The species and functional composition of bird communities in regenerating tropical forests

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GENERAL ABSTRACT

The widespread threat of species extinctions caused by the destruction and degradation of tropical primary forest (PF) could potentially be mitigated by the expansion of regenerating secondary forest (SF). However, the conservation value of SF remains controversial, and is dependent on many site- and landscape-scale factors, such as habitat age and isolation. The aim of this thesis was to assess the role that SF can play in conserving forest bird communities in central Panama. We study a chronosequence of SF aged 20 – 120-years-old, with sites either isolated from or connected to extensive PF. Our results suggest that SF supports high levels of avian species diversity, and similar community composition to PF. Whilst forest age plays a small role in determining compositional similarity to PF, connectivity to extensive PF was the main determinant of community composition. However, despite high species richness and complex community composition, some specialist PF bird species were consistently absent from SF, and isolated PF.

The functional diversity of bird communities did not vary substantially across the forest age and isolation gradient, although we did find some inter-guild differences; with distinct responses in communities of avian insectivores and frugivores. Isolation caused shifts in the trophic traits of insectivores, but resulted in alterations in the dispersal traits of frugivores.

The response of bird and tree community composition to forest age and isolation was similar, although isolation had a stronger impact on bird communities. Bird diversity and composition tracked changes in forest structure over succession.

When examining the role of birds in seed-dispersal networks, we found bird gape width was the key predictor of seed size consumed. Large-gaped birds consume a wider variety of seed-sizes than small-gaped birds, and small-seeded trees attract a greater number of bird species than large-seeded trees. These results imply high levels of redundancy among small-gaped avian frugivores and small-seeded plant species, but low levels of redundancy among large-seeded plant species and their avian dispersers. This suggests that large-seeded plants may be most at risk of dispersal failure following any change in avian frugivore assemblages.

Together, these results suggest that SF can play a key role in sustaining most tropical biodiversity, and in maintaining ecosystem services. Our findings emphasise the importance of integrating SF into conservation strategies to support and buffer tropical PF habitats.

DECLERATION OF AUTHORSHIP

I, Rebekah Jane Watts Mayhew, 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: ____

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Chapter 1: General Introduction

1.1 The importance of tropical forests

Tropical forests are arguably the most important terrestrial biomes on Earth (Malhi *et al.* 2014). They are the most species-rich and diverse of terrestrial ecosystems, hosting over half of all biodiversity, and an even greater proportion of undescribed species (Dirzo & Raven 2003, Pimm & Raven 2000). Tropical forests also provide key ecosystem services; they are an invaluable component of the global carbon cycle, contributing more than 30% of terrestrial carbon stocks and net primary production (Dixon *et al.* 1994, Field 1998, Malhi 2012). They also play a key role in global hydrological cycles, and evapotranspiration from tropical forests contributes to precipitation at higher latitudes as well as within the tropics (Avissar & Werth 2005). In addition, tropical forests provide approximately 500 million people with drinking water, fuel wood and animal protein (Millennium Ecosystem Assessment 2005). Thus, in addition to their intrinsic value, the conservation of tropical forests is critical for both the services and economic benefits they provide (Pearson 2016).

1.2 Changing environments in the tropics

Today, tropical forest landscapes are re-shaped by a growing human population and economy that is driving resource demands and concomitantly increasing and intensifying land-use (Foley *et al.* 2005, Geist & Lambin 2002, Perz *et al.* 2005). Centuries of exploitation have seen primary forests (PF) cleared for agriculture and pasture, or replaced with plantations for the production of commercial crops, such as timber, pulpwood or palm oil (FAO 2006, Sodhi & Smith 2007). The UN’s Food and Agricultural Organisation (FAO) estimates that between 1990 and 2015 there was a net loss of 129 million ha of forest, equivalent to an annual loss of - 0.13 % (FAO 2015). Although the global deforestation rate has slowed, from - 0.18 % per annum in the early 1990s to - 0.08 % in 2015, the largest forest losses are still occurring in the tropics, especially in South America and Africa (FAO 2015). In addition to forest clearance, many more PF ecosystems have been degraded through selective logging practices, infrastructure development, fires and hunting (Parry *et al.* 2009).

The majority of tropical landscapes are now human-modified mosaics of PF fragments, degraded forest and regenerating forest, distributed across a matrix of non-forest habitat (Gardner *et al.* 2009). Although large areas of protected PF remain, recent estimates suggest that the area of degraded and regenerating tropical forest is larger than that of undisturbed PF (Brooks *et al.* 2009, FAO 2015). The deforestation and disturbance of PF in the tropics has had a profound effect on the biodiversity of the region (Achard *et al.* 2002, Hansen & DeFries 2004, Wright 2005). The tropics host the majority of all known biodiversity (Dirzo & Raven 2003) thus the continued loss and degradation of tropical forests has the potential to cause mass species extinctions (Dent & Wright 2009).

1.3 Secondary forests and their potential role in biodiversity conservation

As the spatial extent of regenerating secondary forest (SF) increases (FAO 2015), this habitat has become a major feature in most tropical forest landscapes (Wright & Muller-Landau 2006b). Secondary forests are defined as regrowth on land that was previously cleared of its original vegetation for agriculture, pasturelands or timber extraction (Chazdon *et al.* 2010, Dent *et al.* 2013). Natural disturbances, for example landslides, wild fires or extreme weather events, can also initiate this successional process (Van Breugel 2007, Chazdon 2003). However, human impacts are responsible for most of the world’s SF (Brown & Lugo 1990, Guariguata & Ostertag 2001), with the majority occurring as a consequence of agricultural practices. In the 1980s and 1990s small-scale farmers living in tropical frontier regions, were often seen as the primary driver of deforestation of PF, and subsequent growth of SF (Fox *et al.* 2000, Myers 1993). More recently, the drivers of deforestation have tended to be industrial, such as large-scale agriculture, plantations, and ranching, although there is considerable variation between regions (Butler & Laurance 2008, Laurance 2015, Rudel *et al.* 2009). Today, the majority of SF are regenerating on marginal land in hilly or mountainous areas, which are often abandoned when small-scale farming becomes less attractive, and larger scale agroindustrial practices require large areas of flatter terrain (Asner *et al.* 2009, Rudel *et al.* 2009).

Protection of PF is intrinsic to any tropical conservation strategy, due to their complex structure and high species diversity (Gibson *et al.* 2011), however the importance of SF for biodiversity conservation is less certain. It has been proposed that the decrease in PF may be offset by forest planting and the natural regeneration of SF on previously deforested and degraded land (Wright 2005). However, the conservation value of SF will hinge on whether these habitats can maintain similar species composition and ecosystem functions as PF (Chazdon *et al*. 2009, Dent & Wright 2009).

Numerous studies have examined SF succession in order to elucidate the role that they can play in the conservation of tropical species (e.g. Barlow *et al*. 2007a, Chazdon *et al*. 2009, Dent & Wright 2009, Gibson *et al*. 2011). Most studies indicate that the proportion of PF species present in SF increases with age, but also that a wide range of factors influence these trends, such as landscape context, land-use history, and taxa studied. A major challenge for these studies is the length of time required to observe the successional changes at a single site. Studies of succession therefore often use space-for-time substitutions or chronosequences (Johnson & Miyanishi 2008). This method involves identifying a series of plots differing in age since abandonment, and assumes that these plots represent different stages along a single trajectory of successional development (Saldarriaga *et al.* 1988). However, given that landscape and site history affect the accumulation of PF species in SF (Chazdon *et al.* 2009, Dent & Wright 2009), chronosequence data must be interpreted with caution (Chazdon 2008, Johnson & Miyanishi 2008, Norden *et al.* 2009).

Phases of forest succession

Secondary succession is defined as the developmental change in community composition following a disturbance event (Chazdon 2008). Following abandonment of land, the first seedling shrubs and trees emerge from the seed bank, or from newly dispersed seeds of wind-, bird-, or bat-dispersed species with small seeds that require direct light or high temperatures to germinate (Uhl & Jordan 1984). Remnant trees facilitate colonisation of these bird- and bat-dispersed tree species by offering refuge for their dispersers (Guevara & Laborde 1993, Guevara *et al.* 1986). Dramatic changes in vegetation structure and composition occur during the first decade of succession as woody species quickly colonise abandoned land (Brown & Lugo 1990, Guariguata & Ostertag 2001), and the rapid growth of early colonising ‘pioneer’ trees can bring about canopy closure in only 5 – 10 years (Chazdon 2008).

Canopy closure initiates the second phase of forest succession, as early colonising trees increase in basal area and height, limiting light availability in the understorey (Oliver & Larson 1996). These changes are associated with decreasing stem density, and high seedling mortality of light-demanding species of shrubs, lianas and canopy trees (Capers *et al.* 2005). Low light levels in the understorey favour the establishment of shade-tolerant tree and palm species, the seeds of which are brought in from nearby remnant forest by birds, bats and other mammals (Chazdon 2008). Consequently, 10 – 20 years after abandonment, the abundance and composition of tree species begins to shift, signalling the start of the next phase of succession (Chazdon 2008).

This third phase of succession lasts for decades, or even centuries (Chazdon 2008). It is characterised by the gradual turnover of species composition in canopy and subcanopy layers, as early successional tree species die and are replaced with shade-tolerant tree species (Oliver & Larson 1996). The hypothesis is that this gradual replacement of early-successional species with shade-tolerant species will result in a tree community that is equivalent to PF, but this process is poorly quantified and may take centuries (Oliver & Larson 1996).

Patterns in forest structure in secondary forests

With increasing forest age, structural metrics, such as canopy height, basal area, and above-ground biomass increase, while metrics such as stem density tend to decrease, in SF habitats (Chazdon 2008). Primary forests typically feature complex vertical and horizontal structure, with large volumes of deadwood, and large, living, old trees, as well as highly diverse canopy and understorey vegetation (Budowski 1970). Many studies have shown that SF structure rapidly converges on that of PF (Denslow & Guzman 2000, Guariguata & Ostertag 2001, Peña-Claros 2003, Saldarriaga *et al.* 1988). However, the rates and direction of structural development can vary among sites. Above-ground biomass generally increases with SF age (Brown & Lugo 1990, Guariguata & Ostertag 2001, Silver *et al.* 2000), but the time it takes for SF biomass to converge with PF values varies among sites. A meta-analysis of 74 studies by Martin *et al.* (2013) found that on average above-ground biomass in SF approached similar levels to those found in undisturbed forests within 80 years, although below-ground biomass reached only 50% of PF levels in that time-frame. Above-ground biomass of SF tends to approach PF when there are sufficient large trees, since these stems hold a disproportionally large amounts of total biomass in older forests (Brown & Lugo 1990, Hughes *et al.* 1999).

Patterns in tree species richness and diversity in secondary forests

Plant species richness and diversity tends to recover rapidly during succession (Aide *et al.* 1995, Peña-Claros 2003, Toledo & Salick 2006). In Puerto Rico, Aide *et al.* (1996) found that species richness in abandoned pastures reached PF values within 40 years, whilst Pascarella *et al.* (2000) reported that species richness in abandoned pastures and coffee plantations were the same as PF within 25 to 30 years. Studies examining abandoned agricultural fields report similar findings, with SF species richness approaching that of PF within 20 years in both Central Panama and the Bolivian Amazon (DeWalt *et al.* 2003, Peña-Claros 2003).

Patterns in tree species composition in secondary forests

Although plant species richness and diversity approach PF values within 40 years, recovery of species composition takes considerably longer and may never converge with PF. Studies have found that species composition of old secondary forest (70 – 100 years) is still distinct from that of adjacent PF habitat (Denslow & Guzman 2000, Saldarriaga *et al.* 1988). Whether species composition in SF will ever converge with that of PF is uncertain, although it is thought that this might occur within a 100 – 500 year timescale (Chazdon 2003, Finegan 1996, Guariguata & Ostertag 2001), but to date most SF studied are younger than 100 years. Studies that have examined plant species composition at different life stages in SF have found that similarity between seedlings in SF and adults in PF is often higher than similarity between adults in SF and PF, due to the gradual recruitment of shade-tolerant species into the understorey of SF (Norden *et al.* 2009, Peña-Claros 2003). In Costa Rica, Norden *et al.* (2009) examined four SF plots, aged between 12 and 29-years-old, and two PF plots. They found that, although the tree community composition in the SF plots was dissimilar to those of the PF, both seedling and sapling communities were converging with that of the PF community composition. Thus, Norden *et al.* (2009) conclude that reassembly in tree species composition is occurring gradually over succession.

Chazdon (2008) highlights three factors that likely influence the rate of change in species composition in SF over the course of succession. First, long-lived pioneer species can persist for many decades into the successional process, occupying space and slowing the rate of species turnover (Martínez-Garza & Gonzalez-Montagut 1999). Second, low light availability and the absence of canopy gaps in young and intermediate SF can inhibit the establishment of gap-dependent tree species (Dupuy & Chazdon 2006, Nicotra *et al.* 1999). And last, low seed availability can limit the colonisation of PF tree species, especially in fragmented landscapes for species that are animal dispersed (Holl 1999, Hooper *et al.* 2004, Wijdeven & Kuzee 2000).

Patterns in tree functional composition and ecosystem function in secondary forests

While the community composition of a SF may take many years to converge with PF, it is possible that the functional composition may converge rapidly. For example, Dent *et al.* (2013) found that SF increased in similarity to PF over time in community-level shade tolerance, even whilst species composition did not converge. This implies that the proportion of trees displaying both slow growth and high survival traits increases with SF age (Wright 2010), driving increased similarity in the functional composition of PF and SF, despite distinct species composition. Successional trends have also been reported in the functional composition of seed dispersal modes and other tree species' reproductive traits. A study from Costa Rica found that in the months following clear-cutting, nearly all newly established plants were wind-dispersed species, but within three years, 80% of species present were animal-dispersed, similar to the proportion found in PF (Opler *et al.* 1977).

If SF tree species are functionally similar to PF, then SF have the potential to perform the same ecosystem functions. Many ecosystem functions increase rapidly with successional age, such as accumulation of biomass and carbon storage (Chazdon 2014, Guariguata & Ostertag 2001). For example, analysis of aboveground biomass recovery during SF succession in 45 Neotropical forest sites and 1468 forest plots found that aboveground biomass stocks took a median time of 66 years to recover to 90% of PF values, with several sites between 40 – 100-years-old attaining higher biomass than PF (Poorter *et al.* 2016).

These patterns suggest that there may be ecological redundancy among species, with many different species performing the same ecological function (Walker 1992), thus SF may fulfil key ecosystem functions typically provided by PF even if they are compositionally distinct.

1.4 Factors influencing successional trends in secondary forests

Successional trajectories and rates of SF development are dependent on site and landscape factors. Site specific factors may include soil properties and land-use history. Studies have demonstrated that soil properties, such as fertility and texture, can influence the rate of SF recovery (Johnson *et al.* 2000, Moran *et al.* 2000, Zarin *et al.* 2001). The type, duration and intensity of land-use prior to abandonment can have a strong effect on rate of SF successional regrowth; intense and prolonged land-use slows succession, while short periods of moderate cultivation has the reverse effect (Hughes *et al.* 1999, Wandelli & Fearnside 2015). Intense and prolonged land-use negatively affects local edaphic properties, such as soil organic matter and nutrients, reducing site productivity and slowing

SF succession (Aide & Cavelier 1994, Buschbacher *et al.* 1988, Hughes *et al.* 2002b, 2000, Lawrence 2001, Reiners *et al.* 1994). Furthermore, the availability of propagules from a seed bank and resprouts will be greatly reduced with intensive or prolonged land-use (Nepstad *et al.* 1999). For example, long-term, heavy trampling by livestock on pastures degrades soil structure (Aide *et al.* 1995), and the dominance of grasses in abandoned pastures can impede tree seedling colonisation (Moran *et al.* 2000). In consequence, SF regrowth on pastures may be delayed in comparison with that found on agricultural fields (Aide *et al.* 1995, Moran *et al.* 2000), or coffee plantations (Pascarella *et al.* 2000, Zimmerman *et al.* 1995).

As tropical landscapes become increasingly deforested and fragmented, landscape structure will influence both the pattern and the processes of SF succession (Chazdon 2008). Landscape-level studies show that SF more frequently develop in areas close to or bordering existing PF, and that species diversity and composition recover more quickly in areas close to large forest patches (Thomlinson *et al.* 1996). In Puerto Rico, distance to PF was a key predictor of species richness and diversity in a landscape-scale study of SF (Chinea 2002). While in montane Costa Rica, SF were more likely to occur near PF, at higher elevations, further from roads, and within protected areas (Helmer 2000).

Secondary forest regeneration largely depends on seed rain from remnant forest sources (Wijdeven & Kuzee 2000), especially if the availability of propagules form the site’s seed bank has been reduced due to intense or prolonged land-use (Nepstad *et al.* 1999). Landscape factors, including increasing distance to PF, reduced forest connectivity across the landscape and decreasing proportion of forest in the surrounding landscape, all act to reduce seed arrival in regenerating SF. The abundance and species richness of seeds is strongly negatively related to distance from PF; in abandoned pastures seed rain of woody species was highest near forest edges, and dropped sharply beyond 10 – 20 m from the forest (Aide & Cavelier 1994, Wijdeven & Kuzee 2000). Lawrence (2004) demonstrated that in 9 – 12-year-old swidden fallows in Borneo, the quantity and richness of seed rain declined sharply with distance from PF (< 100 m vs. 300 – 500 m). Within abandoned pastures, seed rain is highest below remnant trees, since they attract seed-dispersing birds and bats (Guevara & Laborde 1993, Guevara *et al.* 1986).

Recruitment failure in fragmented and isolated forest may also be related to extinction, or rarity, of large frugivores, which act as important seed dispersers for large-seeded PF species (Turner *et al.* 1997). For example, on South Pacific islands, where large-bodied frugivores are now extinct, large-seeded plants are no longer dispersed since the large seeds are too big for extant, small-bodied birds to swallow and disperse (McConkey

& Drake 2002, Meehan *et al.* 2002, Rogers *et al.* 2017). If long-distance dispersers of larger-seeded tree species are absent or rare then this can lead to dispersal limitation of many late successional species. Accordingly, inter-site variation in successional trajectories and rates of SF development can be partly explained by a combination of site- and landscape-level factors.

1.5 Plant-animal interactions and animal diversity in secondary forests

Biotic interactions, including the interactions between plant species and their pollinators, seed dispersers, herbivores and pathogens, have a large influence on SF successional trajectories. From an animal's perspective, the changes in vegetation structure and species composition during tropical SF regeneration determine the habitat quality and thus the availability of resources upon which animals depend, such as food, shelter, roosting, nesting and mating sites (Chazdon 2014). From the plant's perspective, reproduction, colonisation, establishment and recruitment are all reliant on the availability of animals that pollinate flowers, disperse seeds, and protect plants from herbivores (Chazdon 2014). Recently abandoned land and young SF provide very different types and amounts of resources for animals than older SF and PF (Bowen *et al.* 2007, DeWalt *et al.* 2003), thus faunal assemblages will change during SF succession as forest matures. Furthermore, the diversity and abundance of animals in the early stages of SF regeneration will also be dependent on the landscape context of the site as well as faunal species' mobility, life history traits, and specialisation (Barlow *et al.* 2007a, Chazdon *et al.* 2009, Dent 2010).

A number of meta-analyses have examined patterns in species richness and composition across a range of animal taxonomic groups, and tend to find that faunal diversity and similarity increase with SF age. Based on 39 datasets, Dunn (2004) concluded that species richness in SF could take as little as 20 – 40 years to recover to PF levels. However, faunal composition of certain taxa, ants and birds in particular, was slower to recover. A later study of 15 taxonomic groups in the Brazilian Amazon found that presence of PF species in SF (14 – 19-years-old) was highly idiosyncratic and varied among taxa; ranging from 95% of PF orchid bees present in SF, to < 60% of PF lizards, dung beetles, leaf-litter amphibians and birds (Barlow *et al.* 2007a). The most comprehensive meta-analysis of SF taxa thus far, found that across 65 studies on average

58% of PF species occurred in SF, and similarity to PF increased with forest age (increasing from 35% in SF < 5 years old to 80% in SF > 50 years old; Dent & Wright 2009).

1.6 The importance of birds in secondary forest research

Many studies that assess tropical land-use change have focused on birds, one of the best studied faunal groups in the tropics (e.g. Barlow *et al.* 2007b, Lees & Peres 2006, Robinson 1999, Stotz *et al.* 1996, Willis 1974). Birds provide important ecosystem services, such as pollination, seed dispersal and herbivore control (Sekercioglu 2006, Whelan *et al.* 2008), and their diverse habitat and dietary requirements mean that their response to habitat disturbance varies across species according to their ecology (Hughes *et al.* 2002a, Petit & Petit 2003). Moreover, they are relatively easy to identify, survey and their taxonomy is well known, making them ideal indicators of habitat quality and value.

Patterns of bird species richness and diversity in secondary forests

Avian species richness and diversity tends to increase with forest age, often recovering to PF levels over time. Studies examining these metrics in young SF have generally found reduced species richness and diversity compared to nearby PF (Barlow *et al.* 2007b, Bowman *et al.* 1990, Terborgh & Weske 1969, Tvardíková 2010). For example, Tvardíková (2010) found 98 species in PF, but only 78 species in 7-year-old SF in Papua New Guinea. While in Amazonia, estimated bird species richness was 70 ± 8.1 in 14 – 19-year-old SF but 106.5 ± 6.3 in PF (Barlow *et al.* 2007b).

In contrast, studies that have focused on older SF have found species richness and diversity to be equivalent, or higher to that of PF (Blake & Loiselle 2001, O'Dea & Whittaker 2007, Schulze & Waltert 2004, Sodhi *et al.* 2005). Sodhi *et al.* (2005) compared 40-year-old SF with PF in Central Sulawesi and found that species richness was almost indistinguishable between the two forest types; the mean species richness of avian forest specialists was 31.99 ± 1.38 for PF, while that of SF was 31.40 ± 0.84. At a site in Amazonia, estimated species richness of nocturnal birds was 12 ± 1.81 in PF and 11 ± 1.28 in 40-year old SF (Sberze *et al.* 2010).

The general trend of increasing species richness with forest age is highlighted in chronosequence studies that have included a range of forest ages (Andrade & Rubio-

Torgler 1994, Borges 2007, Raman 1998). Borges (2007) compared three ages of SF with adjacent PF in the Brazilian Amazon. Although he found lower species richness in the young SF (4 -5 years), species richness in middle-aged SF (7 – 15 years), old SF (20 – 35 years) and PF was similar. When bird communities were assessed across a chronosequence of SF plots in India, estimated species richness increased from 11 ± 0.53 in 1-year-old SF to 23.9 ± 1.43 in 100-year-old SF (Raman 1998). A meta-analysis analysis of avian responses to SF succession, comparing data from 44 tropical SF sites with nearby PF, found that total species richness in SF was 12% lower than in PF (Sayer *et al.* 2017). However, they also found that species richness of avian forest specialists increased with forest age, reaching 99% of PF values after 100 years (Sayer *et al.* 2017).

Patterns in bird species composition in secondary forests

Even when the number of bird species present in SF is similar to PF, the species composition may be very different, thus potentially limiting the conservation value of SF. Studies examining younger SF tend to find low levels of similarity in composition (Barlow *et al.* 2007b, Tvardíková 2010). Barlow *et al.* (2007) found that bird assemblages were markedly different between PF and 14–19-year-old SF sites, and Tvardíková (2010) found composition in 7-year-old SF and PF sites was dissimilar.

However, as with species richness, compositional similarity to PF often increases with SF age. Borges (2007) found that bird species composition followed a well-defined gradient related to forest age. Young SF (4 -5 years) was more similar to that of middle-aged forest (7 – 15 years), which in turn was more similar to that of old SF (20 – 35 years). Whilst bird species composition in the 4-5 year old SF and PF differed significantly, there was no difference between the 20-35 year old SF and PF. Sberze *et al.* (2010) study found that the species composition of nocturnal bird communities in the Brazilian Amazon were indistinguishable in 30-year-old SF and adjacent PF.

Compositional development is not necessarily clear-cut; Dunn's (2004) review examined avian species composition in SF (aged between 7 and 100 years) for three studies and found that composition in 100-year old SF was still distinctly different to PF. Furthermore, some avian PF specialists were also still missing after 100 years of SF growth in India (Raman, 1998). Barlow *et al.* (2007) suggest that the species composition of SF and PF is dissimilar because PF is dominated by specialist (i.e. forest) species, while SF contains fewer specialist species and more generalist (i.e. open-landscape/agricultural) species. However, Dent & Wright (2009) predict that if SF is dominated by generalist species then species composition among SF sites should be highly similar irrespective of age. The studies they reviewed however showed no evidence of this, with the high levels of variation among SF sites, very similar to the variation seen between SF and PF sites. In general, it appears that bird community composition becomes more complex with increasing SF age, and that the proportion of forest species in SF grows over time.

Patterns in bird functional composition in secondary forests

While changes in species richness, diversity and community composition have been well documented in SF, less is known about the potential effects these changes might have on ecosystem functions and services. Species respond very differently to disturbance and responses tend to be dependent on species' ecological and morphological traits (Dent & Wright 2009, Lees & Peres 2008, Newbold *et al.* 2013). For example, the extinction risk of birds has been shown to correlate with body size, habitat and diet specialisation, migratory status and generation length (Owens & Bennett 2000, Sekercioğlu 2007).

The loss of species with specific traits has the potential to affect the delivery of ecosystem services; insectivorous birds play an important role in pest control in ecosystems (Van Bael *et al.* 2003), while frugivores are essential for seed dispersal (Sekercioglu 2006, Wenny *et al.* 2011). Both morphological and ecological traits, for example foraging guild, of bird species have been linked to persistence in highly fragmented forests (Lees & Peres 2008, 2009). Lees and Peres (2008) found that medium- and large-sized, non-flocking, canopy frugivores and omnivores were most tolerant of fragmentation, whereas small, flock-following, terrestrial insectivores were most vulnerable to fragmentation. Newbold *et al.* (2013) also reported that the responses of tropical forest bird species to land-use change were related to their traits. Short-lived, small, migratory, primarily non-frugivorous and non-insectivorous forest generalists were more common and more abundant in disturbed habitats. In contrast, long-lived, large, non-migratory, primarily frugivorous or insectivorous forest specialists were both more common and more likely to occur in undisturbed forest. Newbold *et al.* (2013) conclude that the loss of species from disturbed habitats might have important implications for ecosystem services, such as seed dispersal and pollination.

1.7 Factors influencing bird community recovery in secondary forests

The potential for SF to support bird species that occur in PF increases over time (Dent & Wright 2009, Dunn 2004). Studies have linked greater forest structural complexity to increases in species richness, abundance and composition for birds (Casas *et al.* 2016, MacArthur & MacArthur 1961). Therefore, the rapid recovery of forest structure in SF means that these sites may acquire the structural complexity required by PF birds at a relatively young age (DeWalt *et al.* 2003). However, there are additional factors that can influence the recovery of bird communities in SF.

The landscape context of SF, such as distance to PF source populations and level of isolation within the countryside matrix, plays a critical role in determining avian community reassembly (Chazdon *et al.* 2009, Dent & Wright 2009, Wolfe *et al.* 2015). Many tropical forest birds are strongly dispersal limited with poor gap-crossing abilities, and may not be able to colonise SF unless it is contiguous with PF (Van Houtan *et al.* 2007, Lees & Peres 2009, Moore *et al.* 2008, Tobias *et al.* 2013). Forest isolation has been shown to adversely affect forest-dependent, understorey insectivore species more severely than other functional groups (Barlow *et al.* 2006, Ferraz *et al.* 2007, Stouffer *et al.* 2006).

In addition, bird species occurring in isolated forest patches embedded within a non-forest matrix may be more sensitive to various factors such as population fluctuations and local extinction, and so communities in highly isolated patches may never fully converge with that of PF (Powell *et al.* 2016). Thus, the recovery of bird communities in SF is expected to be mediated by both site and landscape factors, including forest age, level of isolation, and connectivity to PF.

1.8 Plant-bird interactions in secondary forests

There are many complex interactions between species in tropical forests (Burslem *et al.* 2005). Many of the interactions between plants and birds provide key ecosystem services, such as pollination, control of invertebrate herbivores and seed dispersal (Sekercioglu 2006), and can help to drive successional changes, thus benefitting both taxonomic groups (Chazdon 2014).

Birds can play a critical role in the control of insect herbivores in tropical forests (Van Bael *et al.* 2008, 2003, Kalka *et al.* 2008). Insect herbivores can remove between 10% and 30% of a plant’s leaf area per year (Coley & Barone 1996), which may have a profound effects on forest succession, as tree species vary in their tolerance to herbivory, and investments in plant defence (Bazzaz *et al.* 1987). Moreover, early successional plant species support higher densities of herbivores, and sustain greater amounts of herbivory than late successional species (Lewinsohn *et al.* 2005). Therefore, insectivorous birds can reduce plant damage via consumption of insect herbivores with positive impacts for SF succession.

In the Neotropics more than 75% of plant seeds are dispersed by frugivorous vertebrates (Howe & Smallwood 1982). Seed dispersal reduces the effects of density-dependent seedling mortality (Comita *et al.* 2010), as well as facilitating forest regeneration in newly abandoned land (Nathan & Muller-Landau 2000). Bird and mammal frugivores often target different plant species (Pizo 2002), and birds and bats are responsible for the majority of long-distance seed dispersal (Wenny *et al.* 2016). Additionally, in fragmented tropical forests that have lost their large mammals, avian seed dispersal may be the only surviving dispersal pathway (Holbrook *et al.* 2002). Consequently, seed dispersal by birds is critical to the maintenance of tropical forests (Howe 1977, Lundberg & Moberg 2003, Sekercioglu 2006, Wunderle 1997), and has the potential to shape succession in SF (de la Peña-Domene *et al.* 2014, Moran *et al.* 2004).

However, many studies have reported declines in avian frugivores in disturbed landscapes (Gray *et al.* 2007, Moran *et al.* 2004, Sekercioglu 2012), which may impede tree regeneration and result in long-term shifts in tree community composition (Galindo-González *et al.* 2008, Sethi & Howe 2009, Terborgh *et al.* 2008). Large-bodied frugivores are particularly susceptible to habitat disturbance (Dirzo *et al.* 2014), which can disproportionately affect large-seeded plant species that are obligately dependent on a small number of large-bodies species for seed dispersal (Wheelwright 1985, Wotton & Kelly 2011). If frugivorous species are not extirpated, but instead present at lower densities, this could lead to a smaller proportion of the fruit crop being dispersed and consequently fewer seedlings, or a greater proportion of seedlings concentrated under the parent plant (Chimera & Drake 2010, Cordeiro *et al.* 2009, Cordeiro & Howe 2003, Sethi & Howe 2009, Sharam *et al.* 2009, Terborgh *et al.* 2008). These changes might result in alterations to plant community composition, and entire forest communities, or even local extirpation of bird dispersed plants (Cordeiro & Howe 2003, McKinney *et al.* 2009, Muller-Landau 2007, Sharam *et al.* 2009, Wright *et al.* 2007a, b, Wright & Duber 2001).

1.9 Thesis aims and objectives

Deforestation and degradation of tropical PF has the potential to cause mass species extinctions. Expansion of regenerating SF may mitigate the loss of PF (Dent & Wright

2009), but the role that SF can play in conservation of PF species hinges on whether these forest habitats can maintain similar species composition and function as PF.

The overall aims of this thesis were to investigate:

- how bird communities respond to successional changes in SF,
- how the landscape context, such as level of isolation, may mediate bird species recovery and ecosystem function in SF, and
- how morphological traits can predict key ecosystem functions, such as seed dispersal.

Bird community data was collected from a chronosequence of tropical SF (20 – 120-years-old) and PF plots, located within a water-matrix in Central Panama, and integrated with key avian morphological traits. The species and functional composition of the tree community are already described at these sites, allowing us to identify how the composition of birds maps onto that of trees across the successional and isolation gradient. Data was also collected on avian frugivore-plant interactions, and combined with other published Neotropical avian frugivore-plant networks, allowing us to ascertain the key morphological traits involved in avian seed dispersal networks. This dataset presents a unique opportunity to identify how the diversity, and species and functional composition of bird communities relates to that of tree communities in SF, as well as the relative importance of forest age and isolation. The chronosequence encompasses a longer timeframe than any other published study, allowing us to examine successional changes in bird and tree communities over an unprecedented length of time. The specific aims of each chapter are detailed below.

Chapter 2: ***Connectivity with primary forest determines the value of secondary tropical forests for bird conservation***

We examine how the species diversity and composition of bird communities change across a successional and isolation gradient, and investigate the relative importance of forest age versus isolation in determining the conservation value of SF.

We considered three main hypotheses: an increase in forest age is associated with an increase in (1) bird species richness and diversity, (2) bird population density, and (3) the similarity of avian community composition to PF. In all cases, we assessed whether the responses to forest age vary among avian groups, and also the extent to which these responses were mediated by the landscape context, in particular by isolation from and connectivity to extensive PF.

Chapter 3: Using avian morphological traits to assess the functional diversity and composition of tropical bird communities across a gradient of forest age and isolation

We investigate the relative importance of forest age versus isolation in determining functional diversity and composition of bird communities in tropical forests. Specifically, we use the morphological traits of birds, and discuss the implications for two ecosystem processes: insect predation and seed dispersal.

First, we ask 1) how well traditional dietary guilds can be mapped onto morphological trait ordination space, and 2) how the proportional representation of dietary guilds varies with forest age and isolation. Second, we focus specifically on insectivorous and frugivorous birds, to address how the area of occupied functional trait space, functional diversity, and trait structure, change with forest age and isolation.

Chapter 4: High concordance between the composition of tropical bird and tree communities across a gradient of forest age and isolation

We assess the potential similarities in the response of bird and tree community composition to forest age and isolation, and examine the relationship between bird communities and forest structure. We also investigate patterns in community composition between frugivorous birds and bird-dispersed trees to investigate if this relationship is more closely related than the whole community.

We considered the following hypotheses; 1) forest isolation will play a greater role in determining bird communities than forest age, whereas forest age will have a greater impact on tree communities than forest isolation, 2) the number and diversity of birds will be positively correlated with increasing forest structural complexity, but this will be mediated by isolation effects, and 3) patterns in frugivorous bird communities and bird-dispersed tree communities will be more tightly related than patterns across the communities as a whole.

