762	12	0.255

Supplementary table 23. Results of the GLM for *Amazona_1* proportion of revisitations and its response to seasonality and individual sites across the year of 2021. Reference level of season type and site is set to dry and site 1.

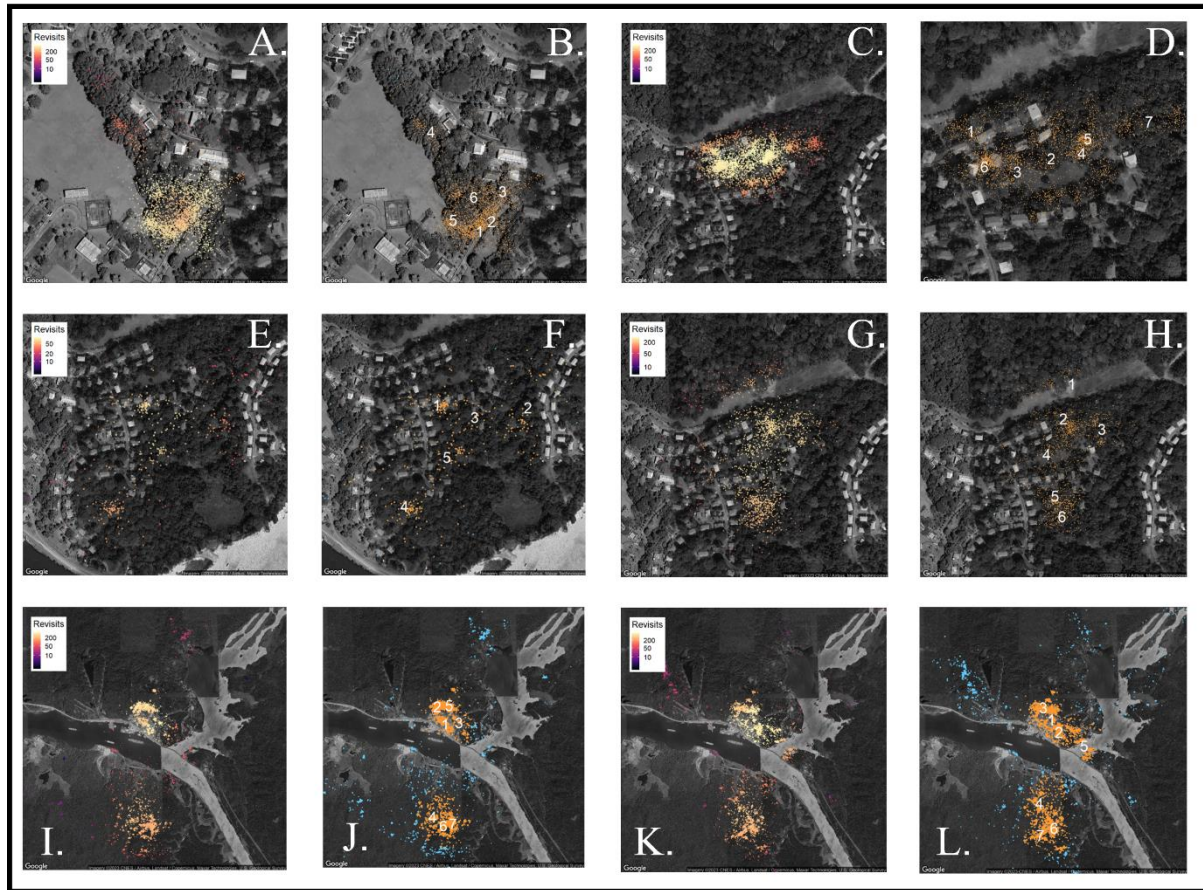
<i>Amazona_2021</i> seasonal site revisitations				
	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-1.103	0.228	-4.841	8.72e-6
Season_Inter	0.118	0.326	0.361	0.719
Season_Wet	-0.358	0.281	-1.272	0.208
Site_2	0.336	0.318	1.059	0.294
Site_3	-0.087	0.334	-0.261	0.795
Site_4	-1.589	0.480	-3.309	0.002
Site_5	-0.394	0.351	-1.124	0.265
Site_6	-3.222	0.936	-3.443	0.001
Site_7	-3.787	1.219	-3.107	0.003
Season_Inter:Site_2	-0.704	0.471	-1.495	0.140
Season_Wet:Site_2	-0.079	0.391	-0.203	0.840
Season_Inter:Site_3	-1.249	0.547	-2.285	0.026
Season_Wet:Site_3	-0.298	0.419	-0.711	0.479
Season_Inter:Site_4	0.385	0.636	0.606	0.547
Season_Wet:Site_4	1.177	0.544	2.164	0.034
Season_Inter:Site_5	-0.384	0.514	-0.747	0.458
Season_Wet:Site_5	-0.645	0.461	-1.397	0.167
Season_Inter:Site_6	2.100	1.021	2.056	0.044
Season_Wet:Site_6	2.950	0.968	3.047	0.003
Season_Inter:Site_7	2.302	1.300	1.770	0.082
Season_Wet:Site_7	3.421	1.245	2.748	0.008

Supplementary table 24. Results for the analysis of deviance for *Amazona_1* proportional revisitation rate and the response to seasonality and specific sites across the year of 2021.

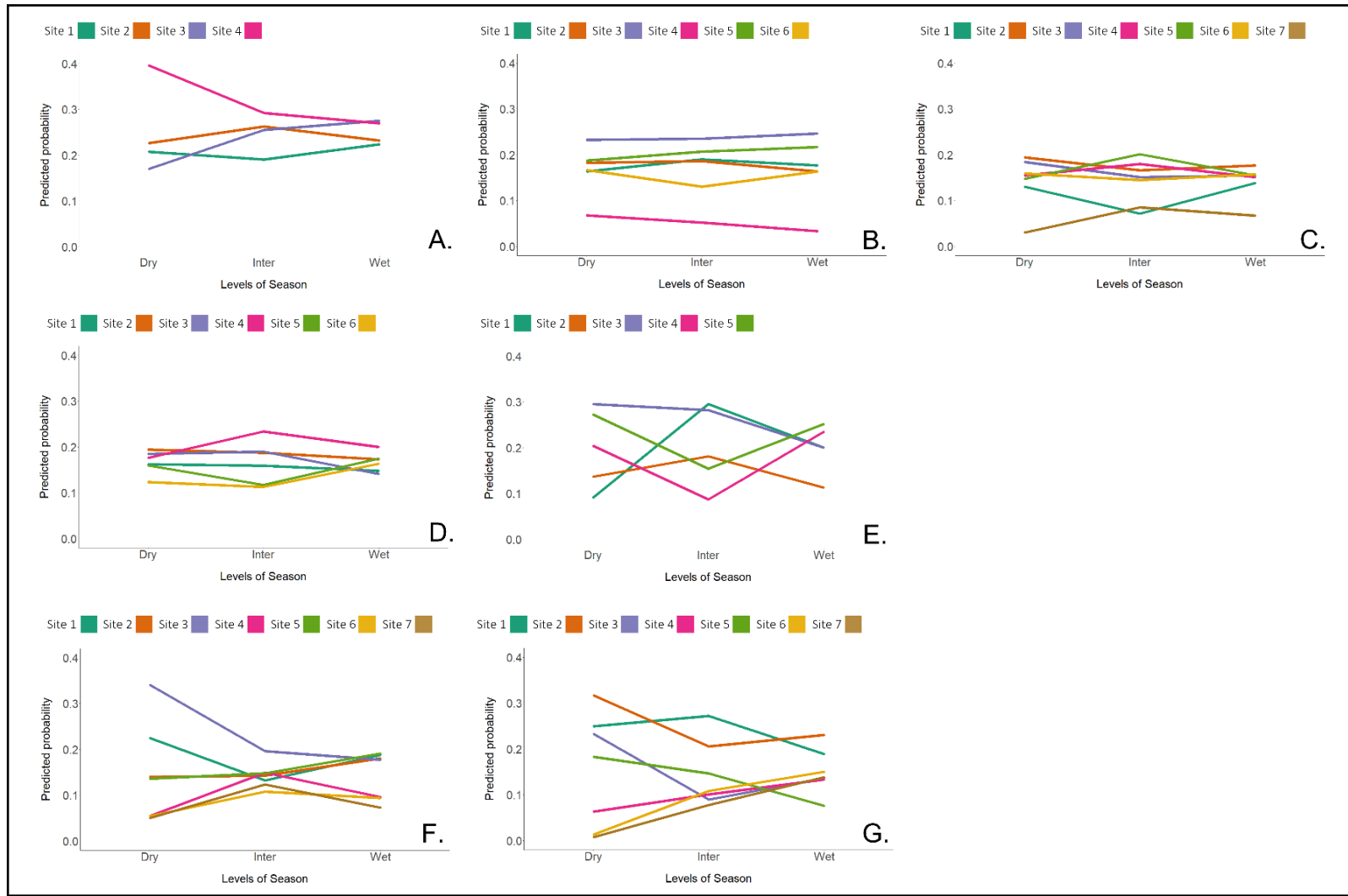
<i>Amazona_2021</i> Analysis of deviance table (Type III tests)			
	LR Chisq	Df	Pr(> z)
Season	3.332	2	0.189
Site	81.956	6	1.408e-15
Season:Site	62.376	12	8.298e-9

Supplementary table 25. Results of the Tukey Post-hoc test for *Amazona_1* to determine how proportional revisitation rates are predicted by the interactions between specific sites and seasonality across the year of 2021.

<i>Amazona_2021</i> Post-hoc Tukey method - seasonal contrasts per site						
Contrasts	Odds ratio	Std.Error	df	null	z.ratio	Pr(> z)
Site 1						
Dry - Inter	0.889	0.290	Inf	1	-0.361	0.931
Dry - Wet	1.430	0.402	Inf	1	1.272	0.411
Inter - Wet	1.609	0.460	Inf	1	1.663	0.220
Site 2						
Dry - Inter	1.798	0.612	Inf	1	1.727	0.195
Dry - Wet	1.548	0.421	Inf	1	1.607	0.243
Inter - Wet	0.861	0.260	Inf	1	-0.496	0.873
Site 3						
Dry - Inter	3.100	1.360	Inf	1	2.579	0.027
Dry - Wet	1.927	0.600	Inf	1	2.108	0.088
Inter - Wet	0.622	0.257	Inf	1	-1.152	0.482
Site 4						
Dry - Inter	0.605	0.330	Inf	1	-0.922	0.626
Dry - Wet	0.441	0.205	Inf	1	-1.760	0.184
Inter - Wet	0.729	0.289	Inf	1	-0.796	0.705
Site 5						
Dry - Inter	1.308	0.518	Inf	1	0.670	0.781
Dry - Wet	2.723	0.997	Inf	1	2.738	0.017
Inter - Wet	2.088	0.807	Inf	1	1.904	0.136
Site 6						
Dry - Inter	0.109	0.105	Inf	1	-2.292	0.057
Dry - Wet	0.075	0.069	Inf	1	-2.798	0.014
Inter - Wet	0.687	0.263	Inf	1	-0.980	0.590
Site 7						
Dry - Inter	0.089	0.112	Inf	1	-1.922	0.132
Dry - Wet	0.047	0.057	Inf	1	-2.526	0.031
Inter - Wet	0.525	0.227	Inf	1	-1.487	0.297



Supplementary figure 1A & B. GPS locations of *Ortalis_3* clustered into six separate sites using a radius of 65m and revisit threshold of >50 revisits. C & D. GPS locations of *Ortalis_4* clustered into seven separate sites using a radius of 50m and revisit threshold of >50 revisits. E & F. GPS locations of *Ramphastos_3* clustered into 5 separate sites using a radius of 135m and revisit threshold of >20 revisits. G & H. GPS locations of *Ramphastos_2* clustered into six separate sites using a radius of 125m and revisit threshold of >100 revisits. I & J. GPS locations of *Amazona_1* (subset by 2020 data) clustered into 7 separate sites using a radius of 500m and revisit threshold of >150 revisits. K & L. GPS locations of *Amazona_1* (subset by 2021 data) clustered into seven separate sites using a radius of 500m and revisit threshold of >150 revisits.



Supplementary figure 2. Interaction plots from individual GLMs, depicting the probability of revisitations to specific sites during different seasons (A - *Ortalis_1*, B - *Ortalis_3*, C - *Ortalis_4*, D - *Ramphastos_2*, E - *Ramphastos_3*, F - *Amazona_1* 2020, G - *Amazona_1* 2021).

**Chapter 4: Unravelling the dietary
composition and interaction networks of
avian frugivores in Central Panama's
tropical forests**

4.1 Abstract

Mutualistic interactions are fundamental to ecological networks, shaping the structure and functioning of natural communities. Frugivore-mediated interactions, specifically seed dispersal networks, play a crucial role in ecosystem functioning at the landscape scale. Given that almost 90% of tropical plants rely on animal-mediated seed dispersal, establishing comprehensive interaction networks within undisturbed tropical forest ecosystems provides a baseline for assessing alterations in seed dispersal services resulting from shifts in land use change or climate change, or changes in animal community composition or behaviour. Investigating the dietary composition of frugivores offers insights into community structure, niche specialisation, and the intricate interactions shaping ecosystems. Despite advancements in tracking methodologies, studying frugivory interactions remains a challenge, which is why this study employs DNA metabarcoding to construct a comprehensive interaction network in Central Panama on the dietary habits of frugivorous birds. We found significant differences in diet composition between different frugivores based on their morphological traits and proportion of frugivory in their diets. We explore the roles of different species in the network and discuss the impact that non-native plant species have on the overall network structure. The findings offer valuable insights into the complex dynamics of frugivore networks, emphasising their role in maintaining ecosystem balance and resilience, even in the face of anthropogenic influences.

4.2 Introduction

Trophic interactions, the exchange of nutrients and energy between organisms within an ecosystem, underpin ecological networks (Clare, 2014). These relationships govern the flow of nutrients and energy, and ultimately shape the structure and functioning of natural communities. The dietary composition of key species can provide an insight into a community's structure and identifies specific roles and niche specialisation, ultimately generating a comprehensive understanding of the complex interactions that shape an ecosystem. (Kartzinel & Pringle, 2020).

Among the numerous interactions that occur in ecosystems, frugivory, the consumption of fruits by animals, is a pivotal ecological process linking plants and animals in a mutually beneficial relationship (Jordano, 1987). Given that almost 90% of tropical plants rely on animal-mediated seed dispersal (Fleming et al, 1987), establishing comprehensive interaction networks within undisturbed tropical forest ecosystems provides a baseline for assessing alterations in seed dispersal services resulting from shifts in land use change or climate change, or changes in animal community composition or behaviour (Bovo et al, 2018). Characterising the dietary composition of frugivorous animals enables us to understand which fruiting plant species provide food resources to which animal species and, reciprocally, the seed dispersal services that those animals provide. In this way frugivory interactions provide a unique window into understanding the complex dynamics of ecosystems. Such insights are

invaluable for understanding the relationships that underpin the health and resilience of tropical ecosystems.

Trophic interactions can provide key information for informing conservation strategies. Investigating dietary composition plays a crucial role in identifying and mitigating instances of human-wildlife conflicts and evaluating the ecological impact of introduced species (Ando et al, 2013; Forian-Wiart et al, 2018; Moorhouse-Gann et al, 2018). For example, by analysing the diet composition of predators, such as eagles (McPherson et al, 2016), researchers can determine the specific prey items being consumed, providing a valuable tool to ascertain whether local people's livestock are being targeted and facilitating the implementation of targeted conservation measures to mitigate human-wildlife conflicts. An understanding of seed dispersal networks can be pivotal for making well-informed decisions regarding ecosystem restoration, enabling restoration practitioners to understand which animal species are critical to seed dispersal and so key to initiating vegetation recovery (Vizentin-Bugoni et al, 2022). Frugivore species with highly specialised niches and fragile interaction networks – i.e. species that eat and disperse a small and specialised group of plant species – can be prioritised through targeted conservation efforts (Clare, 2014).

In tropical environments, birds are a key taxon within frugivore networks, playing a pivotal role in shaping ecological interactions. Previous network analyses have illuminated the intricate patterns of frugivory among avian species, revealing interactions influenced by spatial and temporal variations in resource availability and consumer preferences (Cholewa & Wesołowski, 2011; Shutt et al, 2020). Generalist avian frugivores, in particular, exhibit diverse dietary patterns that encompass a broad range of fruiting plant species (Palacio et al, 2016). Moreover, large-bodied birds often emerge as central figures in frugivore networks due to their capacity to cover extensive foraging ranges, accessing a diverse array of fruiting trees and plants (Naniwadeker et al, 2019). The pivotal role of large birds in seed dispersal is amplified by their ability to consume and transport larger fruits, facilitating the dispersal of seeds across greater distances and thereby contributing significantly to the maintenance of plant diversity and ecosystem health.

Frugivore-mediated mutualistic interactions, such as seed dispersal networks, are pivotal for ecosystem functioning at the landscape-scale (Escribano-Avila et al, 2018). Landscape configuration significantly shapes species richness and interaction links among taxa, for example the presence of large, continuous forest fragments can increase species richness (Hanski et al, 2013). These fragments act as reservoirs of biodiversity, providing stable habitats that can support diverse faunal and floral communities. The interconnected nature of these fragments facilitates the movement of species, promoting gene flow and enhancing ecological resilience (Mueller et al, 2014). Furthermore, the presence of such undisturbed expanses serves as a critical determinant for maintaining the integrity of interaction networks,

particularly those involved in seed dispersal. Habitat fragmentation can disrupt these networks, leading to cascading effects on vital ecosystem services (Bello et al, 2015; Schleuning et al, 2015). For instance, disturbance can alter seed dispersal networks, with knock-on impacts for plant reproduction, seedling distribution and plant communities (Galetti et al, 2013; Kurten, 2013). Species-specific responses to habitat fragmentation, depending on life-history traits, introduce further complexity to these interactions, whereby large-bodied frugivores are critical dispersers of large-seeded plant species but tend to be most impacted by disturbance (Mahoney et al, 2018). Therefore, loss of large frugivores can result in poor regeneration of large-seeded plants with long-term implications for plant community structure (Bello et al, 2015).

Not all species in frugivory networks play equal roles in sustaining community stability. Keystone species, characterised by their disproportionate impact on plant distribution and recruitment relative to abundance, are pivotal for network structure and ecosystem resilience (Power et al, 1996). Keystone species often exhibit strong connections to other species in the network and contribute significantly to community functioning, especially in fragmented landscapes (Peterson et al, 1998). The role of keystone species in predation, competition regulation, or even facilitation, shape the composition and abundance of other species, maintaining a balance within the community. Ecosystem stability, resilience to disturbances, and the overall health of the environment are tied to the presence and functions of keystone species. Animal species vary in their response to fragmentation, small-bodied, abundant, and generalist species are generally less negatively impacted than large-bodied, rare species and habitat or resource specialists (Henle et al, 2004; Devictor et al, 2008). Similarly, rare, and specialised tree species, particularly those pollinated by animals and producing large seeds, are more vulnerable to the adverse effects of fragmentation than broadly distributed, generalist species (Kolb & Diekmann, 2005; Markl et al, 2012; Arasa-Gisbert et al, 2021). The shared vulnerability of large-bodied, rare animal species and specialised tree species to habitat fragmentation not only threatens each group independently but also poses a greater threat by disrupting crucial interactions between these distinct ecological communities.