Chapter 5: The influence of avian frugivore-plant interactions on seed-dispersal networks in the Neotropics

We examine which avian functional traits best predict the seed sizes they consume, and identify the defining traits of bird species that disperse large-seeded (> 10 mm) tree species. We combine our own field data with datasets from 12 published Neotropical frugivore-plant networks, and a corresponding bird and plant functional trait dataset, to identify key relationships in avian frugivore seed-dispersal networks in the Neotropics.

We test four specific hypotheses; 1) there is a positive correlation between size of plant seed consumed and bird gape width, 2) large-gaped birds ingest a greater diversity of seed sizes than small-gaped birds, 3) small-seeded plant species attract a greater number of bird species than large-seeded plant species, and 4) bird species that ingest large seeds will have a diet that is primarily frugivorous, a high dispersal ability, and be more specialised.

Chapter 6: General discussion

We discuss the implications of our findings, highlighting the importance of landscape context in determining the recovery of bird communities in tropical SF. We also consider regional differences in SF succession, and the relative value of SF in the Neotropics, and how this may impact our conclusions on the potential conservation value of SF for bird communities. Finally, we examine the scope for further research and policy implications of our findings.

Chapter 2: Connectivity with primary forest determines the value of secondary tropical forests for bird conservation

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D. H. Dent and J. A. Tobias supervised the project, L. Bunnefeld provided additional supervision, and all authors commented on draft versions of the manuscript.

2.1 Abstract

Predicted species extinctions caused by the destruction and degradation of tropical primary forest may ultimately be mitigated by the expansion of regenerating secondary forest. However, the conservation value of secondary forest remains controversial, and potentially underestimated, since most previous studies have focused on young, single-aged, or isolated stands. Here we use point count surveys to compare tropical forest bird communities in 20–120-yr-old secondary forest and primary forest stands in central Panama. Secondary forest sites were either isolated from or connected to extensive primary forest. We found that species richness and other metrics of ecological diversity, as well as the combined population density of all birds, was greatest in younger (20-yr-old) secondary forests, and declined in older stands. We show that this counter-intuitive result is likely explained by the greater connectivity between young secondary forests and extensive primary forests at our study site, compared with the more isolated older secondary forest sites. Our results suggest that connectivity with primary forest is a more important determinant of avian species richness and community structure than forest age, and highlight the vital contribution secondary forests can make in conserving tropical bird diversity, so long as extensive primary habitats are adjacent and spatially connected.

2.2 Introduction

Between 2010 and 2015 there was an annual loss of approximately 7.6 million ha of forest globally, with most of this deforestation occurring in the tropics (FAO 2015). Given the majority of all known biodiversity is found in the tropics (Dirzo & Raven 2003), the continued loss and degradation of tropical forests has the potential to cause mass species extinctions (Dent & Wright 2009, Wright & Muller-Landau 2006). It has been proposed that the decrease in primary forest (PF) may be offset by forest planting and the natural regeneration of secondary forests (SF) on previously deforested and degraded land (Wright 2005). However, the conservation value of SF will hinge on whether these habitats can maintain similar species composition and ecosystem functions as PF (Chazdon *et al.* 2009, Dent & Wright 2009).

Many studies that assess the conservation value of tropical SF have focused on birds, one of the best studied faunal groups in the tropics (e.g. Barlow *et al.* 2007b, Lees & Peres 2006, Robinson 1999, Stotz *et al.* 1996, Willis 1974). Birds provide important ecosystem services, such as pollination and seed dispersal (Sekercioglu 2006, Whelan *et al.* 2008), and their diverse habitat and dietary requirements mean that their response to habitat disturbance varies across species according to their ecology (Hughes *et al.* 2002, Petit & Petit 2003). Moreover, they are relatively easy to identify and survey, making them convenient indicators of habitat quality and value.

Studies comparing avian species richness and community structure in SF and PF report mixed results. Some studies have found equivalent or higher species richness in SF compared to PF (Andrade & Rubio-Torgler 1994, Blake & Loiselle 2001, Borges 2007, O’Dea & Whittaker 2007, Schulze & Waltert 2004), while other studies report negative trends with reduced species richness in SF (Barlow *et al.* 2007b, Bowman *et al.* 1990, Gibson *et al.* 2011, Terborgh & Weske 1969, Tvardíková 2010). These conflicting results may stem from three key factors: the age of SF studied, the landscape context, and the responses of different avian groups to habitat change.

In terms of SF age, most studies examining avian diversity in tropical SF have only included young, and single-aged stands (less than 35 yr; e.g. Barlow *et al.* 2007b, Blake & Loiselle 2001, Borges 2007, Terborgh & Weske 1969). With increasing forest age, SF develops greater structural complexity, becoming more similar to PF over time (Guariguata & Ostertag 2001, Pena-Claros 2003). More complex forest structure offers an increased breadth of ecological niches for forest birds (DeWalt *et al.* 2003, Zahawi *et al.* 2015). Thus, the structural complexity that develops over secondary forest succession should provide habitats for increasingly diverse and complex bird communities (Casas *et al.* 2016, MacArthur & MacArthur 1961). Studies focusing on species richness in young SF may therefore underestimate the longer-term value of SF for bird conservation. On the other hand, bird species richness in young SF is often inflated by non-forest species, and thus estimates of conservation value need to consider the recovery of species composition and abundance rather than richness alone. Avian species composition in young SF is typically highly dissimilar to PF (Barlow *et al.* 2007a, Borges 2007, Tvardíková 2010), but tends to track changes in forest structure so that similarity increases with time since abandonment (Andrade & Rubio-Torgler 1994, Borges 2007, Raman 1998).

The landscape context of SF, such as connectivity to PF source populations and level of isolation within the countryside matrix, plays a critical role in determining avian community reassembly (Chazdon *et al.* 2009, Dent & Wright 2009, Wolfe *et al.* 2015). Many tropical forest birds are highly dispersal limited with poor gap-crossing abilities, and may not be able to colonise SF unless it is contiguous with PF (Van Houtan *et al.* 2007, Lees & Peres 2009, Moore *et al.* 2008, Tobias *et al.* 2013). In addition, bird species occurring in isolated SF embedded within a non-forest matrix may be more sensitive to various impacts such as population fluctuations and local extinction. Connectivity to PF is an important factor in SF recovery, and the species composition of bird communities in isolated SF may never fully converge with that of PF (Jones *et al.* 2016, Wolfe *et al.* 2015).

Finally, the response of bird species to forest succession may be mediated by the degree of species specialisation. It has been suggested that generalist, migratory or forest-edge species proliferate in SF as their wider niche breadth makes them better adapted to the conditions found in young forest (Barlow *et al.* 2007b, Stotz *et al.* 1996). In contrast, forest specialists are likely to require foraging and nesting resources only found in more mature forest (Barlow *et al.* 2007b, DeWalt *et al.* 2003). Forest isolation has also been shown to adversely affect forest-dependent, understorey insectivore species more severely than other functional groups (Bradfer-Lawrence *et al*. 2018, Barlow *et al.* 2006, Ferraz *et al.* 2007, Stouffer *et al.* 2006). Thus, the conservation value of SF for birds is affected by species-specific responses mediated by both site and landscape factors, including habitat age, and level of isolation and connectivity to PF.

Here, we examine the species richness and composition of bird communities in central Panama across the longest SF chronosequence studied to date, with forest aged from 20 to 120 yrs, as well as PF controls. Across this age gradient, we sampled forests that were either isolated from or connected to extensive PF. This landscape presents an opportunity to examine how bird communities change across both successional and isolation gradients, and to investigate the relative importance of forest age versus isolation in determining the conservation value of SF. Focusing on a partially interconnected mosaic of different forest ages, and a non-forest matrix of both agriculture and water barriers, introduces more complexity than classical forest fragmentation studies, but arguably reflects the reality of most human-modified tropical forest landscapes.

In this context, we assessed the relative role of secondary forest age versus connectivity with primary forest in determining bird diversity—estimated as (1) bird species richness and other diversity metrics, (2) bird population density, and (3) the similarity of avian community composition to PF. In all cases, we examined the extent to which variation in bird communities is mediated by landscape context, such as isolation by water barriers, or varies among different groups of species, including long-distance migrants and habitat specialists.

2.3 Methods

Study sites

Field surveys were conducted in the Panama Canal Watershed, where vegetation is classified as tropical moist forest (Holdridge & Budowski 1956). The climate is seasonal with a distinct dry season, typically from mid-December until early May, with annual rainfall of 1900 – 3600mm (Croat 1978). Study sites were located in the Barro Colorado Nature Monument, Soberania National Park and the adjacent Agua Salud Project (Fig. S1). Barro Colorado Nature Monument (5,600 ha; 26 – 171 m a.s.l.; 9°9’ N, 79°51’ W) is comprised of five peninsulas and Barro Colorado Island, all situated in Lake Gatun, which was formed in 1914 by the flooding of the Panama Canal. Barro Colorado Nature Monument is a mosaic of PF and SF stands of different ages that were used for cattle pasture or fruit production between the 1880s and the establishment of the park in 1979 (Leigh *et al.* 1982). Soberania National Park (22,000 ha; 35 – 225 m a.s.l.; 9°9’ N, 79°44’ W) was established in 1980 and is a mix of PF and very old SF (Van Bael *et al.* 2013). Agua Salud (664 ha; 52 – 302 m a.s.l.; 9°13’ N, 79°47’ W) was once predominantly cattle pasture or small-scale shifting cultivation but, after establishment in 2008, the landscape is now predominantly young SF (Van Breugel *et al.* 2013). The topography in this region of Panama is fairly gentle, although there are areas of relatively steep terrain intersected by ravines. The difference in annual rainfall between our northernmost and southernmost sites (separated by a latitudinal distance of 9.8 km) is 159 mm pa (Rompre *et al.* 2007). This variation is minor compared to a difference of 2100 mm pa across the full rainfall gradient in Central Panama (Rompre *et al.* 2007), so we the study area as a single climatic band (see Fig. S1).

Site selection

Secondary forest sites were located in a chronosequence of approximately 20, 40, 60, 90 and 120 yr since abandonment, with two replicates per forest age. Secondary forest ages were estimated using historical records, aerial photographs and interviews with residents; for details see Denslow & Guzman (2000) and van Breugel et al. (2013). The youngest SF in the Barro Colorado Nature Monument is 40-yr-old, while SF in Agua Salud is 10–34 yr old (mean = 19 yr old). For ease of presentation, Agua Salud sites are referred to as 20-yr-old. Four PF sites were selected, two in a relatively small patch (c. 800 ha) of isolated PF on Barro Colorado Island (henceforth referred to as isolated PF) and two in an extensive area of mainland PF in Soberania National Park (c. 22,000 ha; henceforth referred to as extensive PF). Primary forests are at least 500 yr old and there is no indication that they have ever been logged or cultivated (Piperno 1990). There is no ongoing disturbance (such as logging or hunting) in Barro Colorado Nature Monument, whereas in Agua Salud there may be some forest clearance and disturbance in the wider landscape. Across the Barro Colorado Nature Monument chronosequence average canopy height and structural complexity increases with SF age (DeWalt *et al.* 2003, Mascaro *et al.* 2012). Further details of vegetation structure and composition can be found in Dent *et al.* (2013), DeWalt *et al.* (2003), and Mascaro *et al.* (2012).

Habitat patch size is an important determinant of species' persistence in fragmented landscapes (Bender *et al.* 1998). However, the importance of patch size relates to the composition of the surrounding matrix. The SF sites in our study are embedded within a mixed-age forest matrix, which buffers the effects of fragment size and limits our ability to accurately calculate areas of single-aged fragments. The three forest areas in which study sites are embedded are Barro Colorado Island (1,560 ha), Gigante peninsulas (2,600 ha), and Soberania National Park and surrounding contiguous forest (22,000 ha; see Fig S1 for details). The SF and PF sites in this study experience different connectivity. The 20-yr-old Agua Salud and 90-yr-old Bohio Peninsula SF sites form part of a large forest network connected to extensive PF in Soberania National Park, while both island and Gigante Peninsula SF sites are smaller, isolated areas of forest within a water matrix. Island SF sites (90 – 120 yr old) are connected only with isolated PF, and are separated from extensive mainland PF by water. Secondary forest on the Gigante Peninsula is more extensive, and contains older patches (>200 yr old) interspersed with patches of 40 – 60 yr old SF, but is separated from extensive PF by either water or an agricultural matrix. Thus, we categorise our SF sites as being either isolated from extensive PF (henceforth referred to as isolated SF), or connected to extensive PF (henceforth referred to as connected SF). Primary forest sites were sampled on both island and mainland to examine the effects of forest isolation, and to provide a baseline for studying the effects of SF age on bird communities. Due to the restrictions of available SF in the study landscape, it was not possible to have replicate forest ages for all levels of isolation.

Bird survey methods

At each of the 14 sites, nine point counts were established with each point separated by a minimum of 100 m from other points, and by at least 50 m from forest of a different age (Van Bael *et al.* 2013, Robinson *et al.* 2000). One site was surveyed per morning by two trained observers, with the first count beginning ten mins before sunrise and the last completed by 10:30 h. All nine stations at a site were sampled once during a survey visit, with a minimum of three days between surveys; no surveys were conducted on days with excessive rain or wind.

Point counts were 10 mins in duration, and all birds seen or heard within a 50 m-radius were identified (De Bonilla *et al.* 2012, Martin & Blackburn 2014, O'Dea & Whittaker 2007, Raman & Sukumar 2002). Limiting counts to a 50 m radius can help to reduce the differences in detectability of birds among habitat types due to vegetation structure, and minimises biases and errors in species identification and distance estimates (Petit *et al.* 1995). For each bird seen or heard, observers used a laser rangefinder to estimate the Euclidean distance from the centre of the point count to the bird (Buckland *et al.* 2008). Distance estimates to birds detected only by ear are likely to be less consistent than estimates based on visual detections, but in most cases the location of calling birds can be judged reasonably accurately. Birds flying above the canopy were excluded from the survey. Along with the point count data, we kept a list of additional species encountered as we walked between the point count stations during a survey. Surveys were conducted over three years: July to October 2014, in the wet season, and in January 2015 and January to March 2016, in the dry season. Each site was surveyed a total of ten times over the three years; five times in the wet season and five times in the dry, giving a total of 1,260 point counts.

Observers had considerable ornithological field experience, including in tropical forest habitats. Two observers were Panamanian, with many years' experience of the local avifauna. All observers received training before data collection began, including detection tests to check for any bias in identification ability and for consistency in estimations of distance. Recordings of calls and songs were used intensively to improve identification skills and check identifications based on vocalisations.

Data analysis

Prior to analysis, unidentified birds were removed from the dataset (1.8% of total number of detections). All analyses were conducted on the remaining bird species (henceforth, all birds), and on a dataset restricted to birds with a higher dependency on forest habitats (henceforth, forest specialists). Using a recently published classification of forest dependency (BirdLife International 2018), we scored species with high forest dependence as forest specialists. These species are generally characteristic of the interior of undisturbed forest, and almost invariably breed within forest (BirdLife International 2018, Buchanan *et al.* 2011). We note that classification of forest dependency in birds is potentially subjective, partly because species vary in their habitat selection geographically. We used BirdLife International's classification because it is recent, comprehensive and widely accessible. Results were very similar when we used alternative classifications of forest dependency, including published descriptions by Ridgely & Gwynne (1989), habitat codes of Stotz *et al.* (1996), and habitat scores of Tobias *et al.* (2016).

Rarefaction curves were calculated to compare rates of species accumulation among forest age classes for both all birds and forest specialists. When scaled by number of samples, these showed that curves reached, or were approaching, the asymptote for all forest ages for both all birds and forest specialists suggesting survey effort was adequate (Fig. S2 and S3). However, when rarefaction curves were scaled by number of individuals, asymptotes were not reached for some forest ages for either all birds or forest specialists. This was especially evident for the extensive PF sites, suggesting that these were under-sampled (Fig. S2 and S3). To identify species that were missing from the extensive PF dataset, we compared our dataset to the species list reported in a previous survey of the same extensive PF forest (Robinson *et al.* 2000). This study was of longer duration and utilised more intensive survey methods and so was considered to be a good indication of the species present in the extensive PF sites.

Species richness and the percentage of PF species present in SF were calculated using data combining both the point count data and the additional species encounters. All other analyses used data from point counts only. Relative abundance of each species was calculated using the maximum observed count on any single visit to a site to avoid risk of double-counting bias. Analyses were conducted using R (Version 3.4.1, R Core Team 2017).

Species richness, diversity and dominance

We compared species richness, Shannon-Weiner diversity indices and dominance across forest ages using data from all surveys combined. Dominance was measured as the percentage of individual birds represented by the five most common species in each site.

Bird population density

We used the R package 'Distance' (Laake *et al.* 2015) to estimate bird community population density among forest ages pooled over the 1,260 point counts, following methods set out in Buckland *et al.* (2015). These data are useful as they allow comparisons with previous bird population density estimates from central Panama. Visual and audial detections were pooled, and analyses were stratified by forest age to allow for any differences in detectability among habitats. Using 'ds' ('Distance' R package; Laake *et al.* (2015), we fitted 36 detection functions with various combinations of covariates (year, season, detection method and observer) per forest age and used AIC model selection to choose the best-fit models (Burnham *et al.* 2011). The detection functions provided an estimation of bird population density (number of individuals per hectare) in each of the forest ages. The R package 'Distance' requires a minimum of 80 observations within a category to give reliable estimates per species. While 'Distance' is often used to estimate population densities for individual species, we did not pursue this approach as only between four and nine bird species in each forest age category had more than 80 detections. Our results should be interpreted with caution due to the limitations in pooling community detectability data as this approach assumes that each species is equally detectable across our 14 sites.

Species composition and similarity to primary forest

The percentage of bird species detected in PF that were also detected in SF was calculated separately for both isolated PF and extensive PF sites by pooling data for each forest age category.

All similarity and compositional analyses were conducted with the R package 'vegan' (Oksanen *et al.* 2016). We used the Morisita-Horn abundance-based similarity index (S_{MH}) to compare species composition between pairs of assemblages. The S_{MH} is robust to uneven and insufficient sampling and thus suited to determine if reassembly of PF communities occurs in SF in terms of relative abundance (Chao *et al.* 2006). We examined whether species composition of SF converged with either isolated PF or extensive PF over time by comparing the similarity in composition (S_{MH}) of each SF forest site to each of the PF sites. We examined similarity to isolated and extensive PF sites separately because isolation-related extirpations have altered the island bird communities (Robinson 1999). Similarity values were produced using 'vegdist' ('vegan' R package; Oksanen et al., 2016).

To determine if forest age or geographic location explained patterns in species composition across the different sites, we performed Mantel tests on three matrices of pair-wise distances among sites: Euclidean geographic distance, difference in forest age, and dissimilarity in species composition ($1 – S_{MH}$). Primary forest sites were assigned a nominal age of 500 yr to include these sites in the distance matrix for forest age. Mantel tests were performed using 'mantel' ('vegan' R package; Oksanen et al., 2016).

We explored qualitative similarities in species composition among sites with non-metric multidimensional scaling (NMDS; Anderson *et al.* 2011). This approach uses rank order, rather than absolute abundances of species, to represent the original position of communities in multidimensional space as accurately as possible using a reduced number of dimensions. We used similarity matrices generated from both the S_{MH} abundance-based and Jaccard incidence-based similarity values (S_J). The S_J similarity values were included to investigate whether PF species were present in SF, even if patterns of relative abundance were different from those in PF. Ordinations were performed using 'metaMDS' ('vegan' R package; Oksanen et al., 2016).

To assess the significance of observed differences in species composition in relation to SF age, isolation level (isolated or connected), forest type (SF or PF) and distance to extensive PF, we conducted a series of permutational MANOVAs, an analysis of variance using distance matrices. This analysis uses pseudo-F values to compare among-group to within-group similarity and assesses significance by permutation. We also investigated the effect of season (wet or dry) on species composition by conducting a permutational MANOVA at survey level. Permutational MANOVAs were produced using 'adonis' ('vegan' R package; Oksanen et al., 2016).

We calculated the mean number of migratory bird detections in different forest age categories based on count data with no distance corrections. This gives a relative abundance of migratory birds in habitats for those species with similar detection probabilities. We also used the point count data to list the five most abundant species per forest age, and classified these species using diet and habitat information from Ridgely & Gwynne (1989) and Wilman *et al.* (2014).

2.4 Results

Our surveys recorded a total of 183 bird species from 42 families, of which 55 species from 24 families were forest specialists (Table S1). We detected 13,894 individual birds in fixed radius point counts, of which 5,256 were forest specialists (BirdLife International 2018).

Patterns of species richness, diversity, and dominance

No clear relationship was found between species richness and forest age (Table 1). The youngest SF (20-yr-old) had higher species richness than all other sites, and similar species richness of forest specialists as seen in extensive PF (Table 1). The oldest SF (120-yr-old) had the lowest species richness for all birds and forest specialists. These counter-intuitive patterns of species richness appear to be influenced by differences in connectivity among sites, with higher species richness found in sites that were connected to extensive PF (Fig. 1). Compared with extensive mainland PF sites, the isolated PF sites had lower species richness for both datasets. The same patterns were seen for Shannon-Weiner diversity, while dominance values were highest in isolated sites and lowest in connected sites (Table 1).

Bird population density

There was no clear pattern in bird community population density estimates across the different forest ages or levels of isolation. For all birds, the 20-yr-old SF had the greatest density of birds, estimated at 29 individual birds/ha (95% CI: 26, 31; Fig. 2). This compares with the lowest density estimate of 17 individual birds/ha (95% CI: 16, 19) in the 120-yr-old SF. Qualitatively similar patterns were found for forest specialists.

Table 2.1: Site information and bird species metrics

Approximate forest site age, level of isolation, species richness, Shannon-Weiner diversity index and dominance statistics for bird communities of ten secondary forest and four primary forest sites in central Panama, for all bird species and forest specialists.

			All Birds			Forest Specialists[1]		
Site	Age (yrs)	Level of isolation	Species richness	Shannon–Wiener index	Dominance (%)	Species richness	Shannon–Wiener index	Dominance (%)
1	20	Connected	117	3.97	29.86	40	3.07	46.19
2	20	Connected	113	4.03	27.65	37	3.01	49.22
3	40	Isolated	84	3.63	36.75	26	2.72	54.55
4	40	Isolated	90	3.73	38.01	25	2.75	53.67
5	60	Isolated	76	3.61	37.16	25	2.83	50.00
6	60	Isolated	89	3.73	34.35	30	2.93	45.21
7	90	Connected	95	4.04	22.32	34	3.19	40.05
8	90	Isolated	83	3.77	32.12	26	2.77	54.25
9	120	Isolated	63	3.27	48.37	22	2.45	66.57
10	120	Isolated	62	3.37	46.42	23	2.49	63.84
11	Primary	Isolated	74	3.63	36.89	27	2.78	54.77
12	Primary	Isolated	75	3.64	35.94	28	2.79	54.17
13	Primary	Extensive	99	4.11	21.02	39	3.41	28.74
14	Primary	Extensive	96	3.95	25.13	38	3.20	39.87

[1] Forest Specialists: species that are scored as having high forest-dependence (BirdLife International 2018).

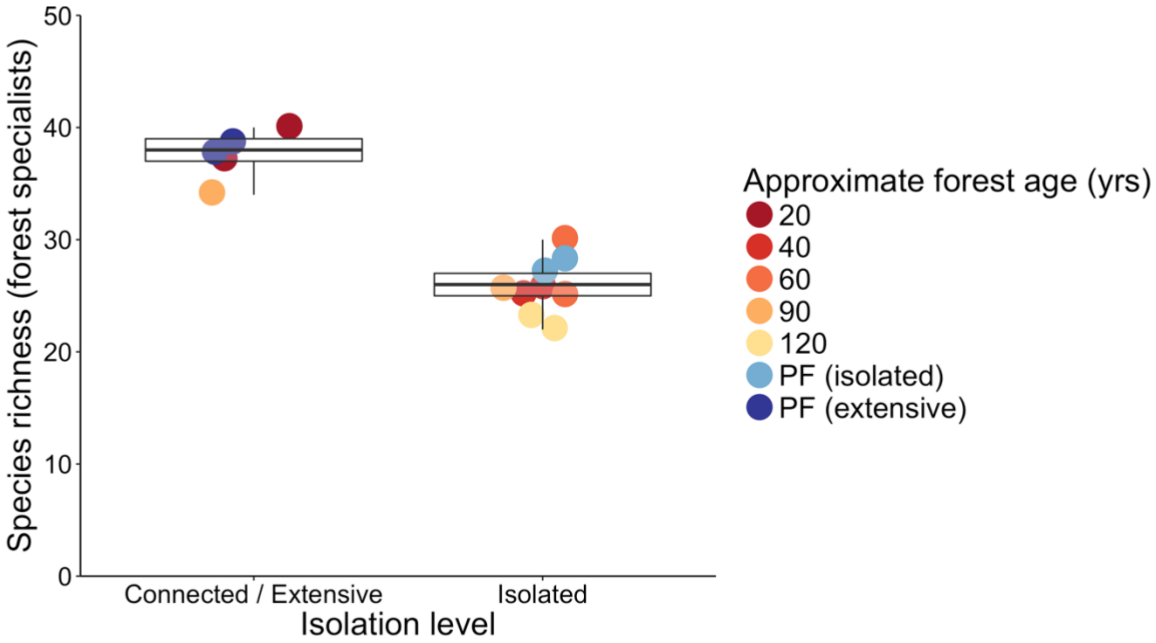

Figure 2.1: Forest specialist species richness with increasing distance to primary forest

Relationship between number of forest specialist bird species detected (in two forest sites in each of five secondary forest (SF) age categories: 20, 40, 60, 90, 120-yr-old SF, and primary forest (PF), and their isolation level. Sites are isolated from or connected to extensive PF. "Forest Specialists" are species that are scored as having high forest-dependence (BirdLife International 2018).

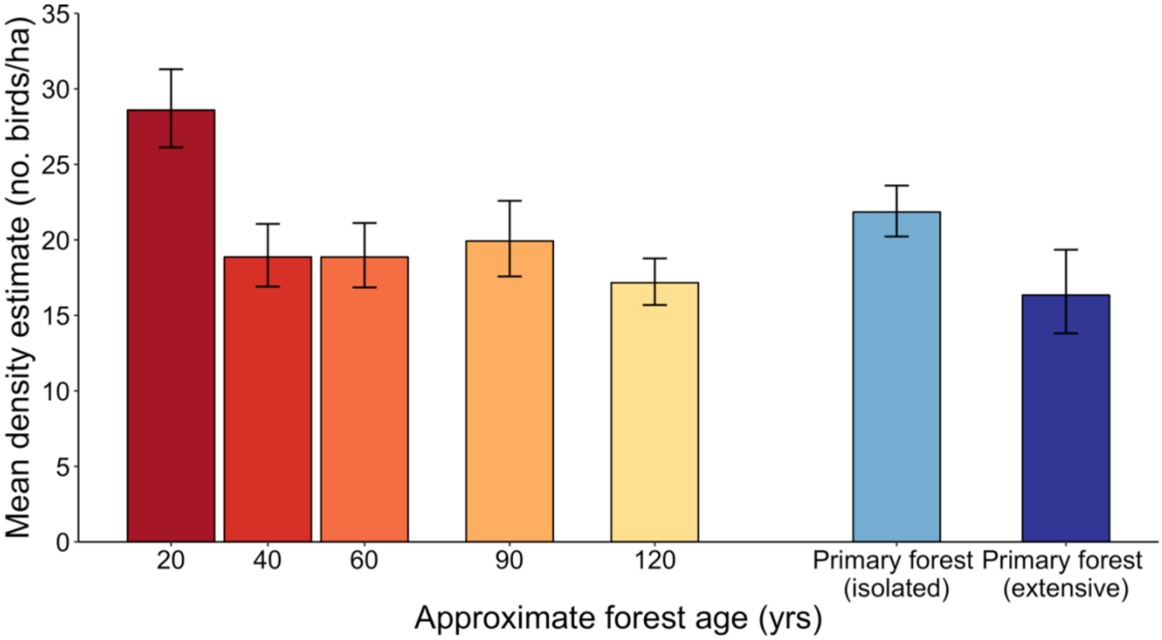

Figure 2.2: Bird population density estimates

Population density estimates and 95% confidence intervals for all bird species (number of birds per hectare) using distance corrections. Species data has been pooled for the two sites in each forest age category.

Similarity to primary forest

Focusing on all birds, we found no clear relationship between SF age and the percentage of PF bird species detected in SF sites (as estimated by our surveys), but there was a relationship between isolation and percentage of PF species present in SF. Percentage of PF species present was consistently highest in connected sites, and lower in isolated sites. When comparing among SF ages, we found that the highest percentage of PF species occurred in the 20-yr-old connected SF (86% when compared with extensive PF sites as estimated by our surveys; Fig. 3). Surprisingly, the 120-yr-old isolated SF had the lowest percentage of PF species present, with only 72 percent in common with isolated PF and 57% in common with extensive PF. This is likely due to shifts in species richness driven by isolation effects in the island PF, where we detected just 62% of the species that we found in extensive mainland PF.

For all birds, similarity in bird species composition increased with forest age in relation to isolated PF, but not extensive PF (Fig. 4). The highest similarity in species composition between PF and SF was recorded on Barro Colorado Island where the community composition of the oldest isolated SF (120-yr-old; n = 2 sites) was very similar to isolated PF (n = 2 sites; similarity index [S_{MH}]: 0.87 ± 0.03). In contrast, the lowest similarity was between the 20-yr-old SF and the isolated PF (0.58 ± 0.03); these sites span the widest range in both isolation level (mainland vs. island) and age (20-yr vs. PF). Similarity was higher between extensive PF sites and 20-yr-old SF (0.69 ± 0.03) than between extensive PF sites and the older, isolated 120-yr-old SF (0.61 ± 0.04). Mantel tests indicated that geographic distance among sites ($R^2 = 0.74$, $P = < 0.001$) explained a greater proportion of variation in species composition than forest age ($R^2 = 0.30$, $P = < 0.05$). Similar patterns were found for forest specialist species, except in this instance forest age was not a significant predictor of species composition (geographic distance: $R^2 = 0.66$, $P = < 0.01$; forest age: $R^2 = 0.21$, $P = 0.06$).

The NMDS of abundance based species composition (S_{MH}) across all bird species showed a separation of sites in relation to both forest age and isolation level (Fig. 5). Sites displayed a clear split along Axis 1 that related to site location (connected or isolated), while the age of forest sites tended to increase along Axis 2. The NMDS comparisons for forest specialists showed very similar patterns as those seen for all birds, as did the NMDS results for both datasets using S_J, although the effect of forest age became less apparent when restricting analyses to species presence/absence data (Fig. 5).

The permutational MANOVA using S_{MH} indicated that forest isolation level explained a greater portion of the variation in community composition of all bird species than forest age or forest type (SF vs PF; Table 2). Distance to extensive PF was not significant. The permutational MANOVA using S_J for all birds showed very similar results (Table 2). Season had a significant effect on community composition, but it did not change the patterns observed for forest isolation, forest age or forest type, although distance to extensive PF became significant (Table 2). Community composition of forest dependent species (using S_{MH} or S_J) was largely dictated by forest connectivity. The same patterns were found for forest specialists as the all-bird dataset when season was taken in to account (Table 2).

Table 2.2: Species composition perMANOVA results

Permutational MANOVA results assessing species composition using community similarity matrices generated with both Morisita-Horn abundance-based similarity index (S_{MH}) and Jaccard incidence-based similarity index (S_J). We tested observed differences between forest age, isolation level (isolated or connected), forest type (SF or PF) and geographic distance to extensive mainland PF. We also investigated the effect of season (wet or dry) on species composition by conducting a perMANOVA at survey level.

		All Birds				Forest Specialists [1]			
		R^2	*F*	df	*P*	R^2	*F*	df	*P*
S_{MH}	Forest isolation	0.15	9.12	1	< 0.01	0.18	6.28	1	< 0.05
	Forest age	0.13	7.80	1	< 0.01	0.02	0.84	1	ns
	Forest type (SF vs PF)	0.08	5.10	1	< 0.01	0.01	0.51	1	ns
	Distance to extensive PF	0.02	1.35	1	ns	0.04	1.31	1	ns
S_J	Forest isolation	0.10	2.19	1	< 0.05	0.11	2.18	1	< 0.05
	Forest age	0.11	2.42	1	< 0.05	0.07	1.37	1	ns
	Forest type (SF vs PF)	0.09	1.93	1	< 0.05	0.06	1.14	1	ns
	Distance to extensive PF	0.06	1.29	1	ns	0.06	1.17	1	ns
S_{MH} [2]	Season (wet v. dry)	0.05	11.69	1	< 0.01	0.04	8.84	1	< 0.01
	Forest isolation	0.03	7.45	1	< 0.01	0.05	9.38	1	< 0.01
	Forest age	0.05	10.29	1	< 0.01	0.04	7.15	1	< 0.01
	Forest type (SF vs PF)	0.03	6.30	1	< 0.01	0.02	5.35	1	< 0.01
	Distance to extensive PF	0.03	5.69	1	< 0.01	0.02	3.56	1	< 0.05

[1] Forest Specialists: species that are scored as having high forest-dependence (BirdLife International 2018).

[2] Data analysed at survey level, with season included

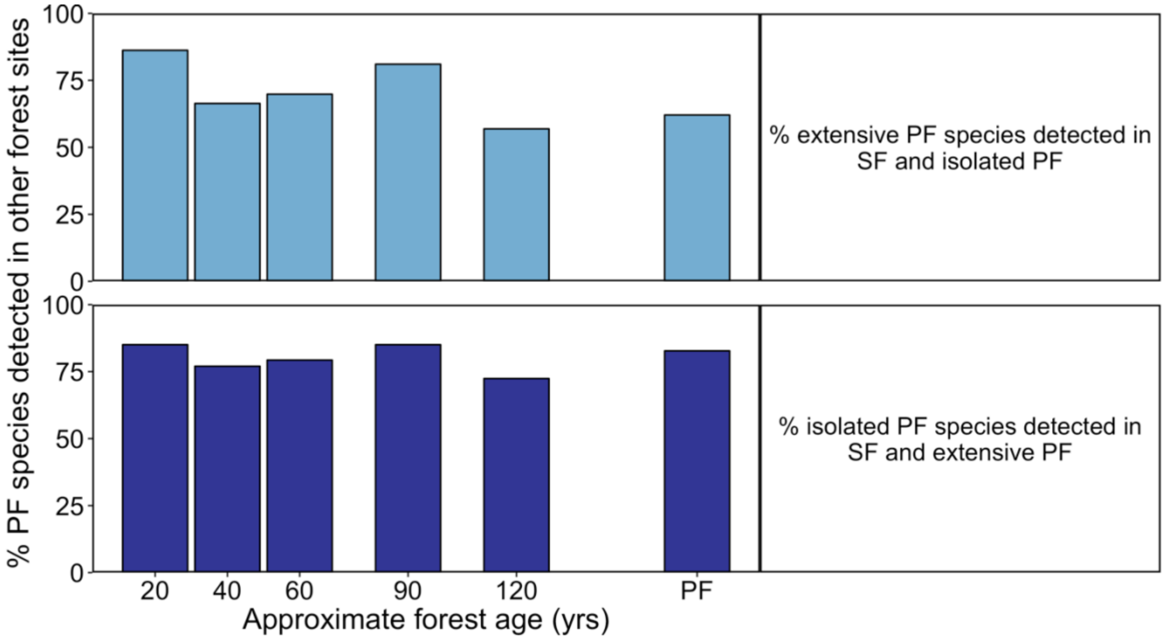

Figure 2.3: Percentage of primary forest species detected in other forest sites

Percentage of bird species detected in primary forest (PF) that were also detected in secondary forest (SF) in five SF age categories for isolated PF sites and extensive PF sites. Species data has been pooled for the two sites in each forest age category.

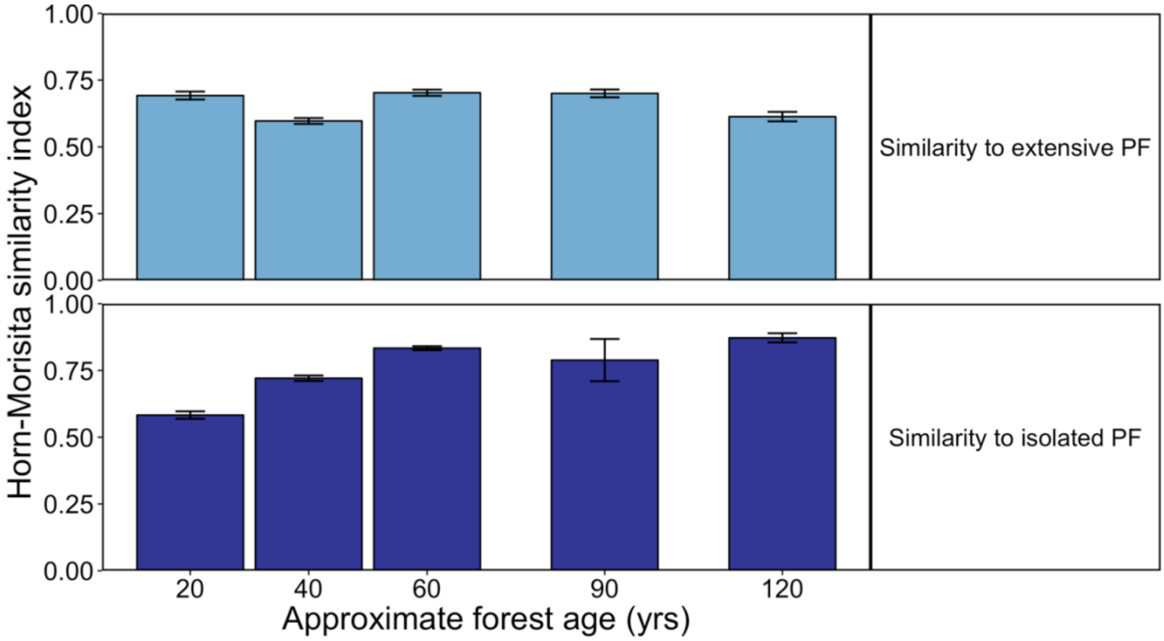

Figure 2.4: Similarity in species composition

Similarity (Morisita-Horn) between secondary forest sites (SF) and both isolated and extensive primary forest (PF). Each bar represents the mean (±1 SE) similarity index of all possible comparisons between the two SF sites in each age category (20, 40, 60, 90 and 120 yr old) and the PF sites. Calculated using the all bird dataset, with data pooled for the two sites in each forest age category.

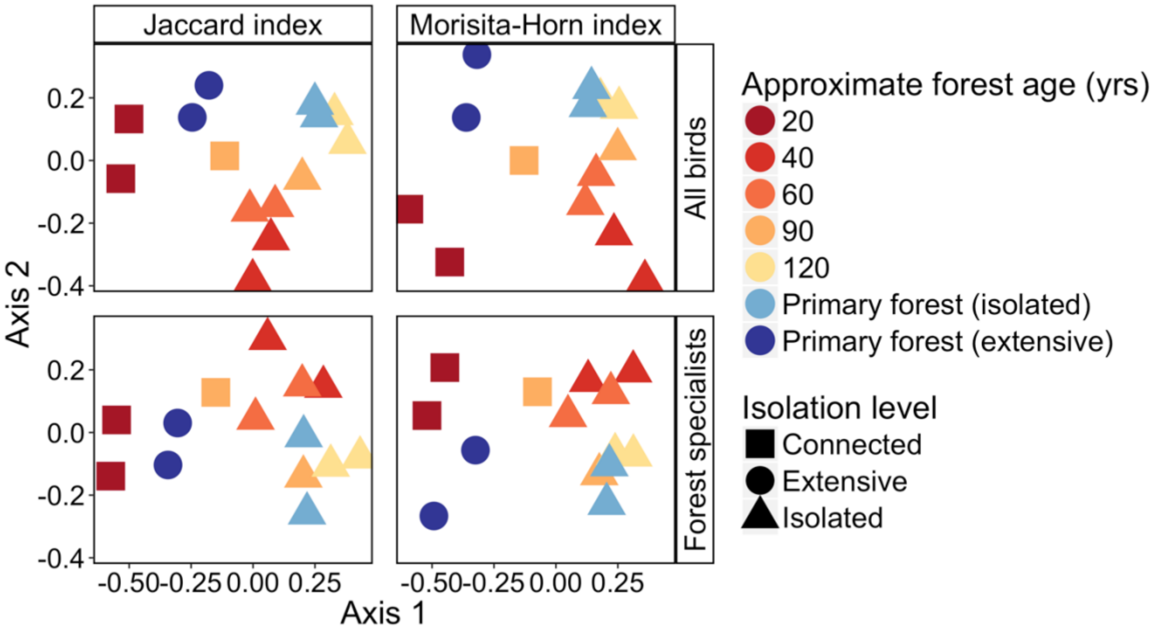

Figure 2.5: NMDS plots of bird communities

Non-metric multidimensional scaling (NMDS) plots of bird communities in two forest sites in each of five secondary forest (SF) age categories (20, 40, 60, 90, 120-yr-old), and isolated primary forest (PF) and extensive PF for all birds, and for forest specialists. NMDS were generated using the Morisita-Horn index (all birds stress = 0.07; forest specialists stress = 0.08) and Jaccard index (all birds stress = 0.07; forest specialists stress = 0.06). Isolation levels are represented by different symbols. “Forest Specialists” are species that are scored as having high forest-dependence (BirdLife International 2018).

Compositional changes

The composition of the five most abundant bird species differed across forest ages (Table S2). Only one species, Black-crowned Antshrike (*Thamnophilus atrinucha*), was consistently abundant across all sites. Southern Bentbill (*Oncostoma olivaceum*) was among the top five most abundant species in the youngest forest sites (20, 40 and 60-yr-old SF), while Red-lored Amazon (*Amazona autumnalis*) appeared in the top five for both the isolated and extensive PF, as well as the 90-yr-old SF. The five most abundant species in the isolated and extensive PF, and the 90-yr-old SF exhibited a greater diversity of feeding guilds and foraging strata than those found in the younger SF sites (Table S2).

We detected 15 species in isolated PF that we did not see in extensive PF, including species such as Crested Guan (*Penelope purpurascens*) that are susceptible to hunting and therefore extirpated from most mainland localities. In contrast, 44 species were detected in extensive PF that were not seen in isolated PF. These were predominantly understorey, insectivorous species, many of which have become extinct on Barro Colorado Island since its isolation (Robinson 1999, Willis 1974).

The number of migratory birds detected per point count was highest in the 20-yr-old SF (0.533 ± 0.091) and declined with increasing SF age to only 0.078 ± 0.032 migrants detected per point count in the 120-yr-old SF (Fig. S4). The number of migrants detected in PF sites was about half the number detected in the 20-yr-old SF (island PF: 0.27 ± 0.07; extensive PF: 0.29 ± 0.06).

2.5 Discussion

Our survey data sampled across tropical SF of varying ages and isolation levels revealed that variation in avian species richness of SF was best explained by connectivity to extensive PF, rather than forest age. We found the highest species richness in the youngest SF sites, which were adjacent to extensive PF. Similarly, connectivity, rather than the age of forest, predicted community composition. Finally, the highest bird population density was also found in young SF, although broader patterns in density did not appear to be driven by either forest age or connectivity.

Species richness, diversity and dominance

High species richness and abundance of birds in SF or successional areas has been documented in many studies (Blake & Loiselle 2001, Johns 1991, Karr 1976, Petit & Petit 2003), supporting the hypothesis that intermediate levels of disturbance may lead to high species richness (Connell 1978). In general, species richness in young SF is boosted by an influx of non-forest, open habitat and generalist species, although it also contains an important component of forest species (Barlow *et al.* 2007b, Dunn & Romdal 2005). Most studies report that species richness and community structure of tropical secondary forests progressively approaches that of PF over time, and tends to track the increasing structural complexity of secondary forests (Raman 1998, Dent & Wright 2009). In our study, however, species richness and abundance did not increase with forest age, and were instead highest in the youngest SF even when non-forest bird species were removed. We also found that species richness and abundance both increased with greater connectivity to extensive PF, suggesting that high species richness in the 20-yr-old SF is driven by proximity to extensive PF in adjacent Soberania National Park.

Proximity to undisturbed habitats has been shown to increase the diversity of bird communities in degraded sites (Johns 1991, Terborgh & Weske 1969, Waltert *et al.* 2004). In La Selva, Costa Rica, PF was the primary habitat and source population for many of the bird species found in SF (Blake & Loiselle 2001). This pattern is supported by our findings where a greater number of forest specialists were found in well-connected 20-yr-old SF, than in isolated PF. Our findings suggest that, in a landscape of mixed ages of SF and varying connectivity among forest patches, the key factor determining the recovery of avian diversity in SF is connectivity to extensive PF, rather than forest age.

Bird population density

The density of birds in SF and PF varied across sites, with the highest density estimates in the youngest SF, matching patterns previously reported for the Neotropics (Blake & Loiselle 2001, Johns 1991, Karr 1976, Petit & Petit 2003). Earlier studies in Soberania National Park have reported densities 2–3 times higher than our PF estimates (Van Bael *et al.* 2013, Robinson *et al.* 2000). The disparity in figures may result from differing methodologies, particularly the spot mapping and smaller point count radius used by previous studies. In contrast, previous population density estimates for young SF (5–6-yr-old) from Agua Salud were about 45 percent lower than estimated population densities from our youngest (20-yr-old) SF, but comparable with our estimates from older SF (Van Bael *et al.* 2013). On the one hand, higher population density in younger forest may in part reflect increased detectability of some species, particularly those associated with the forest canopy, which is harder to survey in PF. On the other hand, our results may reflect the increased resource availability of both fruit and insects often found in young SF (Blake & Loiselle 1991, Levey 1988, Martin 1985), which may encourage birds from PF to use adjacent SF for foraging.

Similarity to primary forest

Most studies comparing the similarity of avian species composition between SF and PF report increasing similarity to PF with SF age (Borges 2007, Dent & Wright 2009, Raman 1998). All our SF sites had high levels of compositional similarity to PF, and upper figures were within the range of similarity found in extensive PF. In line with our hypothesis, SF community composition became increasingly similar to that of isolated PF across the chronosequence. In contrast, SF community composition did not converge on that of extensive mainland PF sites with increasing SF age. Similarly, there was no relationship between SF age and the percentage of PF species detected: the highest percentage of PF species was found in the youngest SF that, critically, was also the least isolated and most well-connected to extensive PF.

Based on our findings, isolation and connectivity to extensive PF plays a greater role than forest age in determining the reassembly of bird communities in SF. Despite the persistence of high-stature PF forest on Barro Colorado Island, many species have disappeared from the local community since it was isolated by the inundation of Lake Gatun (Robinson 1999, Willis 1974). The peninsula sites are also isolated and thus have similar bird communities to the island PF, with relatively low species richness. In contrast, bird communities in extensive mainland PF sites include forest specialists that have been lost from isolated sites and are unlikely to recolonise SF unless it is contiguous with PF that harbours these species. In summary, SF are dependent on contiguous PF source populations, and if these populations have low species richness then SF will never develop the bird communities associated with extensive PF forest stands (Ferraz *et al.* 2007, Jones *et al.* 2016, Stouffer *et al.* 2006). However, if SF sites are adjacent to extensive PF forest specialists may recolonise relatively rapidly; for example, understorey insectivores increased in abundance just 10 yrs after SF was abandoned adjacent to PF in Amazonia (Andrade and Rubio-Torgler, 1994). Our findings highlight that connectivity is critical for reassembly of avian communities in regenerating tropical forests (Barlow *et al.* 2006, Lees & Peres 2009).

Compositional changes

Despite the key role of connectivity in determining avian composition, forest age still influences bird community reassembly, as demonstrated by the increasing similarity of communities in older isolated SF to that of isolated PF. However, six forest species present in isolated PF were missing from the adjacent 120-yr-old SF on the island, including the forest specialists Rufous Piha (*Lipaugus unirufus*), Spot-crowned Antvireo (*Dysithamnus puncticeps*) and Tawny-crowned Greenlet (*Tunchiornis ochraceiceps*). Although a number of studies report a high representation of PF species present in SF (> 70% of PF species), SF communities often lack rare species, or those with highly specialised dietary or habitat requirements (Chazdon *et al.* 2009, Dent & Wright 2009).

The loss of forest species from isolated sites across this landscape is striking, and is especially evident when comparing isolated PF with extensive PF. Barro Colorado Island is a relatively large forest fragment (1560 ha), but it has been isolated for > 100 yr and during this time numerous avian extinctions have been documented (Chapman 1938, Eisenmann 1952, Karr 1990, 1982, Robinson 1999, Willis & Eisenmann 1979); 65 species have been lost from the island, including 30 forest species and 35 edge species (Robinson 1999). Many of the forest species missing from the PF sites on Barro Colorado Island are understorey insectivores such as Dusky Antbird (*Cercomacroides tyrannina*), Ocellated Antbird (*Phaenostictus mcleannani*) and Black-faced Antthrush (*Formicarius analis*). In addition, we only detected two of the ten species identified by Robinson (1999) as forest birds that are close to extirpation on Barro Colorado Island: Black-tailed Trogon (*Trogon melanurus*) and Rufous Piha (*Lipaugus unirufus*). The isolation of Barro Colorado Island within a large waterbody makes recolonization by many forest species highly unlikely as they are poorly adapted to sustained flight, and unwilling or incapable of dispersing across open water (Moore *et al.* 2008, Tobias *et al.* 2013).

Species richness and relative abundance of migratory birds was highest in the youngest SF, with numbers decreasing with increasing SF forest age. Similarly, Van Bael *et al.* (2013) found more migrant species in SF (5 – 6-yr-old) than PF sites in central Panama (0.5 and 0.2 birds/point count for SF and PF respectively). Migrant birds may occupy degraded and open habitats as they are displaced from optimal habitats by resident species, or because they are better able to adapt to the resources offered by SF (Greenberg *et al.* 1994, Willis 1980, Wunderle & Latta 1996). Our results add to a growing body of evidence confirming that secondary and degraded tropical forests are important habitats for migrant bird species (Van Bael *et al.* 2007, Greenberg *et al.* 1994, 1997, Wunderle & Latta 1996).

It is possible that other aspects of community structure, such as functional and phylogenetic composition, may be affected by forest age and connectivity (Bregman et al. 2016, Pigot et al. 2016). For example, if SF provides a simplified range of structural and dietary resources for roosting and foraging birds then young forests may not be able to support as many closely related or functionally similar species driving functional and phylogenetic over-dispersion, while isolation may increase functional and phylogenetic clustering as certain groups are selected against due to their inability to cross gaps between forest fragments (Bregman et al. 2016). Further studies are needed to clarify how forest successional status and connectivity across the wider landscape interact to shape bird community composition.

Caveats

Although survey effort was standardised for all sites, this can potentially generate differences in bird communities because of variation in detectability (Bregman *et al.* 2016). For example, it is possible that estimates of species richness and population density in young SF are inflated because (1) individual birds tend to be more detectable at forest edges and in lower-stature forests (Barlow *et al.* 2007b, Buckland *et al.* 2008, Ruiz-Gutiérrez *et al.* 2010) and (2) PF bird species may have been missed by our surveys because they are relatively quiet, inactive, inconspicuous or occur at low population densities (Terborgh *et al.* 1990). To explore how detectability may have affected our results, we employed a dataset from a previous long-term study located in our extensive PF site (Robinson *et al.* 2000), which involved more intensive survey methods. Compared with these results, we missed 132 species from our censuses of this community. Of these, the majority (65%) fall into one of three categories: 1) birds that are nocturnal, vagrants or migrants and hence may not have been present or active during our surveys in all habitats (45%), 2) birds that are aerial species (swifts and raptors) and were actively excluded from our surveys (15%), 3) birds associated with aquatic landscape features which were not encompassed by any of our survey areas (5%). Once these categories are removed, the number of missing species drops to 46 (or 35%), most of which are rare or difficult to detect. While the absence of these species from our censuses may underestimate the importance of PF for conservation in our analysis, we note that this is a relatively minor component of overall biodiversity and represents a small number of individual birds. Although our species richness estimates are reasonably accurate, we note that our dataset is not suitable for generating estimates of species-specific detectability and abundance, which would require far more intensive sampling. Thus, while our estimates are informative of overall patterns, they should be interpreted with caution. Furthermore, our decision to apply equal survey effort to the dry and wet season in order to record migrant species as well as resident species, may have resulted in lower survey intensity during peak calling periods.

A separate issue relates to the breeding status or viability of populations of forest birds in younger SF. It has been hypothesised that populations of many PF bird species in SF may be non-viable, and therefore less important to conservation, because they are largely made up of (1) transient individuals or (2) temporary territories with infrequent breeding and low breeding success (Tobias *et al.* 2013). We cannot rule out this possibility based on our results, and more research is needed to clarify population demography and viability in SF. However, the relatively high population density of primary forest bird species in young SF suggests that, at a minimum, SF can greatly increase the population carrying capacity of adjacent PF, thus increasing its importance for conservation.

Conclusions

Our results suggest that the link between bird communities and successional trajectories differs between isolated and non-isolated SF sites, with isolated sites converging with bird communities of isolated PF over long time frames, whereas highly-connected SF sites converge rapidly with extensive PF. In addition, we find support for the view that SF, even when relatively young, can support dense populations of PF species, so long as it is connected to extensive PF. Crucially, even if these populations are transitory, SF may theoretically increase the population carrying capacity of PF, reducing the risk of local extinction. These findings emphasise the importance of reforesting and maintaining existing SF at the borders of extensive tropical forest, and highlight the need for improved protection of SF in protected area buffer zones throughout the tropics.

2.6 Acknowledgements

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2.7 Supplementary Information

Table S2.1: Full bird species list

Bird species list from our surveys in central Panama, with ecological classifications used in analyses and species presence/absence in sites.

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tinamus major	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Crypturellus soui	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Penelope purpurascens	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0
Ortalis cinereiceps	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
Odontophorus gujanensis [a]	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Patagioenas speciosa	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0
Patagioenas cayennensis	0	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1
Patagioenas nigrirostris	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1
Geotrygon montana	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Leptotila verreauxi	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Leptotila cassinii	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Columbina talpacoti	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Claravis pretiosa	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Nyctibius griseus [a]	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chordeiles minor [a]	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Nyctidromus albicollis	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Antrostomus rufus	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Florisuga mellivora	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0
Phaethornis striigularis	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1
Phaethornis longirostris	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Heliothryx barroti	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalurania colombica	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Amazilia tzacatl	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amazilia amabilis	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidopyga coeruleogularis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Juliamyia julie	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dromococcyx phasianellus	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Piaya cayana	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Aramides cajaneus	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
Pulsatrix perspicillata	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Leptodon cayanensis	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Elanoides forficatus	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Harpagus bidentatus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Buteogallus anthracinus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Buteogallus urubitinga	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pseudastur albicollis	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Leucopternis semiplumbeus	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Buteo nitidus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Buteo platypterus	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Buteo albonotatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Trogon massena	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Trogon melanurus	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	0
Trogon chionurus	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0
Trogon caligatus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Trogon rufus	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Momotus subrufescens	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Baryphthengus martii	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Electron platyrhynchum	0	1	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Notharchus hyperrhynchus	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0
Notharchus pectoralis	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Malacoptila panamensis	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1
Ramphastos ambiguus	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ramphastos sulfuratus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pteroglossus torquatus	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	0
Campephilus melanoleucos	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Celeus loricatus	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1
Hylatomus lineatus	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1
Melanerpes pucherani	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Melanerpes rubricapillus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrastur mirandollei	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Micrastur semitorquatus	0	0	1	0	1	0	0	1	1	1	1	1	1	1	0	1
Falco rufigularis	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1
Brotogeris jugularis	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1
Pyrilia haematotis	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Pionus menstruus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amazona autumnalis	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Amazona farinosa	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Microrhopias quixensis	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Epinecrophylla fulviventris	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myrmotherula ignota	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Myrmotherula axillaris	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Dysithamnus puncticeps	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1
Cymbilaimus lineatus	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1
Taraba major	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus atrinucha	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cercomacroides tyrannina	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	1
Phaenostictus mcleannani	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1
Gymnopithys bicolor	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Hylophylax naevioides	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Poliocrania exsul	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myrmeciza longipes	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Hylopezus perspicillatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Formicarius analis	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1
Sclerurus mexicanus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sclerurus guatemalensis	0	1	1	1	0	1	0	1	1	0	0	0	1	1	1	1
Deconychura typica	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Sittasomus griseus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
Dendrocincla fuliginosa	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1
Glyphorynchus spirurus	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1
Dendrocolaptes sanctithomae	0	0	1	0	0	1	1	0	1	0	1	1	1	1	0	1
Xiphorhynchus susurrans	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Xiphorhynchus lachrymosus	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	1
Lepidocolaptes souleyetii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Xenops genibarbis	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1
Automolus ochrolaemus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Manacus vitellinus	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Ceratopipra mentalis	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidothrix coronata	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1
Querula purpurata	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Lipaugus unirufus	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0
Onychorhynchus coronatus	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Terenotriccus erythrurus	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tityra semifasciata	0	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1
Pachyramphus polychopterus [a]	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Schiffornis veraepacis	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Platyrinchus coronatus	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Mionectes oleagineus	0	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1
Cnipodectes subbrunneus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Rhynchocyclus aequinoctialis	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
Tolmomyias sulphurescens	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Tolmomyias assimilis	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Myiornis atricapillus	0	0	1	0	0	0	0	1	1	1	0	1	1	1	1	1
Oncostoma olivaceum	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Todirostrum nigriceps	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Zimmerius vilissimus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ornithion brunneicapillus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Camptostoma obsoletum	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0
Tyrannulus elatus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Myiopagis gaimardii	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
Myiopagis viridicata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Attila spadiceus	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Legatus leucophaius	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Pitangus sulphuratus	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0
Megarynchus pitangua	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Myiodynastes maculatus	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0
Myiozetetes cayanensis	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
Myiozetetes similis	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	0
Tyrannus melancholicus	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0
Rhytipterna holerythra	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0
Myiarchus tuberculifer	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Myiarchus crinitus	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
Empidonax virescens	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Contopus cooperi	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Contopus virens	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Vireolanius pulchellus	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1
Tunchiornis ochraceiceps	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Pachysylvia decurtata	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pachysylvia aurantiifrons	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Vireo olivaceus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Microbates cinereiventris	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Ramphocaenus melanurus	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1
Polioptila plumbea	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Microcerculus marginatus	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Pheugopedius fasciatoventris	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	1
Thryophilus rufalbus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Cantorchilus leucotis [a]	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cantorchilus nigricapillus	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Henicorhina leucosticta	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1
Cyphorhinus phaeocephalus	0	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1
Hylocichla mustelina	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Turdus grayi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Euphonia luteicapilla	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Euphonia laniirostris	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Euphonia fulvicrissa	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1
Euphonia minuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhodinocichla rosea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arremonops conirostris	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Arremon aurantiirostris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amblycercus holosericeus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Psarocolius wagleri	0	0	1	1	0	1	0	1	1	1	1	0	0	0	1	1
Cacicus microrhynchus	0	0	1	1	1	0	1	1	1	0	0	0	0	0	1	1
Cacicus cela	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1	0
Icterus chrysater	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0
Parkesia noveboracensis	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Mniotilta varia	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Leiothlypis peregrina	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Setophaga ruticilla	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Setophaga castanea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Setophaga pensylvanica	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	1
Cyanoloxia cyanoides	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1
Habia fuscicauda	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1
Habia carmioli [a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Piranga rubra	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0
Chlorophanes spiza	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1

Scientific Name	Migrant Species	Forest Specialist [1]	Site [2]													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cyanerpes cyaneus	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Cyanerpes lucidus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dacnis cayana	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Saltator grossus	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	1
Eucometis penicillata	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Islerothraupis luctuosa	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Chrysocorypha delatrii	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tangara palmarum	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Tangara inornata	0	0	0	1	0	1	0	1	0	1	1	0	1	1	0	0

[1] Forest Specialists: species that are scored as having high forest-dependence (BirdLife International 2018).

[2] Site details: 1 and 2 = connected 20-year-old SF; 3 and 4 = isolated 40-year-old SF; 5 and 6 = isolated 60-year-old SF; 7 = connected 90-year-old SF; 8 = isolated 90-year-old SF; 9 and 10 = isolated 120-year-old SF; 11 and 12 = isolated PF; 13 and 14 = extensive PF.

[a] Species detected only in encounters, and not in fixed radius point counts.

Table S2.2: Most abundant species in each forest age

Most abundant bird species in each forest age category in Central Panama and their primary foraging substrate, feeding guild and forest specialist status.

Forest age	Scientific name	No. individuals	% of all observations	Foraging Height [1]	Feeding Guild [2]	Forest Specialist [3]
20 (n = 2640 individuals)	*Oncostoma olivaceum*	155	5.9	L	I	0
	Thamnophilus atrinucha	154	5.8	L	I	0
	Cercomacroides tyrannina	140	5.3	L	I	0
	Ramphocaenus melanurus	104	3.9	L	I	1
	Poliocrania exsul	99	3.8	L	I	1
40 (n = 2239 individuals)	*Thamnophilus atrinucha*	248	11.1	L	I	0
	Pachysylvia decurtata	183	8.2	M/U	I	0
	Xiphorhynchus susurrans	121	5.4	L	I	0
	Oncostoma olivaceum	115	5.1	L	I	0
	Tyrannulus elatus	107	4.8	L/M	I	0
60 (n = 2223 individuals)	*Thamnophilus atrinucha*	264	11.9	L	I	0
	Pachysylvia decurtata	169	7.6	M/U	I	0
	Xiphorhynchus susurrans	108	4.9	L	I	0
	Poliocrania exsul	101	4.5	L	I	1
	Oncostoma olivaceum	93	4.2	L	I	0
90 (n = 2534 individuals)	*Pachysylvia decurtata*	161	6.4	M/U	I	0
	Poliocrania exsul	151	6	L	I	1
	Amazona autumnalis	133	5.2	U	F	0
	Thamnophilus atrinucha	115	4.5	L	I	0
	Xiphorhynchus susurrans	100	3.9	L	I	0
120 (n = 2149 individuals)	*Thamnophilus atrinucha*	299	13.9	L	I	0
	Poliocrania exsul	203	9.4	L	I	1
	Pachysylvia decurtata	162	7.5	M/U	I	0
	Xiphorhynchus susurrans	149	6.9	L	I	0
	Hylophylax naevioides	134	6.2	L	I	1

Forest age	Scientific name	No. individuals	% of all observations	Foraging Height [1]	Feeding Guild [2]	Forest Specialist [3]
PF (isolated) (n = 2922 individuals)	*Amazona autumnalis*	272	9.3	U	F	0
	Thamnophilus atrinucha	243	8.3	L	I	0
	Poliocrania exsul	237	8.1	L	I	1
	Pachysylvia decurtata	221	7.6	M/U	I	0
	Hylophylax naevioides	135	4.6	L	I	1
PF (extensive) (n = 2391 individuals)	*Amazona autumnalis*	159	6.6	U	F	0
	Thamnophilus atrinucha	129	5.4	L	I	0
	Pachysylvia decurtata	119	5	M/U	I	0
	Microrhopias quixensis	91	3.8	L/M	I	1
	Zimmerius vilissimus	72	3	C	O	0

[1] Foraging height, classified using information in Ridgely & Gwynne (1989): L = "lower levels" (from ground to about 10 feet above the ground); M = "middle levels" (from about 10 to 30 feet above the ground); U = "upper levels" (everything above 30 feet including the canopy); C = "only canopy" (the very top layer of the forest, within about 10ft of the upper level of leaves only).

[2] Feeding Guild, classified using information in Wilman *et al.* (2014): F = frugivore; I = insectivore; O = omnivore.

[3] Forest Specialist: species that are scored as having high forest-dependence (BirdLife International 2018).

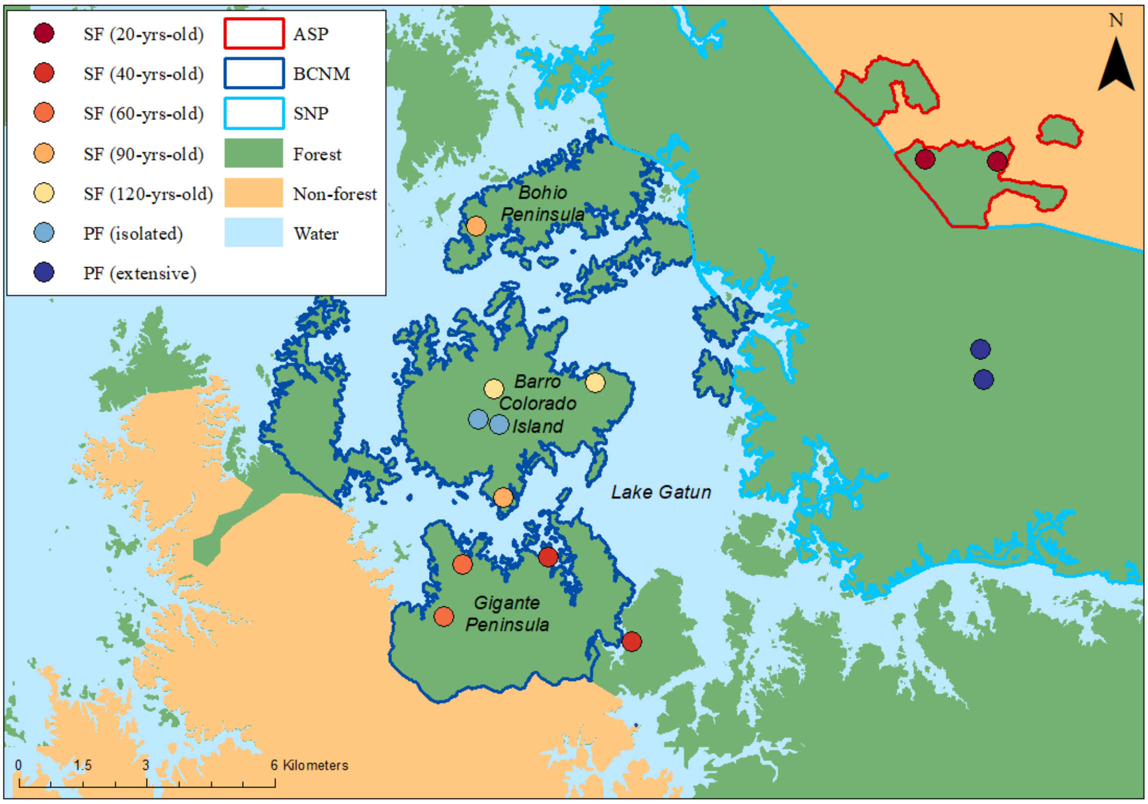

Figure S2.1: Map of study sites

Map of the 14 study sites in central Panama. Sites are colour-coded by forest age (PF = primary forest; SF = secondary forest). This area of central Panama is composed of a mosaic of contiguous different aged forest stands interspersed with a water and agricultural matrix. The main areas in which different aged forest stands are embedded are the Barro Colorado National Monument (BCNM), including Barro Colorado Island (1,560 ha) and Gigante peninsulas (2,600 ha), Soberania National Park (SNP) and surrounding contiguous forest (22,000 ha), including the Agua Salud Project (ASP).