Non-native plant species can significantly affect frugivory networks. Invasive species, often characterised by rapid growth and prolific fruit production, can potentially become integral components of these networks (Rojas et al, 2019; Vizentin-Bugoni et al, 2021). Non-native plants may serve as novel resources for frugivores, offering an alternative food source that supplements diets, especially when other fruit resources are scarce (Greenberg & Walter, 2010). This dynamic can lead to shifts in frugivore foraging behaviour and dietary preferences, potentially influencing the roles within the frugivory network (Costa et al, 2022). Non-native plants may alter the spatial and temporal distribution of fruit resources, influencing the movement patterns and behaviour of frugivorous species over the year and can introduce unpredictability into frugivory networks. The fruiting phenology of non-native

species may differ from native plants, and they may produce fruits with unique nutritional profiles, adding an element of diversity and complexity to the diets of frugivores (Cordero et al, 2023). If native frugivores preferentially forage on non-native species, this can aid dispersal of non-native plants while limiting dispersal of native plant species with cascading effects on population dynamics and community composition (Dáttilo et al, 2023). By assessing the impact of non-native plant species within frugivory networks we can gain insights into the adaptability and resilience of frugivory networks in the face of environmental change.

The dynamics of fruit removal from fleshy-fruited plants are dependent upon a complex interplay between plant traits and the composition of frugivore communities. Plant traits including crop size, fruit size, and the ratio of digestible pulp to indigestible seeds modulate the interaction between plants and frugivores (Cazetta et al, 2007; Blendinger & Villegas 2011; Muñoz et al, 2017). In addition, nutritional constituents in fruit pulp, such as lipids and carbohydrates, exert an influence on frugivore preferences and gut retention times (Lepczyk et al, 2000; Schaefer et al, 2003; Pizo et al, 2021). For frugivorous birds, the key trait in determining frugivory interactions is gape width, which assumes a pivotal role in determining the size of fruits that can be ingested, thereby influencing the range of plant species dispersed by each frugivore species (Muñoz et al, 2017).

While the methodologies for tracking frugivore-plant interactions have advanced, the dietary behaviours of birds, particularly passerine birds, remain relatively underexplored (Shutt et al, 2021; Zurdo et al, 2023). In contrast, bats have been extensively examined using faecal metabarcoding (Mata et al, 2021; Ingala et al, 2021). For forest-dwelling birds that primarily forage in the upper canopy and are often elusive, acquiring precise dietary information through direct observation proves challenging. Methods to study frugivory interactions have advantages and limitations, for example direct observations can introduce observer bias and may miss shy or nocturnal frugivores, while camera traps may not capture the entire fruit crop and so may miss animal visitations. Mist-netting at fruiting trees can underrepresent large frugivores or low-mobility species (Jordano 2016; Schlautmann et al, 2021). Additionally, tree surveys often reveal a high diversity of bird species but comparatively fewer plant species, while faecal eDNA analysis presents the opposite, revealing a large number of plant species but fewer bird species. Therefore, a comprehensive understanding of species interactions often needs the integration of multiple methods (Jordano 2016). Molecular analysis of faecal samples is a promising opportunity to bridge this knowledge gap (Fernandes et al, 2018; Monterroso et al, 2019).

DNA metabarcoding has revolutionised researchers' ability to identify complex dietary interactions. The Internal Transcribed Spacer 2 (ITS2) nuclear gene, uses universal primers to target the most variable region within the gene, has become a powerful tool for dietary analysis (Dunn et al, 2018; Moorhouse-Gann et al, 2018). This method is particularly valuable for studying elusive species and for

informing the conservation of threatened species (Ingala et al, 2021). However, molecular analysis of faecal samples has some key limitations in informing dietary patterns: (1) gut retention times and digestion processes may affect detection rates differently between species, complicating interspecies comparisons; (2) while presence/absence data are reliable, relative abundance information (DNA quantity) that determines the quantity of diet items is unreliable (King et al, 2008); (3) DNA assays can possibly misattribute diet items when prey items themselves contain dietary DNA in their digestive system (e.g., predatory insects; King et al, 2008); (4) the method of sequence matching is dependent on the diet items barcode being present in the genomic library; for example, sequences from many species of tropical plants will be missing and identification may be restricted to genus or family (Hoenig et al, 2022). DNA-barcoding analyses may become more limited in tropical areas because of sample processing, collection, and preservation as well as the lack of DNA sequence data for many species, some not even known, which limits the use of these molecular techniques in megadiverse areas (Quintero et al, 2022)

Here we present a frugivorous interaction network from Central Panama generated using DNA metabarcoding to analyse defecated and regurgitated seeds – a novel and robust approach to construct frugivory networks. We aim to provide a more complete understanding of how frugivory shapes ecological processes within tropical forests of Central Panama. Importantly, this method reveals the post-dispersal stage of seeds, linking species interactions to the dispersal dynamics of fleshy-fruited plant species.

Study aims

We provide a comprehensive summary and comparison of the dietary preferences of a selection of largely frugivorous avian species in Central Panama. We identify native fruiting species that are used by a substantial portion of the species, along with non-native species that may hold comparable importance. Furthermore, we explore the roles of bird species within the network and identify potential significant traits which may result in species centrality. Lastly, we consider the effect that non-native plant species may have on frugivory network structure.

Specifically, we hypothesise:

- I. Significant differences in diet composition among species is driven by morphological traits such as beak width, extent of frugivory in the diet, body size and the position occupied in the forest layers, in relation to the corresponding plant traits (seed size, fruit size etc).
- II. Frugivores with larger body sizes and larger beak width/length/gapes will occupy more central roles within the network.

- III. Non-native plant species will have a significant, negative effect on the structure and key network attributes (*connectance*, *nestedness* & *robustness*) of the frugivory network.

4.3 Methods

4.3.1 Study area

This study was performed in Gamboa, a village on the banks of the Chagres River in Central Panama, situated in between two protected forests; Soberania National Park and Forest Protector Arraijan (see Figure 1A & 1B; -79.69707, 9.11624). The local forest is a mixture of secondary forest (20-80 years old) and old-growth lowland moist forest, whilst the local village contains residential areas, gardens (often with non-native species), forest patches and open grasslands. Panama has a tropical climate with a mean annual temperature of 28 °C and a unimodal precipitation regime of an average rainfall of 2226mm, with the dry season lasting from December – April and the wet season from May – November. All birds were captured between January – March 2022 using mist nets placed in the forest canopy at six different locations in the vicinity of Gamboa.

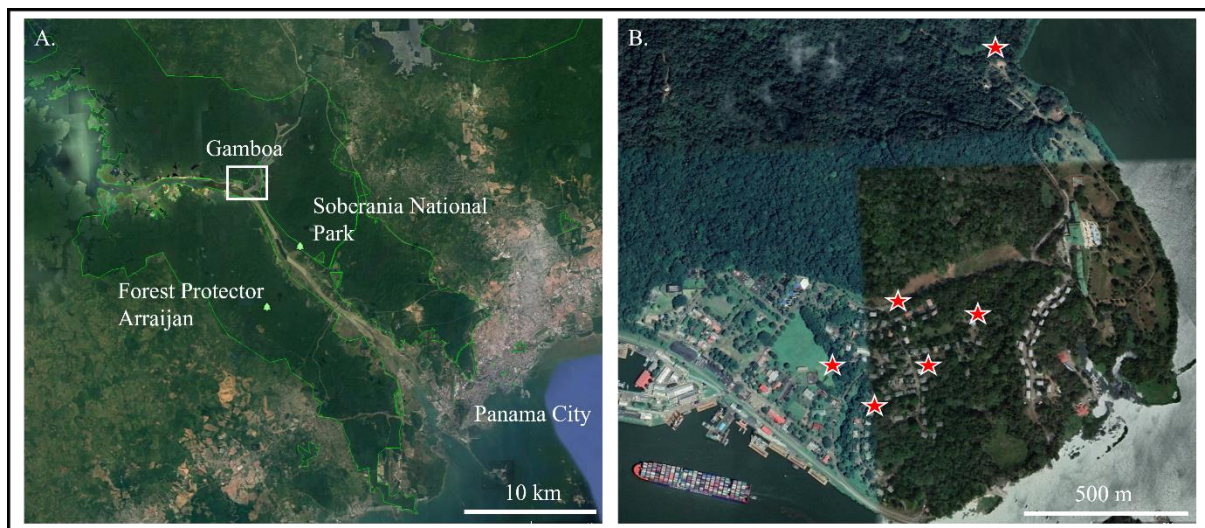


Figure 1A. Map of the location of Gamboa, in relation to Panama City and the two protected forests; Soberania National Park and Forest Protector Arraijan. 1B. The village of Gamboa with stars representing the locations of mist netting for faecal sampling.

4.3.2 *Data collection*

Trapping effort was identical to that described in the methodology for Chapter 3, with faecal samples collected concurrently with the periods dedicated to trapping larger frugivores for movement analysis. Due to time restraints, our primary objective was to prioritise the capture and tagging of larger frugivores, leading us to concentrate our efforts in areas most likely to yield these target species, rather than aiming for an even distribution of effort across all six sites.

Nylon mist nets with dimensions 6 x 12 m and with mesh size of 60 x 60 mm were positioned in six distinct locations around Gamboa, with the aim being to capture a representative sample of frugivorous birds inhabiting diverse ecological niches in the study site. These locations were chosen to encompass a range of environmental conditions, from urbanised areas to primary forest edges, and ranged in height from ground to canopy nets (i.e. 4 to 15 meters above the forest floor). This approach ensured that we could sample frugivores foraging at different strata, including the forest floor, understory, midstory, and canopy levels.

Mist nets were opened at the onset of daylight, around 05:00 Eastern Standard Time (EST), to coincide with the activity period of many avian frugivores. Nets were operational until 10:30 EST, after which they were closed. Nets were reopened at 16:00 EST and closed again at 18:30 EST, just before dusk. Throughout the operational hours, each net was continuously monitored to ensure that any captured birds did not experience prolonged exposure to high temperatures or stress.

Once removed from the nets, birds were placed in small pet carry crates that had been modified to create a darkened environment to minimise stress on the birds. Fresh paper lining the crate floor was provided for each individual caught to maintain hygienic conditions and ensure no cross contamination between samples. Captured birds were held for a maximum of 20 minutes. Almost all individuals freely defaecated within this timeframe. Each faecal sample was collected from the crate floor and carefully transferred into a small, sterile plastic vial. To maintain the integrity of the collected samples, all vials were stored in a cool box containing ice packs and transported from the field site to the laboratory as soon as possible after collection. Samples were maintained in the cool box for a maximum of three hours before being transferred to a freezer set at -20°C for long-term storage.

All handling protocols were approved by both the Animal Welfare and Ethical Review Body (AWERB) at the University of Stirling and the IUCAC of Smithsonian Tropical Research Institute. Our data collection methods were designed to prioritise the welfare of captured birds while obtaining valuable faecal samples for our study.

4.3.3 Focal bird species

In Panama, 675 bird species inhabit forested areas (*BirdLife International Data Zone*), of which 203 (30%) have a diet consisting of > 50% fruit and seeds (Wilman et al, 2014). Our aim was to sample species from this pool of fruit-eating species and to encompass a diverse cross-section of frugivores, considering factors such as body size, morphological measurements, and their vertical distribution within the forest layers (ground, understory, midstory and canopy). This comprehensive approach allowed us to explore how different frugivore species contribute to plant-frugivore interaction networks across various strata of the forest ecosystem.

4.3.4 DNA extraction

DNA was extracted from our faecal samples at Naos Marine & Molecular Laboratories, Panama City by Kristin Saltonstall and Marta Vargas, who then sent over the final processed DNA sequences.

DNA samples were extracted using the QIAamp PowerFecal DNA Kit (*Qiagen*), starting with 250 mg of material or the entire faecal pellet if it was less than that. An Illumina metabarcoding library was prepared using a two-step PCR approach. The first PCR (PCR1) was conducted in triplicates to amplify the ITS region with primers ITS2-S2F and ITS2-S2R in a 10 µl reaction mix, consisting of 5 µl PCR buffer, 0.075 µl KAPA3G plant DNA polymerase (*Roche*), 0.2 µl each of 10 mM forward and reverse primers, and 1 µl of DNA. Subsequently, a second PCR was performed to add the indexes in a 10 µl reaction, using 5 µl Platinum II Hot-Start PCR Master Mix (*Thermofisher*), 1 µl each of 2.5 mM forward and reverse primers (with a unique index combination per sample), and 1 µl combined product of the PCR1 triplicates.

PCR products were then purified using the Just-a-Plate™ 96 PCR Normalization and Purification Kit (*Charm Biotech*) and combined into a single library. The final library was concentrated using Kapapure beads (*Roche*) at a 1X concentration. The library was sequenced on an Illumina Miseq using a 600-cycle V3 sequencing kit. PCR1 conditions included an initial denaturation at 95°C for 3 minutes, followed by 35 cycles of 95°C for 45 seconds, 56°C for 45 seconds, and 72°C for 45 seconds, with a final extension at 72°C for 5 minutes. Index PCR conditions involved an initial denaturation at 94°C for 3 minutes, followed by 6 cycles of 94°C for 45 seconds, 50°C for 60 seconds, and 72°C for 90 seconds, with a final extension at 72°C for 10 minutes.

4.3.5 Bioinformatics and sequencing

Quality control of sequence data was performed using the DADA2 V1.16 pipeline (Callahan et al, 2016) and all further bioinformatics analysis and sequencing was undertaken by myself using Rstudio 4.3.1.

Quality control of sequence data was performed using the *DADA2* V1.16 pipeline (Callahan et al, 2016). Following a similar protocol to Clever et al (2022), sequences were removed if they had more than two expected errors ($\text{maxEE} = 2$), at least one ambiguous nucleotide ($\text{maxN} = 0$), or at least one base with a high probability of erroneous assignment ($\text{truncQ} = 2$). Following visual inspection of base quality score plots, the forward sequences were trimmed to 260 base pairs and reverse sequences were trimmed to 200 base pairs. This was to remove low quality bases while maintaining adequate overlap. Any sequences identified as chimeras were removed and the final sequences dereplicated and used to produce Amplicon Sequence Variants (ASVs). A total of 2727 ASVs were produced.

4.3.6 Taxonomic assignment

Before assigning the ASVs to taxonomic identities, we first created a suitable reference database. We used two databases unique to Panama and a third global database. The first Panama specific database incorporated 19,663 sequences from 9,393 plant species from Panama (Saltonstall et al, 2023a), and the second was limited to 80 plant species found on Barro Colorado Island (Saltonstall et al, 2023b; 9°9'42.36"N, 79°50'15.67"W) located approximately 16 km from our study site. Our study site includes many gardens and cultivated areas, and it is highly likely that there are non-native species present, thus, to allow for identification of non-native species we included a third database as a comprehensive list of world vascular plants and this included 96,990 sequences from 59,718 species (Banchi et al, 2020). We created a subset of only those species found in Central America using the “World Checklist of Vascular Plants” (POWO, 2023) and “Tree Atlas of Panama” (Perez & Condit, 2023) to describe a comprehensive list of plant species present in Central America, both native and non-native. We integrated the two local Panama databases and the World ITS2 database subset by species in Central America generating a database of 13,041 sequences from 5,433 plant species.

To ensure that all databases were usable and could be successfully combined, taxonomic differences in the classification of species among databases were standardised. The reference sequences were analysed to determine duplicates across the different databases (95% similarity). Duplicated species were removed and one identifier with the longest sequence length was retained per species. Our final reference library consisted of 5165 plant species with one sequence each. See *Supplementary figure 1* for the complete decision workflow for creating our customised ITS2 reference database.

We then matched the sequence data to the reference library. We identified all ASVs present in at least 1% of all samples, to species level. If this was not possible using *DADA2* pipeline, then we used the Basic Local Alignment Search Tool (*BLAST*) to find the most appropriate matches for the sequences (182 ASVs). We used a minimum query coverage of 95% and a minimum percentage identity of 90% to filter out probable species. Finally, we filtered out any singletons, ASVs which occurred just once

across all of the samples (61 ASVs), and a local botanist reviewed the final list of species to assess the likelihood of species occurrence.

4.3.7 *Statistical analysis*

For all following statistical analysis, we used the presence/absence of each taxonomic unit within a faecal sample. Using relative read abundance (*RRA*) was not appropriate because of variability in rate of digestion and breakdown of organic material across bird and plant species. We therefore calculated the more conservative frequency of occurrence (*FOO* - the proportion of samples in which each plant species was found) to identify the most prevalent taxa within a species diet and used binary matrices, as opposed to abundance matrices, to determine interaction network metrics.

Differences in dietary composition across all samples and species were visualised using non-metric multidimensional scaling analysis (NMDS) via *metaMDS* in the *vegan* package. We performed the NMDS using Jaccard distance in two-dimensional space ($k=2$; Figures 3A & 3B; *Supplementary figure 2*). For the NMDS analysis, we used the whole frugivore network, including plant species that do not produce fleshy fruits. For the further analysis, we subset the network to only include plant species that produced fleshy fruits to capture the dynamics of the mutualistic relationships between birds and their food plants through the process of seed dispersal.

To first understand the composition of the plant-frugivore network, we calculated *nestedness* and *modularity* using the *bipartite* package. *Nestedness* refers to the structured pattern where the diet of one species is a subset of the diet of another, and specialists closely interact with subsets of generalist species (James et al, 2012). *Modularity* provides a quantitative measure of the network's compartmentalisation into distinct modules and the structural organisation of the plant-frugivore interactions (Nordbotten et al, 2018). These modules represent subsets of species that exhibit stronger interactions among themselves than with species in other modules, often reflecting both phylogenetic and functional affinities (Olesen et al, 2007). High modularity indicates that interactions are predominately confined within modules, with minimal connections beyond these subsets.

We then assessed the role of each frugivore species within the interaction network by employing three species-level metrics that indicate the centrality of a species within the broader network. The first metric, *degree*, quantifies the number of interactions between each frugivore species and plant species, where species with high values are considered generalists. The second metric, *betweenness*, measures the proportion of the shortest paths linking any pair of nodes in a network. A species with high *betweenness* will have a large number of shortest paths going through their node. The final metric, *closeness*, is calculated based on the reciprocal of the sum of the shortest paths from one node to all

other nodes in the network. Nodes connected by shorter paths and have higher closeness centrality are considered more central in the network.

Similar to other studies (Acevedo-Quintero et al, 2020; Da Silva et al, 2022; Moulatlet et al, 2023; Goebel et al, 2023), we utilised these species-level network metrics to perform a Principal Component Analysis (PCA) with the objective of identifying a proxy measure for centrality (*Supplementary figure 3A & 4A*). The first PCA axis (PC1) captured a large portion of the variance in our network (78%), and we used this as a proxy for the position of frugivore species within the interaction network. We employed the same measures as mentioned in Olesen et al, 2007, for identifying the critical cz -value thresholds. These measures included identifying peripheral species by low z values < 2.5 and low c values < 0.62 , whereas connector species had low z values < 2.5 but high c values > 0.62 . Peripheral species occupy the periphery of the interaction network, connector species link different modules of the network.