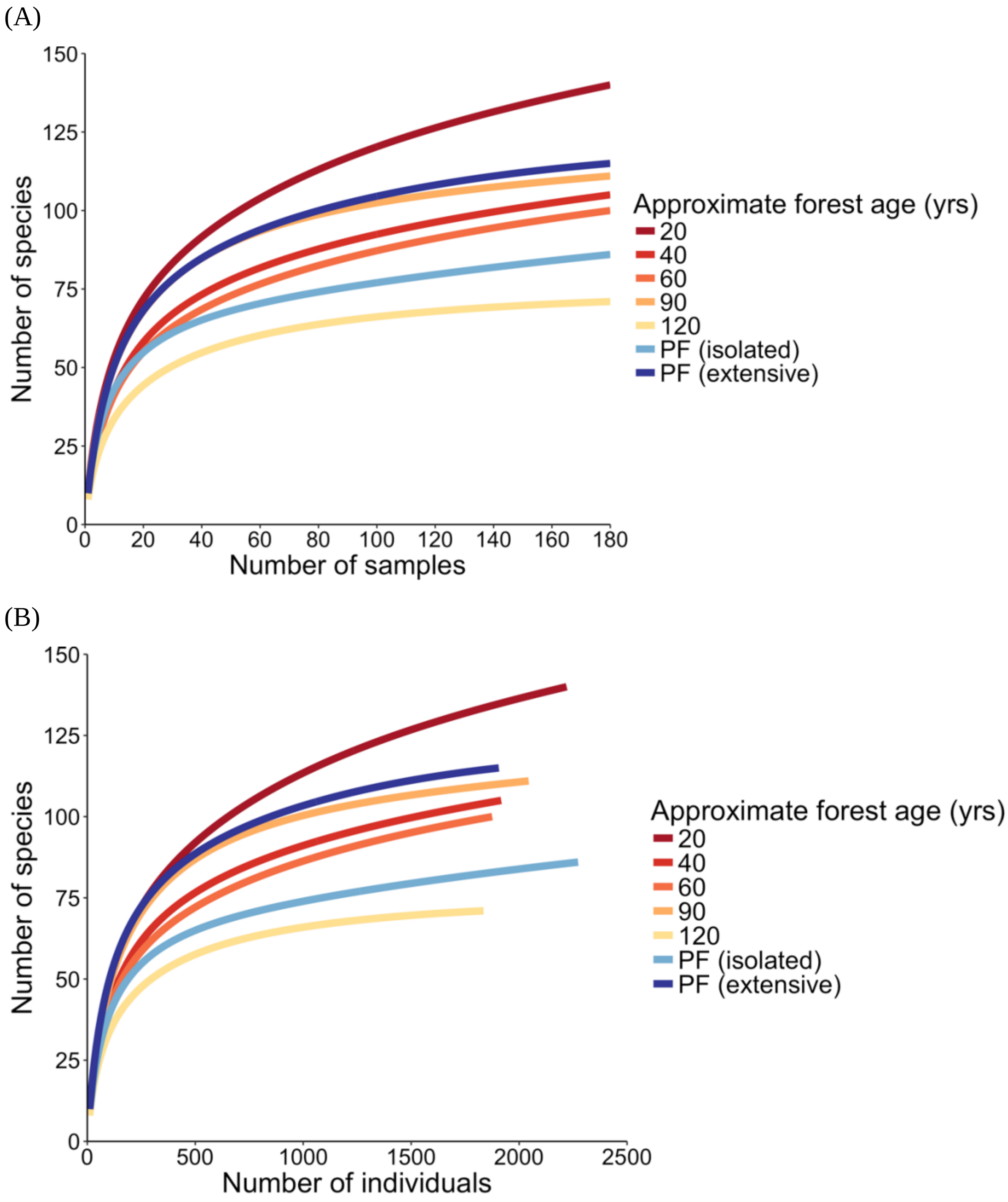

Figure S2.2: Species accumulation curves for all birds

Species accumulation curves scaled by (A) sample and (B) by number of individual birds detected for bird communities in each of five secondary forest (SF) age categories: 20, 40, 60, 90, 120-yr-old, and isolated primary forest (PF) and extensive PF for all birds.

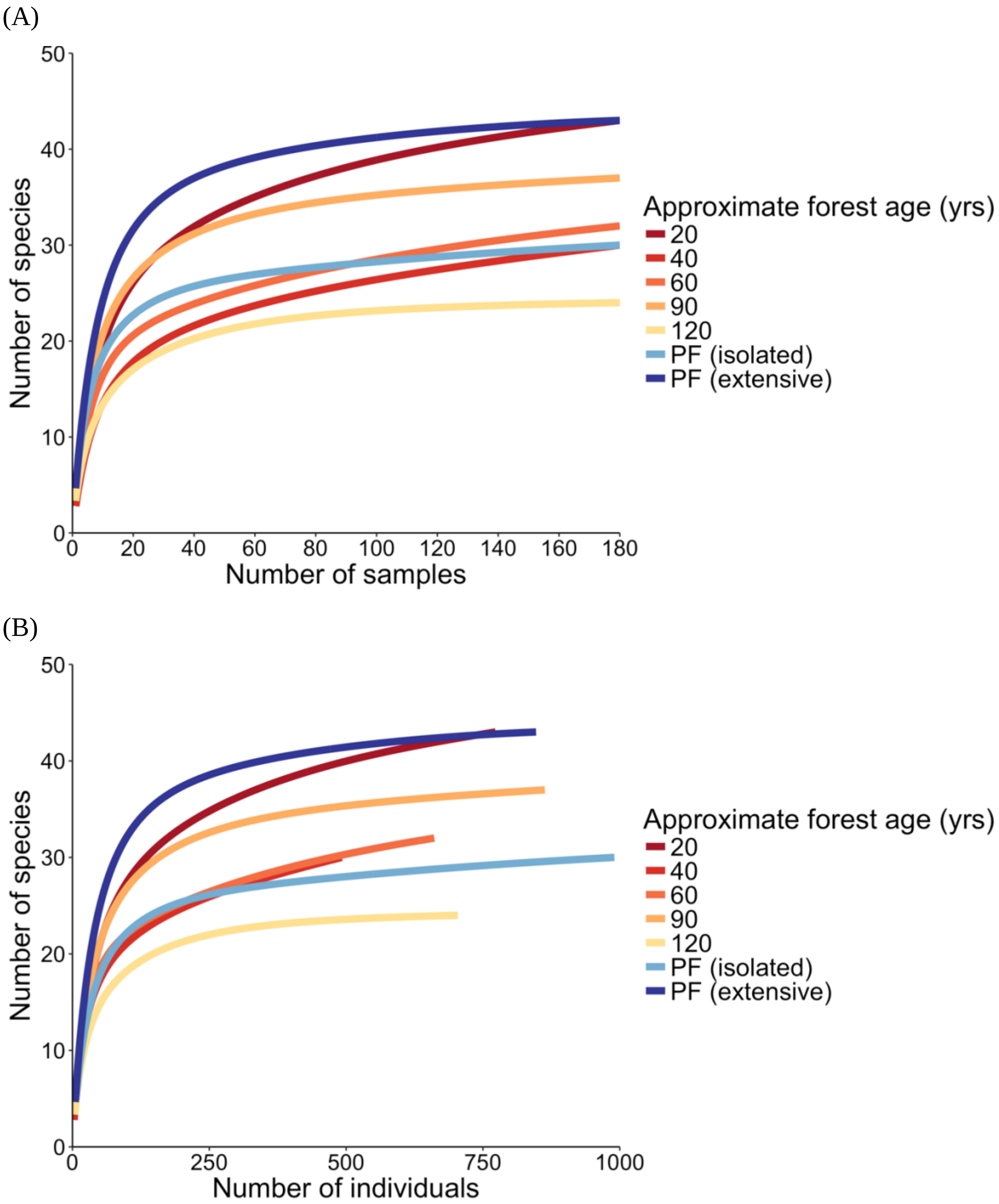

Figure S2.3: Species accumulation curves for forest specialists

Species accumulation curves scaled by (A) sample and (B) by number of individual birds detected for bird communities in each of five secondary forest (SF) age categories: 20, 40, 60, 90, 120-yr-old, and isolated primary forest (PF) and extensive PF for forest specialists. “Forest Specialists” are species that are scored as having high forest-dependence (BirdLife International 2018).

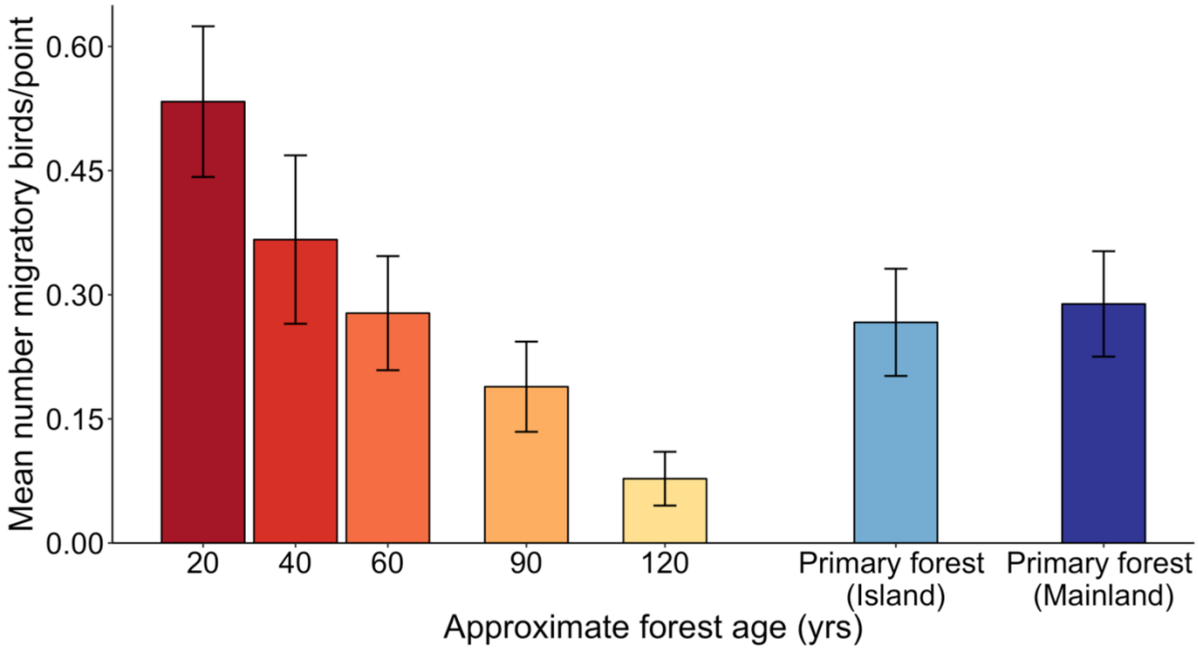

Figure S2.4: Mean detections of migratory birds in each age class

Mean detections (or number of birds) per point count for migratory birds only (±1 SE).

Chapter 3: Using avian morphological traits to assess the functional diversity and composition of tropical bird communities across a gradient of forest age and isolation

D. H. Dent and J. A. Tobias supervised the project, L. Bunnefeld provided additional supervision, and D. H. Dent commented on draft versions of the chapter.

3.1 Abstract

Bird communities play a vital role in many key ecosystem processes that underpin the long-term resilience of tropical forests. Maintaining these ecosystem processes (such as control of arthropod pests and seed dispersal) in disturbed forests depends on whether degraded forest habitats can retain similar levels of avian functional diversity to those found in intact primary forest. Here we examine the effects of forest age and isolation on morphological traits of insectivorous and frugivorous bird communities in central Panama and discuss the implications for two ecosystem processes: insect predation and seed dispersal. We found significant effects of forest age and isolation on certain aspects of community structure, but generally the impact of forest age and isolation on the functional diversity and trait structure of insectivore and frugivore communities in this study landscape were minimal. For insectivorous birds, forest isolation reduced the functional dispersion of traits, and lowered the area of trait space occupied by the community. Trophic traits of insectivores also differed between isolated and connected forests, highlighting the loss of species with long, narrow beaks from isolated forests. For frugivorous birds, the area of trait space occupied was lower in both secondary forest, and isolated sites. Frugivore dispersal traits varied with isolation; communities in isolated forests had higher dispersal ability. Overall our results suggest that both isolated forest, and secondary forest have the capacity to retain significant avian functional diversity, thus maintaining the network of trophic interactions regulating seed dispersal by birds, and herbivory by insects. The lack of clear relationships between functional diversity and habitat type may be explained by the maturity of the secondary forests in this study (20 – 120 years) and low levels of ongoing disturbance across all sites. Our results suggest that if secondary forests are left to regenerate without further disturbance they can provide similar ecosystem functions to undisturbed primary forest, highlighting the need to conserve and protect secondary forests within the broader landscape.

3.2 Introduction

Tropical forests are one of the world's most biodiverse ecosystems; home to over 70% of the world's terrestrial species and vital for the functioning of our biosphere (Foley *et al.* 2007). However, the continuous forests that historically covered many tropical regions have been transformed by expanding urban areas, intensifying agriculture, and forest clearance, causing the loss and degradation of primary forest (PF) habitats (Laurance 2015). This often results in a matrix of isolated patches of remnant and regenerating forest scattered across inhospitable landscapes of non-forest habitats (FAO 2015). It has been proposed that the loss of PF may be offset by forest planting and the natural regeneration of secondary forest (SF) on previously deforested and degraded land (Wright 2005). However, the maintenance of species and ecosystem processes within SF will depend on site-specific factors including SF age and extent of the forest patch (Chazdon *et al.* 2009, Dent & Wright 2009). Moreover, as patches of secondary forest are embedded within the surrounding matrix, there are additional influences acting at the landscape scale, such as surrounding land cover and distance to PF, that will also determine which forest species can persist in a network of forest patches, how they utilise different habitat patches, and how they disperse through the landscape (Powell *et al.* 2015b, Wolfe *et al.* 2015). Thus, it is vital to determine the role that SF can play in the long-term conservation of tropical forest biodiversity and ecosystem processes.

Many animal species are involved in key ecosystem processes such as seed dispersal, pollination and invertebrate control (Jordano 2016), and understanding how animal communities are affected by environmental change enables us to make inferences about the knock-on effects for the ecosystem processes that underpin tropical forest functioning. For example, frugivorous birds play an important role in seed dispersal, which is critical to the long-term resilience of forests (Howe 1977, Lundberg & Moberg 2003, Wunderle 1997). A reduction in avian frugivores in tropical forest habitats has the potential to impede tree regeneration resulting in long-term shifts in tree community composition (Galindo-González *et al.* 2008, Sethi & Howe 2009, Terborgh *et al.* 2008), especially among some large-seeded plant species that are obligately dependent on large birds for seed-dispersal (Wheelwright 1985, Wotton & Kelly 2011). Insectivorous birds also play a key role in forest ecosystem processes, since insectivores predate herbivorous insects controlling herbivore damage to plants (Van Bael *et al.* 2003, Marquis & Whelan 1994). Reductions in insectivores can negatively impact plant growth and seedling mortality as the result of elevated herbivory (Van Bael *et al.* 2008, Dunham 2008).

Maintaining bird communities, and the ecosystem functions they provide, in the face of forest disturbance is vital to preserve the future of tropical forests. Many studies have shown that avian species richness and diversity enhance ecosystem functioning (Cardinale *et al.* 2012, Hooper *et al.* 2005). However, the functional diversity of avian communities may provide more valuable insights into ecosystem processes than simple metrics of species numbers (Cadotte *et al.* 2011, Diaz & Cabido 2001, Gagic *et al.* 2015, McGill *et al.* 2006, Monnet *et al.* 2014). Functional diversity allows for differences among species to be quantified in terms of their morphological or functional traits (such as, beak shape or wing length), which in turn enables greater understanding of ecosystem processes since these traits relate to specific functional roles (Monnet *et al.* 2014, Naeem *et al.* 2012).

Functional traits are defined as any measurable feature of an individual that potentially affects its performance or fitness; thus influencing its environmental tolerances, habitat requirements and contributions to ecosystem processes (Cadotte *et al.* 2011). Indices of functional diversity convey the range of species' traits within a community, and so changes in these indices, over time or space, illustrate the community-wide response to environmental change. Communities tend to respond to increasing habitat disturbance in one of two ways: either species with highly-specialised and ecologically distinct traits are lost, leading to a decrease in functional diversity (Flynn *et al.* 2009, Hidasi-Neto *et al.* 2012, Villéger *et al.* 2010); or the number of species performing ecologically similar roles within the community falls, lowering functional redundancy (Laliberte *et al.* 2010).

Previous studies have highlighted that environmental change can affect the functional trait structure of bird communities. Yet understanding how this impacts ecosystem processes is complex and requires the identification of distinct groups of traits that impact specific processes (Naeem *et al.* 2016, Trisos *et al.* 2014). For example, to understand how changes in bird community structure affects seed dispersal we need to isolate the traits the affect seed consumption and dispersal (such as gape width, body mass and wing shape; Dehling *et al.* 2016). Distinct dietary guilds may differ in their responses to disturbance, suggesting that different facets of an ecosystem will be affected by disturbance in distinct ways (Bregman *et al.* 2016, Luck *et al.* 2013, Vandewalle *et al.* 2010). For example, the negative impact of forest isolation is much greater for understory insectivores than frugivores and omnivores (Sekercioğlu 2007). This suggests that the herbivory control provided by insectivores in forest fragments may be lost more rapidly after disturbance compared with the seed dispersal functions provided by frugivores.

Exploring functional variation, both within and between dietary guilds, is key to understanding the implications of disturbance for community composition and ecosystem function since even within single guilds different species may perform distinct ecological roles (Galetti *et al.* 2013, Hoehn *et al.* 2008). For instance, the body size and gape width of avian frugivores dictates the size of seed that a species is capable of dispersing. Hence larger species with larger gape widths are able to disperse a greater diversity of seeds than smaller species within the same guild (Levey 1987).

Here we examine tropical bird communities across forest age and isolation gradients in Central Panama. Earlier research tended to rely on qualitative descriptors of bird feeding guilds, based on observational work. Here, we take a more quantitative approach, separating bird communities into specific dietary guilds based on their functional morphology. Rather than relying on broad categorical dietary guilds, this approach is more nuanced, and so offers the opportunity to better elucidate the effects of both forest age and isolation level on ecosystem processes. We utilise continuous functional traits for all species of our community, but with specific emphasis on the frugivore and insectivore groups, since these are the two largest functional groups in our dataset and perform the key functions of insect predation and seed dispersal.

We sampled SF aged from 20 to 120 years, as well as PF controls. Across this age gradient, we sampled forests that were either isolated from or connected to extensive PF. This landscape presents a unique opportunity to examine how bird communities' functional diversity changes across a successional and isolation gradient, and to investigate the relative importance of forest age versus isolation in determining ecosystem function and resilience. First, we ask i) how well traditional dietary guilds can be mapped onto morphological trait ordination space, and ii) how the proportion of dietary guilds varies with forest age and isolation. Second, we focus specifically on insectivorous and frugivorous birds, and consider how functional diversity changes with forest age and isolation.

3.3 Methods

Study site and species

Field surveys were conducted in the Panama Canal Watershed. Study sites were located in Barro Colorado Nature Monument, Soberania National Park and the adjacent Agua Salud Project (Fig. S3.1). Barro Colorado Nature Monument (5,600 ha; 9°9' N, 79°51' W) is comprised of five peninsulas and Barro Colorado Island, all situated in Lake

Gatun which was formed in 1914 by the flooding of the Panama Canal. Barro Colorado Nature Monument is a mosaic of PF and SF stands of different ages, with PF covering roughly half of Barro Colorado Island and small areas on the peninsulas. Secondary forests are located on areas of land that were used for cattle pasture or fruit production between the 1880s and the establishment of the Barro Colorado Nature Monument in 1979 (Leigh *et al.* 1982). Soberania National Park (22,000 ha; 9°9’ N, 79°44’ W) was established in 1980 and is a mix of very old SF and PF (Van Bael *et al.* 2013). Agua Salud Project (664 ha; 9°13’ N, 79°47’ W) was once predominantly cattle pasture or small-scale shifting cultivation, but farming ceased in 2008 and the landscape is now predominantly young SF (Van Breugel *et al.* 2013).

We surveyed birds at 14 sites. Secondary forest sites were located in forests aged between 20 and 120 years old (n = 10). These ages were estimated using historical records, aerial photographs and interviews with residents; for details see Denslow & Guzman (2000) for sites in Barro Colorado Nature Monument, and van Breugel *et al.* (2013) for sites in Agua Salud Project. The SF sites in this study experience different connectivity. The Agua Salud SF (20 yr old) and Bohio Peninsula (90 yr old) sites form part of a large forest network connected to extensive PF in Soberania National Park, while both island and Gigante Peninsula SF sites are smaller, isolated areas of forest within a water matrix. Island SF (90 – 120 yr old) sites are connected only with isolated PF, and are separated from extensive mainland PF by water. Secondary forest on the Gugante Peninsula is more extensive, and contains older patches (>200 yr old) interspersed with patches of 40 – 60 yr old SF, but is separated from extensive PF by either water or an agricultural matrix. Four PF sites were selected, two in a relatively small patch (c. 800 ha) of isolated PF on Barro Colorado Island, and two in an extensive area of mainland PF in Soberania National Park (c. 22,000 ha). There is no indication that these PF sites have ever been logged or cultivated (Piperno 1990). Gigante Peninsula and island sites were combined into one category, hereafter termed ‘isolated’ (n = 9). This generated four forest categories; extensive primary forest (PFe; n = 2), isolated primary forest (PFi; n = 2), connected secondary forest (SFc; n = 3) and isolated secondary forest (SFi; n = 7).

At each of the 14 sites, nine point counts were established with each point separated by a minimum of 100 m from other points, and by at least 50 m from forest of a different age (Van Bael *et al.* 2013, Robinson *et al.* 2000). One site was surveyed per morning by two trained observers, with the first count beginning ten mins after sunrise and the last completed by 10:30 h. All nine stations at a site were sampled once during a survey visit, with a minimum of three days between surveys; no surveys were conducted on excessively rainy or windy days.

Point counts were 10 mins in duration, and all birds seen or heard within a 50 m-radius were identified (Martin & Blackburn 2014). Birds flying above the canopy were recorded but excluded from analyses. Surveys were conducted over three years: July to October 2014, in the wet season, and in January 2015 and January to March 2016, in the dry season. Each site was surveyed a total of ten times over the three years; five times in the wet season and five times in the dry, giving a total of 1,260 point counts.

This study detected 13,925 individual birds and a total of 178 bird species in fixed radius point counts (Table S2.1 in Chapter 2). We included all 178 species in our analyses, rather than solely forest specialists. Previous work has demonstrated that similar species richness, diversity and composition patterns were found for forest species, and for all species (pooled forest and non-forest species; as presented in Chapter 1). In addition, bird species have the potential to assume the functional roles of extirpated competitors (Touchton & Smith 2011), suggesting that all bird species may potentially play a role in forest ecosystem functioning. The relative abundance of each species was calculated using the maximum observed count on any single visit to a site to avoid risk of double-counting bias.

Functional trait sampling

For this study, we selected seven functional traits relating to trophic niche, locomotory and dispersal abilities: beak length, width and depth; wing length; Kipp's distance (the distance between the tip of the longest primary/wing tip and the first secondary feather measured on the folded wing); tail length and tarsus length. Beak dimensions predict the size and type of food items selected by birds, providing an index of trophic niche (Hsu *et al.* 2014, Miles *et al.* 1987, Schoener 1965, Wheelwright 1985). Locomotory traits (tail, tarsus and wing length) are associated with foraging substrate and manoeuvrability (Miles *et al.* 1987, Miles & Ricklefs 1984, Tobias *et al.* 2014). Finally, a measure of dispersal ability was calculated from Kipp's distance and wing length to produce the hand-wing index. This index reflects wing shape and flight ability, providing information about dispersal limitation and gap-crossing ability (Claramunt *et al.* 2012).

We measured bird specimens in museum collections to generate biometric trait data for all 178 species recorded in our surveys. We selected specimens collected as close to the study location as possible to ensure that they were regionally appropriate phenotypes. Of the 848 specimens measured, most were from the Smithsonian Tropical Research Institute, Panama (n = 431). Gaps were filled using specimens stored at the Natural History Museum, Tring, UK (n = 243), the Museu Paraense Emílio Goeldi, Belém, Brazil (n = 126), as well as smaller samples of specimens at Louisiana State University Museum of Zoology, USA (n = 5) and the American Museum of Natural History, USA (n = 5). A small number of measurements were also taken from live specimens from mist-netting projects within the study's locality (n = 38).

The three beak measurements were taken from the anterior edge of the nostrils: 1) length to the tip of the beak, 2) width and 3) depth (as vertical height). Wing length was the distance between the carpal joint and the wing tip of the unflattened wing. Kipp's distance was measured from the tip of the longest primary feather to the tip of the first secondary on the closed wing. Tail length was taken from the point at which the two central rectrices meet the skin to the tip of the longest rectrix. Tarsus length was measured from the middle of the rear ankle joint (i.e. the notch between the tibia and tarsus), to the end of the last scale of the acrotarsium. All measurements were taken with digital callipers to the nearest 0.01 mm, apart from wing length and tail length, which were measured using an end-ruler to the nearest mm. Mean body mass values were taken from Wilman *et al.* (2014).

We aimed to measure a minimum of two males and two females per species. For 69 specimens, we were unable to identify the sex confidently and these specimens were recorded as unsexed. We measured a mean of 4.8 ± 1.6 specimens per species (2.2 ± 0.9 males; 2.3 ± 0.9 females and 2.0 ± 1.5 unsexed). We generated a mean value for each functional trait by averaging data across all specimens (male, female and unsexed) for each species, which were then normalised with $\log^{10}$ transformations.

Dietary guild

Species were assigned a dietary guild based on Wilman *et al.* (2014). Guilds were defined by the food that composed > 50% of a species diet, following methods set out in Bregman *et al.* (2016). Six guilds were represented in our dataset; carnivore, frugivore, granivore, insectivore, nectivore and omnivore. Species were classified as omnivores when no primary diet was apparent (i.e. all dietary components were less than 50%).

The percentage of individual birds in each guild was calculated for each forest type using species relative abundance data. Negative binomial generalised linear mixed-effect models (GLMMs) were performed to examine if percentage of individuals in each dietary guild varied across the four forest types. Percentage of individuals was used as the response, with guild, forest age (PF and SF), isolation level (extensive/connected or isolated), and their interactions used as predictors. Site was included as a random effect to account for any inter-site variation unrelated to forest age or isolation level.

PCA of functional traits

We used principle components analysis (PCA) to examine how traditional dietary guilds are mapped onto morphological trait ordination space, by visualising the relationships among species, the seven $\log^{10}$ transformed functional traits, and dietary guilds (details of the PCA loadings and proportion of variance for the PCA can be found Table S3.1).

Morphological traits were highly correlated with each other and with body mass ($r = 0.32 – 0.96$). To prevent these correlations biasing analyses towards detecting only processes associated with body size, we used PCA to derive independent trait axes, following methods set out in Bregman *et al.* (2016) and Trisos *et al.* (2014). We used a two-step PCA on the morphological trait data that generated three trait axes related to different ecological characteristics, hereafter termed ‘derived’ traits. PCAs were performed on trophic (beak length, width and depth) and locomotory (wing, tail and tarsus lengths) traits separately. The first components of the trophic and locomotory PCAs were both strongly correlated with body mass (Table S3.2). Therefore, these two first components were combined into a second PCA to produce a single body size axis. The second components of the trophic and locomotory PCAs were independent of body mass, and were therefore used as the trophic and locomotory trait axes for further analyses (details of the PCA loadings and proportion of variance for the two-step PCA can be found Table S3.2). These three derived traits (locomotory, trophic and size) were independent of each other (Table S3.5). A final fourth axis consisted of the $\log^{10}$ transformed hand-wing index as an indicator of dispersal ability. This was negatively correlated with the locomotory trait (Table S3.5). All traits were standardised to a mean of 0 and unit variance to give the same weight to each trait (Villéger *et al.* 2008).

The two-step PCA analysis was also performed for insectivore and frugivore communities individually (details of the PCA loadings and proportion of variance for the insectivore and frugivores can be found Tables S3.3 and S3.4 respectively, along with correlation values for the four derived traits in Table S3.5). For both the insectivore and frugivore two-step PCAs, the locomotory trait explained 14% and 19% of the variation respectively and represented the tarsus to tail/wing length ratio, where larger values are associated with a shorter tarsus and longer tail and wing. The trophic trait explained 10% and 3% of the variance for insectivore and frugivores respectively, and was an index of beak shape; larger values are associated with longer and narrower beaks. The size trait explained 89% and 86% of the variation for insectivores and frugivores respectively, and was an index of overall body size, with larger values associated with larger birds. The dispersal trait was an index of wing shape, with larger values associated with more pointed wings.

Functional trait variation of two key guilds – insectivores and frugivores

We conducted analyses on insectivore and frugivore guilds separately as they have been shown to respond differently to forest disturbance and land-cover change (Bregman *et al.* 2014, Lees & Peres 2008). They were also the most numerous of the six dietary guilds detected across our sites, with 106 insectivore species and 34 frugivore species recorded. Two key analyses were performed. Firstly, the two-step PCA method was performed for insectivore and frugivore communities in each forest category to generate the functional trait distribution of three derived traits (trophic, locomotory and size). A 95% CI ellipse that encompassed the occupied morphospace was plotted for each of these trait distributions. The area of the ellipse was calculated to compare the area of functional morphospace occupied across forest types. Secondly, the two-step PCA method detailed above was performed for insectivore and frugivore communities to calculate the four derived traits (dispersal, trophic, locomotory and size) across the complete dataset. These values were then used to calculate site-level values of three measures of functional diversity: functional dispersion (FDis), functional divergence (FDiv) and functional evenness (FEve), using species relative abundance data. FDis calculates the mean distance of all species to the community mean trait value in functional trait space (Laliberte & Legendre 2010). FDiv represents how abundance is spread along a functional trait axis, and FEve examines the evenness of abundance distribution in functional trait space (Villéger *et al.* 2008). Community-weighted mean (CWM) values of the four derived traits were calculated for each site. Binomial GLMs were performed to investigate if values of functional diversity or CWMs varied across sites. Predictors included forest age (PF and SF), isolation level (extensive/connected and isolated), and their interaction. Model selection was performed on all functional diversity indices and CWM GLMs, based on Akaike's information criterion corrected for small samples (AICc; Akaike 1973). Models were ranked according to their AICc value, and only those with a difference (ΔAICc) of < 2 were considered to be equally supported. The importance of each predictor was assessed by Akaike weight (wi), which indicates the probability that the particular model is the best fit for the data (Burnham & Anderson 2002). All analyses were conducted in R (R Core

Team 2017). The three functional diversity indices, and the CWMs were calculated using the ‘FD’ package (Laliberté *et al.* 2015) and model selection was performed using the ‘MuMIn’ package (Burnham and Anderson, 2002).

3.4 Results

Dietary guild and functional traits for all species

In this bird community, multivariate analysis of functional traits identified only nectivores as a distinct dietary group. Carnivores and granivores were moderately dissimilar to the rest of the community, but the distribution of frugivores, insectivores and omnivores overlapped considerably in trait space (Fig 3.1). The first principal component (PC) explained 64% of the variation. However, the location of individual species within the morphospace suggests that PC1 and six morphological traits (bill length, width and depth, wing, tail and tarsus length) were highly correlated with body size. PC2 explained 19% of the variance and was correlated with the hand-wing index.

A second PCA, which used derived morphological (trophic, locomotory, dispersal and size) traits, indicated similar patterns to the first PCA (Fig. 3.2). This method, which accounted for the high correlation of many morphological traits with body size by combining the first components of trophic (beak length, width and depth) and locomotory (wing, tail and tarsus lengths) PCAs into a single body size axis, showed that nectivores were recognisable as a distinct group but frugivores, insectivores and omnivores overlapped in morphospace. PC1 explained 47% of the variance and was an index of dispersal and locomotory traits, while PC2 explained 27% of the variance and was an index of size and trophic traits.

The percentage of species represented by the six dietary guilds (nectivores, carnivores, granivores, frugivores, insectivores and omnivores) did not vary significantly with forest age or isolation (Table 3.1). Insectivores were the largest guild in all forest types, followed by frugivores, whilst carnivores generally represented the smallest proportion (Table 3.2). There were slightly higher numbers of nectivores and lower numbers of carnivores in connected SF compared to other forest types, while extensive PF had a very small percentage of granivores compared with other forest types. The body mass distribution of bird communities did not vary across forest types (Fig. 3.3).

Species richness and functional traits for insectivores and frugivores

Species richness was highest for both frugivores and insectivores in connected SF and lowest in the most isolated sites (Figs 3.4 and 3.5). This effect was not a reflection of reduced sampling in PF sites, as confirmed by rarefaction curves (Fig S3.2; although see caveats for further discussion). The functional trait structure of communities across forest types was visualised by plotting derived trophic (the second component of the beak length, width and depth PCA), dispersal (hand-wing index) and size (the first component of the trophic and locomotory PCAs combined) traits of insectivores and frugivores in morphospace (Figs 3.4 and 3.5 respectively). The area of morphospace occupied by both insectivores and frugivores was very similar across forest types for all traits. However, there were some trends. For insectivores, the area of occupied morphospace was highest in the least isolated sites, reflecting the patterns seen in species richness. For frugivores, the area of morphospace occupied was consistently highest in extensive PF sites, despite lower species richness than connected and isolated SF.

Table 3.1: GLMMs examining relative proportions of dietary guilds across sites

Negative binomial generalised linear mixed-effects model (GLMM) results for percentage of individual birds in each dietary guild as a function of forest age and isolation level. This was calculated using species relative abundance data. (Forest Age = PF or SF; Isolation Level = connected/extensive or isolated).

term	estimate	SE	Z-statistic	*P*
(Intercept)	-0.531	0.418	-1.272	0.203
guildFrugivore	3.496	0.424	8.237	**0.000**
guildGranivore	0.905	0.642	1.408	0.159
guildInsectivore	4.828	0.424	11.389	**0.000**
guildNectivore	1.236	0.507	2.439	**0.015**
guildOmnivore	1.671	0.554	3.016	**0.003**
Forest Age	-0.604	0.544	-1.110	0.267
Isolation Level	-0.480	0.740	-0.648	0.517
Forest Age:Isolation Level	0.000	0.121	0.001	0.999
guildFrugivore:Forest Age	0.522	0.546	0.956	0.339
guildGranivore:Forest Age	0.977	0.765	1.277	0.201
guildInsectivore:Forest Age	0.592	0.548	1.082	0.279
guildNectivore:Forest Age	1.122	0.617	1.820	0.069
guildOmnivore:Forest Age	0.772	0.681	1.133	0.257
guildFrugivore:Isolation Level	0.516	0.745	0.693	0.488
guildGranivore:Isolation Level	-0.364	0.969	-0.375	0.707
guildInsectivore:Isolation Level	0.486	0.742	0.655	0.512
guildNectivore:Isolation Level	0.781	0.749	1.043	0.297
guildOmnivore:Isolation Level	0.156	0.810	0.192	0.848

Table 3.2: Percentage of dietary guilds across forest types

Percentage of individual birds in each dietary guild within four forest types, based on relative abundance of species (PFe = extensive primary forest (n = 2); PFi = isolated primary forest (n = 2); SFc = connected secondary forest (n = 3); SFi = isolated secondary forest (n = 7)).