Using PC1 as a proxy for centrality within the network, we fitted linear models to test if centrality could be predicted by bird species traits including body mass, beak length, beak width, hand-wing index, tail length, proportion of frugivory within diet and foraging strata. Predictor variables were extracted from *AVONET* (Tobias et al, 2022) and *EltonTraits* (Wilman et al, 2014). Body mass was logged to account for the skewed distribution. We provide the results of the F-tests, P-values, and summary tables for each of the models in *Supplementary tables 4A & 4B*.

To assess the *robustness* of the plant-frugivore interaction network, we employed the network extinctions method implemented in the *bipartite* package in R. This approach involves systematically removing species from the network and observing the effect on network integrity. Bird species would be removed one by one and the rate of extinctions in the second trophic level (plant species) would be observed. Various extinction scenarios were considered, including removing species with traits identified that significantly predicted centrality using the linear modelling for centrality measures. Specifically, species were selected for removal based on the number of connections each species has: descending frugivory rate within their diets, descending tail length, and removal at random. By systematically evaluating the network's response to the removal of specific bird species based on their increased centrality in the network, this approach allowed for an exploration of the factors influencing the stability and resilience of the plant-frugivore interaction network.

To examine the impact of non-native plants on the plant-frugivore interaction network, we used null models where we systematically removed all 19 non-native plant species from the network, and then calculated *connectance*, *nestedness*, and *robustness* metrics. Subsequently, to account for stochasticity, we selected 19 plant species at random for removal in 1000 iterations. For each iteration, we calculated *connectance*, *nestedness*, and *robustness* metrics. To calculate statistical significance, the observed

metrics from removal of non-native plants were compared to the distributions from random removals. This approach provided a rigorous framework for assessing the ecological implications of non-native species in the context of the plant-frugivore interaction network. *All statistical analysis was undertaken in R 4.3.1.*

4.4 Results

4.4.1 Composition of faecal samples

We found a total of 127 unique plant species across 94 faecal samples from 21 bird species. The number of unique plant species per bird species ranged from three (Yellow-green Tyrannulet) to 71 (Clay-coloured Thrush), with a mean of 15 species (Table 1); and the number of unique plant species per faecal sample ranged from 1 (Clay-coloured Thrush) to 22 (Slaty-tailed Trogon), with a mean of 8 (Figure 4). The most common species detected were *Myrcia sylvatica*, *Syzygium cumini* and *Myrcia guianensis*; found in 79%, 69% and 64% of all samples, respectively. All other plant species were found in < 50% of the samples and 33 species were present in only one sample. *Fabaceae*, *Rubiaceae*, *Poaceae*, *Arecaceae*, and *Euphorbiaceae* were the most common families, each with 12, 12, nine, eight, and eight species, respectively. However, *Myrtaceae* emerged as the most abundant family found in all samples.

The plant species presented 95 native species and 32 non-native species, 69 fleshy-fruited species and 58 non-fleshy-fruited species and 95 woody species and 32 non-woody species (Figure 2A). On average, all bird species consumed a larger percentage of fleshy-fruited, native and woody species than non-native, non-fleshy, and non-woody species (Figure 2B). The exceptions were the Crimson-collared Tanager, Olive-throated Parakeet, Common ground Dove and White-tipped Dove (Table 1). It is likely that three of the non-native plant species identified, namely chickpea (*Cicer arietinum*), carrot (*Daucus carota*), and onion (*Allium cepa*), were consumed from garden food waste. Additionally, four other non-native cultivated species - banana (*Musa acuminata*), coffee (*Coffea arabica*), mango (*Mangifera indica*), and passionfruit (*Passiflora edulis*) – could have been consumed as garden waste material or from fruiting plants in the local landscape. Eight bird species had these species in their diets: (Clay-coloured Thrush – passionfruit, mango, banana; Masked Tityra – onion, coffee; Gartered Trogon – mango, carrot; Slaty-tailed Trogon – coffee, Gray-headed Chachalaca – chickpea; White-tipped dove – carrot; Great kiskadee – banana; Palm Tanager – banana and Tropical Mockingbird – mango) (Figure 4).

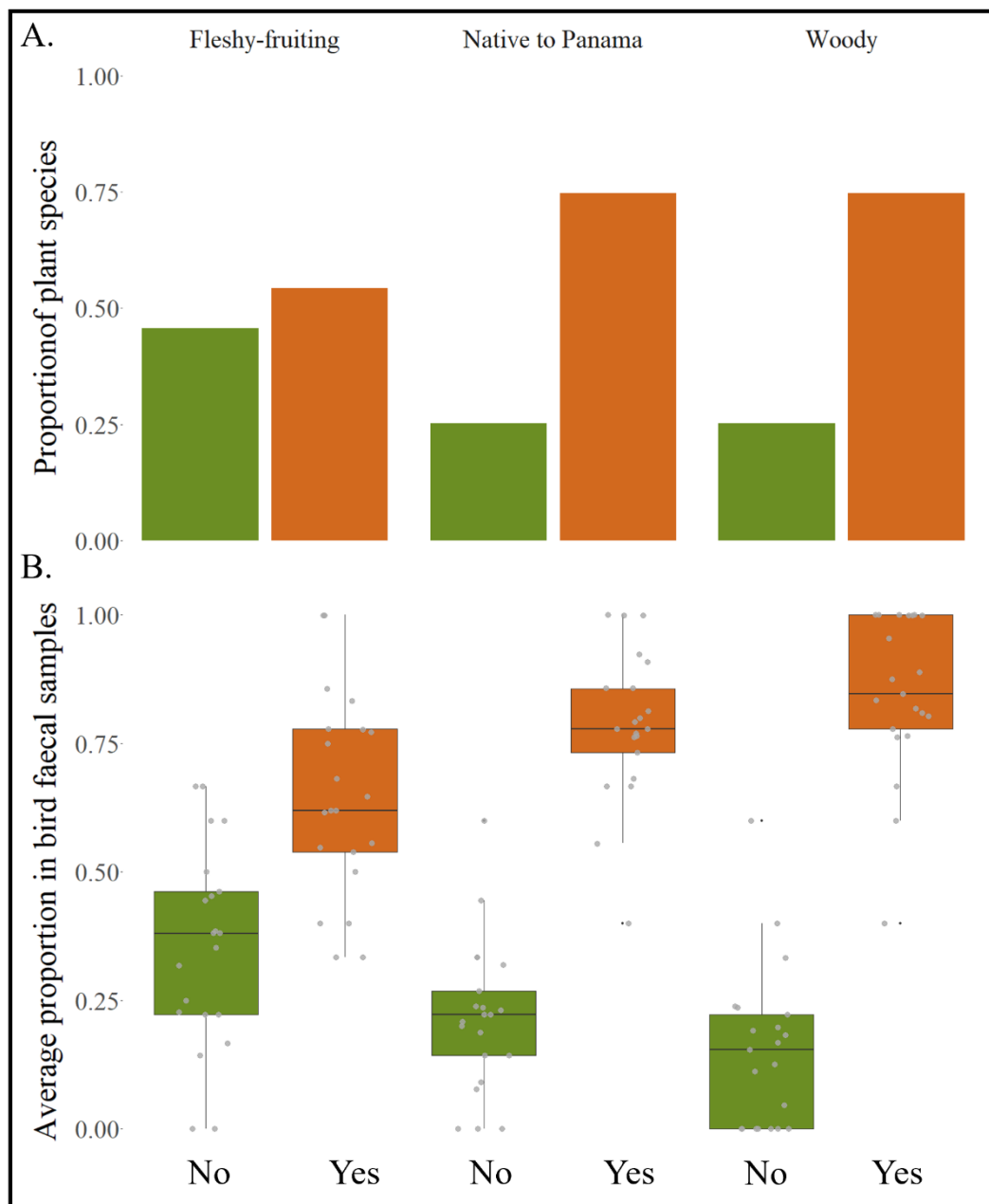


Figure 2A. The proportion of fleshy-fruited, native and woody stemmed plant species out of 127 species found in all faecal samples. Figure 2B. The average proportion of fleshy-fruited, native and woody stemmed plant species found across all 21 frugivorous bird species.

NMDS analysis showed distinct species diet compositions among the studied bird species (Supplementary table 2A). Notably, we observed repeated and significant differences in several species, including Whooping Motmot (*Momotus subrufescens*), Great Kiskadee (*Pitangus sulphuratus*), Black-cheeked Woodpecker (*Melanerpes pucherani*), Gartered Trogon (*Trogon caligatus*), Blue-gray Tanager (*Thraupis episcopus*), and Gray-headed Chachalaca (*Ortalis cinereiceps*), as determined through permutational analysis of variance (Supplementary table 2B).

Body mass and frugivory rate both significantly influenced dietary preference in the permutation test outcomes based on the Jaccard index of dissimilarity (Figure 3A). It is evident from Figure 3A that NMDS2 scales with frugivory rate, with those that have a higher proportion of fruit in their diet placing at the top of the plot, and those with a lower proportion of fruit placing towards the bottom of the plot.

Further NMDS analysis identified 42 plant species (33%) as significant contributors in grouping different bird species together based on diet compositions (Figure 3B). This selection of plants included 11 non-native species and 27 fleshy-fruited species (Supplementary table 2B). To the top right of the NMDS plot diets are dominated by the non-native plant species, *Eugenia*, *Syzygium* and *Myrcia*, whilst the bottom right sees a clustering of palm species, *Brahea*, *Kentiopsis*, *Bactris*, *Areca*, *Oenocarpus*.

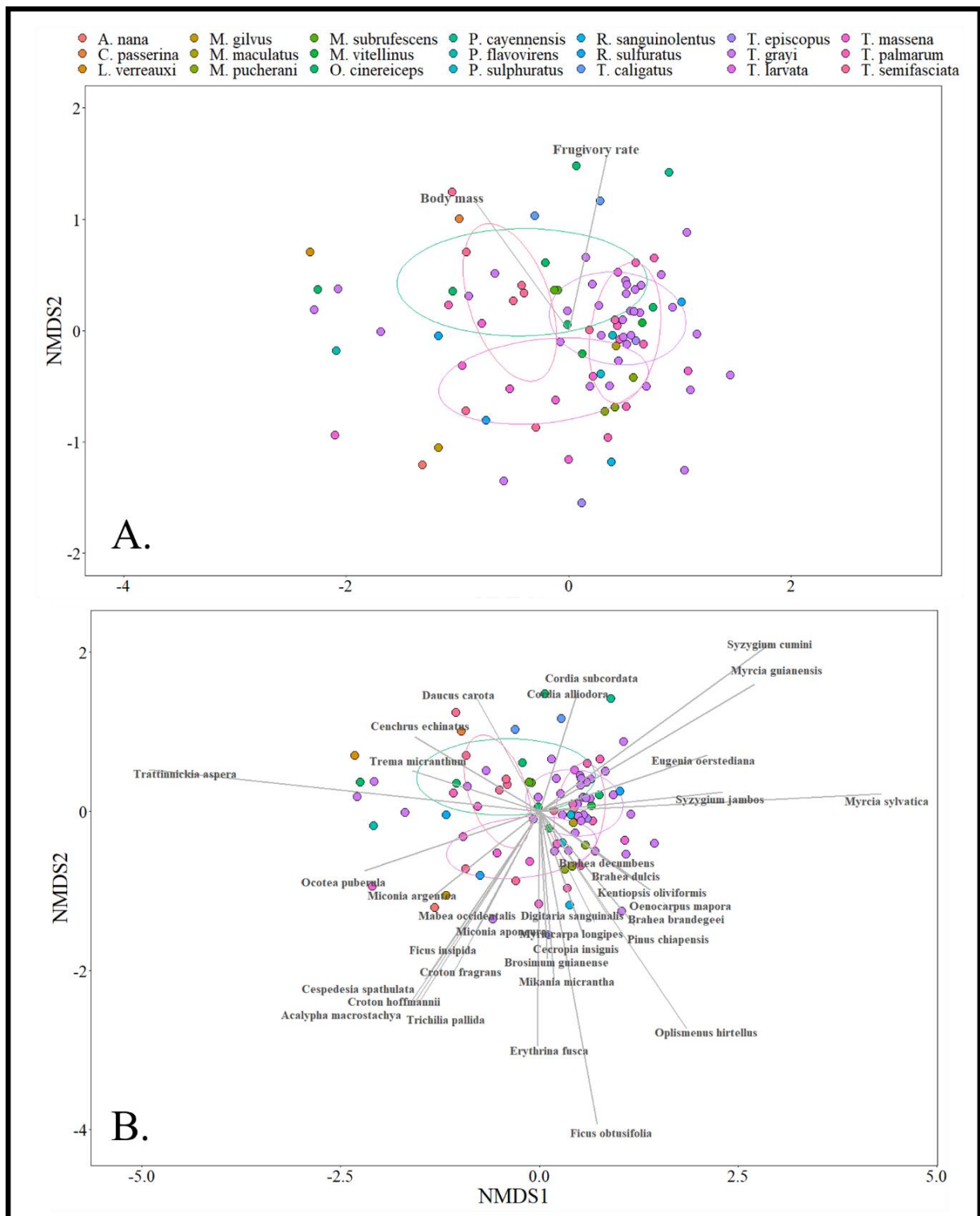


Figure 3A. NMDS analysis of bird traits and B. plant species influencing the diet composition of 94 faecal samples from 21 bird species.

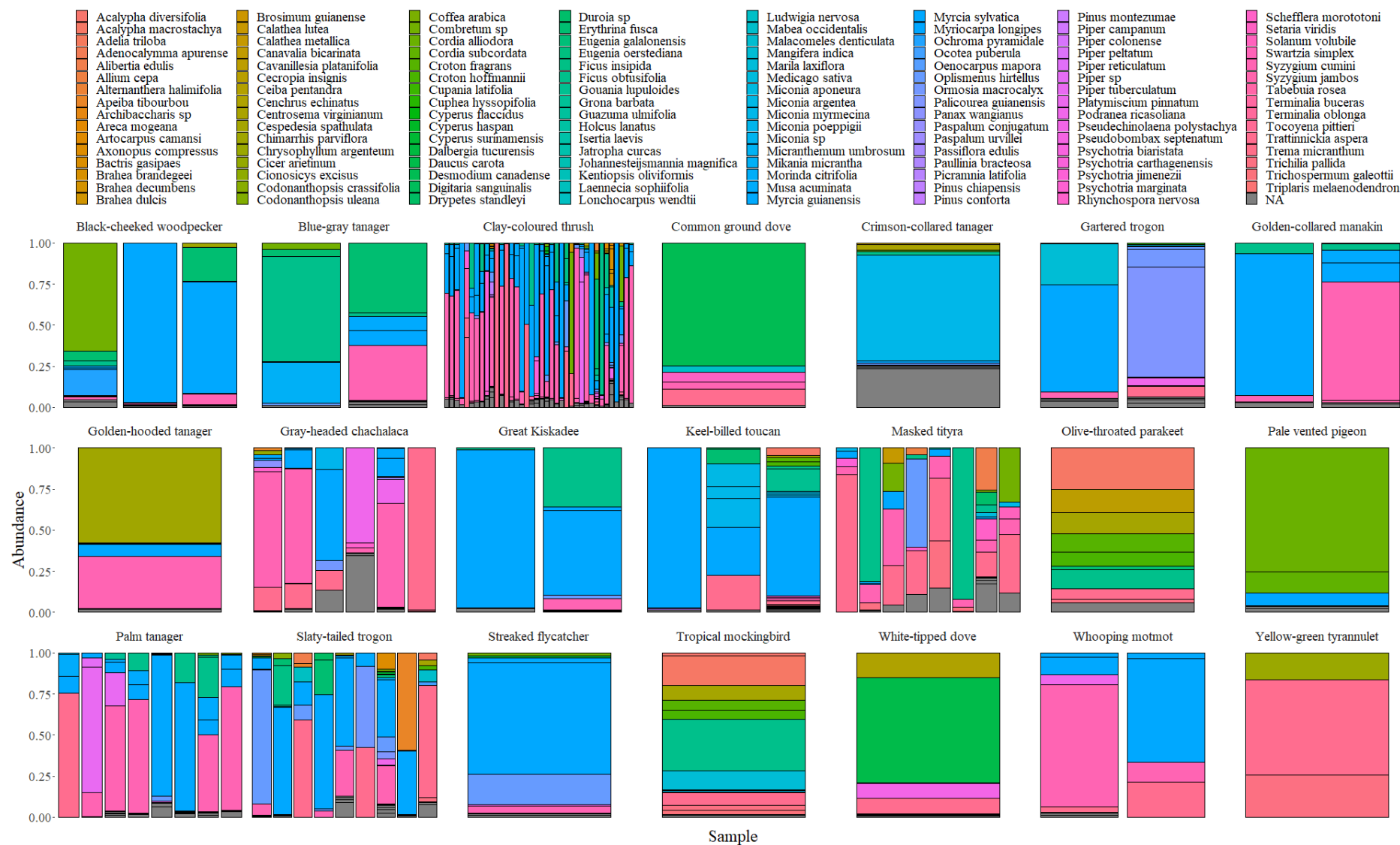


Figure 4. The proportion of plant species found in each of the individual faecal samples, grouped by bird species with each column representing a different faecal sample.

Table 1. List of bird species sampled in Central Panama (21) and the total number of samples per species (total samples = 94). The number of unique plant species, genera and families found across all samples of the same species. Average proportion of native, non-native, fleshy-fruited, non-fleshy-fruited, woody stemmed and non-woody stemmed plant species.

Bird species	Number of samples	Unique plant species	Unique plant genera	Unique plant families	Native species (%)	Non-native species (%)	Fleshy fruit species (%)	Non-fleshy fruit species (%)	Woody species (%)	Non-woody species (%)
Clay-coloured Thrush	38	71	55	33	73	27	62	38	80	20
Slaty-tailed Trogon	9	42	38	20	86	14	55	45	81	19
Palm Tanager	8	24	20	16	79	21	75	25	83	17
Keel-billed Toucan	3	22	17	15	91	9	68	32	95	5
Masked Tityra	8	22	21	15	68	32	77	23	82	18
Gray-headed Chachalaca	6	21	18	13	76	24	62	38	76	24
Gartered Trogon	2	17	16	14	76	24	65	35	76	24
Black-cheeked Woodpecker	3	16	15	12	81	19	50	50	88	12
Blue-gray Tanager	2	13	11	9	77	23	62	38	85	15
Tropical Mockingbird	1	13	10	9	92	8	54	46	100	0
Crimson-collared Tanager	1	9	9	7	100	0	33	67	67	33
Golden-collared Manakin	2	9	7	5	78	22	78	22	100	0
Great Kiskadee	2	9	7	6	56	44	78	22	78	22
Olive-throated Parakeet	1	9	8	7	100	0	33	67	100	0
Streaked Flycatcher	1	9	8	6	78	22	56	44	89	11
Golden-hooded Tanager	1	7	6	4	86	14	86	14	100	0
Whooping Motmot	2	6	5	4	67	33	83	17	100	0
Common ground Dove	1	5	5	5	40	60	40	60	60	40
White-tipped Dove	1	4	5	4	80	20	40	60	40	60
Pale vented Pigeon	1	3	2	2	67	33	100	0	100	0
Yellow-green Tyrannulet	1	3	3	3	100	0	100	0	100	0

4.4.2 *Modularity of network*

Modularity analysis revealed a significant degree of structuring within the network, as indicated by a modularity score of 0.41 with all plants species and 0.37 with just fleshy-fruited species. The network naturally partitioned into six communities, highlighting the presence of distinct clusters of nodes (where each node is either a bird or a plant species) within the network, each characterised by a higher degree of internal connectivity compared to connections between other communities (Figure 5). NMDS analysis, and the subsequent permutational analysis of variance, provided additional support for the existence of distinct communities within the network, showing that communities one (green), three (purple) and six (orange) had significantly different dietary compositions (*Supplementary table 3A*; *Supplementary figure 2*; $p < 0.1$). Frugivory rate and habitat were the only two bird morphological/life-history traits that explained observed differences between these six communities (*Supplementary table 3A*). Whereas 36 specific plant species emerged as key determinants in shaping the distinct ecological profiles of these communities (*Supplementary table 3B*). The network also displayed a significantly high level of *nestedness* when calculated with all plant species (31.72) (Figure 6) and with just fleshy-fruited species (41.71).