Dietary Guild	PFe	PFi	SFc	SFi
Carnivore	0.32	0.58	0.16	0.33
Frugivore	19.8	19.34	18.42	17.67
Granivore	0.11	1.82	1.19	1.91
Insectivore	75.57	72.52	72.59	73.17
Nectivore	2.18	2.62	4.95	3.26
Omnivore	2.02	3.11	2.69	3.66

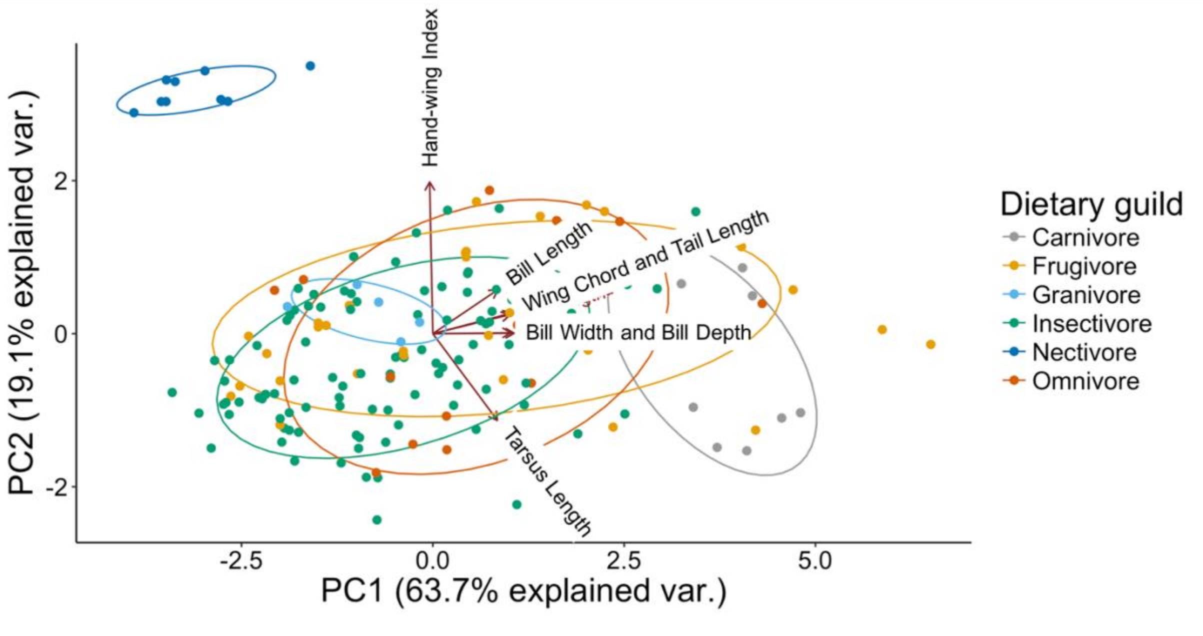

Figure 3.1: PCA of individual functional traits

Principal Component Analysis (PCA) using all species and seven functional (log^{-10} transformed) traits. Colours indicate dietary guild assigned to species using data from Wilman *et al.* (2014).

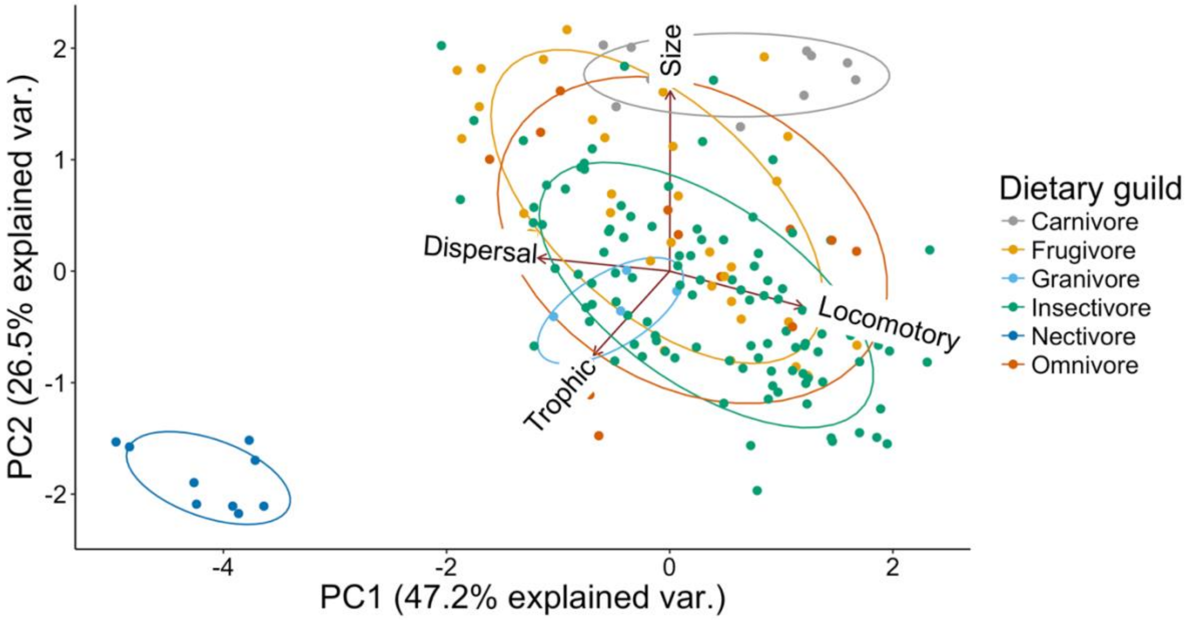

Figure 3.2: PCA of derived functional traits

Principal Component Analysis (PCA) using four derived functional traits. PCAs were performed on trophic (beak length, width and depth) and locomotory (wing, tail and tarsus lengths) traits separately. The first components of the trophic and locomotory PCAs were both strongly correlated with body mass and so were combined into a second PCA to produce a single body size axis. The second components of the trophic and locomotory PCAs were independent of body mass, and were therefore used as the trophic and locomotory trait axes for further analyses. Dispersal was calculated from the hand-wing index (Claramunt *et al.* 2012). Colours indicate dietary guild assigned to species using data from Wilman *et al.* (2014).

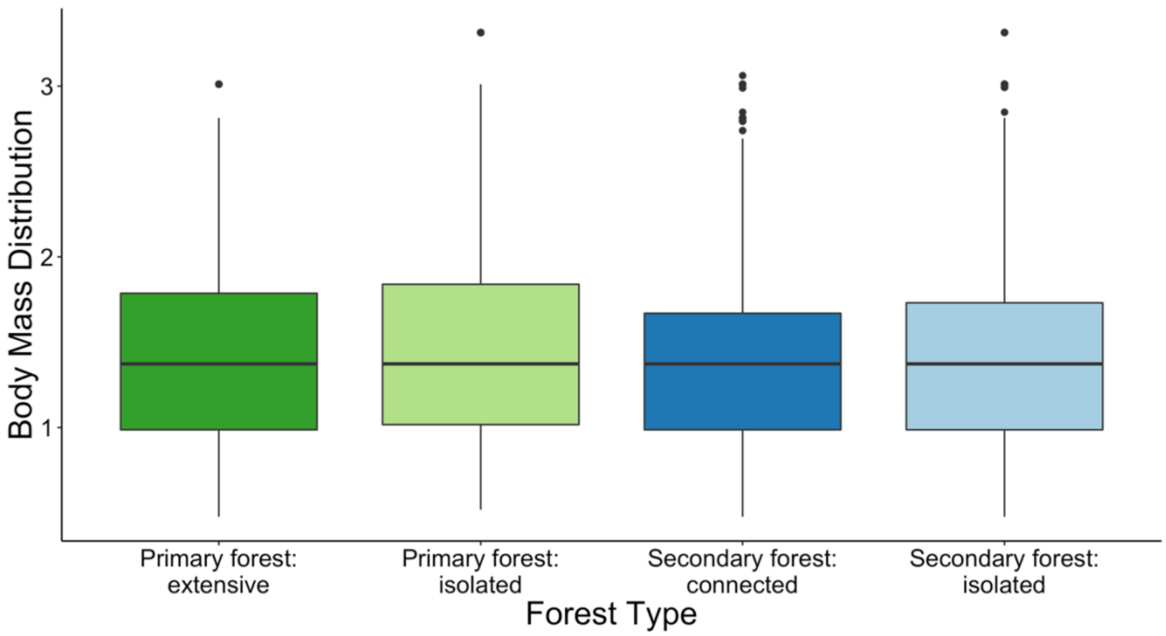

Figure 3.3: Body mass distribution across forest types

Body mass distribution ($\log^{-10}$ transformed) for birds in four forest types. Calculated using species relative abundance data.

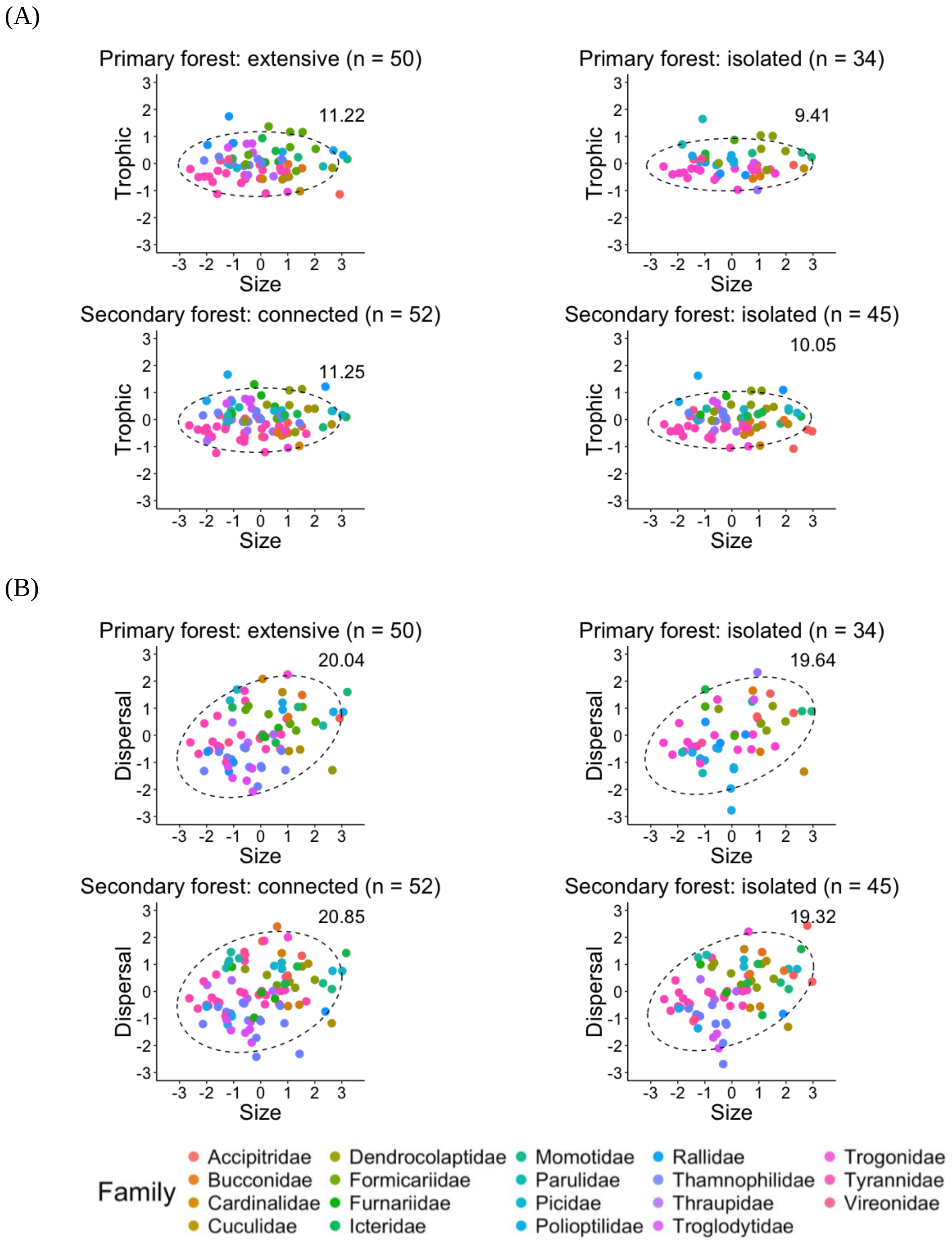

Figure 3.4: Trait distributions for insectivores across forest types

Functional trait distribution of insectivores across four forest types for (A) size and trophic traits, and (B) size and dispersal traits, allowing a visual assessment of relative morphospace. Ellipses represent 95% CI of the occupied morphospace, numbers indicate the area of functional morphospace occupied by the ellipse. Traits have been scaled and centred and are therefore directly comparable.

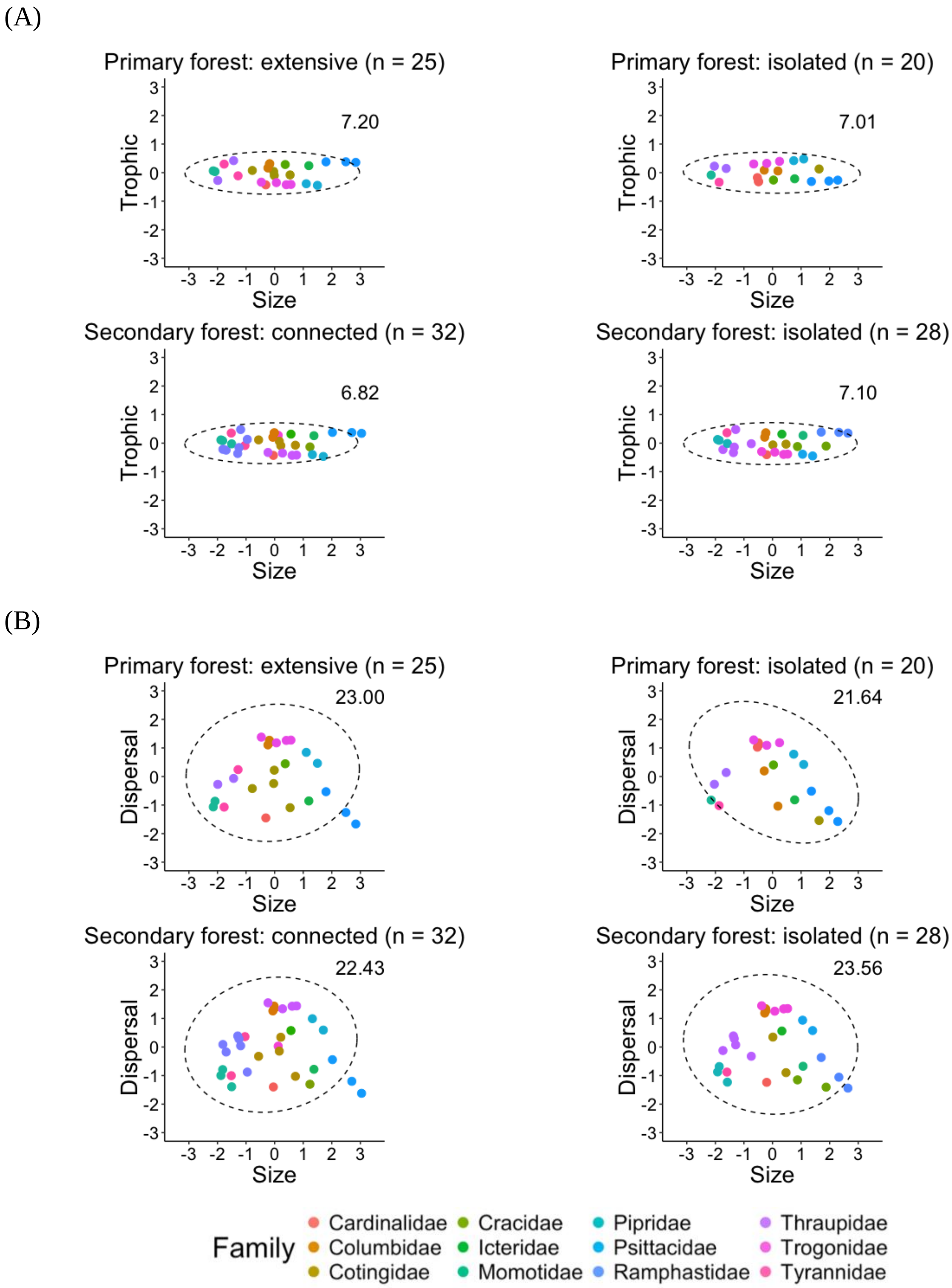

Figure 3.5: Trait distributions for frugivores across forest types

Functional trait distribution of frugivores across four forest types for (A) size and trophic traits, and (B) size and dispersal traits, allowing a visual assessment of relative morphospace. Ellipses represent 95% CI of the occupied morphospace, numbers indicate the area of functional morphospace occupied by the ellipse. Traits have been scaled and centred and are therefore directly comparable.

Functional diversity

There was no significant difference in FDiv or FEve in insectivore communities across forest types (Figs 3.6 and 3.7). However, FDis of insectivores varied with forest isolation; extensive PF and connected SF had significantly higher FDis than isolated PF and SF (Figs 3.6 and 3.7). These patterns were confirmed using AICc model selection (Table S3.6).

FDis, FDiv and FEve were not significantly different for frugivore communities across forest categories (Figs 3.8 and 3.9); although FDis was highest in isolated SF and lowest in connected SF, with intermediate levels in extensive and isolated PF (Fig. 3.8), as confirmed my models selection using AICc (Table S3.7).

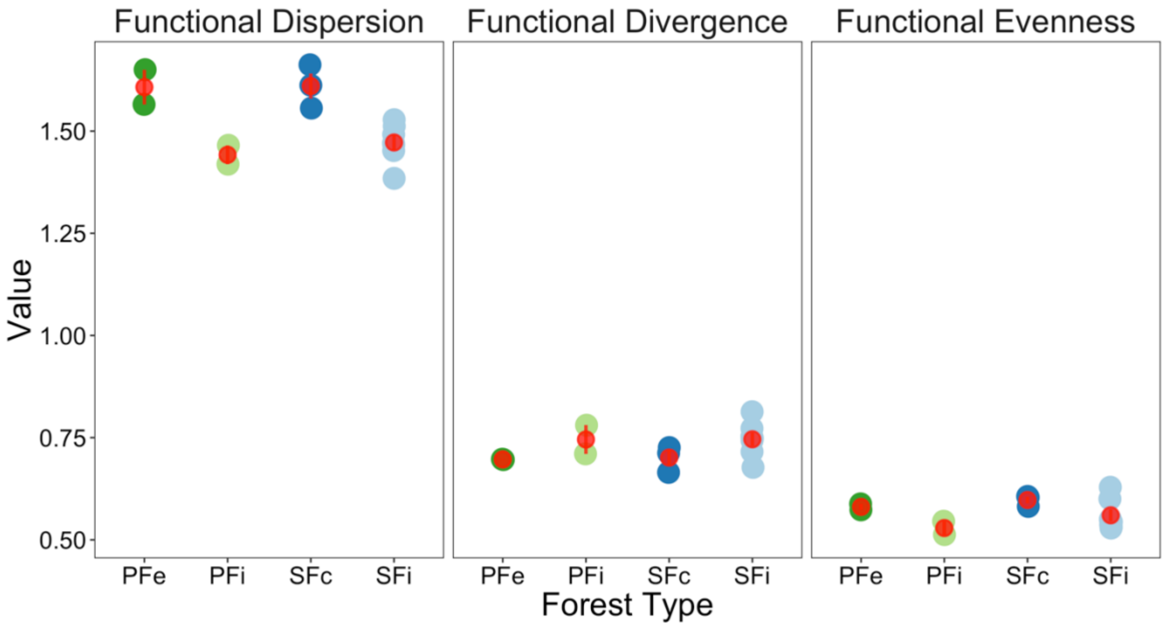

Figure 3.6: Functional diversity indices for insectivores across forest types
Three functional diversity indices for four forest types for insectivorous birds. Values for individual sites are plotted in green or blue, mean and standard errors for each forest type are plotted in red. Values are calculated using species relative abundance data. (PFe = extensive primary forest (n = 2); PFi = isolated primary forest (n = 2); SFc = connected secondary forest (n = 3); SFi = isolated secondary forest (n = 7)).

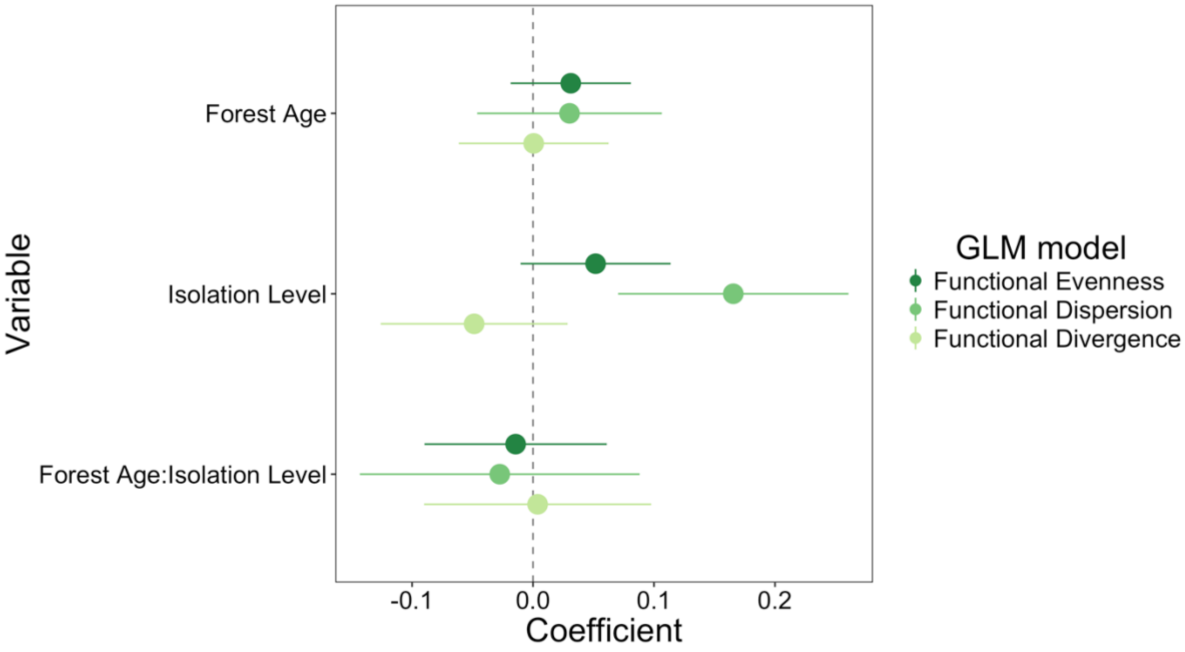

Figure 3.7: GLM results for functional diversity indices for insectivores

Coefficient estimates of the effect sizes from Generalised Linear Models (GLM) with two predictor variables and their interaction for insectivorous birds. The different colours indicate individual linear regression models for three functional diversity indices. The centre point denotes the mean, the bars denote the 95% lower and upper confidence limits; where the confidence limits do not intersect the dotted line, the effect is significant. . Model selection results are reported in Table S3.6.

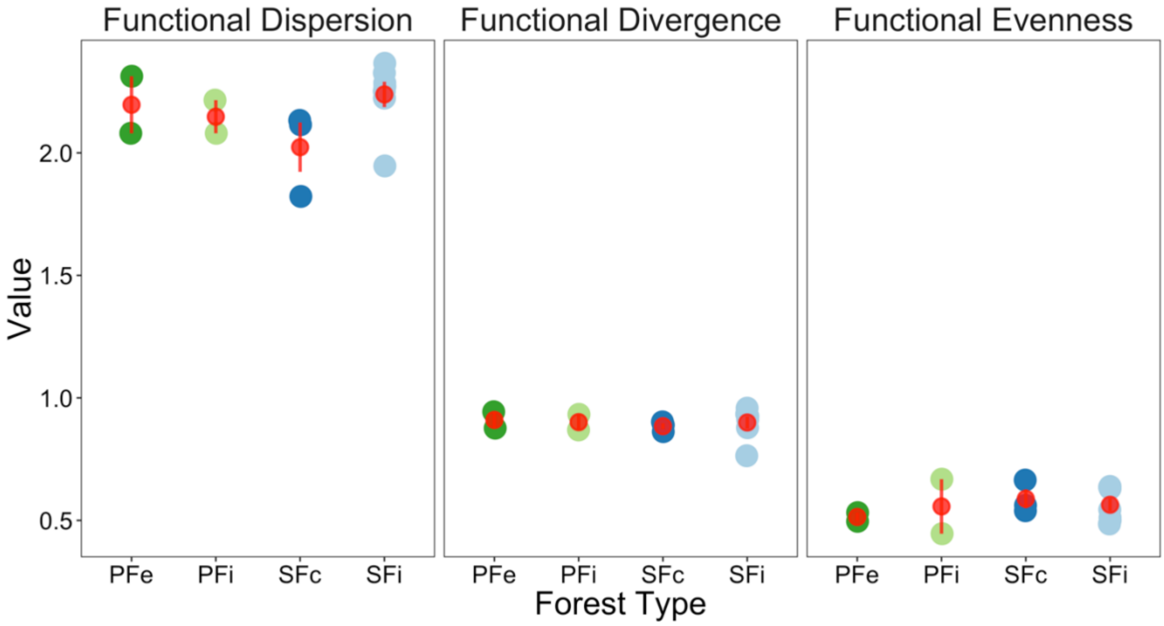

Figure 3.8: Functional diversity indices for frugivores across forest types

Three functional diversity indices for four forest types for frugivorous birds. Values for individual sites are plotted in green or blue, mean and standard errors for each forest type are plotted in red. Values are calculated using species relative abundance data. (PFe = extensive primary forest (n = 2); PFi = isolated primary forest (n = 2); SFc = connected secondary forest (n = 3); SFi = isolated secondary forest (n = 7)).

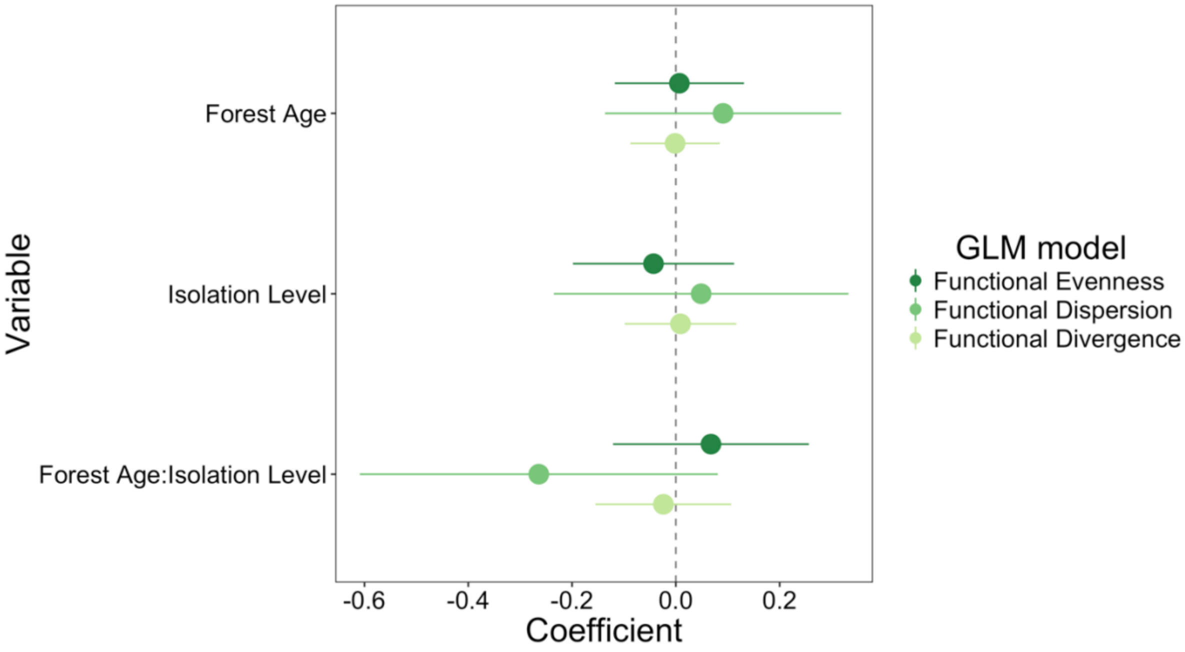

Figure 3.9: GLM results for functional diversity indices for insectivores

Coefficient estimates of the effect sizes from Generalised Linear Models (GLM) with two predictor variables and their interaction for frugivorous birds. The different colours indicate individual linear regression models for three functional diversity indices. The centre point denotes the mean, the bars denote the 95% lower and upper confidence limits; where the confidence limits do not intersect the dotted line, the effect is significant. . Model selection results are reported in Table S3.7.

Functional composition of community-weighted mean traits in communities

For the insectivore community, the trophic trait (the second component of the beak length, width and depth PCA) varied significantly with forest age and isolation (Figs 3.10 and 3.11). Extensive PF and connected SF sites had a higher trophic value than isolated sites, indicating a greater number of species with longer and narrower beaks, and SF had a higher trophic value than PF. Although, the latter result was driven primarily by the very low trophic trait values recorded in isolated PF. No clear pattern was found for the other three traits (Fig. 3.10). These patterns were confirmed using AICc model selection (Table S3.8).

For frugivores, the dispersal (hand-wing index) trait varied significantly with the interaction between forest age and isolation; isolated PF and SF both had higher dispersal values than extensive PF and connected SF, indicating a greater number of species with narrow, pointed wings (Figs 3.12 and 3.13). The same pattern was seen for the locomotory (the second component of the wing, tail and tarsus length PCA) and size (the first component of the trophic and locomotory PCAs) trait. Isolated PF and SF had higher values than extensive PF and connected SF equivalents suggesting that species in isolated sites generally have longer tarsus to tail/wing ratio, and a larger body size, although these results were not significant (Figs 3.12 and 3.13). For the trophic trait, the pattern was reversed and extensive PF and connected SF sites had higher values than isolated sites, suggesting longer, narrower beaks, though again this result was not significant (Figs 3.12 and 3.13). These patterns were confirmed using AICc model selection (Table S3.9).

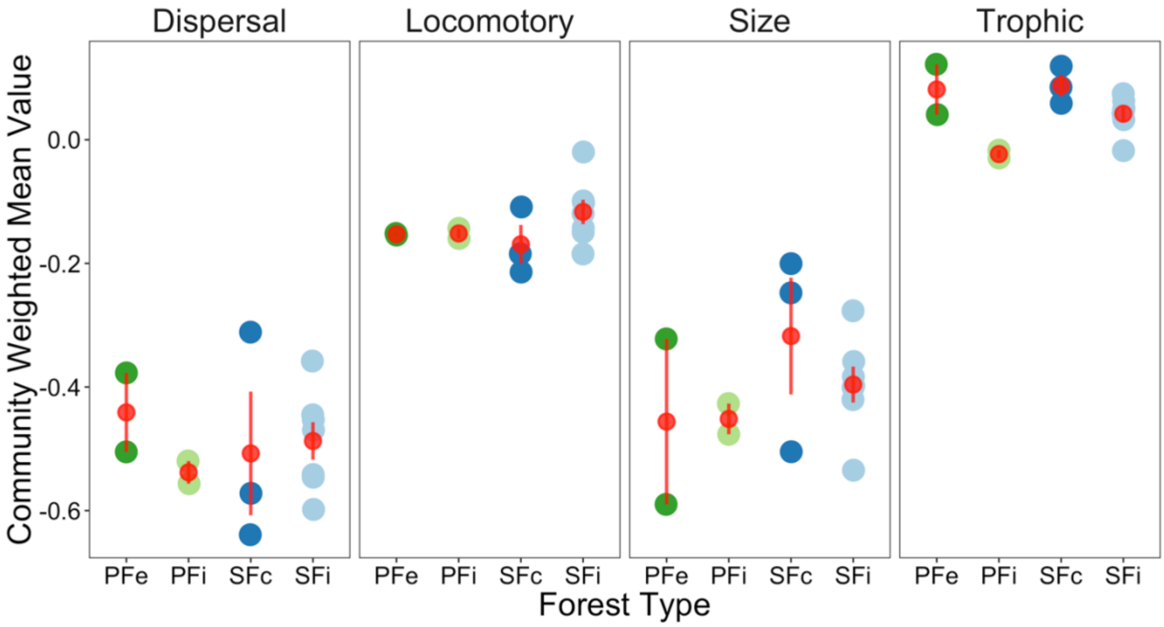

Figure 3.10: Community-weighted mean traits for insectivores across forest types Community-weighted mean values of four traits for insectivorous birds across four forest types. Traits have been scaled and centred, and are calculated on species relative abundance data. Values for individual sites are plotted in green or blue, mean and standard errors for each forest type are plotted in red. (PFe = extensive primary forest (n = 2); PFi = isolated primary forest (n = 2); SFc = connected secondary forest (n = 3); SFi = isolated secondary forest (n = 7)).