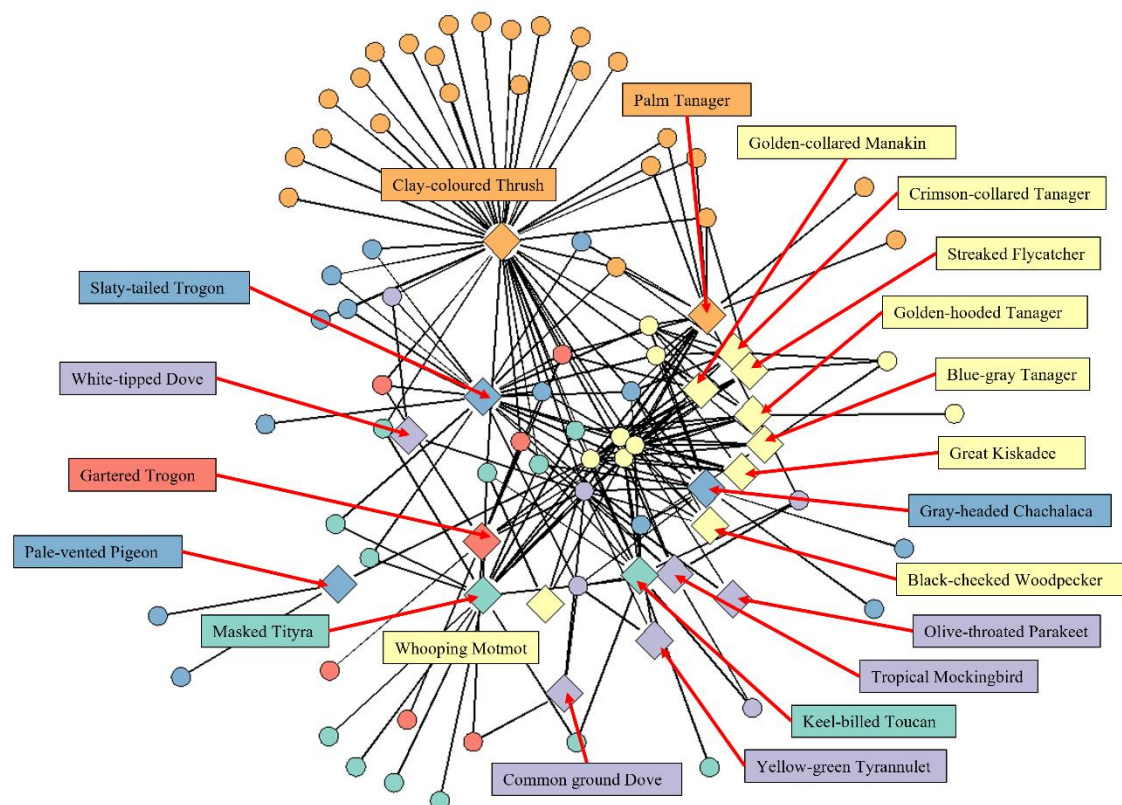


Figure 5. Interpretation of modularity within the frugivory network of fleshy-fruited plant species only, denoting six distinct communities (represented by colour). Bird species are denoted by square labels, plant species are denoted by circles.

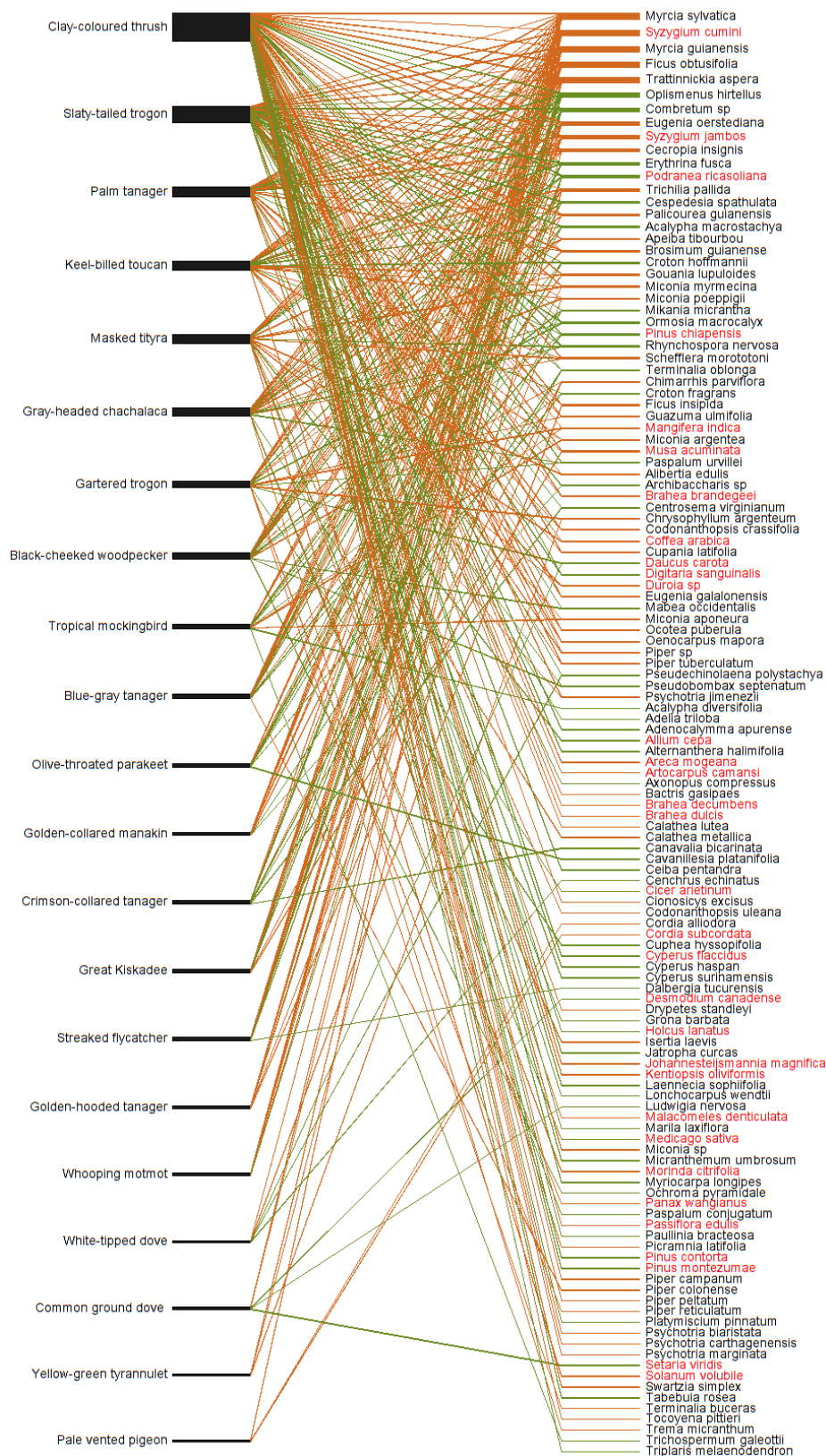


Figure 6. The bipartite frugivory interaction network of 21 bird (left) and plants species (right) in Gamboa, Central Panama. Size of species boxes represents frequency of occurrence in faecal samples. Orange colour denotes fleshy-fruited plants, and green denotes non-fleshy-fruited species. Non-native plant species are labelled in red text.

4.4.3 *Species roles & centrality*

The Keel-billed Toucan, Slaty-tailed Trogon, Gray-headed Chachalaca, Clay-coloured Thrush, and Palm Tanager were crucial module connector species (Figure 7A). These species are key intermediaries that facilitate interactions across different modules within the network. In contrast, all other species were categorised as peripheral, indicating their relatively more localised influence on the network structure.

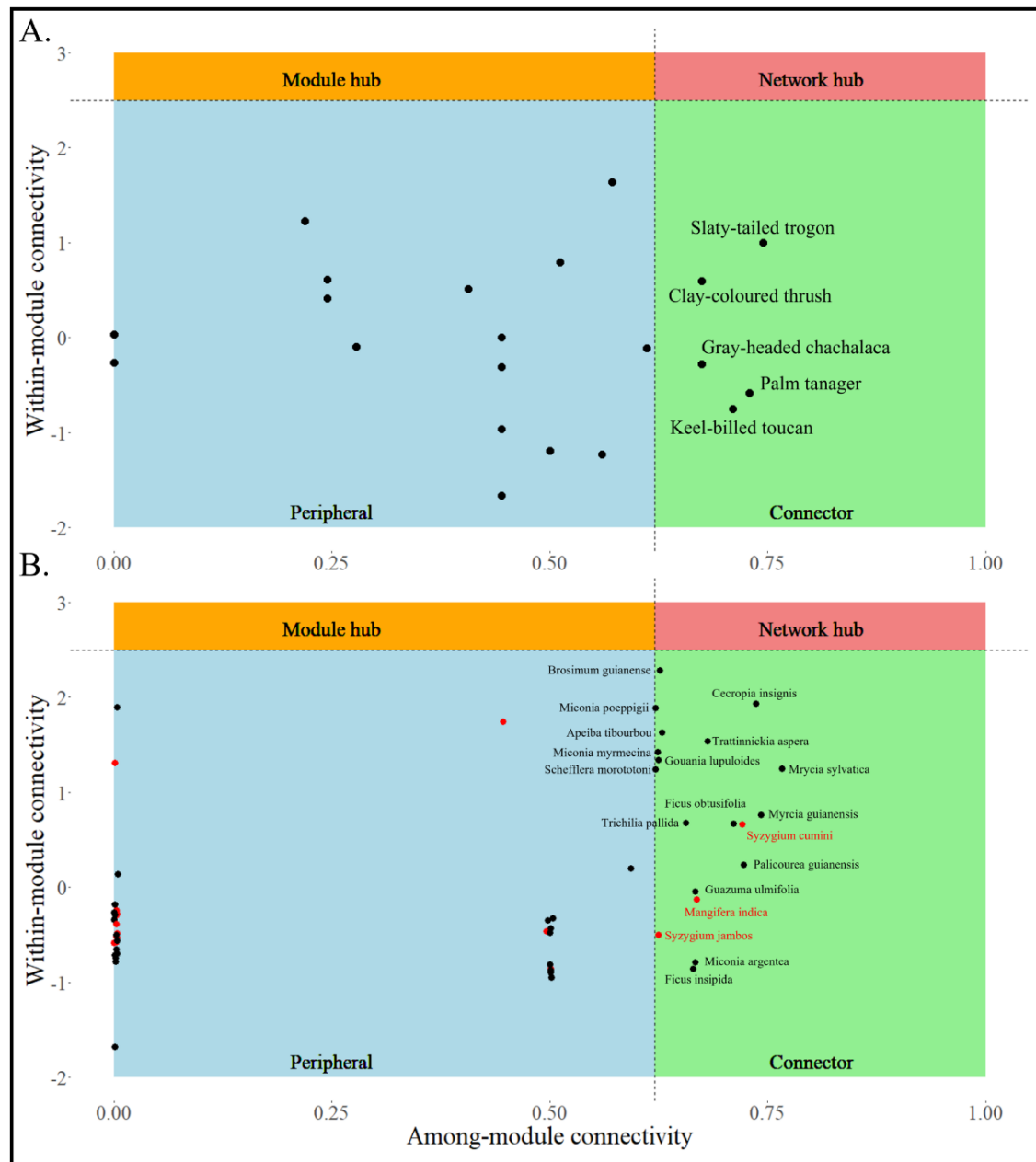


Figure 7A. Module roles of birds within the frugivory network. 16 peripheral species ($C < 0.62$ & $Z < 2.5$) and 5 connector species ($C \geq 0.62$ & $Z < 2.5$). 7B. Module roles of plants within the frugivory network. 50 peripheral species and 19 connector species. Non-native species denoted by red labels.

The PCA indicated that frugivory rate diet (centrality estimate $\pm$ std. error = 0.027 ± 0.012 , $p < 0.05$; *Supplementary table 4A & Figure 3B*) and tail length (centrality estimate $\pm$ std. error = 1.240 ± 0.540 , $p < 0.05$; *Supplementary table 4B & Figure 3C*) were key traits that explained the centrality of a species. PCA analysis for our centrality values explained 78% of the total variation (*Supplementary figure 3A*). Other traits such as body mass, beak width, beak length, hand to mid-wing index, and foraging area demonstrated no discernible impact on species centrality and were consequently removed from the model.

For plants, 28% of species were module connectors, including 3 non-native plants: *Syzygium cumini*, *Syzygium jambos* and *Mangifera indica* (*Figure 7B*). Plant height significantly affected centrality values (centrality estimate $\pm$ std. error = 0.040 ± 0.016 , $p < 0.05$; *Supplementary table 4B*) and larger plants were more central to the network (*Supplementary figure 4B*). Nativeness, woodiness, and seed size (centrality estimate $\pm$ std. error = -0.006 ± 0.018 , $p = 0.74$; *Supplementary table 4B*), had no significant effect on centrality within the network.

4.4.4 Robustness & extinction scenarios

The extinction simulation results indicated that the removal of species with higher frugivory rates and elongated tail lengths yielded extinction curves that exhibited steeper declines, indicative of heightened vulnerability to network disruption (Figure 8). The most pronounced impact on network integrity was observed when species with the highest number of connections were removed. This same pattern can also be seen in the *robustness* values, with degree of connectivity = 0.265, rate of frugivory = 0.426, length of tail = 0.516 and random removals = 0.602. Values closer to 1 indicate a higher robustness level to extinctions, whereas values closer to 0 indicate less robust networks.

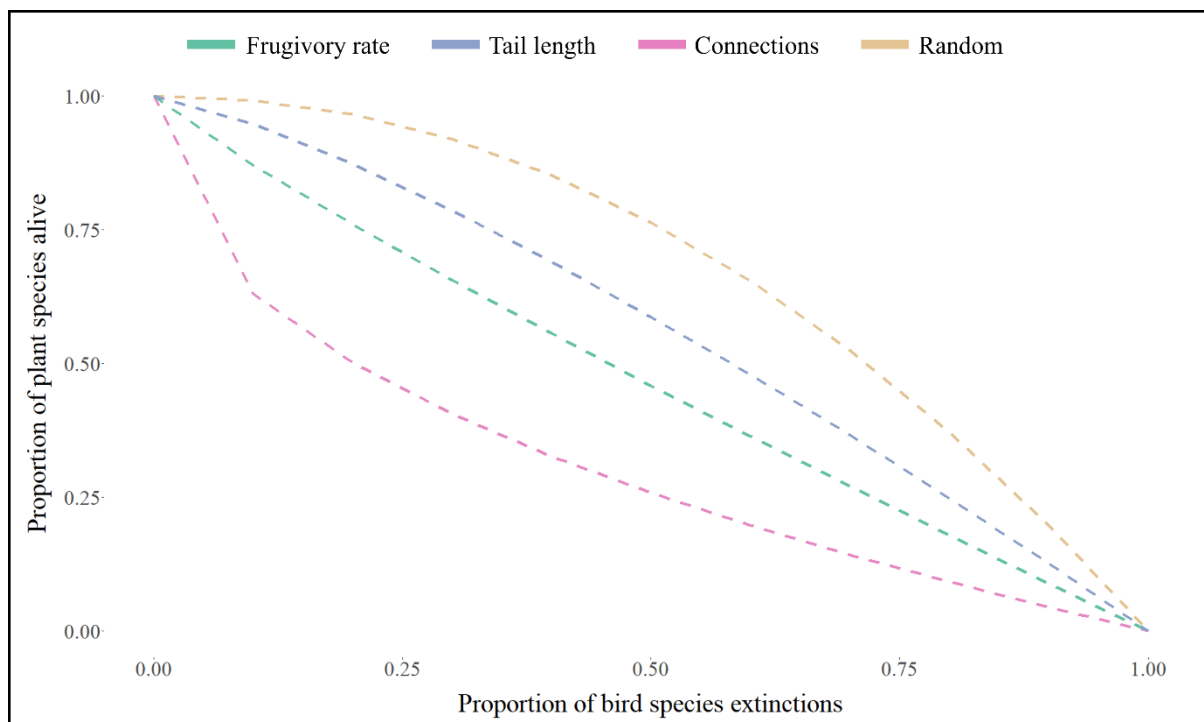


Figure 8. Network robustness to cumulative extinctions following four different simulation procedures. Pink = Removal of most connected bird species first. Green = Removal of species with highest rate of frugivory in diet first. Purple = Removal of species with the longest tail length first. Yellow = Random bird species removal.

4.4.5 Impact of non-native, fleshy-fruited plant species on the frugivorous network

Permutation analysis showed that *nestedness* ($p = 0.287$) and *connectance* ($p = 0.226$) of the overall network was not significantly affected by the removal of non-native plants, but there was a significant increase in network *robustness* when the 19 non-native plants were removed compared to the removal of 19 species at random ($p = 0.008$) (Figure 9).