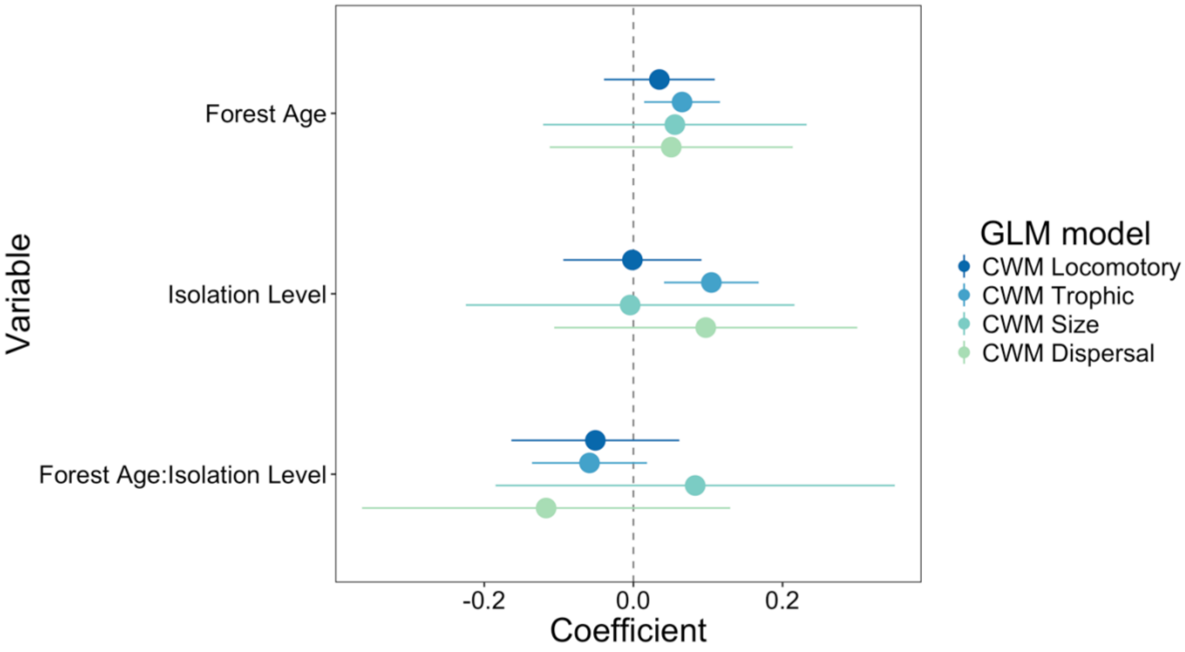

Figure 3.11: GLM results for community-weighted mean traits for insectivores
Coefficient estimates of the effect sizes from Generalised Linear Models (GLM) with two predictor variables and their interaction for insectivorous birds. The different colours indicate individual linear regression models for four community-weighted mean traits. The centre point denotes the mean, the bars denote the 95% lower and upper confidence limits; where the confidence limits do not intersect the dotted line, the effect is significant. Model selection results are reported in Table S3.8.

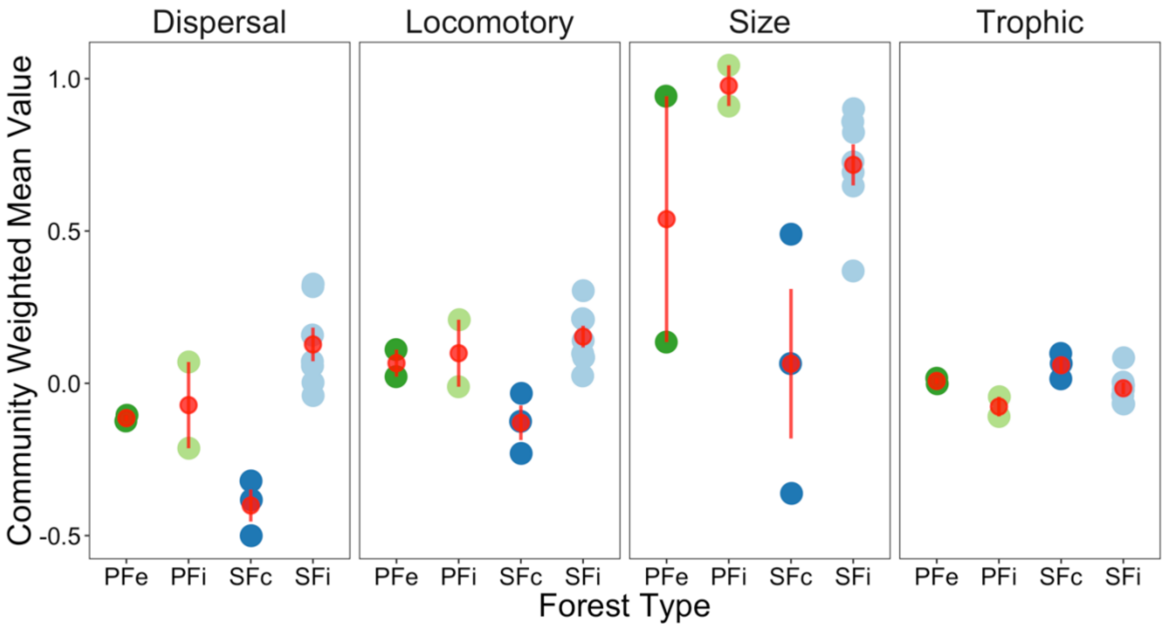

Figure 3.12: Community-weighted mean traits for insectivores across forest types Community-weighted mean values of four traits for frugivorous birds across four forest types. Traits have been scaled and centred, and are calculated on species relative abundance data. Values for individual sites are plotted in green or blue, mean and standard errors for each forest type are plotted in red. (PFe = extensive primary forest (n = 2); PFi = isolated primary forest (n = 2); SFc = connected secondary forest (n = 3); SFi = isolated secondary forest (n = 7)).

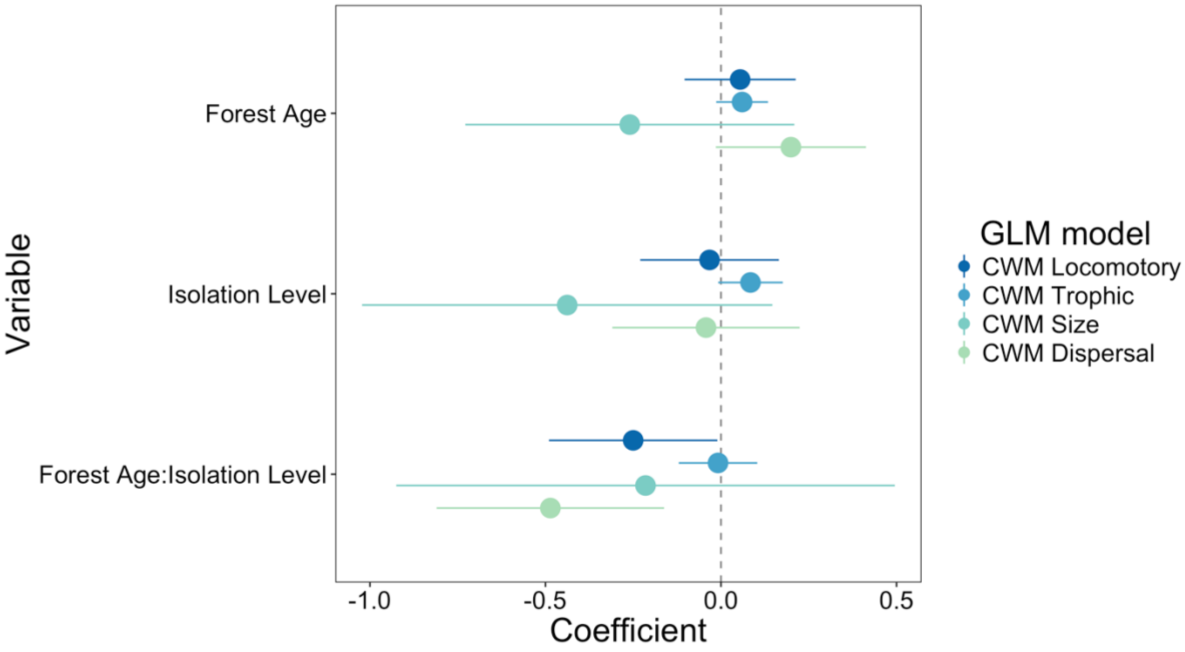

Figure 3.12: GLM results for community-weighted mean traits for frugivores Coefficient estimates of the effect sizes from Generalised Linear Models (GLM) with two predictor variables and their interaction for frugivorous birds. The different colours indicate individual linear regression models for four community-weighted mean traits. The centre point denotes the mean, the bars denote the 95% lower and upper confidence limits; where the confidence limits do not intersect the dotted line, the effect is significant. . Model selection results are reported in Table S3.9.

3.5 Discussion

Our results suggest that dietary guild structure does not vary with forest age or isolation, and overall forest age and isolation appear to have little impact on the functional diversity of frugivore and insectivore communities in tropical forests. The significant effects that were observed suggest that frugivores and insectivores differ in their responses to forest isolation and age, indicating that habitat change has different implications for distinct dietary guilds.

Relationships between dietary guilds and functional traits

Only species that have highly distinctive morphology (nectivores) were distinguishable as a discrete dietary group from multivariate analysis of morphological traits. All other dietary groups showed considerable overlap in multivariate trait space. The high overlap of different dietary guilds in trait space may be representative of overlap in diets. Some species can clearly be assigned to a single guild; for example the Red-lored Amazon (*Amazona autumnalis*), which only consumes fruit, or the Dot-winged Antwren (*Microrhopias quixensis*) whose diet consists solely of invertebrates (Wilman *et al.* 2014). However, most species exhibit a greater diversity in their diet and are not easily allocated to a single dietary guild; for example, the Keel-billed Toucan (*Ramphastos sulfuratus*) is estimated to consume 60% fruit, 20% invertebrates, 10% mammals/birds, and 10% reptiles/amphibians and yet is classed as a frugivore, and the Black-throated Trogon (*Trogon rufus*) is estimated to eat 60% insects and 40% fruit and yet is classed as an insectivore (Wilman *et al.* 2014). This has obvious implications for where to draw the boundary lines between dietary groups in multivariate space, and so may confound conclusions regarding responses of different guilds to habitat change. Furthermore, species may be incorrectly categorised due to a lack of detailed dietary information. Precise dietary information is known for many species, but for others it is based on only a few brief observations, or extrapolated from data from congeneric species (Wilman *et al.* 2014). Thus, our certainty of whether a bird is, for example, primarily insectivorous, is dependent on the quality and quantity of original observations.

It is also possible that the morphological traits selected are inappropriate for fully explaining dietary guild. There is debate about which traits are most appropriate for assessing community functional diversity (Petchey & Gaston 2006), since the traits used will influence where species are plotted in multivariate space and will dictate the relevance of these analyses to ecosystem processes. However, the traits selected for this study are broadly accepted as being highly correlated with functional roles (Bregman *et al.* 2016, 2015, Trisos *et al.* 2014), and multiple studies have shown a connection between these traits and their corresponding ecosystem processes (e.g. Claramunt *et al.* 2012, Hsu *et al.* 2014, Miles *et al.* 1987, Miles & Ricklefs 1984, Schoener 1965, Tobias *et al.* 2014, Wheelwright 1985).

Impacts of forest age and isolation on functional diversity

Secondary forests can support similar functional diversity in bird communities relative to PF, but the provision of ecosystem services in younger regrowth may be less stable, and will be dependent on forest connectivity and disturbance history (Sayer *et al.* 2017). However, distinct dietary guilds tend to differ in their responses to disturbance (Bregman *et al.* 2016, Luck *et al.* 2013, Vandewalle *et al.* 2010).

Previous studies have found that insectivores are particularly sensitive to habitat disturbance and isolation, and many species are unable to sustain populations in fragmented landscapes due to changes in vegetation structure (Pavlacky *et al.* 2015, Stratford & Stouffer 2015), altered microclimates (Patten & Smith-Patten 2012, Pollock *et al.* 2015, Stratford & Robinson 2005), reduced availability of suitable habitat (Sodhi *et al.* 2008, Stouffer *et al.* 2011), increased nest predation (Crooks & Soulé 1999, Robinson & Sherry 2012) and dispersal limitation (Barlow *et al.* 2006, Ferraz *et al.* 2007, Moore *et al.* 2008, Powell *et al.* 2015a, 2013, Stouffer *et al.* 2006).

In our study, the insectivore community in both SF and isolated sites supported similar levels of FDiv and FEve relative to extensive PF, suggesting that insectivore communities in disturbed habitats have similar levels of niche differentiation compared to PF, and thus low resource use competition. Communities were also similarly distributed in niche space, allowing for the effective utilisation of the entire range of available resources (Mason *et al.* 2005). However, FDis was higher in extensive PF and connected SF relative to isolated forest, which suggests that in isolated sites the mean distance of all species to the community mean trait value is reduced. In addition, the total area of morphospace occupied was greatest in extensive PF and connected SF sites, and lowest in isolated sites for insectivores. These findings suggest that there is a narrower range of traits present in insectivore communities in isolated forests compared to continuous forest.

Barro Colorado Island has well-documented cases of isolation-related extirpations, particularly among understorey insectivore species (Robinson 1999, Willis 1974), which has reduced the diversity of insectivorous birds in isolated forests across our study site. In contrast, we found that even young SF sites that are connected to extensive PF can have high functional and species diversity. This is probably because increased matrix permeability aids the movement of dispersal limited species. Thus, these connected SF sites tend to have a greater functional diversity of insectivores, compared to communities in isolated SF.

Forest age did not appear to impact the functional diversity of insectivores in our study, with extensive PF and connected SF supporting similar levels of functional diversity and occupied trait space. Our SF sites are between 20 and 120-years-old and so tend to have high structural complexity that may support a diverse community of birds (DeWalt *et al.* 2003). Other studies have also suggested that the functional diversity of insectivores is boosted in SF habitats by the influx of non-forest insectivores (Bregman *et al.* 2016, Sekercioğlu *et al.* 2002), although this did not seem to be the case at our sites where we detected only limited numbers of non-forest birds (see Chapter 2). A recent meta-analysis that compared SF (1 – 100-years-old) with nearby PF at 44 tropical forests sites also found little effect of forest age on the functional diversity of bird communities, with only FEve being slightly higher in SF (Sayer *et al.* 2017). In contrast, studies of younger SF (6 – 22-years-old), have found trait structure of avian insectivore communities in SF is limited compared to neighbouring PF (Bregman *et al.* 2016). However, with increasing SF age, tree species composition and many structural aspects of SF become more similar to PF, providing an increased number of nesting, roosting and foraging resources for birds (DeWalt *et al.* 2003).

Few studies have investigated the impacts of habitat disturbance on the functional diversity of frugivorous bird communities. Bregman *et al.* (2016) found that increasing habitat disturbance led to a reduction in the trait space occupied by frugivorous bird communities, and Cottee-Jones *et al.* (2015) reported decreasing FDis of frugivores at isolated *Ficus* trees with increasing distance from intact forest. In contrast, the functional diversity (FDiv, FEve and FDis) of our frugivore community did not change across either forest age or isolation gradients. However, the impact of both forest age and isolation was evident when examining the total area of morphospace occupied by individual niche axes, indicating that frugivore trait diversity is reduced for each niche axis in both isolated and SF habitats, compared to extensive PF. These results indicate that frugivores may be particularly susceptible to altered resource availability (i.e. fruiting trees) in disturbed habitats. Frugivorous species often have large home ranges, and are generally highly dispersive because they are adapted to tracking temporally and spatially patchy food resources (Salisbury *et al.* 2012, Tobias *et al.* 2013). These adaptations may enable frugivorous bird species to persist in fragmented landscapes, where fruiting trees are scarce are patchily distributed across the landscape (Chiarello 2000, Schulze *et al.* 2000). However, results from this study, Bregman *et al.* (2016) and Cottee-Jones *et al.* (2015) would suggest that there is a filtering of certain traits from the frugivorous community in disturbed habitats; with changes in body size, trophic and dispersal traits across disturbance gradients.

Variation in trait structure

Habitat disturbance can select for a subset of morphological traits, illustrated by shifts in community-weighted mean traits for insectivores and frugivores, and particularly forest insectivores (Bregman *et al.* 2016). We found that insectivores had lower trophic trait values in isolated forest, indicating that these sites are comprised of species with shorter and wider beaks. This highlights the loss of insectivorous species with long, narrow beaks from isolated sites. Long, narrow beaks are typical of the understorey insectivores that have been lost from Barro Colorado Island as the result of isolation-related extirpations, including the Song Wren (*Cyphorhinus phaeocephalus*), White-breasted Wood-wren (*Henicorhina leucosticta*) and Tawny-throated Leaftosser (*Sclerurus mexicanus*; Robinson 1999, Willis 1974). These understorey insectivores may be among the most sensitive to habitat isolation; studies have shown that this group is often the first to disappear when forests are disturbed (Pavlacky *et al.* 2015, Stratford & Stouffer 1999). As a result, the insectivore community in isolated sites is increasingly dominated by foliage-gleaning species, that forage using an upward-striking motion to capture prey, and by aerial-foraging species, that use a hawking method (Fitzpatrick 1985, Trisos *et al.* 2014). These are foraging tactics employed by insectivorous bird species that are less likely to be associated with the understorey; their wider bills being more suited to acquiring food in the vegetation structure found in higher levels of the forest.

Species with poor dispersal ability and an unwillingness to cross open areas are also more sensitive to forest isolation (Lees & Peres 2008), and our results suggest that frugivore communities in isolated habitats had greater dispersal ability compared to extensive PF and connected SF sites. Non-significant trends in the other derived traits (size, locomotory and trophic), indicated that frugivorous species in isolated sites tended to have larger body size, longer tarsus to tail/wing ratio, and shorter, wider beaks. This suggests that species present in isolated sites may be more adept at feeding on a wider range of fruits than those in well-connected sites, since these traits allow them to track fluctuating fruit resources across the landscape (Price 2004). In contrast to our study, others have shown that large frugivore species were more sensitive to habitat change, and were absent from fragmented and disturbed habitats (Bregman *et al.* 2016, Galetti *et al.* 2013, Pérez-Méndez *et al.* 2016). These findings may be due to the increased hunting pressure frequently found in disturbed and fragmented habitats (Holbrook & Loiselle 2009, Markl *et al.* 2012, Peres & Palacios 2007, Wright 2003). Our study site is unusual in that the isolated sites have limited accessibility, as they are located within a reservoir, and are in a strictly protected area, regularly patrolled by park rangers. In contrast, the mainland sites (extensive PF and connected SF) are more accessible and more susceptible to hunting pressure. Thus, in our study landscape, the abundance of larger birds may not be reduced in isolated sites relative to extensive PF and connected SF mainland sites. This suggests that, at least for larger forest patches, habitat fragmentation per se does not lead to the extirpation of large species, and that previous studies may have failed to account for the confounding impact that hunting pressure can have on bird community composition.

Implications for ecosystem processes

Our results suggest that the ecosystem services carried out by frugivores and insectivores are minimally affected by isolation and forest age in this study landscape. However, there are some effects of forest age and isolation on both seed dispersal and insect predation, which have the potential to influence the long-term resilience of forests (Howe 1977, Lundberg & Moberg 2003, Wunderle 1997). Insectivores and frugivores had different responses to forest age and isolation highlighting the importance of analysing functional groups and ecological niches separately so as not to mask patterns and responses in ecological processes following habitat change. In addition, by using functional traits separated into ecological niche axes we can identify limiting traits, and potentially detect morphologically-distinct specialist species (located on the edge of trait space) that may fulfil previously unrecognised ecological roles.

For insectivores, shifts in trophic behaviour in isolated forest sites may alter herbivorous insect populations (Van Bael *et al.* 2003, Marquis & Whelan 1994), which in turn may impact plant growth and seedling mortality (Van Bael *et al.* 2008, Dunham 2008). However, the loss of certain trophic traits within the community does not necessarily mean that ecosystem processes will be altered, as other species may fill the vacant functional niche. The loss of the socially dominant ant-following bird, the Ocellated Antbird (*Phaenostictus mcleannani*), from Barro Colorado Island has been partially mitigated by the compensatory response of the socially subordinate Spotted Antbird (*Hylophylax naevioides*; Touchton & Smith 2011). The Spotted Antbird's presence at ant swarms has tripled since the extirpation of the Ocellated Antbird from the island > 20 years ago (Touchton & Smith 2011), supporting the hypothesis that functional redundancy may buffer the effects of species loss on ecosystem processes in disturbed habitats. Similarly, research examining the diversity and composition of avian functional traits in the Atlantic Forest, Brazil, has suggested that degraded forest sites provide alternative rather than fewer functions (De Coster *et al.* 2015). This was caused by a decrease in the provisioning of some functions, and an increase in others, along with strong within-guild species turnover, and a replacement of specialists by generalists.

For frugivores, the filtering of dispersal-limited bird species from isolated sites could have implications for seed dispersal (Galetti *et al.* 2013, Sethi & Howe 2009, Terborgh *et al.* 2008). Our results suggest that frugivorous species that remain in isolated habitats tend to be larger, with wider beak shapes (although both these results were not significant). Other studies have shown that frugivores with wide beaks are capable of consuming and dispersing the widest range of fruit sizes, whereas those species with narrow beaks/gapes only disperse small-fruited plants (Wheelwright 1985). This suggests that seed dispersal services may be minimally affected by the shifts in frugivore communities resulting from increased forest isolation.

Caveats

The landscape where this study was conducted is largely forested with extensive old SF (20-120 years old). The isolated sites are well-protected with little ongoing-disturbance, and the youngest SF sites are well connected to a large tract of undisturbed extensive PF. These landscape factors, combined, suggest that our results should be treated as a best-case scenario for the effects of forest succession and isolation on the functional diversity of avian communities. The findings from this study are landscape-specific and should be interpreted in the context of the disturbance levels, forest age and connectivity in central Panama.

The decision to standardise survey effort across all sites could potentially have generated differences in bird communities because of variation in detectability between different sites (for further discussion see Chapter 2). Comparisons between our data and a previous long-term study located in our extensive PF, which involved more intensive survey methods (Robinson *et al.* 2000), highlighted a number of species that were missing from our extensive PF dataset. Of these missing species, the majority (65%) were nocturnal, vagrant, migrant, aerial or aquatic birds and hence may not have been present or active during our surveys (for details see Chapter 2). The remaining 35% were rare species that occur at low abundances, and were not morphologically distinct. Only when a species occurs at a relatively high abundance, and with a distinctive suite of traits, will it be likely to have an effect on functional diversity indices. Thus, these missing species’ contribution to the overall functional diversity of traits in PF sites was considered to be limited.

Conclusions

Our results suggest that isolated forests and SF have the capacity to retain a significant portion of avian functional diversity, potentially contributing to the maintenance of interaction networks that regulate seed dispersal and herbivory. This has important implications for the resilience of tropical forests in human-modified landscapes, and highlights the need to conserve and protect secondary forest to help maintain ecosystem processes in changing tropical landscapes.

3.6 Acknowledgements

I would like to thank Tom Bradfer-Lawrence, Nick Gardner, Ovidio Jaramillo, Samuel Jones and Juan Pablo Rios for their valuable assistance with bird identification and verification, as well as their support during fieldwork. I would also like to thank the Smithsonian Tropical Research Institute (STRI) for providing logistical support, and the members of the Tropical Ecology and Conservation (TEAC) group at the University of Stirling for many helpful discussions. Research was supported by a Carnegie Research Grant (R.J.M.), a Gilchrist Travel Grant (R.J.M.), a Santander University Travel Grant (R.J.M.), and the Natural Environment Research Council (J.A.T.).

3.7 Supplementary Information

Table S3.1: PCA factor loadings for individual traits for all birds

Factor loadings (eigenvectors) and proportion of variance explained for principal components (PCs) from the principal component analysis including all seven functional traits

	PCA loadings						
Functional Trait	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Bill Length	0.356	0.241	0.597	0.654	-0.117	0.127	0.015
Bill Width	0.429	0.005	0.289	-0.598	0.101	0.579	0.173
Bill Depth	0.446	0.003	0.247	-0.357	-0.172	-0.700	-0.305
Tarsus Length	0.354	-0.475	-0.356	0.174	-0.465	0.308	-0.426
Tail Length	0.422	0.104	-0.333	0.182	0.772	-0.015	-0.266
Wing Chord	0.432	0.113	-0.428	0.096	-0.213	-0.188	0.726
Hand Wing Index	-0.017	0.832	-0.279	-0.121	-0.299	0.165	-0.313
Proportion variance	**0.637**	**0.191**	**0.090**	**0.042**	**0.026**	**0.008**	**0.006**

Table S3.2: PCA factor loadings for derived traits for all birds

Principal component analysis (PCA) for all birds showing factor loadings (eigenvalues) and the proportion of variance explained. PC1 from both trophic and locomotory trait analyses were combined in a secondary PCA to create an axis representing overall body size. The second PC for both trophic and locomotory traits captured variation independent of body size.

Functional Trait	PC	Proportion variance	PCA loadings			Correlation with body mass
			Tarsus length	Tail length	Wing length	*r*
Locomotory	1	0.83	0.537	0.587	0.607	0.950
	2	0.14	0.829	-0.500	-0.250	0.001
			Beak length	Beak width	Beak depth	*r*
Trophic	1	0.86	0.537	0.591	0.602	0.770
	2	0.12	0.838	-0.453	-0.304	-0.180
Size			Trophic PC1	Locomotory PC1		*r*
	1	0.88	0.707	0.707		0.920

Table S3.3: PCA factor loadings for derived traits for insectivores

Principal component analysis (PCA) for insectivorous birds showing factor loadings (eigenvalues) and the proportion of variance explained. PC1 from both trophic and locomotory trait analyses were combined in a secondary PCA to create an axis representing overall body size. The second PC for both trophic and locomotory traits captured variation independent of body size.

Functional Trait	PC	Proportion variance	PCA loadings			Correlation with body mass
			Tarsus length	Tail length	Wing length	*r*
Locomotory	1	0.78	0.509	0.592	0.625	0.940
	2	0.19	-0.841	0.495	0.216	-0.042
			Beak length	Beak width	Beak depth	*r*
Trophic	1	0.86	0.561	0.572	0.598	0.860
	2	0.1	0.759	-0.644	-0.096	0.073
Size			Trophic PC1	Locomotory PC1		*r*
	1	0.89	0.707	0.707		0.950

Table S3.4: PCA factor loadings for derived traits for frugivores

Principal Component Analysis (PCA) for frugivorous birds showing factor loadings (eigenvalues) and the proportion of variance explained. PC1 from both trophic and locomotory trait analyses were combined in a secondary PCA to create an axis representing overall body size. The second PC for both trophic and locomotory traits captured variation independent of body size.

Functional Trait	PC	Proportion variance	PCA loadings			Correlation with body mass
			Tarsus length	Tail length	Wing length	*r*
Locomotory	1	0.85	-0.534	-0.596	-0.600	0.950
	2	0.13	-0.845	0.402	0.353	-0.081
			Beak length	Beak width	Beak depth	*r*
Trophic	1	0.96	0.571	0.580	0.581	-0.730
	2	0.03	0.821	-0.418	-0.389	-0.051
Size			Trophic PC1	Locomotory PC1		*r*
	1	0.86	-0.707	0.707		0.910

Table S3.5: Correlations among derived traits

Correlation table showing *r* values for derived functional traits used in two-step PCA analyses for all species, frugivorous species and insectivorous species.

Dietary Group	Functional Trait	Functional Trait		
		Dispersal	Locomotory	Trophic
All Species	Dispersal			
	Locomotory	-0.740		
	Trophic	0.240	-0.270	
	Size	-0.033	-0.085	-0.100
Frugivores	Dispersal			
	Locomotory	0.780		
	Trophic	-0.270	-0.460	
	Size	-0.096	0.055	0.066
Insectivores	Dispersal			
	Locomotory	0.610		
	Trophic	-0.230	-0.360	
	Size	0.250	0.051	0.040

Table S3.6: GLM simplification for FD indices for insectivores

Results from Generalised Linear Models (GLM) simplification for models for three functional diversity indices with two predictor variables and their interaction for insectivorous birds. Models are ranked by AICc. A '+' indicates that the predictor was included in the model.

	Model	Forest Age	Isolation Level	Forest Age:Isolation Level	df	logLik	AICc	ΔAIC	*wi*
Functional Evenness	3		+		3	29.648	-50.9	0	0.472
	1				2	27.385	-49.7	1.22	0.257
	4	+	+		4	30.739	-49	1.86	0.186
	2	+			3	27.727	-47.1	3.84	0.069
	8	+	+	+	5	30.836	-44.2	6.72	0.016
Functional Dispersion	3		+		3	24.429	-40.5	0	0.842
	4	+	+		4	24.688	-36.9	3.53	0.144
	8	+	+	+	5	24.839	-32.2	8.28	0.013
	1				2	15.362	-25.6	14.82	0.001
	2	+			3	15.389	-22.4	18.08	0
Functional Divergence	3		+		3	27.752	-47.1	0	0.616
	1				2	25.166	-45.2	1.86	0.243
	4	+	+		4	27.758	-43.1	4.03	0.082
	2	+			3	25.283	-42.2	4.94	0.052
	8	+	+	+	5	27.762	-38	9.08	0.007

Table S3.7: GLM simplification for FD indices for frugivores

Results from Generalised Linear Models (GLM) simplification for models for three functional diversity indices with two predictor variables and their interaction for frugivorous birds. Models are ranked by AICc. An 'X' indicates that the predictor was included in the model.

	Model	Forest Age	Isolation Level	Forest Age:Isolation Level	df	logLik	AICc	ΔAIC	*wi*
Functional Eveness	1				2	17.271	-29.5	0	0.662
	2	+			3	17.648	-26.9	2.56	0.184
	3		+		3	17.276	-26.2	3.3	0.127
	4	+	+		4	17.65	-22.9	6.6	0.024
	8	+	+	+	5	17.987	-18.5	10.98	0.003
Functional Dispersion	1				2	6.819	-8.5	0	0.503
	3		+		3	8.078	-7.8	0.79	0.339
	2	+			3	6.819	-5.2	3.31	0.096
	4	+	+		4	8.121	-3.8	4.75	0.047
	8	+	+	+	5	9.543	-1.6	6.96	0.015
Functional Divergence	1				2	22.948	-40.8	0	0.699
	2	+			3	23.02	-37.6	3.17	0.143
	3		+		3	22.968	-37.5	3.27	0.136
	4	+	+		4	23.058	-33.7	7.13	0.02
	8	+	+	+	5	23.148	-28.8	12.01	0.002

Table S3.8: GLM simplification for CWM traits for insectivores

Results from Generalised Linear Models (GLM) simplification for models for four community-weighted mean traits with two predictor variables and their interaction for insectivorous birds. Models are ranked by AICc. An ‘X’ indicates that the predictor was included in the model.

	Model	Forest Age	Isolation Level	Forest Age:Isolation Level	df	logLik	AICc	ΔAIC	*wi*
Locomotory	1				2	23.333	-41.6	0	0.497
	3		+		3	24.555	-40.7	0.87	0.323
	2	+			3	23.606	-38.8	2.76	0.125
	4	+	+		4	24.681	-36.9	4.66	0.048
	8	+	+	+	5	25.213	-32.9	8.65	0.007
Trophic	4	+	+		4	29.1	-45.8	0	0.392
	3		+		3	27.069	-45.7	0.02	0.388
	8	+	+	+	5	30.515	-43.5	2.23	0.129
	1				2	23.684	-42.3	3.48	0.069
	2	+			3	24.215	-40	5.73	0.022
Size	1				2	11.516	-17.9	0	0.556
	2	+			3	12.407	-16.4	1.53	0.259
	3		+		3	11.697	-15	2.95	0.127
	4	+	+		4	12.837	-13.2	4.71	0.053
	8	+	+	+	5	13.089	-8.7	9.26	0.005
Dispersal	1				2	13.584	-22.1	0	0.702
	3		+		3	13.644	-18.9	3.19	0.142
	2	+			3	13.586	-18.8	3.3	0.134
	4	+	+		4	13.644	-14.8	7.23	0.019
	8	+	+	+	5	14.224	-10.9	11.13	0.003

Table S3.9: GLM simplification for CWM traits for frugivores

Results from Generalised Linear Models (GLM) simplification for models for four community-weighted mean traits with two predictor variables and their interaction for frugivorous birds. Models are ranked by AICc. An ‘X’ indicates that the predictor was included in the model.