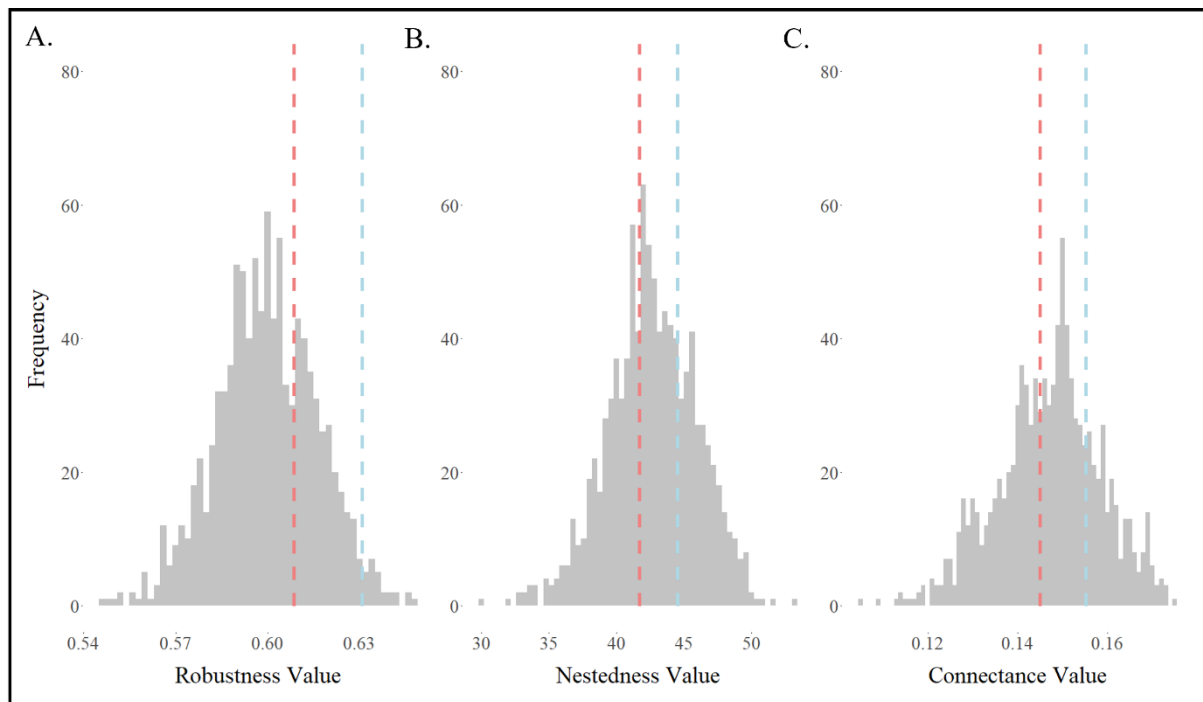


Figure 9. Null distributions of (A) *robustness*, (B) *nestedness* and (C) *connectance* of the frugivory network when 19 non-native plants are removed (blue line) and when 19 random plant species are removed (red line).

4.5 Discussion

4.5.1 Comprehensive dietary preferences and compositions

The dietary composition of frugivorous avian species in Central Panama revealed a complex network of ecological interactions. In 94 faecal samples from 21 bird species, we detected 127 distinct plant species. This diversity of plant species reflects the diversity in dietary preferences and variation in foraging behaviours within the frugivorous avian community. The Clay-coloured Thrush was the most comprehensively studied species (> 40% of samples were from this species) and had 71 plant species detected in faecal samples, illustrating the high dietary diversity of frugivorous birds in this region. In contrast some species may be dietary specialists or may be omnivorous and so consume a low quantity and diversity of fruit. For example, results for the Pale-vented Pigeon and Yellow-green Tyrannulet suggest that they consume just three plant species.

Native plant species dominated the diet of most birds (95 of the identified plants), but 32 non-native plant species were present in the dietary analysis, suggesting plasticity to novel food resources. The non-native species chickpea, carrot, and onion, that do not grow in lowland Panama suggest that some birds explore household waste as a novel food resource in human-altered environments. This adaptability aligns with observations in other ecosystems where avian species display a capacity to incorporate anthropogenic elements into their diets, highlighting the ecological flexibility of frugivorous communities (Ottoni et al, 2009). For example, numerous parrots species (Scarlet Macaw, Golden-capped Parakeet and Blue-winged Parrotlet) have been found to feed heavily on non-native, cultivated plant species across anthropogenic landscapes in Costa Rica and Brazil (Matuzak et al, 2008; Silva & Melo, 2013; Silva & Melo, 2018). Interestingly, some primarily forest species (including the Masked Tityra and Gartered Trogon) consumed these plant species that are typical of household waste, suggesting that even forest birds may venture out of preferred habitats to consume food resources, potentially because these resources are more easily available and reliable. Other studies have observed that gardens in Sri Lanka (Perera et al, 2017) and landfill sites in Iran (Malekian et al, 2021) are capable of attracting large numbers of species, likely following the constant and reliable resources.

In total, almost 25% of the plant species identified as key contributors to dietary patterns were non-native species (Figure 3B), suggesting that non-native species are integrated into the dietary repertoire of frugivores, potentially influencing the broader frugivory network. This can have negative consequences for the mutualistic relationship between local native plants and their dispersers. For example, if native and non-native plants fruit synchronously, this can increase competition for seed dispersal services and potentially redirect frugivores away from native plants, ultimately reducing the recruitment of native plants across the landscape (Traveset et al, 2012; Helano et al, 2013). Equally, if

non-native species take advantage of available temporal niches - such as fruiting outside the primary native fruiting season – then they will likely attract a large number of seed dispersers which will likely facilitate further dispersal into the local landscape (Ramos-Robles et al, 2018; Vergara-Tabares et al, 2018). The incorporation of non-native species into frugivore diets highlights the adaptability and resilience of frugivore networks to environmental changes, including the introduction of non-native plant species (Rojas et al, 2019; Costa et al, 2022). Understanding the role of these non-native plants in avian diets is crucial for comprehending the adaptability of frugivore networks to anthropogenic influences and changes in plant community composition, whether this be as a novel food source or as a direct competitor to native species.

The network analysis revealed significant differences in diet compositions among species, with some species having distinct diet compositions such as Whooping Motmot, Great Kiskadee, Black-cheeked Woodpecker, Gartered Trogon, Blue-gray Tanager, and Gray-headed Chachalaca. These differences in dietary composition may be a result of the ecological niches occupied by these species (Sherry, 1990; Boyle et al, 2011; Yoshikawa & Isagi, 2012). For example, the Gartered Trogon is a forest canopy species and exhibit preferences for fruits available in the upper canopy (i.e. *Chrysophyllum argenteum*, *Guazuma ulmifolia* and *Mangifera indica*) in contrast to ground-feeding species like the Gray-headed Chachalaca. Omnivorous species like the Great Kiskadee and Black-cheeked Woodpecker eat a large proportion of arthropods and may only feed on specific plant material and at certain times of the year. Differences in diet were influenced by body mass, frugivory rate and foraging strategy. Larger-bodied species with great rates of frugivory in their diets had a more diverse diet composition than other, smaller-bodied frugivores. Similar patterns of dietary differentiation based on morphological traits have been observed in other frugivorous bird communities (Yoshikawa & Isagi, 2012). Moran & Caterall (2010) revealed that frugivory rate, coupled with beak gape, significantly accounted for a substantial proportion of the overall taxonomic composition and diversity of plants consumed by frugivorous species. Additionally, their study suggests that taxonomic relatedness and phylogenetically derived tolerance of secondary chemical compounds may play pivotal roles in influencing the patterns of plant species consumption among frugivorous birds.

4.5.2 Modularity and species roles

The modularity analysis showed that the frugivory network was structured into six distinct communities, where each community exhibited a higher degree of internal than external connectivity, suggesting distinct subgroups within the network. Keystone species, such as the Keel-billed Toucan and Gray-headed Chachalaca, then act as module connectors facilitating interactions across different network modules. Connector species tended to be large-bodied species with diets composed of a large proportion of fruit. Frugivory studies from India, Malaysia and Brazil also find that large-bodied

frugivores often act as network module connectors (Naniwadekar et al, 2021; Ong et al, 2022; Goebel et al, 2023). Large-bodied frugivores possess anatomical (beak shape) and physiological (extended digestive tract; ability to cope with secondary compounds) adaptations that enable them to efficiently consume a diverse range of fruits, often spanning different sizes and types (Valenta & Nevo, 2020; Nelson & Whitehead, 2021). The reliance of these large-bodied species on a diet dominated by fruits may drive foraging activities, navigating different habitats in search of abundant and varied fruit resources (Naniwadekar et al, 2019). This foraging behaviour, coupled with their capacity to act as module connectors, underscores their importance in maintaining the functionality of frugivory networks across various ecosystems. Module connectors play a pivotal role in maintaining network cohesion and facilitating ecological interactions across different ecological niches (Olesen et al, 2007). In contrast, the peripheral species had localised influence on the overall network structure and tended to be smaller-bodied individuals, with a lower proportion of frugivory in their diets. These findings underscore the importance of specific keystone species in maintaining the integrity and connectivity of frugivorous networks and highlight the need for focussed conservation efforts.

Species with higher frugivory rates and elongated tail lengths played more central roles within the network, acting as crucial connectors. Similar observations of these traits influencing species centrality have been documented in other frugivore networks (Carnicer et al, 2007; Mello et al, 2015; Sebastian-Gonzalez, 2017). Long-tail length may be associated with increased dispersal ability, which is often associated with network centrality (Montoya-Arango et al, 2019), and may provide greater stability and balance in navigating dense forest vegetation and allowing species to access a greater diversity of fruits (Pell & Jones, 2015; Revelo Hernandez et al, 2016; Li et al, 2022). Longer dispersal distances and increased mobility may facilitate interactions with a more diverse array of plant species driving network centrality.

Our findings challenge the conventional expectations regarding the roles of body size and gape width, other studies have found that increased body and beak size are associated with network centrality (Montoya-Arango et al, 2019). This is because larger birds with large gape widths tend to eat a wide variety and quantity of fruits and seeds (Moulatlet et al, 2022), and large gape widths are typically linked to the ability to access a broader range of food resources (Wheelwright, 1985; Levey, 1987). However, higher frugivory rates and longer tail lengths were associated with centrality and these traits may ultimately be associated with a similar dietary strategy i.e. consumption of a large diversity and quantity of fruits, in the group of birds that we studied.

In our study, several connector species were smaller-bodied, generalist species, such as the Clay-coloured Thrush and Palm Tanager. The ability of smaller, generalist species to bridge distinct communities underscores the complex dynamics at play in frugivore networks and suggests that factors

beyond body size and beak size contribute to species' roles in shaping network structure. Generalist species often exhibit a much greater dietary flexibility, allowing them to exploit a broader range of resources (Palacio et al, 2016). In addition, these two species are highly abundant at the study site and represent a large proportion of the faecal samples studied, which increases the likelihood of diet overlap with other species both within our sampling design but more broadly across the ecosystem and can ultimately drive central positions in the network.

The robustness of our findings regarding the identification of module connectors within the frugivore network, specifically the prominent roles of the Clay-coloured Thrush (Turdidae) and Palm Tanager (Thraupidae), could be questioned given the highly uneven sample sizes of the individuals and these species featuring prominently in the total samples. However, the alignment of our observations with established knowledge from previous studies, particularly the work of Pizo et al. (2021) and Quintero et al. (2020), serves to validate our conclusions and underscores the potential significance of these species in the local frugivore network structure of Panama. Pizo et al. (2021) highlighted the significant contributions of *Turdidae* (thrush) and *Thraupidae* (tanager) families to frugivory in the Neotropics, reinforcing our observation that these species are likely to act as pivotal connectors within the local frugivore network. Similarly, Quintero et al. (2020) emphasised the diverse diet of thrushes, tanagers, and toucans, which includes a wide range of fruit species and sizes, supporting our inference that these species play a central role in the network due to their versatile dietary preferences.

4.5.3 Robustness to different extinction scenarios

The frugivore network was vulnerable to the targeted removal of species with higher frugivory rates and elongated tail lengths. This refers to the network's sensitivity and potential disruption when specific species are selectively removed. It highlights how susceptible the network is to alterations caused by the loss of certain frugivorous bird species. Frugivory rate is a pivotal indicator of a species' dependence on fruits for sustenance, and these species tend to play important roles in seed dispersal and plant regeneration. On the other hand, tail length, often associated with foraging strategies and habitat utilisation, can influence a species' access to certain fruit resources (Luck et al, 2012; Pigot et al, 2016; Pena et al, 2021), shaping its position within the network. The loss of species from the network was more rapid when species with higher frugivory rates and elongated tail lengths were selectively removed, compared to the rate of extinctions when species were removed at random. This outcome suggests these species play pivotal roles in maintaining network integrity and their removal may trigger cascading effects, disrupting the balance of interactions within the frugivore network (Naniwadekar et al, 2019; Lamperty & Brosi, 2022). These species, which are central to the network, connect a larger number of nodes across the network and contribute significantly to the stability and functioning of the entire ecosystem.

4.5.4 Impact of non-native plants on frugivory network

Almost 28% of plant species were connectors within the network, including three non-native plant species (*Syzygium jambos*, *Syzygium cumini* and *Mangifera indica*). Plant height significantly influenced the centrality of species within the network, where taller plants had a greater number of interactions and connectivity within the network. Taller plants, extending into various canopy layers, potentially provide resource accessibility to a broader spectrum of frugivorous avian species (Vissoto et al, 2022) and have a larger crop size and so provide greater abundance of resources (Wright et al, 2007). Contrastingly, other plant traits, including seed size, nativeness, and woodiness, did not demonstrate a discernible impact on species centrality.

The inclusion of non-native plant species as connectors suggests that certain non-native plants have successfully integrated themselves into the frugivory network. This inclusion may be indicative of a competitive advantage, where non-native species are outcompeting native species for dispersers (Cordero et al, 2023). The inclination of frugivores to prefer non-native fruits may disrupt established seed dispersal patterns for native species, thereby influencing their ability to regenerate and sustain viable populations, ultimately leading to a shift in community composition over long-term (Spotswood et al, 2012; Vizentin-Bugoni et al, 2021). However, while competition for dispersers may have negative implications for native plant reproduction, the provisioning of resources during seasons of dormancy or non-fruiting periods among native plants could offer a novel resource for the frugivore community (Heleno et al, 2013). The dynamics of this interaction merit further investigation to discern whether non-native plants are providing complementary resources or if their introduction has led to the displacement of native counterparts. This adaptability of non-native species to assume connector roles may have implications for the overall stability and functioning of the ecosystem. While these non-native connectors contribute to the overall connectivity, their introduction may also introduce new interactions, altering the traditional relationships between frugivores and native plants.

The removal of non-native plants, via permutation analysis, did not impact network *nestedness* (the order and organization of interactions within a network) or *connectance* (quantifies the proportion of realised interactions in a network relative to all possible interactions). This implies that, at least in the context of our study, the overall arrangement of interactions and the density of connections in the frugivore network remained relatively stable when non-native plants are removed. Our findings are complimented by the study Ribeiro da Silva & Pizo (2020) that highlighted that, despite non-native plants forming a substantial part of the generalist core of interacting species, the simulated removal of these species had no discernible impact on the key metrics characterising network topology. These results suggest that the fundamental structure of the frugivore network remains unchanged post non-native plant removal, pointing to potential adjustments in frugivore foraging behaviours towards native

plants. i.e. a compensatory shift in dietary preferences. It is expected that this shift in foraging behaviour will likely benefit and favour plants with the most connections and interactions (Barabási & Albert, 1999; Ribeiro da Silva & Pizo, 2020) or else increase the interactions of already previously connected plant species (Costa et al, 2018). This adaptability could contribute to the maintenance of *nestedness* and *connectance*, as frugivores dynamically respond to changes in resource availability.

In contrast network *robustness* (refers to the ability of a network to maintain its structure and functionality despite the removal of nodes or links) increased with removal of non-native species compared to random species. This suggests that the frugivore network, in our study area, may be more resilient and less susceptible to disruptions when non-native plant species are not present. This could be attributed to the reduction of competition between native and non-native plant species, and ultimately the reduction of functional redundancy (Traveset & Richardson, 2006; Kuebbing & Nunez, 2016). The removal of non-native species allows native species to succeed without constraints on resources and/or local seed dispersers, thereby reinforcing the stability of the network (Heleno, 2020). The heightened network robustness indicates that the removal of non-native plants contributes to the overall stability and functionality of the frugivore interaction network.

4.5.5 Caveats

While our study provides valuable insights into the dietary preferences, network structure, and species roles within the frugivore community of Central Panama, it is crucial to acknowledge several limitations that may influence the interpretation of our findings. A significant limitation of our study is the relatively small sample sizes of the individuals analysed for each species. Small sample sizes can lead to skewed results, especially when attempting to infer broader ecological patterns or behaviours from a limited dataset. This is particularly relevant when identifying a species role within the network, as the species found to be connector species are represented by a larger proportion of the samples analysed. Therefore, the prominence of certain species as module connectors may be an artifact of sample size rather than a true reflection of their network centrality. This limitation necessitates cautious interpretation of our findings and calls for further research with larger sample sizes to validate and expand upon our observations.

A further limitation to acknowledge is that our methodology only provides a snapshot of these interactions at a specific time and within defined spatial subsets. While our deployment of mist nets across various ecological niches, from urbanised areas to primary forest edges, aimed to cover a broad spectrum of habitats, the actual sampling effort may still reflect a temporal and spatial limitation. Given the dynamic nature of ecological systems, especially those involving frugivorous birds and their plant hosts, our findings should be considered within the context of the specific conditions under which they were obtained. Future studies could benefit from expanding the temporal scope and increasing the

spatial coverage to further enrich our understanding of the complex web of trophic interactions within this ecosystem.

4.5.6 Conclusion

Our study contributes to the global understanding of frugivore interaction networks, emphasising the fundamental principles governing dietary preferences, network structure, and species roles. The adaptability of frugivores to anthropogenic influences mirrors broader trends observed in avian communities worldwide where many species are adjusting their foraging strategies in order to exploit opportunities presented by human-altered landscapes and capitalise on novel food resources. The identification of keystone and peripheral species aligns with established ecological network principles where keystone species typically exhibit characteristics such as large body size, large beak gape, and a high proportion of frugivory in their diets (Escribano-Avila et al, 2018). The impacts of traits on network robustness resonate with broader ecological studies that the removal of species with high connectivity and specific traits (frugivory rate, tail length) disproportionately weakens network robustness highlighting the crucial influence of keystone species on frugivory networks (Ramos-Robles et al, 2018).

The resilience of the frugivore network to certain non-native plants confirm trends observed in other ecosystems undergoing rapid environmental changes. The network analysis explained significant differences in diet compositions among bird species, revealing a complex interplay of body mass, frugivory rate, beak width, and foraging strategy in shaping dietary profiles. The identification of specific plant species, such as *Myrcia spp*, *Syzygium spp* and *Trattinnickia aspera* (Supplementary table 2C; figure 3B), as key contributors to dietary patterns adds depth to our understanding, highlighting the pivotal role played by not only native plant species but also non-native plant species in shaping the local ecological landscape.

The structured network, partitioned into distinct communities, stresses the modular nature of frugivore interactions, where keystone species are crucial intermediaries facilitating interactions across distinct modules. Contrary to conventional expectations, our analysis of centrality challenged the expected roles of body size and beak size, where larger birds and those with larger beaks tend to have heightened centrality. Instead, we found that central species had longer tail lengths or a greater proportion of frugivory in their diets, which emphasises the need for further exploration of the factors influencing species centrality within frugivore networks. The role of non-native plants on frugivory networks also deserves further study as we found that removal of non-native plants drove increases in network robustness suggesting that these non-native species can increase network instability.

Our findings have far-reaching implications for conservation strategies, emphasising the need for a comprehensive approach that considers both native and non-native plants, and highlights that the preservation of keystone frugivore species is paramount for ensuring the stability and resilience of frugivorous networks in the face of ongoing environmental changes. These findings pave the way for future research avenues, and further exploration of the ever-changing relationships between frugivorous avian species and their plant counterparts in tropical ecosystems.

4.6 Supplementary material

Supplementary table 1. Faecal samples from 97 individuals across 21 bird species in Gamboa, Central Panama between January-March 2022. Collected from six different netting sites.