	Model	Forest Age	Isolation Level	Forest Age:Isolation Level	df	logLik	AICc	ΔAIC	*wi*
Locomotory	3		+		3	11.793	-15.2	0	0.674
	4	+	+		4	12.178	-11.9	3.27	0.131
	8	+	+	+	5	14.621	-11.7	3.44	0.12
	1				2	7.748	-10.4	4.78	0.062
	2	+			3	7.763	-7.1	8.06	0.012
Trophic	4	+	+		4	25.294	-38.1	0	0.467
	3		+		3	22.949	-37.5	0.65	0.338
	1				2	20.179	-35.3	2.88	0.111
	2	+			3	20.946	-33.5	4.65	0.046
	8	+	+	+	5	25.31	-33.1	5.02	0.038
Size	4	+	+		4	-0.813	14.1	0	0.484
	3		+		3	-3.036	14.5	0.4	0.396
	1				2	-6.707	18.5	4.44	0.053
	8	+	+	+	5	-0.57	18.6	4.57	0.049
	2	+			3	-6.163	20.7	6.66	0.017
Dispersal	3		+		3	6.045	-3.7	0	0.503
	8	+	+	+	5	10.415	-3.3	0.36	0.42
	4	+	+		4	6.054	0.3	4.03	0.067
	1				2	0.302	4.5	8.18	0.008
	2	+			3	0.401	7.6	11.29	0.002

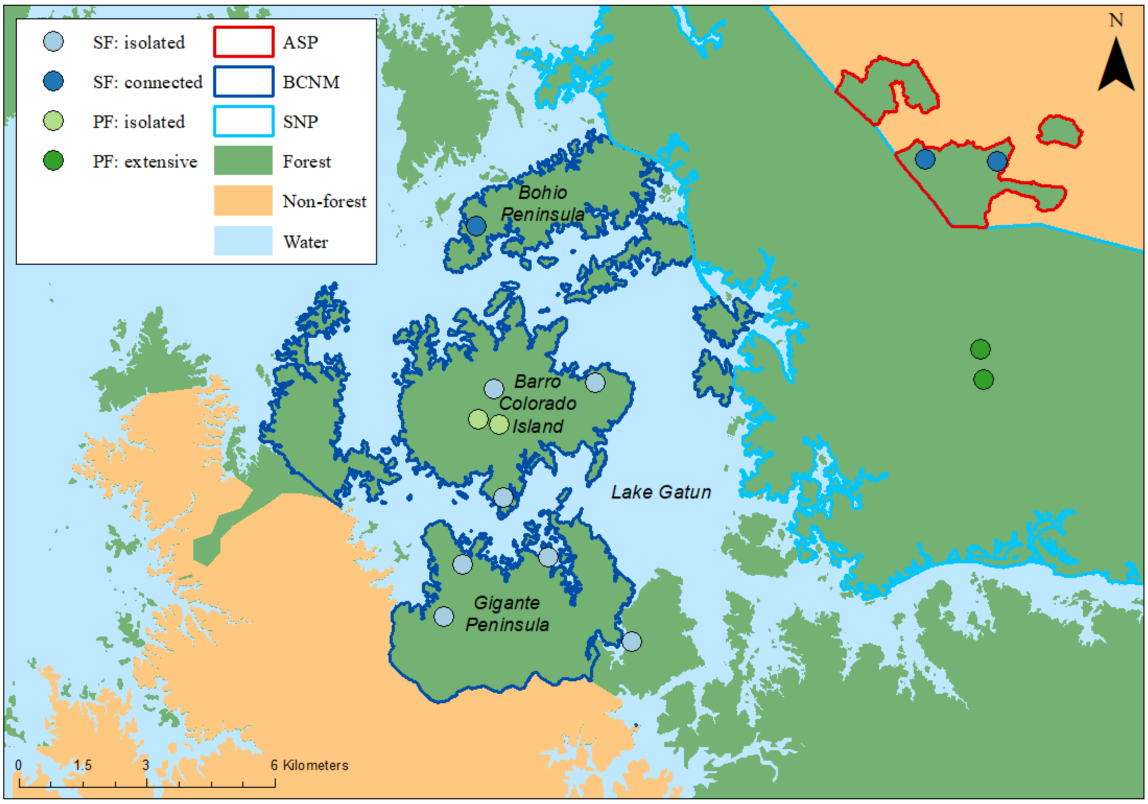

Figure S3.1: Map of study sites

Map of the 14 study sites in central Panama. Sites are colour-coded by forest age (PF = primary forest; SF = secondary forest). This area of central Panama is composed of a mosaic of contiguous different aged forest stands interspersed with a water and agricultural matrix. The main areas in which different aged forest stands are embedded are the Barro Colorado National Monument (BCNM), including Barro Colorado Island (1,560 ha) and Gigante peninsulas (2,600 ha), Soberania National Park (SNP) and surrounding contiguous forest (22,000 ha), including the Agua Salud Project (ASP).

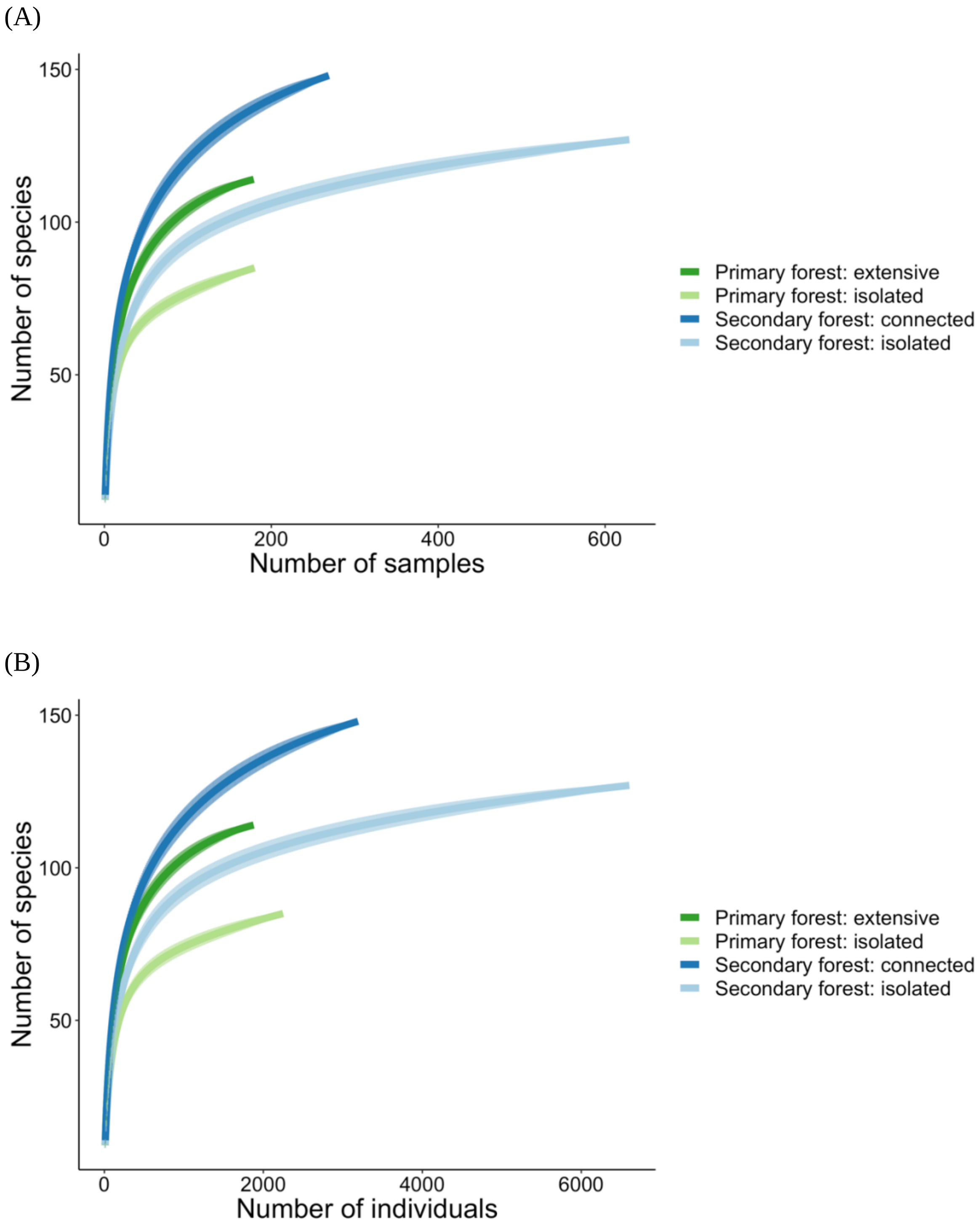

Figure S3.2: Species accumulation curves across forest types

Species accumulation curves scaled by (A) sample and (B) by number of individual birds detected for bird communities in 14 sites in four forest types. (Primary forest: extensive (n = 2); Primary forest: isolated (n = 2); Secondary forest: connected (n = 3); Secondary forest: isolated (n = 7)).

Chapter 4: High concordance between the composition of tropical bird and tree communities across a gradient of forest age and isolation

D. H. Dent and J. A. Tobias supervised the project, ForestGEO-CTFS provided tree community data for primary forest sites, and D. H. Dent provided tree community data for secondary forest sites. D. H. Dent also commented on draft versions of the chapter.

4.1 Abstract

Deforestation and degradation of tropical primary forests increasingly threatens biodiversity and ecosystem functions, but the widespread expansion of secondary forests may help to mitigate this threat. The degree to which secondary forests can replicate primary forest biodiversity is mediated by landscape and site factors such as forest age and isolation, and therefore the role they might play in averting an extinction crisis has been a subject of much debate. We assess compositional similarities of bird and tree communities in response to forest age and isolation, and examine the relationship between bird communities and forest structure. We also investigate the relationship between frugivorous bird community composition and bird-dispersed trees. We found high levels of compositional concordance between bird and tree communities, in that site compositions for both taxa responded to forest disturbance in similar ways. However, forest age played a greater role in determining bird community composition compared to tree community composition. Similarly, forest isolation had a greater impact on the bird community compared to the tree community. Bird diversity was related to forest structure (mean tree diameter and number of stems per hectare); with more diverse bird communities associated with greater structural complexity. Bird community composition was also significantly correlated with metrics of forest structure. Communities of frugivorous bird species and bird-dispersed plant species were not as well matched as the full bird and tree communities, possibly due to the relatively small scale at which we were able to examine the relationship. These results have important implications for conservation; restoring one is not possible without the other. Moreover, additional resources in SF will aid passive restoration, highlighting the value of SF and the need for improved protection of SF throughout the tropics. SF are important components of tropical landscapes that can act to increase habitat connectivity or provide buffer zones for protected areas.

4.2 Introduction

Changes in tropical landscapes

Over the last 100 years, tropical primary forests (PF) have been cleared and replaced with agriculture, pasture and plantations at unprecedented rates (Chazdon 2014). The subsequent abandonment of many of these areas initiates forest succession, resulting in widespread and expanding areas of regenerating secondary forests (SF) across the tropics (Chazdon *et al*. 2009). Secondary forests may retain more forest species than alternative land uses such as intensive agriculture (Lindenmayer & Franklin 2002), and combined with the increasing area in the tropics (Aide *et al*. 2013, FAO 2015), this means these habitats could be of particular importance for biodiversity conservation. However, their potential ability to preserve forest biodiversity is dependent on both site- and landscape-level factors, such as forest extent, age, connectivity and configuration of the surrounding habitat matrix (Brook & Bradshaw 2006, Chazdon *et al*. 2009, Dent & Wright 2009, Gardner *et al*. 2007, Laurance 2006, Wright & Muller-Landau 2006a, b).

Tree community development in secondary forests

Regenerating SF can reach levels of tree species richness and diversity similar to PF within 20 – 30 years (DeWalt *et al*. 2003, Pascarella *et al.* 2000). Sites are initially colonised by fast-growing pioneer tree species, and accumulate more shade-tolerant, late successional, species over time (Dent *et al*. 2013), so that SF tree community composition becomes increasingly similar to that of PF (Letcher & Chazdon 2009, Norden *et al*. 2009). The rate of recovery is influenced by site-level factors, such as historical land-use, as well as broader landscape-level factors (Guariguata & Ostertag 2001). A history of intensive land-use practices, such as fires, heavy grazing or agriculture, high-impact logging or bulldozing, can all reduce residual vegetation and seed sources and create highly disturbed and compacted soils that will slow forest regeneration (Guariguata & Ostertag 2001). Landscape factors, such as the presence of PF (as a seed source and as habitat for vertebrate seed dispersers), can help to accelerate forest regrowth and species colonisation, whilst habitat fragmentation and isolation will impede these processes (Dent & Wright 2009, Guevara & Laborde 1993).

Consequences for faunal recovery

Changes in forest structure and tree species composition that occur during SF regeneration have important consequences for animal populations. As SF matures, forest structural complexity increases, providing habitat and food resources for animal species (DeWalt *et al.* 2003), and so the diversity of most animal taxa increases over time in SF, mirroring changes in structural complexity and tree species composition (Chazdon *et al.* 2009, Dent & Wright 2009, Wright 2010).

Tracking changes in the conservation value of SF as the habitat develops requires a tractable taxon. Much of the research assessing the conservation value of tropical SF has focused on birds (e.g. Barlow *et al.* 2007b, Powell *et al.* 2013, Raman 1998). Birds are one of the best studied faunal groups in the tropics and provide important ecosystem services, such as pollination and seed dispersal (Sekercioglu 2006, Whelan *et al.* 2008). As a group, birds have diverse habitat and dietary requirements such that their response to habitat development varies across species according to their ecology (Hughes *et al.* 2002a, Petit & Petit 2003). Moreover, birds are relatively easy to identify and survey, making them convenient indicators of habitat quality and value.

Bird community development in SF

The site and landscape factors that affect community reassembly of tree communities in SF also influence bird communities. Bird species richness and diversity is capable of returning to PF levels in as little as seven years (Borges 2007). However, the species present may be very different and there is typically little overlap between the avian species composition in young SF and that of nearby PF (Barlow *et al.* 2007a, Borges 2007, Tvardíková 2010). Changes in avian community composition tend to follow changes in forest structure, so that similarity to PF increases with SF age (Andrade & Rubio-Torgler 1994, Borges 2007, Raman 1998). The landscape context of SF, such as distance to PF source populations and level of isolation within the countryside matrix, plays a critical role in determining avian community reassembly (Chazdon *et al.* 2009, Dent & Wright 2009, Wolfe *et al.* 2015). Many tropical forest birds are strongly dispersal limited with poor gap-crossing abilities, and may not be able to colonise SF unless it is contiguous with PF (Van Houtan *et al.* 2007, Lees & Peres 2009, Moore *et al.* 2008, Tobias *et al.* 2013). In addition, bird species occurring in isolated forest patches embedded within a non-forest matrix may be more sensitive to stochastic population fluctuations and local extinction (Wolfe *et al.* 2015).

Differing responses of tree and bird communities to isolation and succession

The initial stages of tropical forest succession can progress quickly, and the rapid growth of early-colonising pioneer tree species can bring about canopy closure only 5–10 years after land abandonment (Chazdon 2008). Many structural aspects of SF (such as, large living tree density) can resemble those of PF within 70 years (DeWalt *et al.* 2003). However, the gradual turnover of tree species composition in canopy and subcanopy layers, from pioneer to shade-tolerant forest species, can take centuries (Chazdon 2008, Oliver & Larson 1996). In contrast, the bird community composition in SF may converge with PF more quickly than trees, as recovery of bird communities in SF is more strongly influenced by structural development (e.g. Andrade & Rubio-Torgler 1994, Borges 2007, Bowman *et al.* 1990, Dunn 2004, Raman 1998).

Both floral and faunal communities develop over the course of succession, but this is mediated by isolation, which may limit colonisation of new habitat patches and precipitate extirpations from mature communities in recently fragmented areas. However, the time-scales at which these effects present themselves will vary between the taxa (Bender *et al.* 1998, Fahrig 2003, Turner 1996). Bird species have much shorter generation cycles than tree species, thus the consequences of fragmentation and isolation may be seen more rapidly in bird communities than in tree communities. Bird species are often extirpated from forest patches. For example, understorey insectivores and flocking species were found to be nearly absent from two 100-ha forested islands in Amazonia that had been isolated for approximately 25 years in a manmade reservoir (Wolfe *et al.* 2015). Conversely, tree communities in the same area maintained species richness and composition comparable with nearby continuous forest sites (Benchimol & Peres 2015).

The relationship between tree and bird communities

Forest bird communities are inherently dependent on the tree communities in which they live. The species richness and abundance of forest birds increases with structural complexity (Casas *et al.* 2016, MacArthur & MacArthur 1961). More complex forest structure offers more diverse ways to exploit resources and can therefore sustain more specialist species (Casas *et al.* 2016). Thus, the structural complexity that develops over secondary forest succession should provide habitats for increasingly diverse and complex bird communities.

In turn, trees are dependent on birds for ecosystem functions such as pollination, seed dispersal and protection from insect herbivory (Sekercioglu 2006). For example, avian frugivores play a critical role in seed dispersal, which is vital to seedling recruitment and the long-term resilience of forests (Howe 1977, Lundberg & Moberg 2003, Wunderle 1997). More than 75 percent of plants are dispersed by frugivorous vertebrates in the Neotropics (Howe & Smallwood 1982, Wenny *et al.* 2016), and birds are particularly important seed dispersers in tropical habitats modified by land-use change (Şekercioğlu *et al.* 2015). Declines in frugivorous birds may disrupt seed-dispersal networks and inhibit tree regeneration resulting in long-term shifts in tree community composition (Galindo-González *et al.* 2008, Sethi & Howe 2009, Terborgh *et al.* 2008), especially among large-seeded plant species that are thought to be obligately dependent on large birds for seed-dispersal (Wheelwright 1985, Wotton & Kelly 2011). Given the interdependence of frugivores and fruiting trees, we might expect a strong association between the structure of the two communities.

The potential for compositional concordance between bird and tree communities, (i.e. do the taxa mirror each other in their response to forest disturbance), would imply that the they are closely interrelated, and that responses in one taxon can be used as a proxy for responses in the other. This would imply that conservation actions need to take place at an ecosystem scale, rather the taxon-level.

Assessing the potential for SF to conserve tropical forest species requires detailed species inventory data over a wide range of SF ages, with comparable PF controls (Chazdon *et al.* 2009). While this data exists for a number of tropical bird communities (e.g. Andrade & Rubio-Torgler 1994, Barlow *et al.* 2007b, Blake & Loiselle 2001, Borges 2007, Bowman *et al.* 1990, Casas *et al.* 2016, Raman 1998), comparable species data for the corresponding tree communities rarely exists (although, see Barlow *et al.* 2007b and Casas *et al.* 2016). Of the few studies that have described bird and tree communities concurrently, the majority examine only metrics of forest structure (Van Bael *et al.* 2013, Blake & Loiselle 2001, Borges 2007, Sodhi *et al.* 2005b) or survey trees at such a small spatial scale that it limits inference (Bowman *et al.* 1990, Raman 1998, Schulze & Waltert 2004).

Study aims

Here we present data from tropical bird and tree communities across a forest age and isolation gradient. Both taxa received comparable, detailed survey effort, allowing us to draw robust conclusions regarding their interactions. We sampled four ages of SF (40 – 120-years-old), as well as PF controls. Sites were located in a water-matrix across an isolation gradient of island, peninsula and mainland. This landscape presents a unique opportunity to examine how bird and tree communities change across a successional and isolation gradient, and to investigate the relative importance of forest age versus isolation in determining the conservation value of SF. Our aim was to assess the potential similarities in the response of bird and tree community composition to forest age and isolation, as well as explore the relationship between bird communities and forest structure. Finally, we examined patterns in community composition between frugivorous birds and bird-dispersed trees to investigate if this relationship is more closely related than the whole community. We considered the following hypotheses; 1) forest isolation will play a greater role in determining bird communities than forest age, whereas forest age will have a greater impact on tree communities than forest isolation, 2) the number and diversity of birds will be positively correlated with increasing forest structural complexity, but this will be mediated by isolation effects, and 3) patterns in frugivorous bird communities and bird-dispersed tree communities will be more tightly related than patterns in the entire communities.

4.3 Methods

Study sites

Field surveys were conducted in the Panama Canal Watershed. Study sites were located in Barro Colorado Nature Monument and Soberania National Park (Fig. S4.1). Barro Colorado Nature Monument (5,600 ha; 9°9’ N, 79°51’ W) is comprised of five peninsulas and Barro Colorado Island, all situated in Lake Gatun, which was formed in 1914 by the flooding of the Panama Canal. Barro Colorado Nature Monument is a mosaic of PF and SF stands of different ages, with PF covering roughly half of Barro Colorado Island and small areas on the peninsulas. Secondary forests are located on areas of land that were used for cattle pasture or fruit production between the 1880s and the establishment of the Barro Colorado Nature Monument in 1979 (Leigh *et al*. 1982). Soberania National Park (22,000 ha; 9°9’ N, 79°44’ W) was established in 1980 and is a mix of very old SF and PF (Van Bael *et al*. 2013).

This study was conducted in a chronosequence consisting of two replicate stands of approximately 40, 60, 90 and 120-year-old SF, and four stands of PF (> 500 years). The SF stands are all located within the Barro Colorado Nature Monument and ages were estimated using historical records, aerial photographs and interviews with residents, for details see Denslow & Guzman (2000). Further descriptions of the forest history, soil properties and understorey light levels of the SF can also be found in Denslow & Guzman (2000). PF sites were selected, two in a relatively small patch (c. 800 ha) of isolated PF on Barro Colorado Island (henceforth referred to as isolated PF) and two in an extensive area of mainland PF in Soberania National Park (c. 22,000 ha; henceforth referred to as extensive PF). There is no indication that these PF sites have ever been logged or cultivated (Piperno 1990). The SF sites in our study experience different connectivity across an isolation gradient of island, peninsula or mainland. The Bohio Peninsula (90 yr old) site forms part of a large forest network connected to extensive PF in Soberania National Park. Island and Gigante Peninsula SF sites are smaller, isolated areas of forest within a water matrix. Island SF sites (90 – 120 yr old) are connected only with isolated PF, and are separated from extensive mainland PF by water. Secondary forest on the Gigante Peninsula is more extensive, and contains older patches (>200 yr old) interspersed with patches of 40 – 60 yr old SF, but is separated from extensive PF by either water or an agricultural matrix. In this chapter, we use a finer scale of forest isolation (referred to as island, peninsula or mainland) than in previous chapters as it better reflects the observed patterns.

Bird surveys

At each of the 12 sites, nine point counts were established; points were separated by a minimum of 100 m, and located at least 50 m from forest of a different age (Van Bael *et al.* 2013, Robinson *et al.* 2000). This method gave an estimated total survey area of nine ha per site. One site was surveyed per morning by two trained observers, with the first count beginning ten minutes after sunrise and the last completed by 10:30 am. All nine points at a site were sampled once during a survey visit, with a minimum of three days between repeat surveys at the same site; no surveys were conducted on excessively rainy or windy days.

Point counts were 10 minutes in duration, and all birds seen or heard within a 50 m-radius were identified (Martin & Blackburn 2014). Birds flying above the canopy were excluded from the survey. Surveys were conducted over three years: July to October 2014 (during the wet season), and in January 2015 and January to March 2016 (during the dry season). Each site was surveyed a total of ten times over the three years; five times in the wet season and five times in the dry, generating a total of 1,260 point counts. Further details of the bird survey methods can be found in Chapter 2.

We detected 13,925 individual birds and a total of 178 bird species from 35 families in fixed radius point counts (Table S2.1 in Chapter 2). We did not analyse solely forest species, and all 178 species were retained for analyses. Previous analysis of this dataset has demonstrated that similar species richness, diversity and composition patterns were found for forest species, and for all species (pooled forest and non-forest species; as presented in Chapter 2). Relative abundance of each species was calculated using the maximum observed count on any single visit to a site to avoid risk of double-counting bias.

Vegetation sampling

At each of the 12 sites, vegetation data was collected from one hectare forest plots located in the centre of the 9-ha bird survey area. The plots are part of two long-term tropical forest monitoring networks: the PF sites are part of the ForestGEO-CTFS network (Hubbell 1999, Hubbell *et al.* 2005), and the SF plots comprise the Barro Colorado Nature Monument chronosequence (Denslow and Guzman 2000, Dent *et al*. 2013). All free-standing woody plants within these plots were surveyed following the ForestGEO-CTFS census protocol, where all trees ≥ 1 cm diameter at breast height (DBH) are measured, mapped and identified to species level (Condit 1998). The SF sites were surveyed between 2011 and 2017, and the PF sites were surveyed in 2015. The two isolated PF sites are within Barro Colorado Island's 50-ha forest plot; we therefore selected two 1-ha plots from within the 50-ha plot (located in the centre of each of the two 9-ha bird survey areas) to use for our analyses. The two extensive PF plots are 1-ha plots from the ForestGEO-CTFS network within the Panama Canal watershed.

We analysed data from all living, woody stems ≥ 5 cm DBH, which we defined as the 'adult' community that determine forest structure (although individual trees are not necessarily reproductive at this size). This gave us a dataset of 9778 individual stems, and a total of 289 species in 58 families.

Data analyses

All analyses were conducted with the R package 'vegan' (Oksanen *et al*. 2016), using R version 3.4.1 (R Core Team 2017). Rarefaction curves were calculated to compare rates of species accumulation among forest age classes for bird and tree communities. When scaled by number of samples, these showed that curves reached, or were approaching, the asymptote for bird communities in all forest ages suggesting bird survey effort was adequate (Fig. S4.2). However, when rarefaction curves were scaled by number of individuals, asymptotes were not reached for all sites, suggesting that bird communities in some forest sites were under-sampled (Fig. S4.2; for further discussion see the caveats section in Chapter 2). Rarefaction curves for tree communities showed that most curves were only beginning to approach the asymptote (when scaled by both number of samples and number of individuals), suggesting that 1ha plots were perhaps not sufficient to capture the full range of species present in this study area (Fig. S4.3).

To compare patterns in species composition between bird and tree communities, we generated a dissimilarity matrix using the Morisita-Horn abundance-based similarity index (S_{MH}). The S_{MH} is robust to uneven and insufficient sampling and thus suited to determine whether reassembly of PF communities occurs in SF in terms of relative abundance (Chao *et al.* 2006).

To determine if forest age or geographic location explained patterns in species composition across the sites, we performed Mantel tests on three matrices of pair-wise distances among sites: Euclidean geographic distance, difference in forest age, and dissimilarity in species composition (S_{MH}), for each of our community datasets. Primary forest sites were assigned a nominal age of 500 years to allow inclusion of these sites in the analysis.

We explored qualitative similarities in species composition among sites with non-metric multidimensional scaling (NMDS), for both bird and tree communities. We used similarity matrices generated from S_{MH} that were undertaken with two dimensions as the stress levels were deemed sufficiently low (birds stress = 0.067, tree stress = 0.099; Kruskal 1964).

To investigate similarities in community composition between bird and tree communities we used Procrustes rotation (Peres-Neto & Jackson 2001). The first two axes from each of the bird and tree NMDS analyses were scaled and rotated to find an optimal superimposition that maximised fit. The stress levels from the NMDS analyses for both bird and tree communities were ‘good’, indicating that a high level of variation in the datasets was explained by these first two axes of the NMDS. The sum of the squared residuals (m_{12}) between the Procrustes configurations in their optimum superimposition is used as a metric of association (Gower 1971), where lower values indicate a greater degree of association between ordinations (i.e. high concordance between datasets). A permutation procedure (PROTEST) was then used to assess the statistical significant of the Procrustean fit (Jackson 1995). This test produces a correlation-like statistic which is interpreted in a way similar to the Pearson’s correlation index r (Peres-Neto & Jackson 2001); larger values indicate a better concordance between the two matrices, with $r = 1$ indicating identical matrices.

To assess the significance of observed differences in species composition in relation to forest age, degree of isolation (island, peninsula or mainland), and distance to extensive PF, we conducted a permutational multivariate analysis of variance (perMANOVA); an analysis of variance using the S_{MH} distance matrices for each community dataset.

Finally, to examine the relationship between bird communities and forest structure, we calculated species richness and Shannon-Weiner diversity indices (H) per site for bird communities, and mean DBH of stems, and number of stems/ha per site for the tree communities. We then investigated relationships among these variables using multi-predictor generalised linear models (GLM), using species richness or diversity (H) of birds as the response and forest structural metrics as the predictor. Model selection was based on Akaike's information criterion corrected for small samples (AICc; Akaike 1973). Models were ranked according to their AICc value, and only those with a difference (DAICc) of < 2 were considered to be equally supported. The importance of each predictor was assessed by Akaike weight (wi), which indicates the probability that the particular model is the best fit for the data (Burnham & Anderson 2002). Employing Pearson's correlation, we further explored relationships between forest structure and bird community composition, using the first and second axes from the NMDS ordinations.

Frugivorous bird and bird-dispersed tree subset

We created a subset of data to investigate the relationship between frugivorous birds and tree species that are dispersed by birds. Bird species were assigned a dietary guild based on Wilman *et al.* (2014). Guilds were defined by the food type that composed > 50% of a species diet, following methods set out in Bregman *et al.* (2016). Six guilds were represented in our dataset; carnivore, frugivore, granivore, insectivore, nectivore and omnivore. Species were classified as omnivores when no primary diet was apparent (i.e. all dietary components were less than 50%). From this data, we selected bird species from our community dataset that were classed as frugivores (n = 33). Tree species from our community dataset were selected if their fruit was dispersed by birds (n = 186), based on information from Muller-Landau & Hardesty (2005) and Wright *et al.* 2007.

We examined the relationship between these subsets of bird and tree communities, hereafter termed 'frugivorous birds' and 'bird-dispersed trees', investigating the relationships among the number of bird and tree species, and the diversity (H) of bird and tree species per site. We also investigated the community composition of these datasets through NMDS (frugivorous birds stress = 0.123, trees dispersed by birds stress = 0.095) and Procrustes rotation analyses, as described above.

4.4 Results

Community composition

Geographic distance among sites explained a greater portion of species composition patterns than forest age for both bird and tree communities (Mantel tests using S_{MH}; Table 4.1). The S_{MH} NMDS of species composition for birds showed a separation of sites in relation to both forest age and level of isolation (Fig. 4.1). Axis 1 appears to correlate with forest age; younger forests had more negative values and older forests more positive values. Sites displayed a clear split along Axis 2 that related to site location, with mainland and peninsula sites grouped together at one end of the axis and island sites at the other. Similar patterns were seen for the S_{MH} NMDS for tree communities but the separation of PF and SF sites along Axis 1 was less distinct, while separation following patterns of isolation was more pronounced along Axis 2 (Fig. 4.1).

Forest isolation explained a greater portion of the variation in community composition for bird species than forest age, while distance to extensive PF was not significant (perMANOVA using S_{MH}; Table 4.2). For tree communities, the perMANOVA using S_{MH} found no significant patterns.

Similarities in bird and tree community structure

Procrustes rotation analyses using PROTEST revealed significant concordance between bird and tree communities ($m_{12} = 0.202$, $r^2 = 0.893$, $P = < 0.001$; Fig. 4.2). However, even though composition of bird and tree communities were closely matched, metrics of bird and tree diversity were not correlated. Both bird and tree species richness per site, and bird and tree diversity (H) per site were unrelated (Fig. 4.3, Table 4.3 and Table 4.4).

Table 4.1: Mantel test results for bird and tree communities

Mantel test results assessing the correlation between similarity distance matrices for both bird and tree communities (using community similarity matrices generated from the Morisita-Horn abundance-based similarity index), with forest age, and geographic location. The significance of the statistic is evaluated by permuting rows and columns of the first similarity matrix.

Data Subset	Explanatory Variable	Mantel Statistic R^2	P
Birds	Forest Age	0.346	**<0.05**
	Geographic Location	0.756	**<0.001**
Trees	Forest Age	0.256	**<0.05**
	Geographic Location	0.672	**<0.001**

Table 4.2: perMANOVA results for bird and tree communities

Permutational MANOVA results (an analysis of variance using distance matrices) assessing the significance of observed differences in species composition between forest age, degree of isolation (island, peninsula or mainland), and geographic distance to extensive mainland PF, using community similarity matrices generated from Morisita-Horn abundance-based similarity index.

Explanatory Variable	Birds				Trees			
	R^2	F	df	P	R^2	F	df	P
Forest isolation	0.432	11.843	2	< **0.01**	0.218	1.607	2	0.099
Forest age	0.114	6.23	1	< **0.05**	0.07	1.032	1	0.396
Distance to extensive PF	0.032	1.729	1	0.129	0.086	1.267	1	0.257

Table 4.3: GLM simplification for bird species richness and forest structure

Results from Generalised Linear Models (GLM) simplification for models examining relationships between bird species richness and three predictor variables.

Model	Mean DBH of tree stems	Number of tree stems/ha	Tree species richness	df	logLik	AICc	ΔAIC	*wi*
3		-0.5881		3	-43.698	96.4	0	0.395
2	0.5393			3	-44.182	97.4	0.97	0.244
1				2	-46.244	97.8	1.43	0.194
4	0.2843	-0.4122		4	-43.221	100.2	3.76	0.06
5			-0.2188	3	-45.949	100.9	4.5	0.042
7		-0.5998	0.02842	4	-43.691	101.1	4.7	0.038
6	0.5162		-0.102	4	-44.098	101.9	5.51	0.025
8	0.2834	-0.4204	0.01859	5	-43.219	106.4	10.04	0.003

Table 4.4: GLM simplification for bird diversity (H) and forest structure

Results from Generalised Linear Models (GLM) simplification for models examining relationships between bird diversity (H) and three predictor variables.

Model	Mean DBH of tree stems	Number of tree stems/ha	Tress diversity (H)	df	logLik	AICc	ΔAIC	*wi*
2	0.6434			3	3.625	1.7	0	0.444
3		-0.5567		3	2.645	3.7	1.96	0.167
6	0.6261		0.3278	4	4.837	4	2.29	0.141
1				2	0.419	4.5	2.75	0.113
4	0.4844	-0.257		4	4.058	5.6	3.85	0.065
5			0.3608	3	1.256	6.5	4.74	0.042
7		-0.4912	0.2003	4	2.965	7.8	6.04	0.022
8	0.5553	-0.1174	0.2932	5	4.929	10.1	8.39	0.007

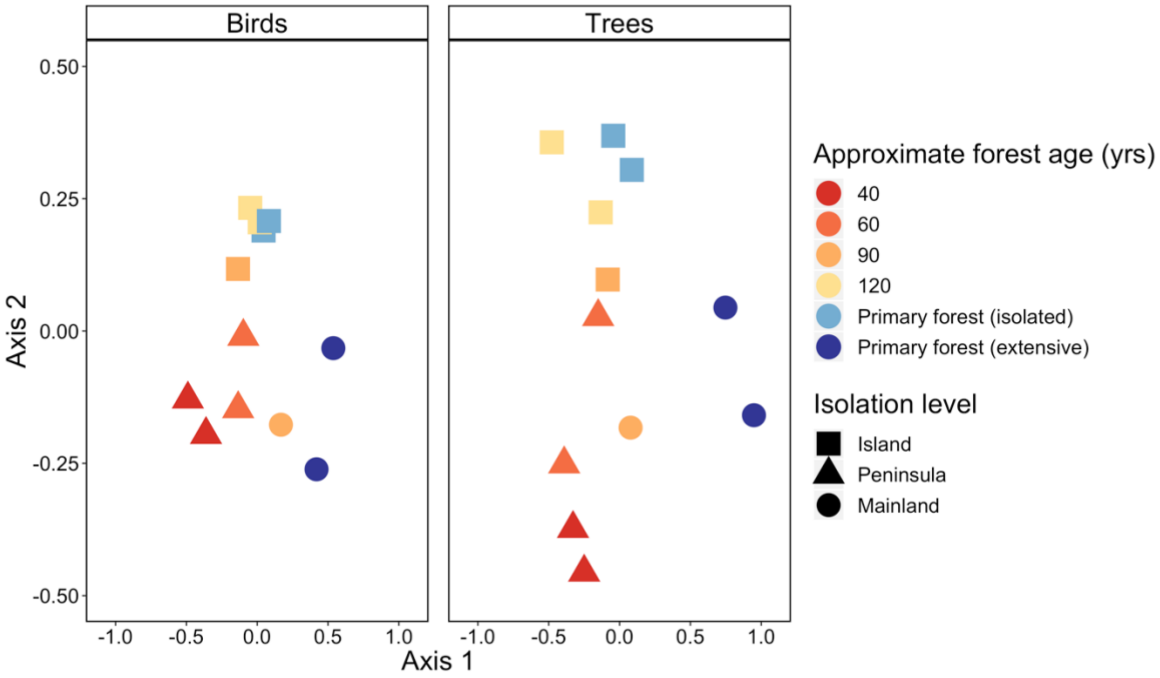

Figure 4.1: NMDS plots of bird and tree communities

Non-metric multidimensional scaling (NMDS) plots of bird and tree communities at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. NMDS were generated using the Morisita-Horn index (bird stress = 0.067; tree stress = 0.099). Isolation levels are represented by different symbols.