Species	Latin name	Date	Time	Sample	Site
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	10:10	1	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	13:20	2	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	14:25	3	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	15:10	4	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:00	5	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:25	6	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:30	7	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:40	8	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:40	9	School
Clay-coloured Thrush	<i>Turdus grayi</i>	13/01/2022	16:45	10	School
N/A	N/A	N/A	N/A	11	N/A
Palm Tanager	<i>Thraupis palmarum</i>	13/01/2022	16:50	12	School
Palm Tanager	<i>Thraupis palmarum</i>	13/01/2022	17:30	13	School
Palm Tanager	<i>Thraupis palmarum</i>	13/01/2022	17:30	14	School
Clay-coloured Thrush	<i>Turdus grayi</i>	14/01/2022	09:50	15	School
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	10:55	16	Resort
Palm Tanager	<i>Thraupis palmarum</i>	15/01/2022	11:25	17	Resort
Palm Tanager	<i>Thraupis palmarum</i>	15/01/2022	11:30	18	Resort
Palm Tanager	<i>Thraupis palmarum</i>	15/01/2022	11:35	19	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	15/01/2022	11:50	20	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	15/01/2022	11:55	21	Resort
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	14/01/2022	08:00	22	School
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	12:00	23	Resort
Palm Tanager	<i>Thraupis palmarum</i>	15/01/2022	12:10	24	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	13:00	25	Resort
Palm Tanager	<i>Thraupis palmarum</i>	15/01/2022	13:20	26	Resort
Masked Tityra	<i>Tityra semifasciata</i>	15/01/2022	13:50	27	Resort
Masked Tityra	<i>Tityra semifasciata</i>	15/01/2022	15:20	28	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	16:15	29	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	16:45	30	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	15/01/2022	16:55	31	Resort
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	14/01/2022	08:00	32	School
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	14/01/2022	09:10	33	School
Masked Tityra	<i>Tityra semifasciata</i>	15/01/2022	16:55	34	Resort
Masked Tityra	<i>Tityra semifasciata</i>	16/01/2022	07:10	35	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	16/01/2022	09:45	36	Resort
Great Kiskadee	<i>Pitangus sulphuratus</i>	16/01/2022	10:45	37	Resort
Keel-billed Toucan	<i>Ramphastos sulfuratus</i>	15/01/2022	16:05	38	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	16/01/2022	10:55	39	Resort

Great Kiskadee	<i>Pitangus sulphuratus</i>	16/01/2022	14:10	40	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	16/01/2022	14:30	41	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	16/01/2022	15:00	42	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	16/01/2022	15:15	43	Resort
Blue-gray Tanager	<i>Thraupis episcopus</i>	16/01/2022	16:50	44	Resort
Masked Tityra	<i>Tityra semifasciata</i>	16/01/2022	17:00	45	Resort
Masked Tityra	<i>Tityra semifasciata</i>	16/01/2022	17:25	46	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	08:15	47	Resort
Golden-collared Manakin	<i>Manacus vitellinus</i>	17/01/2022	08:25	48	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	09:25	49	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	09:45	50	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	10:45	51	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	10:45	52	Resort
Blue-gray Tanager	<i>Thraupis episcopus</i>	17/01/2022	11:10	53	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	13:00	54	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	17/01/2022	14:00	55	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	17/01/2022	16:00	56	Resort
Golden-collared Manakin	<i>Manacus vitellinus</i>	18/01/2022	08:10	57	Resort
Crimson-collared Tanager	<i>Ramphocelus sanguinolentus</i>	18/01/2022	10:00	58	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	18/01/2022	10:30	59	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	19/01/2022	07:45	60	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	19/01/2022	14:30	61	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	19/01/2022	10:45	62	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	20/01/2022	07:20	63	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	20/01/2022	07:45	64	Resort
Yellow-green Tyrannulet	<i>Phylloscartes flavovirens</i>	20/01/2022	09:00	65	Resort
Masked Tityra	<i>Tityra semifasciata</i>	20/01/2022	09:20	66	Resort
Masked Tityra	<i>Tityra semifasciata</i>	20/01/2022	09:30	67	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	20/01/2022	09:30	68	Resort
Black-cheeked Woodpecker	<i>Melanerpes pucherani</i>	20/01/2022	11:00	69	Resort
Black-cheeked Woodpecker	<i>Melanerpes pucherani</i>	20/01/2022	11:00	70	Resort
Golden-hooded Tanager	<i>Stilpnia larvata</i>	20/01/2022	11:15	71	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	20/01/2022	11:45	72	Resort
Streaked Flycatcher	<i>Myiodynastes maculatus</i>	20/01/2022	12:30	73	Resort
Slaty-tailed Trogon	<i>Trogon massena</i>	21/01/2022	07:30	74	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	21/01/2022	08:30	75	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	23/01/2022	08:45	76	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	23/01/2022	09:15	77	Resort
Clay-coloured Thrush	<i>Turdus grayi</i>	23/01/2022	10:45	78	Resort
Black-cheeked Woodpecker	<i>Melanerpes pucherani</i>	23/01/2022	14:15	79	Resort
Gartered Trogon	<i>Trogon caligatus</i>	23/01/2022	15:00	80	Resort
Common ground Dove	<i>Columbina passerina</i>	26/01/2022	15:45	81	Jims
Whooping Motmot	<i>Momotus subrufescens</i>	27/01/2022	08:00	82	Jims
Gartered Trogon	<i>Trogon caligatus</i>	27/01/2022	14:30	83	Jims

Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	28/01/2022	09:00	84	Jims
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	30/01/2022	09:45	85	Jims
Slaty-tailed Trogon	<i>Trogon massena</i>	30/01/2022	10:00	86	Resort
Gray-headed Chachalaca	<i>Ortalis cinereiceps</i>	14/02/2022	09:20	87	School
White-tipped Dove	<i>Leptotila verreauxi</i>	15/02/2022	10:55	88	School
Whooping Motmot	<i>Momotus subrufescens</i>	15/02/2022	11:45	89	School
Keel-billed Toucan	<i>Ramphastos sulfuratus</i>	22/02/2022	11:00	90	Marsh
Slaty-tailed Trogon	<i>Trogon massena</i>	24/02/2022	16:30	91	Marsh
Tropical Mockingbird	<i>Mimus gilvus</i>	12/03/2022	07:45	92	Park
Pale vented Pigeon	<i>Patagioenas cayennensis</i>	15/03/2022	06:30	93	Roundabout
Olive-throated Parakeet	<i>Eupsittula nana</i>	16/03/2022	07:45	94	Roundabout

Site Coordinates:

School – 9.1176, -79.6995
Marsh – 9.1214, -79.6942

Resort – 9.1271, -79.6946
Roundabout – 9.1187, -79.6958

Jims – 9.1192, -79.6981
Park – 9.1180, -79.6969

Supplementary table 2A. Test results of Jaccards dissimilarity index for bird traits influencing the difference in diet composition across 94 faecal samples.

Permutation test results of Jaccard's dissimilarity index for bird traits					
Vectors					
	MDS1	MDS2	r2	Pr(>r)	
Body mass	-0.586	0.810	0.058	0.063	
Log body mass	-0.580	0.815	0.034	0.199	
Frugivory rate	0.213	0.977	0.072	0.037	
Beak length - culmen	-0.777	-0.629	0.011	0.604	
Beak length - nares	-0.535	-0.845	0.013	0.564	
Beak width	-0.524	-0.851	0.049	0.097	
Beak depth	-0.554	-0.832	0.044	0.118	
Tarsus length	-0.162	0.987	0.048	0.103	
Wing length	-0.851	0.523	0.033	0.205	
Secondary length	-0.600	0.800	0.040	0.158	
Tail length	-0.666	0.746	0.033	0.221	
Hand wing index	-0.421	-0.907	0.030	0.242	
Factors					
Foraging strategy			0.117	0.022	
Habitat			0.078	0.013	
Trophic niche			0.146	0.001	
Analysis of Variance					
	Df	Sum sq	Mean sq	F value	Pr(>F)
Species	20	2.361	0.118	5.017	1.7e-07
Residuals	73	1.718	0.234		

Supplementary table 2B. Permutation of variance analysis results of differences in diet composition for all significant bird species combinations.

Permutation test of variance	
Significant species combinations	P value
<i>M. subrufescens</i> - <i>O. cinereiceps</i>	0.001
<i>M. subrufescens</i> - <i>M. vitellinus</i>	0.005
<i>M. subrufescens</i> - <i>P. sulphuratus</i>	0.001
<i>M. subrufescens</i> - <i>T. caligatus</i>	0.001
<i>M. subrufescens</i> - <i>T. episcopus</i>	0.001
<i>M. subrufescens</i> - <i>T. grayi</i>	0.027
<i>M. subrufescens</i> - <i>T. massena</i>	0.001
<i>M. subrufescens</i> - <i>T. palmarum</i>	0.021
<i>M. subrufescens</i> - <i>T. semifasciata</i>	0.005
<i>M. pucherani</i> - <i>T. massena</i>	0.007
<i>M. vitellinus</i> - <i>O. cinereiceps</i>	0.045
<i>M. vitellinus</i> - <i>P. sulphuratus</i>	0.001
<i>M. vitellinus</i> - <i>T. caligatus</i>	0.001
<i>M. vitellinus</i> - <i>T. episcopus</i>	0.005
<i>M. vitellinus</i> - <i>T. massena</i>	0.005
<i>O. cinereiceps</i> - <i>P. sulphuratus</i>	0.027
<i>P. sulphuratus</i> - <i>T. caligatus</i>	0.003
<i>P. sulphuratus</i> - <i>T. episcopus</i>	0.001
<i>P. sulphuratus</i> - <i>T. massena</i>	0.005
<i>P. sulphuratus</i> - <i>T. semifasciata</i>	0.039
<i>T. caligatus</i> - <i>T. episcopus</i>	0.001

Supplementary table 2C. Test results of Jaccard's dissimilarity index for plant species influencing the difference in diet composition across 94 faecal samples.

Permutation test results of Jaccard's dissimilarity index for plant species				
	Vectors			
	MDS1	MDS2	r2	Pr(>r)
<i>Alibertia edulis</i>	-0.57872	0.81553	0.049	0.077
<i>Areca mogeana</i>	0.80932	-0.58737	0.0605	0.069
<i>Bactris gasipaes</i>	0.80932	-0.58737	0.0605	0.069
<i>Brahea decumbens</i>	0.80932	-0.58737	0.0605	0.069
<i>Brahea dulcis</i>	0.80932	-0.58737	0.0605	0.069
<i>Cavanillesia platanifolia</i>	-0.48222	-0.87605	0.0671	0.079
<i>Chrysophyllum argenteum</i>	-0.81983	0.57261	0.0524	0.082
<i>Combretum sp</i>	0.08435	-0.99644	0.053	0.099
<i>Cordia alliodora</i>	0.30664	0.95183	0.0697	0.059
<i>Cordia subcordata</i>	0.30664	0.95183	0.0697	0.059
<i>Kentiopsis oliviformis</i>	0.80932	-0.58737	0.0605	0.069
<i>Mabea occidentalis</i>	-0.47437	-0.88033	0.0637	0.054
<i>Piper colonense</i>	0.03875	-0.99925	0.0694	0.068
<i>Brahea brandegeei</i>	0.81536	-0.57896	0.0817	0.028
<i>Brosimum guianense</i>	0.05618	-0.99842	0.0962	0.014
<i>Cecropia insignis</i>	0.3367	-0.94161	0.0756	0.024
<i>Cenchrus echinatus</i>	-0.85805	0.51357	0.0927	0.013
<i>Daucus carota</i>	-0.48461	0.87473	0.0812	0.025
<i>Digitaria sanguinalis</i>	0.55155	-0.83415	0.0711	0.036
<i>Ficus insipida</i>	-0.54245	-0.84009	0.0953	0.013
<i>Miconia aponeura</i>	-0.46243	-0.88666	0.0772	0.034
<i>Miconia argentea</i>	-0.78282	-0.62225	0.0861	0.016
<i>Myriocarpa longipes</i>	0.44868	-0.89369	0.0673	0.048
<i>Oenocarpus mapora</i>	0.81536	-0.57896	0.0817	0.028
<i>Pinus chiapensis</i>	0.64173	-0.76693	0.0965	0.017
<i>Trema micranthum</i>	-0.95196	0.30622	0.0779	0.032
<i>Croton fragrans</i>	-0.47031	-0.8825	0.1438	0.002
<i>Mikania micrantha</i>	0.08804	-0.99612	0.126	0.01
<i>Ocotea puberula</i>	-0.94688	-0.32158	0.1498	0.002
<i>Acalypha macrostachya</i>	-0.54741	-0.83686	0.2278	0.001
<i>Cespedesia spathulata</i>	-0.5642	-0.82564	0.1808	0.001
<i>Croton hoffmannii</i>	-0.55847	-0.82953	0.2261	0.001
<i>Erythrina fusca</i>	-0.00927	-0.99996	0.2421	0.001
<i>Eugenia oerstediana</i>	0.94756	0.31957	0.1379	0.001
<i>Ficus obtusifolia</i>	0.18075	-0.98353	0.4452	0.001
<i>Myrcia guianensis</i>	0.86045	0.50953	0.2746	0.001

<i>Myrcia sylvatica</i>	0.99867	0.05151	0.5173	0.001
<i>Oplismenus hirtellus</i>	0.56153	-0.82746	0.3038	0.001
<i>Syzygium cumini</i>	0.80952	0.5871	0.3577	0.001
<i>Syzygium jambos</i>	0.99431	0.10652	0.1499	0.001
<i>Trattinnickia aspera</i>	-0.99432	0.10643	0.6769	0.001
<i>Trichilia pallida</i>	-0.53416	-0.84538	0.2231	0.001

Supplementary table 3A. Test results of Jaccards dissimilarity index for bird traits influencing the difference in diet composition across the 6 distinct communities in the network.

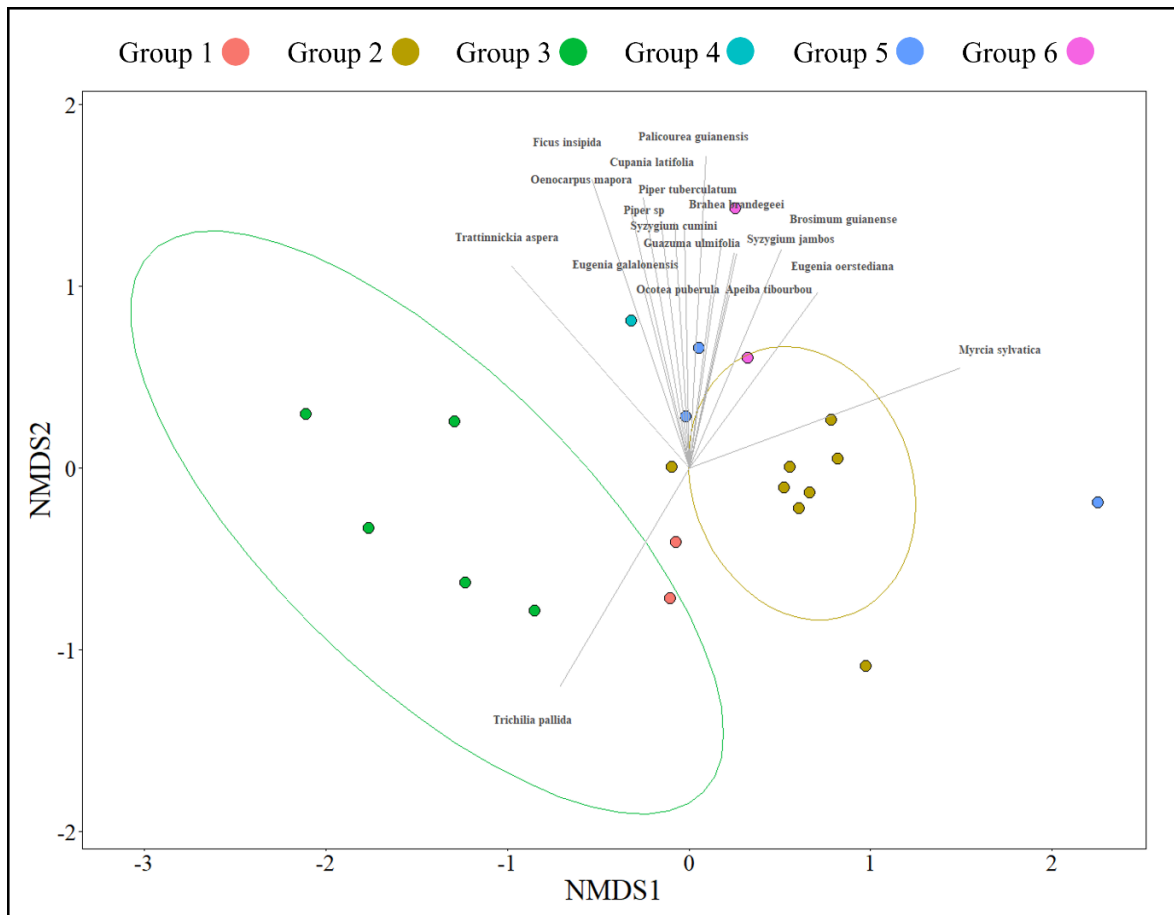
Permutation test results of Jaccard's dissimilarity index for bird traits					
Vectors					
	MDS1	MDS2	r2	Pr(>r)	
Body mass	0.855	0.519	0.006	0.951	
Log body mass	0.708	0.707	0.021	0.847	
Frugivory rate	0.455	0.890	0.282	0.051	
Beak length - culmen	0.088	-0.996	0.027	0.745	
Beak width	0.162	-0.987	0.051	0.599	
Beak depth	-0.092	-0.996	0.057	0.577	
Tarsus length	0.447	-0.894	0.003	0.973	
Wing length	0.537	0.844	0.017	0.862	
Secondary length	0.751	0.661	0.011	0.925	
Tail length	-0.346	0.938	0.014	0.889	
Hand wing index	-0.326	0.945	0.018	0.862	
Factors					
Foraging strategy			0.193	0.660	
Habitat			0.212	0.094	
Trophic niche			0.243	0.169	
Analysis of Variance					
	Df	Sum sq	Mean sq	F value	Pr(>F)
Groups	15	0.226	0.045	2.38	0.088
Residuals	15	0.284	0.019		
Permutation test of variance – Significant community combinations:					
Group 1 – Group 3					0.047
Group 1 – Group 6					0.001

Supplementary table. 3B Test results of Jaccards dissimilarity index for all significant plant species influencing the difference in diet composition across the 6 distinct communities in the network.

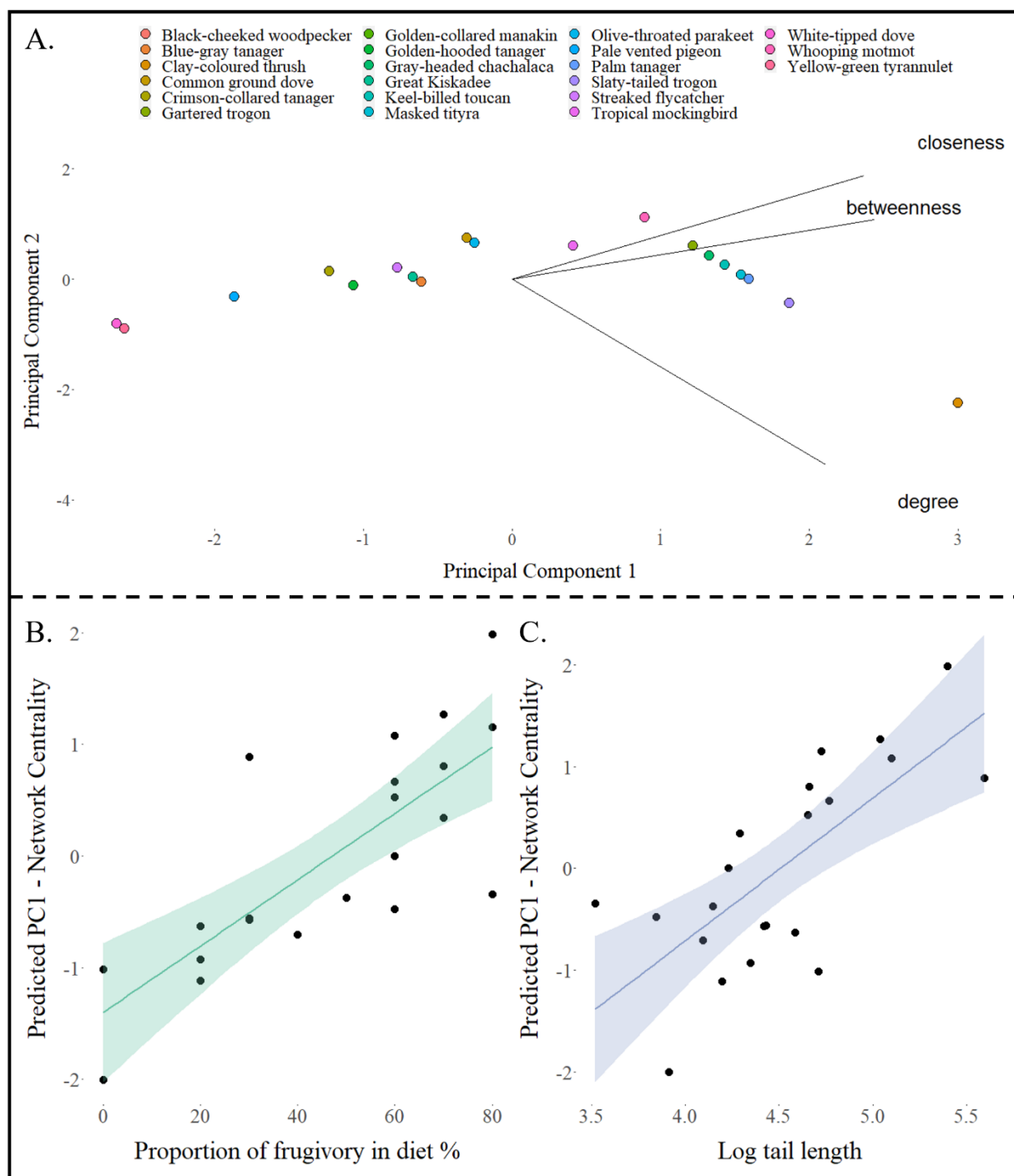
Permutation test results of Jaccard's dissimilarity index for plant species influencing the differences in communities in the network				
	Vectors			
	MDS1	MDS2	r2	Pr(>r)
<i>Areca mogeana</i>	0.06111	0.99813	0.3129	0.052
<i>Artocarpus camansi</i>	0.06111	0.99813	0.3129	0.052
<i>Bactris gasipaes</i>	0.06111	0.99813	0.3129	0.052
<i>Brahea decumbens</i>	0.06111	0.99813	0.3129	0.052
<i>Brahea dulcis</i>	0.06111	0.99813	0.3129	0.052
<i>Calathea lutea</i>	0.06111	0.99813	0.3129	0.052
<i>Cionosicyx excisus</i>	0.06111	0.99813	0.3129	0.052
<i>Johannesteijsmannia magnifica</i>	0.06111	0.99813	0.3129	0.052
<i>Kentiopsis oliviformis</i>	0.06111	0.99813	0.3129	0.052
<i>Miconia sp</i>	0.06111	0.99813	0.3129	0.052
<i>Passiflora edulis</i>	0.06111	0.99813	0.3129	0.052
<i>Piper campanum</i>	0.06111	0.99813	0.3129	0.052
<i>Piper peltatum</i>	0.06111	0.99813	0.3129	0.052
<i>Psychotria biaristata</i>	0.06111	0.99813	0.3129	0.052
<i>Psychotria carthagenensis</i>	0.06111	0.99813	0.3129	0.052
<i>Psychotria marginata</i>	0.06111	0.99813	0.3129	0.052
<i>Swartzia simplex</i>	0.06111	0.99813	0.3129	0.052
<i>Tocoyena pittieri</i>	0.06111	0.99813	0.3129	0.052
<i>Myrcia sylvatica</i>	0.89686	0.44232	0.7271	0.001
<i>Trattinnickia aspera</i>	-0.86043	0.50956	0.5713	0.001
<i>Apeiba tibourbou</i>	-0.00169	1	0.4484	0.007
<i>Eugenia oerstediana</i>	0.41064	0.9118	0.3904	0.006
<i>Ficus insipida</i>	-0.24704	0.96901	0.3794	0.008
<i>Guazuma ulmifolia</i>	-0.00005	1	0.47	0.004
<i>Palicourea guianensis</i>	0.08494	0.99639	0.474	0.004
<i>Brahea brandegeei</i>	0.05101	0.9987	0.3498	0.018
<i>Brosimum guianense</i>	0.17753	0.98412	0.3668	0.016
<i>Cupania latifolia</i>	0.09666	0.99532	0.339	0.023
<i>Eugenia galalonensis</i>	0.05101	0.9987	0.3498	0.018
<i>Ocotea puberula</i>	0.05101	0.9987	0.3498	0.018
<i>Oenocarpus mapora</i>	0.05101	0.9987	0.3498	0.018
<i>Piper sp</i>	0.09666	0.99532	0.339	0.023
<i>Piper tuberculatum</i>	0.09666	0.99532	0.339	0.023
<i>Syzygium cumini</i>	0.31805	0.94807	0.3385	0.027
<i>Syzygium jambos</i>	0.38525	0.92281	0.3119	0.044
<i>Trichilia pallida</i>	-0.5669	-0.82378	0.2832	0.041

Supplementary table 4A & 4B. Results of the LMs for predicting the centrality values of bird species (4A) and plant species (4B) using different traits.

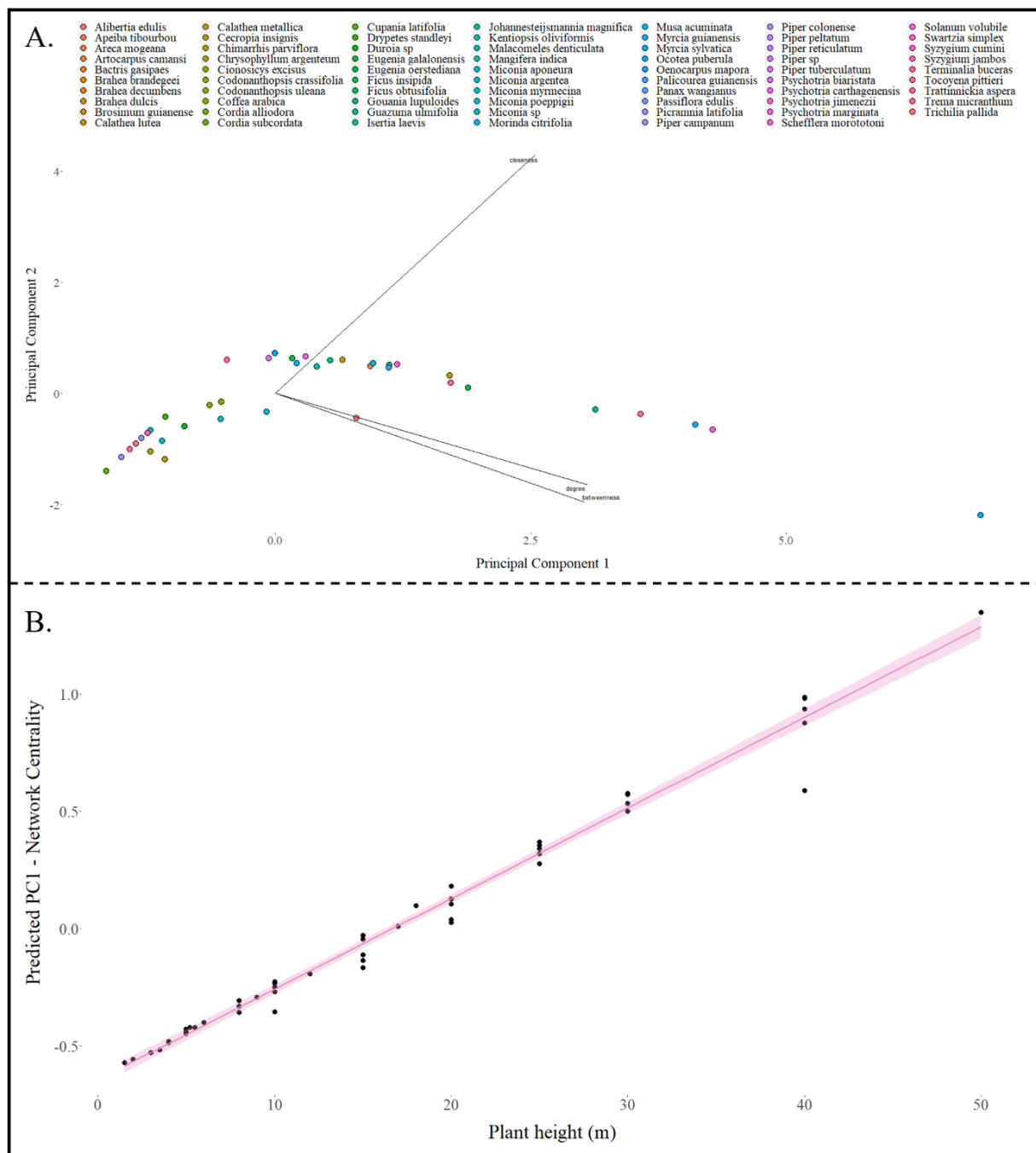
Linear model for predicting bird centrality				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	-6.855	2.441	-2.810	0.012
Frugivory rate (%)	0.027	0.011	2.520	0.021
Log (tail length)	1.240	0.540	2.300	0.034
Linear model for predicting plant centrality				
	Estimate	Std. Error	t value	Pr(> t)
Intercept	-0.626	0.321	-1.951	0.057
Plant height (m)	0.040	0.016	2.510	0.015
Seed length (mm)	-0.006	0.018	-0.329	0.744



Supplementary figure 2. NMDS analysis of plant species which significantly influence the diet compositions of the 6 distinct communities found within the frugivory network.



Supplementary figure 3A. PCA of three network-level metrics (*closeness*, *betweenness* & *degree*) explaining 77% of variation across 21 bird species. 3B. An increase in the proportion of frugivory within a birds diet significantly increases the centrality of the species in the network. 3C. An increase in length of tail significantly increases the centrality of the species in the network.



Supplementary figure 4A. PCA of three network-level metrics (closeness, betweenness & degree) explaining 78% of variation across 69 plant species. 4B. An increase in the height of the plant species significantly increases the centrality of the species in the network.

Chapter 5: General Discussion

5.1 Background – The importance of tropical forests and ecosystem services such as seed dispersal

Tropical forests, comprising only 7% of the Earth's land, host over two-thirds of the world's terrestrial biodiversity and provide crucial ecosystem services (Laurance, 1999; Gardner et al, 2009). These services include maintaining biodiversity, stabilising soils, controlling climates, and acting as carbon sinks (Laurance, 1999; Bonan, 2008; Edwards et al, 2014). Despite their high value, only 10% of tropical forests are protected and their long-term viability is threatened by adjacent human activities (Wittemyer et al, 2008; Schmitt et al, 2009). Deforestation is the primary threat to tropical forests driving habitat loss and fragmentation (Bradshaw et al, 2009). Global tropical forest cover has decreased to less than 30% of its original extent, with 4.1 million hectares of tropical forest cover lost in 2022 alone (Whitmore, 1997; Laurance, 1999; Chazdon, 2014; Pro et al, 2023). Many tracts of continuous forest have been converted to human-modified landscapes, characterised by isolated forest fragments in an agricultural and urban matrix. Human-modified landscapes may not be able to sustain biodiversity as landscape structure impact ecological processes like seed dispersal and pollination (Saunders et al, 1991; Fahrig, 2003; Fischer & Lindenmayer, 2006). As the global population increases, demand for food drives agricultural expansion, a key driver of deforestation. In line with this, tropical nations with high population growth rates show positive correlations with deforestation rates (Hurt et al, 2011). Predictions suggest that by 2050, half of the world's population will inhabit the tropics (Edelman et al, 2014; Lewis et al, 2015; Barlow et al, 2018). Continued habitat fragmentation, land use changes, and climate change could lead to mass species extinctions in tropical forests (Laurance & Useche, 2009). One group of species that is becoming increasingly vulnerable to these changes is frugivorous animals (Newbold et al, 2014; Bregman et al, 2016; Bonfim et al, 2021).

Frugivores are essential for maintaining the process of seed dispersal in global ecosystems (Jordano et al, 2011; Estrada & Fleming, 2012). Understanding and conserving seed dispersal is paramount for the preservation of tropical forests. Seed dispersal, maintained by multiple interactions between plants and animal dispersers, underpins biodiversity maintenance and ecosystem resilience (Peterson et al, 1998; Elmqvist et al, 2003). This ecological process promotes diversity by allowing plant species to colonise new areas, thus avoiding competition with parent plants (Howe & Miriti, 2004). Moreover, it contributes to the resilience of ecosystems, aiding in recovery from disturbances (Sansevero et al, 2011; McConkey et al, 2012). Mutualistic relationships between plants and frugivorous animals are critically important for the health and functionality of tropical forest ecosystems where frugivores can disperse up to 90% of tree species (Howe & Smallwood, 1982; Gentry, 1988). To effectively conserve seed dispersal, a focus on the conservation of the animal species involved is essential (Telleria et al, 2005; Mittelman et al, 2020). Given that a significant proportion of tropical plant species rely on animal-mediated dispersal, conservation efforts must prioritise the fauna that play key roles in this process. Recognising the dominance of animal-mediated dispersal in the tropics, particularly in comparison to

temperate regions, emphasises the need to safeguard these ecological interactions (Wunderle Jr, 1997). Additionally, understanding seed dispersal is vital for adapting to climate change, as it enables plants to establish in new potentially suitable habitats (Mokany et al, 2014). In essence, unravelling the complexities of seed dispersal is not only about the dispersal of individual plant species but also about safeguarding the broader ecological interactions that can sustain and restore invaluable tropical forest ecosystems.

5.2 Navigating fragmented tropical landscapes; understanding how forest fragmentation affects frugivore behaviour

5.2.1 Current knowledge of seed dispersal and knowledge gaps

Our systematic review (*Chapter 2*) shows that the theme of seed dispersal is increasingly well studied, with an exponential increase in frugivorous tracking publications over the last 20 years. Numerous studies have uncovered important information regarding the species that govern seed dispersal. For example, we know that species traits hold key insights into their ecological roles (Mello et al, 2015; Pigot et al, 2016). The morphological adaptations of frugivores, such as beak structure in birds or digestive systems in mammals, further underscore the co-evolutionary relationships between these species and the fruits they consume, and ultimately, the effectiveness of their seed dispersal abilities (Paulino-Neto et al, 2016; Pegman et al, 2017). For example, frugivorous birds with larger beaks will often exhibit a more diverse diet because of their ability to consume a larger selection of fruits, ranging from smaller ones to larger ones (Valido et al, 2011; Brodie, 2017; Velenta & Nevo, 2020). Some frugivores exhibit specialised dietary preferences, focusing on specific fruit types, while others embrace a generalist approach, consuming a broad range of fruits (Schleuning et al, 2011; Dehling et al, 2021). These dietary differences influence frugivore impact on seed dispersal patterns and, consequently, the structure of the plant-frugivore network (Acevedo-Quintero et al, 2020). Habitat preferences of frugivores contribute significantly to their ecological dynamics; for example, some species thrive in undisturbed primary forests while others successfully navigate the challenges of fragmented landscapes, agricultural expanses, and even urban environments (Grass et al, 2014; Da Silveira et al, 2016). Understanding these preferences is crucial for predicting how frugivore communities respond to ongoing habitat changes, especially in the context of widespread deforestation and human-induced landscape modifications.

To understand the response to the changing environment, we first need to understand frugivore behaviour or a typical baseline for their movements. This is where movement ecology comes in to play. The spatial movements of frugivores play a vital role in the seed dispersal process. The ranging patterns, migration behaviours, and home range sizes of frugivores influence the spatial distribution of seeds and

contribute to genetic diversity across landscapes (Pizo & dos Santos, 2011; Cortes & Uriarte, 2013; Borah & Beckman, 2022). Observing the temporal dynamics of frugivore activities, including feeding and movement patterns throughout the day and across seasons, adds a temporal dimension to our understanding, enabling a more comprehensive view of their ecological contributions. *Chapter 2* (Fell et al, 2023) highlights the substantial increase in tracking studies over the last 20 years, which has been facilitated by advancements in tracking technology, but also shows that there are definite knowledge gaps that need to be addressed to improve our understanding of seed dispersal. Global distribution patterns revealed in the review emphasise the importance of considering movement ecology in different ecosystems. The concentration of studies in tropical regions, coupled with the identified gaps in tracking efforts, underscores the potential for movement ecology to guide targeted research. Further studies are needed in Africa, boreal regions, and Central Asia. Integrating tracking approaches can help overcome challenges associated with fieldwork in dense tropical forests, facilitating a greater understanding of frugivore movement in critical tropical regions.

The focal taxa of global studies, particularly the intensive tracking of birds and bats, aligns with movement ecology principles and seed dispersal theory. Frugivorous birds and bats are highly mobile and capable of covering large distances and play key roles in connecting fragmented landscapes through deposition of seeds in different fragments or across the matrices (Galindo-González et al, 2000; de la Pena-Domene et al, 2014). Integrating movement ecology with seed dispersal ecology allows researchers to explore how bird and bat species navigate and utilise diverse habitats, aiding to a more complete understanding of seed dispersal dynamics. We found very few studies focussed on the role of reptiles as dispersers, but reptiles can be important dispersers particularly for island habitats, which often lack a diverse mammal and bird population (Valido & Olesen, 2019). Thus, additional research is required to investigate the involvement of reptiles in tracking studies and their potential significance for seed dispersal.

Chapter 2 reinforced the conclusion of a positive correlation between frugivore body mass and seed dispersal distances (Vidal et al, 2013; Naniwadekar et al, 2019). Larger species tend to have more extensive foraging areas and contribute significantly to long-distance seed dispersal. By incorporating movement ecology principles, researchers can further refine seed dispersal kernels based on the specific characteristics of frugivores, such as their morphological traits, flying capabilities, and behaviour. This would help contribute to more accurate estimations of seed dispersal distances (Nield et al, 2020). The findings from *Chapter 2* led us to develop plans for *Chapter 3*, where we track multiple large-bodied avian frugivores in Central Panama to explore if species of similar size vary in dispersal capabilities due to other traits and behaviours.

5.2.2 Integrating movement ecology into seed dispersal.

The results presented in *Chapter 3* offer compelling insights into the movement behaviours of four species of frugivorous birds and emphasise the need to integrate movement ecology and seed dispersal ecology. The traditional assumption that species' body size alone determines movement behaviour (aforementioned in *Chapter 2*) is challenged by the distinct strategies exhibited by the studied *Amazona*, *Ortalis*, and *Ramphastos* species. We show that the inclusion of additional factors such as wing morphology, ecological preferences, and seasonal variations in resource availability enriches our understanding of the complexities involving animal movement, decision making and in seed dispersal dynamics. This indicates that general theories may not universally apply to all landscapes and local ecosystems and recognises the complexity in ecological systems, where outcomes may not always neatly align with initial expectations.

The observed influence of species traits and life-history characteristics on home ranges and movement patterns revealed a multifaceted relationship between frugivore characteristics and their spatial behaviours. Given the previous general expectation of a positive correlation between body mass and home range size, we would have expected very similar home range sizes between *Amazona*, *Ortalis*, and *Ramphastos* species. However, this study demonstrates the potential significance of traits like wing morphology and foraging preferences (such as vertical stratification within the forest) in shaping movement behaviours (Sheard et al, 2020; Thiel et al, 2021; Weeks et al, 2022). This approach improves our comprehension of the ecological strategies employed by these specific species, providing crucial implications for their role in seed dispersal dynamics. The distinct home range estimates among the studied species, where *Amazona* displaying the largest home-range followed by *Ramphastos* and then *Ortalis*, supports our hypothesis that wing morphology, enabling sustained flight, plays a pivotal role in determining range size. Moreover, we found that the role of life-history, particularly the potential influence of longevity on the extensive home ranges of *Amazona* individuals, underscores the importance of considering temporal factors in movement ecology. Long-lived species with enhanced memory capacities can contribute significantly to seed dispersal as they can track seasonal variations in resource availability optimising their foraging efforts and minimising energy expenditure. This concept of longevity, memory and long-term knowledge of food resources is one which has not yet been fully explored and would make an interesting project if long-term tracking technology could allow it (Baert et al, 2022; Martins et al, 2024).

The variation in daily distance travelled and median step-lengths of the different species unveils diverse foraging strategies. *Amazona* species, with their larger daily distances, show an inclination towards extensive exploration and wide-ranging foraging. This aligns with their wing morphology, enabling sustained flight and efficient coverage of larger areas (Bjork, 2004; Stahala, 2008). In contrast, the

longer median 2-hour step lengths in *Ramphastos* species suggest more focused movements over shorter intervals, potentially reflecting a targeted exploitation of specific resources within localised areas. Whereas *Ortalis* have smaller step-lengths but comparable daily distances to *Ramphastos* which suggests fine-scale and localised foraging behaviour in the understory. The relationships between movement patterns and foraging behaviours among these species offer a window into their ecological roles as seed dispersers. The observed movements suggest that *Amazona* and *Ramphastos* species could be instrumental in enhancing gene flow and promoting plant population resilience over larger spatial scales. In contrast, *Ortalis* species, while limited in their spatial coverage, may play a crucial role in shaping the composition and structure of plant communities in specific microhabitats.

The proportion of home range defined for core use across all species suggests a general ecological strategy, highlighting specific areas for critical activities and broader areas for exploration and wider foraging. However, the observed intra-specific differences in range distribution patterns, particularly among *Ramphastos* and *Ortalis* species, emphasise the importance of habitat accessibility. Larger forest fragments or undisturbed areas encouraged greater dispersal for individuals of each of these species. This helps contribute to the overall understanding of how movement patterns can be influenced by landscape features (Graham, 2001; Diaz Velez et al, 2015; Paxton et al, 2023). This result further encourages the use of comparative studies among different landscape types to investigate if this strategy is indicative of broader patterns across other species in different habitats and at different spatial scales.

Understanding the seasonal dynamics of range distributions is pivotal in unravelling the complexities of frugivorous bird movement ecology due to the distinct fruiting phenologies of different plants and ecosystems. While some of the bird species studied exhibit stable monthly range distributions, others show lagged responses to historical weather patterns. This shows that long-term monitoring is vital in capturing fine-scale variation in movement patterns, emphasising the need for adaptable strategies to effectively track varying food resources. Similarly, our tracking data for one of the *Amazona* individuals reveals that single individuals can present contrasting behaviour across temporal scales. For example, for 18-months this individual did not stray further than ~10 km away from its central home range and then abruptly travelled 25 km south-west through agricultural land uses and then stayed in this area for 8-weeks (Sept-Nov) before returning to the original home range. Previous monitoring in this region suggest that this species does not commonly occupy these habitats (Bradfer-Lawrence, 2019), therefore without long-term monitoring this long-distance movement behaviour would not have been captured.

In conclusion, the integration of movement ecology and seed dispersal ecology emerges as imperative, given the intricate species-specific and individual-specific movement behaviours observed among frugivorous birds. From challenging conventional correlations between body size and movement to unravelling the temporal dynamics of range distributions, this study lays a foundation for a more

inclusive understanding of the role of frugivores in shaping tropical ecosystems. As the study showcases the divergent movement strategies among these species, it underscores the need for integrated approaches in seed dispersal ecology to address ecological challenges and contribute to the study of resilience and diversity of plant communities in their respective habitats.

5.2.3 Frugivory network interactions and what they can tell us about frugivorous networks.

Chapter 4 added yet another level of complexity to understanding seed dispersal by integrating frugivore network interactions into the study of frugivorous communities presented insights into the complex mechanisms of seed dispersal within Central Panama. We revealed the dietary preferences and foraging behaviours of a large group of frugivorous bird species common across Central Panama. We identified key seed dispersers and shed light on the adaptability of frugivores to feed on both native and non-native plant species. This quantification of interactions between birds and plants, coupled with their movement patterns, can allow researchers to estimate the quantity and diversity of seeds moved across landscapes, contributing to our understanding of the spatial distribution patterns of plant species.

The identification of modular structures within frugivore interaction networks represent distinct communities, possibly corresponding to different ecological niches, habitats, or traits. Understanding which bird species act as connectors between these modules provides insights into the spatial distribution of seeds across diverse habitats, creating localised seed shadows. Interestingly, the species studied in *Chapter 3* - *Ramphastos* and *Ortalis* - were module connectors, suggesting that these large-bodied frugivores are potentially important in distributing different plant species across the landscape. We also found the Clay-coloured Thrush and Palm Tanager were module connectors. These smaller species, typically exhibiting greater dietary flexibility and in greater abundances, may serve as crucial links between different plant communities (Walker, 2007; Yoshikawa & Isagi, 2012). Their ability to bridge distinct communities within the network underscores the importance of considering not only the larger, more conspicuous species but also the ecological roles played by smaller, but more abundant frugivores in shaping the spatial distribution of seeds (Moran et al, 2004).

We observed a large proportion of non-native plant species present in the diets of bird species, with several identified as key connectors within the frugivory network. While this finding suggests that non-native plants may serve as an alternative food source, it also implies potential competition with native plant species. If native and non-native plants fruit simultaneously, competition for seed dispersal services may intensify, diverting frugivores away from native plants and ultimately reducing the recruitment of native plants across the landscape (Traveset et al, 2012; Helano et al, 2013). If non-native species instead exploit temporal niches by fruiting outside the primary native fruiting season, they could attract numerous seed dispersers which would facilitate their dispersal into the local landscape (Ramos-Robles et al, 2018; Vergara-Tabares et al, 2018). Understanding the role of these non-native plants in

tropical avian diets is essential for comprehending how frugivore networks adapt to anthropogenic influences and changes in plant community composition.

5.3 Ecological & conservational implications and wider impacts

In the context of conservation and restoration, the insights from these studies guide strategies for preserving biodiversity and managing tropical forests. Identifying keystone species and understanding the role of non-native plants in the network can inform conservation efforts, particularly in the face of ongoing environmental changes and habitat alterations. The integration of network interactions with movement ecology further enhances the predictive power of seed dispersal studies; by linking individual bird movement patterns with dietary preferences and their roles within the network (i.e. module connectors or peripheral species), researchers gain a more comprehensive understanding of the spatial patterns of seed dispersal and how these patterns may respond to alterations in bird populations or environmental conditions. Overall, these studies deepen our understanding of frugivore ecology and offer practical applications for ecosystem management, conservation, and restoration by providing an insight into seed dispersal dynamics across diverse landscapes.

The integration of findings from all three chapters offers a comprehensive understanding of the ecological dynamics of seed dispersal in Central Panama, with far-reaching implications for conservation and ecosystem management. *Chapter 2* provides a theoretical foundation for understanding the ecological importance of seed dispersal across global ecosystems and incorporating insights from this chapter into the subsequent empirical studies helped explore practical implications of seed dispersal dynamics. *Chapter 3* details the individual movement patterns of key frugivorous species and linking the behaviour of these birds to the observed dietary patterns (documented in *Chapter 4*) enriches our comprehension of how local landscapes are navigated and utilised by seed dispersers. This information is pivotal for predicting and managing seed dispersal patterns, especially in fragmented or changing habitats. For example, Toucans and Parrots may be key to moving seeds outside of continuous forests and connecting smaller, fragmented patches, whereas Chachalacas may be more important for creating local seed shadows and influencing seedling survival. Understanding the movement ecology of key species identified by specific traits in *Chapter 3* allows for targeted conservation efforts, ensuring that critical corridors and habitats are preserved to facilitate effective seed dispersal. *Chapter 4* unveils the complex network of interactions between frugivorous birds and plants, showcasing the adaptability of avian communities to both native and non-native plant species. The identification of keystone species and connectors within the frugivore network becomes a cornerstone for conservation strategies. Protecting these key species - not just large-bodied frugivores but smaller, abundant generalists - and the habitats where they play vital roles ensures the maintenance of robust seed dispersal networks, critical for sustaining biodiversity.

At a local scale, the ecological implications are profound. The integration of these chapters reinforces the importance of preserving intact ecosystems and minimising anthropogenic disturbances. The identification of keystone and connector species within frugivore networks emphasises the importance of specific birds in maintaining the integrity of seed dispersal processes. Understanding the roles of individual species and their responses to environmental changes is crucial for the preservation of biodiversity within the local landscape. Moreover, the resilience of frugivore networks to certain non-native plants in our study region, as revealed in *Chapter 4*, challenges traditional conservation paradigms, and necessitates a different approach that recognises the complexity of species interactions. While the removal of non-native plants did not significantly affect the overall structure of the frugivore network, the increase in network robustness suggests that these non-native plants may introduce instability and without them, the frugivory network is more resilient and less susceptible to disruptions. The removal of non-native species may reduce competition between them and the native species, leading to a potential decrease in functional redundancy. This could allow the native plant species to thrive without competition and constraints on resources. This calls for a comprehensive approach that considers the dynamics of both native and non-native plants to ensure the stability and resilience of frugivorous networks.

My thesis is able to contribute valuable insights with broader implications for understanding and managing tropical ecosystems at a global scale. The findings from *Chapter 2* provide a comprehensive overview of the current state of knowledge in the field, informing global conservation efforts by highlighting the critical role of frugivores in maintaining biodiversity and ecosystem functionality. It also establishes a baseline of our current state of knowledge in using movement ecology to estimate seed dispersal distances. This chapter recognises gaps in global knowledge about dispersal and frugivore movement and identifies key taxa and regions that deserve further research. *Chapter 3* advances our understanding of the behaviour of multiple, large-bodied avian species in tropical landscapes, offering crucial long-term information on the daily movements and foraging strategies of different species. This knowledge has implications for global conservation strategies, especially considering the increasing threats to tropical ecosystems worldwide. By identifying species-specific movement patterns, we can help contribute to the development of targeted conservation measures that address the specific needs of key frugivores. Our findings can, for example, help to guide forest restoration efforts by providing information such as recommended minimum distances among forest fragments and guidelines for tree planting/ and forest regeneration planning at the landscape scale. This landscape scale oversight can help to promote frugivores, and the key services they provide, within restoration areas. It also establishes a baseline for typical, natural movements of the study species, that can be compared to changes in landscape use and seasons. *Chapter 4* reveals the ecological relationships among frugivorous birds and their plant counterparts in tropical ecosystems. Understanding the factors influencing dietary preferences, network structure, and the roles of different species has global

implications for conservation. The adaptability of frugivorous communities to anthropogenic influences, including the incorporation of non-native plants into their diets, underscores the need for broad conservation approaches that consider both native and non-native plant species and suggests that conservation strategies must also address the dynamics of introduced species in other environments. Our findings also support and acknowledges the fact that small, generalists species may be just as important to maintaining frugivory networks as large-bodied frugivores and that studies and conservation efforts should not focus solely on the large, enigmatic species.

In summary, my thesis provides a foundation for global conservation efforts by uncovering the complexities of frugivore interactions in tropical ecosystems. The identification of key species, movement patterns, and network dynamics informs conservation practitioners and policymakers, guiding efforts to preserve biodiversity, ecological connectivity, and the long-term health of tropical landscapes.

5.4 *Future research*

The combined insights from the three chapters brings together a review of global literature, frugivore tracking approaches and detailed descriptions of frugivore diets. This multifaceted approach to understanding seed dispersal processes offers a foundation for future research, so we can develop more comprehensive studies of the dynamics that govern seed dispersal processes.

Integration of advanced technologies, such as GPS tracking and molecular analysis, into future research can continue to provide more precise data collection. This technological advance promises a more detailed understanding of spatial patterns and can contribute to the refinement of predictive models, advancing our capacity to anticipate and manage changes in seed dispersal dynamics. Coupling this technological advancement with long-term monitoring emerges as a critical chance for future research, with a focus on unravelling the temporal dynamics of seed dispersal networks. The integration of temporal aspects can reveal how frugivore networks adapt or succumb to climate change and human-induced alterations in tropical habitats. Such longitudinal studies are paramount for predicting and managing the potential cascading effects and resilience of seed dispersal networks. Such studies would enable us to observe how seasonality and climate change are likely to impact the movement of frugivores.

Exploring the behavioural plasticity of frugivorous birds in response to a habitat disturbance gradient is key to understanding the impacts of land-use change. Integrating tracking technologies in different habitats, ranging from primary forests to heavily disturbed areas, can show how avian species change movement behaviours and seed dispersal in the face of land-use changes. Comparative studies tracking frugivore movements in primary forest ecosystems versus disturbed areas would provide an understanding of how habitat alterations influence fine-scale movement and behaviour. Tracking individual birds across these contrasting environments can shed light on whether behavioural plasticity allows for the adaptation of movement patterns, foraging strategies, and dietary preferences. This knowledge is crucial for anticipating how tropical ecosystems might respond to ongoing disturbances and guiding conservation efforts in landscapes altered by human activities.

Delving deeper into the roles and impacts of non-native plant species within seed dispersal networks is a pressing topic for future research. Understanding how frugivores adapt to the presence of non-native plant species is crucial, as it sheds light on the behavioural plasticity of avian species in response to changing ecological conditions. If frugivores can adapt to eat non-native plants in periods of low native fruit availability, then this can support frugivore persistence. However, the adaptability of frugivores to non-native plants holds implications for the broader dynamics of seed dispersal, potentially non-native plants could compete with native plants for dispersal services by frugivores which could have negative impacts on the dispersal of native species. Understanding whether the inclusion of non-native species

enhances or hinders the dispersal of native seeds informs our grasp of the overall consequences of global change on seed dispersal processes. It becomes essential to discern how these interactions contribute to or disrupt the balance between frugivores and native plants, influencing plant community composition and ecosystem dynamics.

The recognition of keystone and connector species within seed dispersal networks underscores the need for targeted conservation strategies to ensure network stability and functionality. Future research should prioritise the development of conservation approaches that specifically identify and target these key ecological species. Habitat restoration is a key conservation strategy and understanding how habitat restoration initiatives can support and sustain keystone and connector species is essential for effective conservation planning. Such understanding involves exploring how restored habitats provide the necessary resources and ecological conditions to foster the activities of these species. By focusing on the habitat preferences, foraging behaviours, and movement patterns of keystone and connector species, researchers can inform habitat restoration strategies that align with the ecological needs of these species. This targeted approach ensures that restored landscapes are supportive environments for the key species instrumental in seed dispersal networks.

Employing molecular tools alongside tracking techniques can offer insights into the connectivity of bird dietary composition across different habitats. Understanding whether there are differences between dietary composition of birds in primary forests compared to disturbed areas can provide an extensive view of the ecological and evolutionary implications of behavioural plasticity in dietary flexibility and downstream seed dispersal processes. Our results provide insights into the adaptability of frugivores to changes in habitat structure and plant community composition. Understanding whether changes in habitat structure can lead to shifts in dietary preferences, influencing seed dispersal dynamics, is a key area for future research. This knowledge is crucial for anticipating the ecological consequences of habitat disturbances and how this may be buffered by behavioural plasticity in seed dispersal, and for guiding conservation efforts in landscapes shaped by human activities.

Expanding the conceptual framework developed in this research beyond frugivorous birds to encompass mammals, particularly bats, could broaden the applicability of the findings and provides insights into seed dispersal dynamics in various taxa. Bats cover extensive distances during foraging, making them pivotal for long-distance seed dispersal. Their unique ability to defecate in flight further accentuates their role in shaping plant communities across diverse habitats.

5.5 Synthesis

Rooted in the tropical landscapes of Central Panama, this thesis navigates the complex dynamics of avian movement ecology and seed dispersal networks. Driven by the need to comprehend the mechanisms governing these interactions, the study unfolds in three chapters: a comprehensive systematic review, an exploration of the movement ecology of large-bodied frugivorous birds, and an analysis of diet composition and network interactions among frugivorous avian species and native and non-native plant species. Commencing with a systematic review, the study examines the existing body of knowledge on tracking frugivorous animals and uses this data to inform seed dispersal distances. Showing that increased body mass of frugivores and the ability to fly are associated with longer dispersal distances. Subsequently, the movement ecology chapter delves into empirical observations, revealing the complex patterns of avian movements influenced by morphological traits and temporal variations. The key results were that species of similar body sizes exhibit highly different movement behaviours and the patterns of site selection and revisitation suggest individualised strategies rather than species-level patterns. This has profound implications for seed dispersal dynamics, with *Amazona* species potentially contributing to long-distance seed dispersal due to their extensive ranging behaviour. The unique movement patterns displayed by *Ramphastos* suggest bursts of high intensity foraging and a potential for contributions to broader seed dispersion. *Ortalis* species displayed a more concentrated foraging behaviour, which may create denser seed shadows, impacting local seed dispersal and seedling survival. The final chapter analyses frugivorous avian diets, where we unravelled the adaptability of these frugivore networks to anthropogenic changes and explored the centrality of specific species. We found that large-bodied frugivores as well as smaller, abundant, generalist species were key connector species within the networks. Similarly, non-native plant species were highly integrated across the frugivore network, with many bird species consuming non-native plants. Collectively, these chapters provide a comprehensive understanding of avian frugivores in tropical ecosystems, shedding light on the relationships governing frugivorous birds and the process of seed dispersal.

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