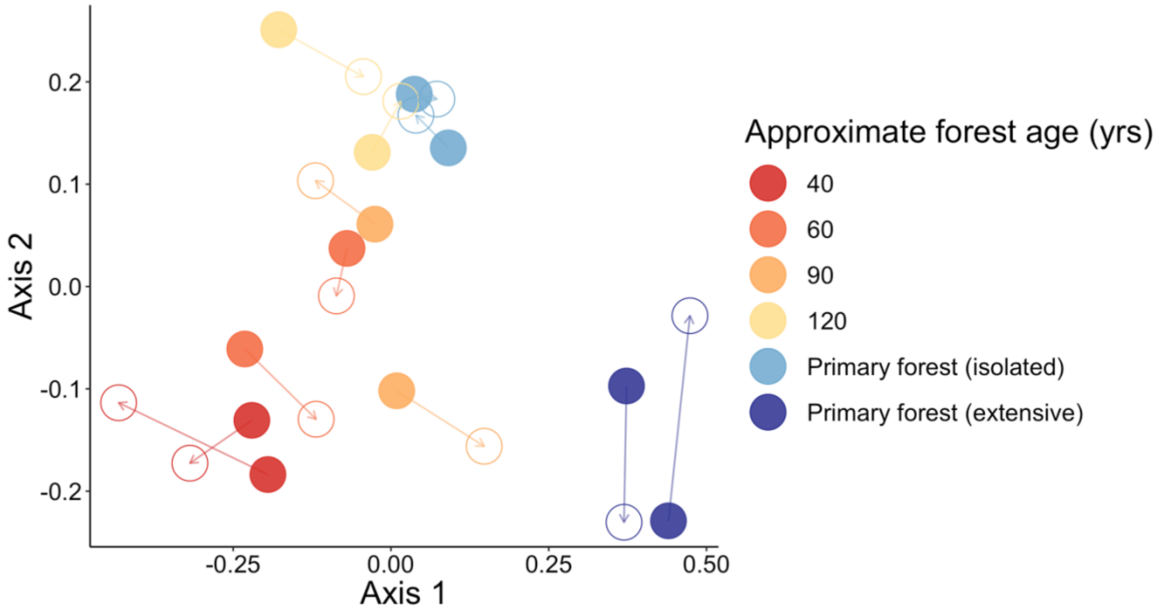

Figure 4.2: Procrustes rotation of bird and tree communities

Procrustes rotation comparing the first two axes from Morisita-Horn (S_{MH}) NMDS ordinations of bird (open circles) and tree (closed circles) communities at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. PROTEST results revealed a high level of concordance between the two datasets (m_{12} = 0.202, r^2 = 0.893, P = < 0.001).

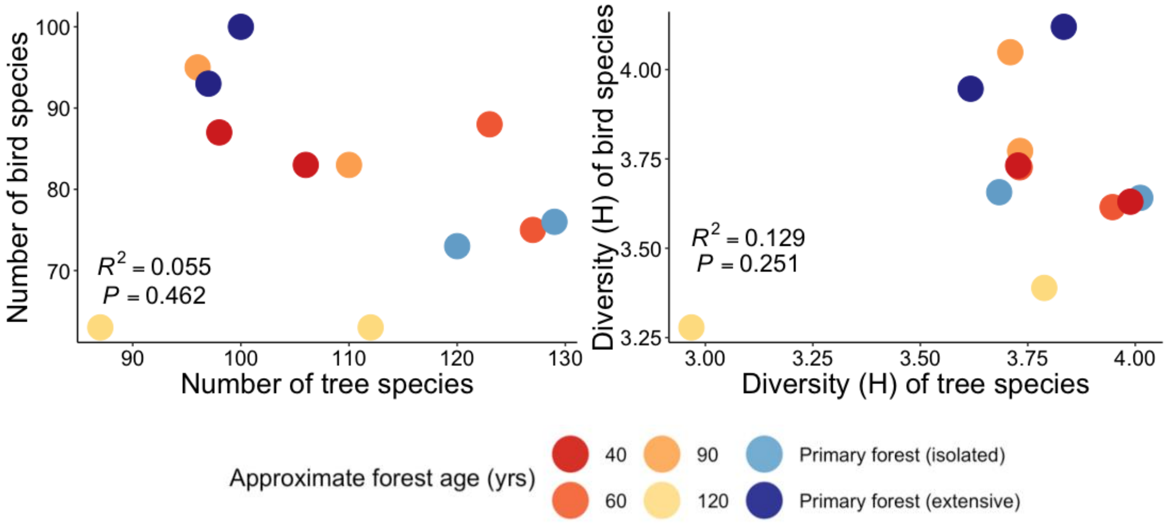

Figure 4.3: Relationship between bird and tree species metrics

Relationship between number and diversity (H = Shannon-Weiner diversity index) of bird and tree species at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. Results from GLMs are displayed on individual graphs.

Forest structure and bird communities

Mean DBH significantly increased with forest age (Pearson's correlation: r = 0.73, P = < 0.01), and stem density (number of stems/ha) decreased with forest age although this was not significant (r = -0.54, P = 0.07). When examining the relationship between the bird species richness and forest structure metrics (mean DBH and stems/ha), AIC model selection did not exclude the null model, suggesting that there was no relationship between the bird species richness and forest structure (Fig. 4.4, Table 4.3). However, for the relationship between the bird diversity (H) and forest structure metrics the models ranked highest during model selection suggested either mean tree DBH or stem density was influential (Table 4.4). Bird diversity (H) increased with mean tree DBH, and decreased with stem density per site (Fig. 4.4).

When forest structural metrics were examined in relation to bird community composition, mean DBH was significantly correlated with the first axis of the S_{MH} NMDS ordination (r = 0.82, P = < 0.01), and number of stems/ha was significantly correlated with the second axis (r = 0.62, P = < 0.05).

Frugivorous bird and bird-dispersed tree subset

The S_{MH} NMDS analyses of frugivorous birds and bird-dispersed trees showed similar patterns of separation among sites as the NMDS analyses using the full bird and tree datasets, but sites were less clustered in ordination space (Fig. 4.5). There was significant concordance between the frugivorous bird and bird-dispersed tree communities' ordinations (m_{12} = 0.367, r^2 = 0.795, P = < 0.001; Fig. 4.6), but it showed lower levels of concordance than that of the full bird and tree community ordinations. There were no significant relationships between metrics of species richness or diversity for frugivorous birds and bird-dispersed tree species (Fig. 4.7, Table 4.5).

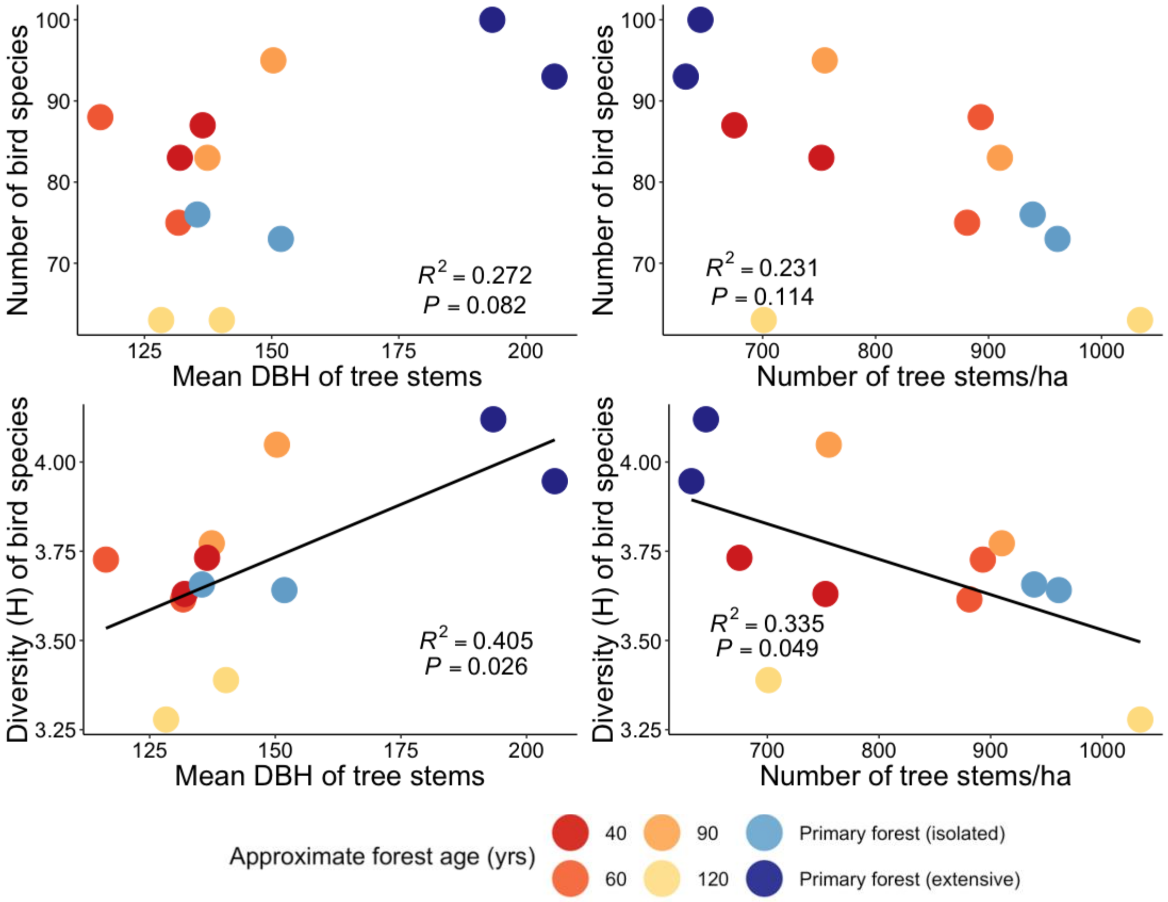

Figure 4.4: Relationship between bird species metrics and forest structure

Relationship between number and diversity (H = Shannon-Weiner diversity index) of bird species and forest metrics in two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. Results from GLMs are displayed on individual graphs, with regression lines for significant relationships.

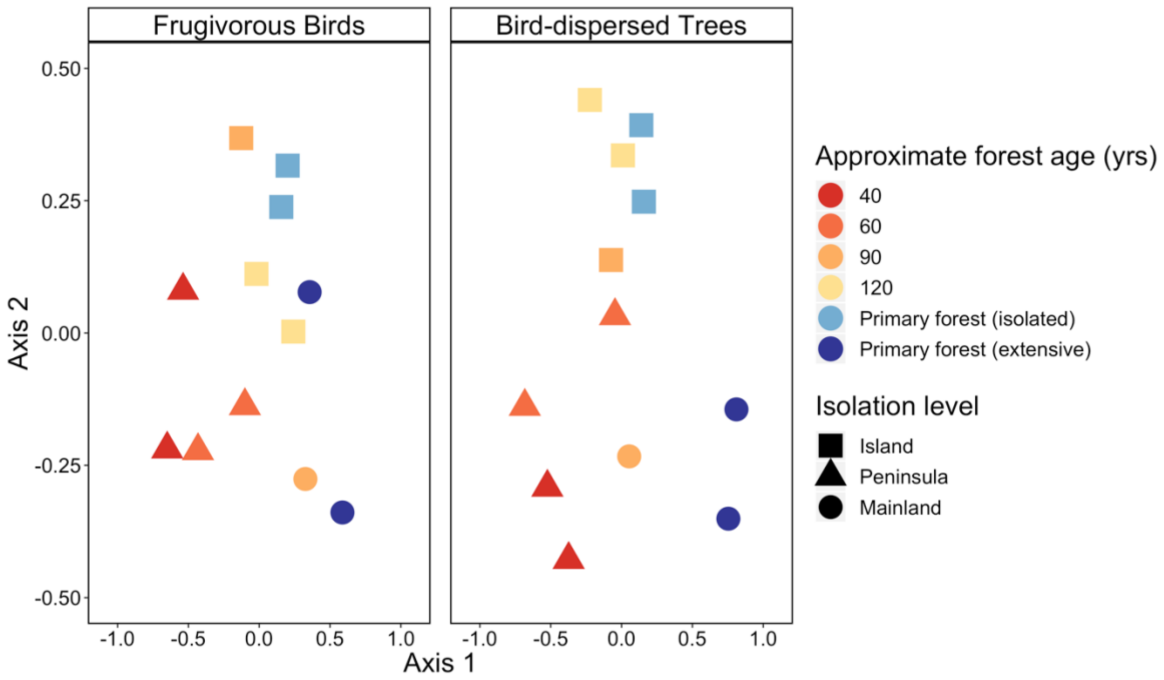

Figure 4.5: NMDS plots of frugivorous birds and tree community subsets

Non-metric multidimensional scaling (NMDS) plots of frugivorous birds (diet composed of > 50% fruit), and bird-dispersed tree communities at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. NMDS were generated using the Morisita-Horn index (frugivorous birds stress = 0.123; trees dispersed by birds stress = 0.095). Isolation levels are represented by different symbols.

Table 4.5: GLM results for frugivorous birds and bird-dispersed trees

Single predictor relationships between frugivorous bird and bird-dispersed tree communities from Generalised Linear Models (GLM).

Response	Explanatory Variable	Estimate	SE	*t*	*P*	R^2
Frugivorous bird species richness	Bird-dispersed tree species richness	-0.082	0.073	-1.109	0.293	0.11
Frugivorous bird species diversity (H)	Bird-dispersed tree species diversity (H)	0.302	0.183	1.65	0.13	0.214

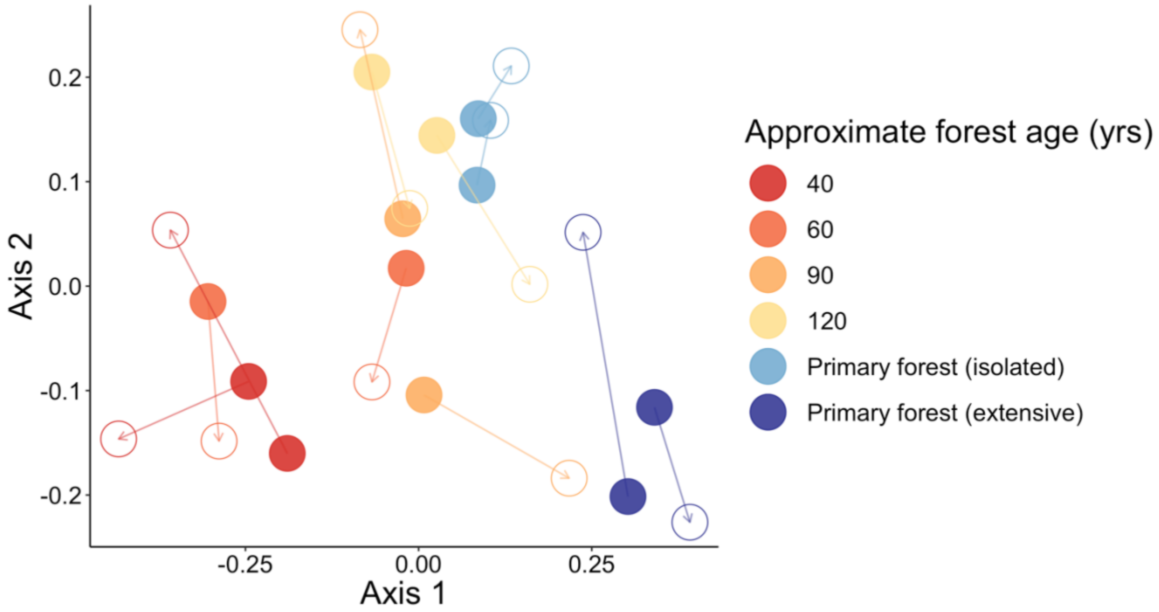

Figure 4.6: Procrustes rotation of frugivorous bird and tree community subsets

Procrustes rotation comparing the first two axes from Morisita-Horn (S_{MH}) NMDS ordinations of frugivorous bird (open circles), and bird-dispersed tree communities (closed circles) at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. PROTEST results revealed a high level of concordance between the two datasets (m_{12} = 0.367, r^2 = 0.795, *P* = < 0.001).

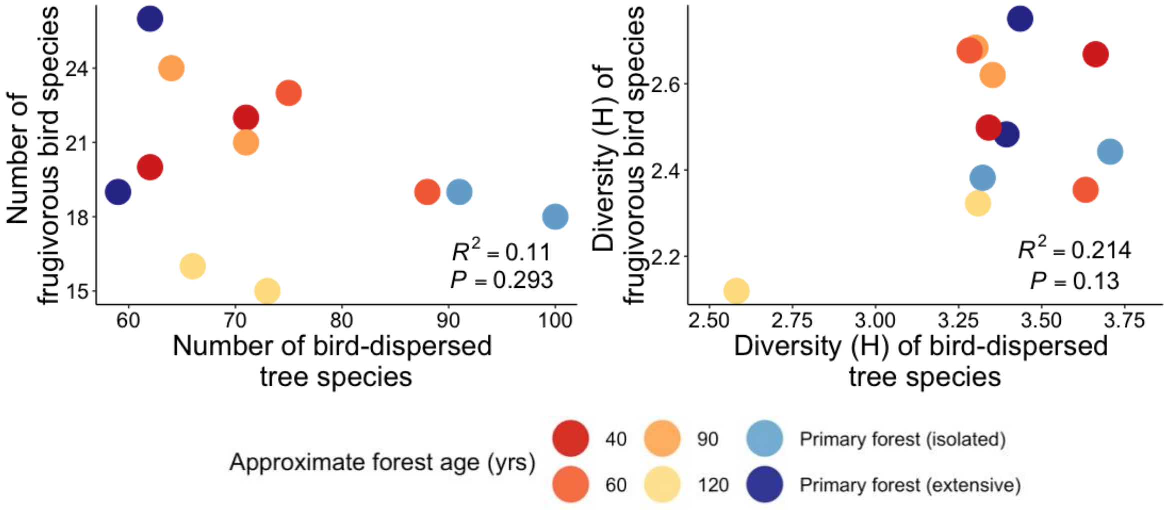

Figure 4.7: Relationship between species metrics of frugivorous bird and tree subsets

Relationship between frugivorous bird species (diet composed of > 50% fruit) and bird-dispersed tree species at two forest sites in each of four secondary forest age categories (40, 60, 90, 120-year-old), and isolated primary forest and extensive primary forest. (H = Shannon-Weiner diversity index). Results from GLMs are displayed on individual graphs.

4.5 Discussion

We found that the composition of bird and tree communities was tightly matched across our study landscape. However, forest age and isolation only had a significant effect on bird community composition and not on tree community composition. Bird species diversity and community composition were significantly correlated with metrics of forest structure; bird diversity increased with mean DBH and decreased with increasing stem density. Finally, patterns in community composition of frugivorous birds and bird-dispersed trees were similar to those found for the whole community. Although, contrary to our hypothesis, there was a lower concordance between frugivorous birds and bird-dispersed trees than there was between the complete bird and tree communities.

The role of forest age in determining bird and tree community composition

Many studies have documented rapid recovery of forest structure (Denslow & Guzman 2000, Guariguata & Ostertag 2001, Peña-Claros 2003, Saldarriaga *et al.* 1988), as well as tree species richness and diversity over tropical forest succession (Brown & Lugo 1990, Chazdon 2003, Chazdon *et al*. 2007, Guariguata & Ostertag 2001). However, tree species composition lags behind the recovery of species richness (Chazdon 2003, Dent *et al*. 2013, Finegan 1996, Guariguata & Ostertag 2001). From current studies it is unclear if tree species composition of SF will ever converge with PF, as the timescale required to observe these changes at a single site exceeds potential study timeframes; but many studies postulate that recovery of species composition is likely to take centuries (Chazdon 2003, Dent *et al*. 2013, Finegan 1996, Guariguata & Ostertag 2001, Norden *et al*. 2009). In our study, forest age did not explain variation in species composition of tree communities, potentially because our sites are relatively old (40 – 120-years-old) compared with many other SF studies.

Alternatively, differences in site history and landscape composition may mean that sites are progressing along distinct successional trajectories. Site factors (such as previous land-use and differences in early colonising vegetation) and landscape factors (such as distance to PF; Janzen 1988, Mesquita *et al*. 2001), can drive distinct successional pathways even among forests of similar ages. For example, the low similarity in species composition between the two 120-year-old stands at our study site may be due to the relative abundance of *Gustavia superba*, which accounted for 31% of individuals in one stand, compared to only 4% of individuals in the other. *Gustavia superba* is abundant in regenerating SF elsewhere in the Panama Canal watershed because its large seeds are dispersed into disturbed sites by rodents, and seedling survival in open pasture is high (Hooper *et al*. 2004).

Many studies that have compared bird species richness in SF with neighbouring PF have reported equivalent or higher richness in SF (Andrade & Rubio-Torgler 1994, Blake & Loiselle 2001, Borges 2007, O'Dea & Whittaker 2007, Schulze & Waltert 2004). However, as with tree communities, the reassembly of bird species composition in SF is less certain; some studies have reported that composition is strongly dissimilar to PF (Barlow *et al*. 2007a, Borges 2007, Tvardíková 2010), while others have shown that the similarity of bird species composition to PF increases with SF age (Andrade & Rubio-Torgler 1994, Borges 2007, Raman 1998). Forest age influenced the species composition of bird communities at our study sites, and qualitative examination of NMDS ordinations showed that the community composition of 120-year-old SF was very similar to isolated PF. Despite this, six forest species present in isolated PF were missing from the adjacent isolated 120-year-old SF on the island, including the forest specialists Rufous Piha (*Lipaugus unirufus*), Spot-crowned Antvireo (*Dysithamnus puncticeps*) and Tawny-crowned Greenlet (*Tunchiornis ochraceiceps*). This suggests that while many PF species may be present in SF (> 70% of PF species, see Chapter 2), SF communities may lack rare species, or those with highly specialised dietary or habitat requirements (Chazdon *et al*. 2009, Dent & Wright 2009).

The role of forest isolation in determining bird and tree community composition

Isolation from extensive PF reduces availability of parent trees as seed sources and restricts populations of animal dispersers, therefore affecting SF regeneration (Goosem *et al*. 2016). However, forest isolation did not play a role in explaining tree species composition at our sites. This may be a consequence of the relatively large areas of PF that remain in the landscape and low-levels of ongoing disturbance. The SF sites in this study are regenerating in a complex landscape, where forests are either isolated on islands but contiguous with PF, or regenerating on peninsulas in extensive forested areas that contain older forest patches (> 200-year-old) interspersed with patches of 40 – 60-year-old SF (total forest area on the peninsula = approximately 2600 ha). Although some sites are isolated within a water matrix, the large island area (1560 ha) and extensive forest cover at the landscape scale may maintain seed dispersal. A meta-analysis examining the effects of human disturbance on seed dispersal by animals in tropical systems found that reduction in forest area following fragmentation had little effect on frugivore visitation rates, number of seeds removed or seed dispersal distance (Markl *et al*. 2012). This suggests that seedling recruitment may be maintained in fragmented and isolated landscapes, although the authors posit that the resilience of seed dispersal to forest fragmentation is likely driven by small-seeded plant species dispersed by many generalist frugivore species (Markl *et al.* 2012). However, further investigation of avian frugivore communities at our sites suggests that seed dispersal of large-seeded plant species may be not be excessively affected by isolation (see chapter 3 for further discussion).

Despite finding no influence of isolation, NMDS ordinations imply that there are distinct tree communities seen across our study landscape. Environmental factors, such as underlying parent material, soil fertility, and slope, may explain the dissimilarities observed between isolated and extensive PF tree communities (Chazdon 2008). These same environmental factors will also influence the regeneration of SF tree communities, selecting for particular species that possess the appropriate set of traits to establish at a site (Goosem *et al.* 2016, Lebrija-trejos *et al.* 2010). Thus, the dissimilarities between isolated SF and extensive PF tree communities may be a consequence of factors other than forest age or isolation.

In contrast to tree communities, and in line with our hypothesis, forest isolation played a greater role in shaping the bird community composition across the study landscape. Indeed, bird communities in the 90-year-old SF located on the mainland was more similar to the extensive mainland PF sites than to the isolated 90-year-old SF located on Barro Colorado Island. Barro Colorado Island is a relatively large forest fragment (1560 ha), but it has been isolated for > 100 years and during this time numerous avian extinctions have been documented (Chapman 1938, Eisenmann 1952, Karr 1990, 1982, Robinson 1999, Willis & Eisenmann 1979); 30 forest species and 35 edge species have been lost from the island (Robinson 1999). These results are comparable to many other studies that have found that bird species, and particularly understorey insectivores, are sensitive to habitat disturbance and isolation. Many species are unable to sustain populations in fragmented landscapes due to changes in vegetation structure (Pavlacky *et al.* 2015, Stratford & Stouffer 2015), altered microclimates (Patten & Smith-Patten 2012, Pollock *et al.* 2015, Stratford & Robinson 2005), limited habitat availability (Sodhi *et al.* 2008, Stouffer *et al.* 2011), increased nest predation (Crooks & Soulé 1999, Robinson & Sherry 2012) or dispersal limitation (Barlow *et al.* 2006, Ferraz *et al.* 2007, Moore *et al.* 2008, Powell *et al.* 2015a, 2013, Stouffer *et al.* 2006).

Differences in the response of bird and tree communities to forest age and isolation

The greater impact of forest isolation on bird communities compared to tree communities may arise from different tolerances to isolation, and the taxa's varying response times to habitat disturbance. Many tropical forest birds are highly dispersal limited with poor gap-crossing abilities (Van Houtan *et al.* 2007, Lees & Peres 2009, Moore *et al.* 2008, Tobias *et al.* 2013). Therefore, birds may respond to stochastic processes (such as population reductions and extirpations caused by fragmentation and isolation) more quickly than trees. Additionally, if pollination and seed dispersal services are not disrupted by landscape configuration, then the demographic processes that maintain tree populations may be conserved, preserving tree communities in isolated sites (Hill & Curran 2003). Seeds of tropical forest plants that are dispersed by abiotic methods, such as wind, typically disperse beyond forest edges, as well as, or better than, they do within forests (Ingle 2003). Frugivorous animals tend to be highly dispersive, due to the wide spatial and temporal distribution of fruiting trees, and frugivores can track food resources over entire landscapes (Garcia *et al.* 2011, García & Ortiz-Pulido 2004, Symes *et al.* 2002). Even small frugivorous birds, such as manakins, have been shown to disperse seeds over 600 m through a fragmented landscape in southern Costa Rica (Şekercioğlu *et al.* 2015). Thus, the life cycles of trees may be less affected by habitat isolation than that of birds.

The response time of a species to habitat isolation depends on its life-history traits (Bender *et al.* 1998, Fahrig 2003, Turner 1996). The generation lengths of many tropical tree species are measured in centuries, whereas for bird species it is generally less than a single decade (BirdLife International 2017). Assuming that isolation effects require at least one generation to become apparent, bird community composition will begin to reflect landscape change more rapidly than the tree community. Consequently, the full effect of habitat isolation may not yet be apparent in the adult tree community of our isolated sites, given that they have been isolated for just over 100 years.

The relationship between forest structure and bird communities

The developing complexity of forest structure with increasing age is the foundation for faunal recovery (Dent & Wright 2009, DeWalt *et al.* 2003). Similar to other studies, we found that forest structural metrics were correlated with bird diversity and composition (Blake & Loiselle 2001, Casas *et al.* 2016, Diaz *et al.* 2005, Jankowski *et al.* 2013, Raman 1998, Willson 1974). Greater structural heterogeneity enables a greater diversity of bird species to coexist, since a wider range of resources are provided by more structurally complex habitats (DeWalt *et al.* 2003). Avian community assembly can be rapid for birds dependent on structural traits that develop quickly. For example, in SF contiguous with PF in the Colombian Amazon, species richness of understorey insectivorous birds increased approximately 10 years after abandonment, as the understorey micro-climate began to resemble PF (Andrade & Rubio-Torgler 1994). However, recovery is slower for birds dependent on structural traits or plant species that develop less rapidly. For example, a study of forest birds in Chile found species that primarily feed and nest in large, tall trees and snags tend to be restricted to PF, with species either absent or only rarely detected in early-successional SF (4 – 20-years-old; Diaz *et al.* 2005). SF habitats lacked the key structural requirements of these species, such as large emergent canopy trees, and standing and fallen dead trees (Diaz *et al.* 2005).

The relationship between frugivorous birds and bird-dispersed trees

In the Neotropics, vertebrate frugivores play a much greater role in the dispersal of early successional plants than wind or other abiotic dispersal mechanisms (Muller-Landau & Hardesty 2005). Over three-quarters of Neotropical plant species are dispersed by animals, with birds and bats responsible for most of the long-distance dispersal (Howe & Smallwood 1982, Wenny *et al.* 2016). At one site in Panama, seed dispersal of *Virola surinamensis* was found to be limited to only six bird species, with one toucan (*Ramphastos ambiguus*) accounting for almost half the interactions (Howe & Kerckhove 1981). We hypothesised that there should be a close relationship between frugivorous birds and bird-dispersed trees arising from their mutual interdependence; as a food source for birds, and as seed dispersal agents for plants.

Unexpectedly, we found lower concordance between the community composition of frugivorous birds and bird-dispersed trees than we found between the full communities of these two taxa. This result may be a product of the scale at which we examined the relationship. Fruit resources are located at the level of individual trees, not at the plot scale and frugivorous birds track these highly dispersed resources across the landscape, and are known to congregate at specific fruiting trees (Garcia *et al.* 2011, García & Ortiz-Pulido 2004, Guevara & Laborde 1993, Symes *et al.* 2002). With fruit only present on single trees for short periods of time during the year (Mulwa *et al.* 2013), an exhaustive, localised survey effort would be required to investigate the probable link between frugivores and fruiting trees. Hence, the plot-scale bird data presented here might not reflect the full value of a patch of forest for frugivorous birds. At the wider landscape-scale there may be differences in fruiting tree availability among different forest types, which would be reflected in frugivorous bird community composition (García & Ortiz-Pulido 2004, Kissling *et al.* 2007), but to confirm this link requires mapping the phenology of individual trees across a much wider area.

Caveats

Given that landscape and site history affect the accumulation of PF species in SF (Chazdon *et al.* 2009, Dent & Wright 2009), interpretation of chronosequence data must be cautious (Chazdon 2008, Johnson & Miyanishi 2008, Norden *et al.* 2009). Space-for-time substitutions often make unrealistic assumptions, such as assuming similar abiotic and biotic conditions across space as well as over time (Chazdon 2008). However, the length of time required to observe successional changes at a single site means that studies of succession using chronosequences are often the only option to investigate these processes.

Our study area is representative of regeneration throughout much of Central America, where forests regenerate on abandoned agricultural land embedded in a mosaic of farmland, PF and SF patches (Asner *et al.* 2009). However, our results should be treated as a best-case scenario for the effects of forest succession and isolation on the recovery of avian and tree communities due to the combination of the maturity of our SF, as well as the high level of environmental protection and low ongoing disturbance in the isolated sites.

We standardised avian survey effort across all sites, which may have generated differences in bird communities due to variation in detectability among sites (for further discussion see Chapter 2). Comparisons between our data and a previous long-term study located in the extensive PF study site, which involved more intensive survey methods (Robinson *et al.* 2000), highlighted a number of species that were missing from our extensive PF dataset. The majority (65%) of these missing species were either nocturnal, vagrant, migrant, aerial or aquatic birds and hence may not have been present or active during our surveys (for details see Chapter 2). The remaining species (35%) were mainly rare, with naturally low abundances. Thus, their contribution to the overall community in PF sites was considered to be limited. However, it is possible that our survey methodology may underestimate the importance of PF for the conservation of avian community diversity. We also note that the rarefaction curves of tree species per site suggest that tree communities may have been under-sampled, and thus we may also underestimate the diversity of these communities at some sites.

Conclusions

Our findings suggest that although there may be high levels of concordance between bird and tree communities across forest age and isolation gradients, bird communities are more responsive than trees to successional changes in forests, and the detrimental impacts of habitat isolation. These results highlight the value of SF and the need for improved protection of SF throughout the tropics. SFs are important components of tropical landscapes that, if left undisturbed, can provide valuable habitat, increasing connectivity across the landscape and potentially serving as buffer zones for protected areas.

4.6 Acknowledgements

I would like to thank Tom Bradfer-Lawrence, Nick Gardner, Ovidio Jaramillo, Samuel Jones and Juan Pablo Rios for their valuable assistance with bird identification and verification, as well as their support during fieldwork. I would also like to thank the Smithsonian Tropical Research Institute (STRI) for providing logistical support, and the members of the Tropical Ecology and Conservation (TEAC) group at the University of Stirling for many helpful discussions. Research was supported by a Carnegie Research Grant (R.J.M.), a Gilchrist Travel Grant (R.J.M.), and the Natural Environment Research Council (J.A.T.).

In addition, I am grateful to the Barro Colorado Island forest dynamics research project for sharing their ForestGEO-CTFS census data. The Barro Colorado Island forest dynamics project was founded by S.P. Hubbell and R.B. Foster, and is now managed by R. Condit, S. Lao, and R. Perez under the Centre for Tropical Forest Science and the Smithsonian Tropical Research in Panama. Numerous organizations have provided funding for the Barro Colorado Island forest dynamics research project, principally the U.S. National Science Foundation, and hundreds of field workers have contributed. Finally, I would also like to thank the all field workers who contributed to the collection of vegetation census data in the BCMN chronosequence.

4.7 Supplementary Information

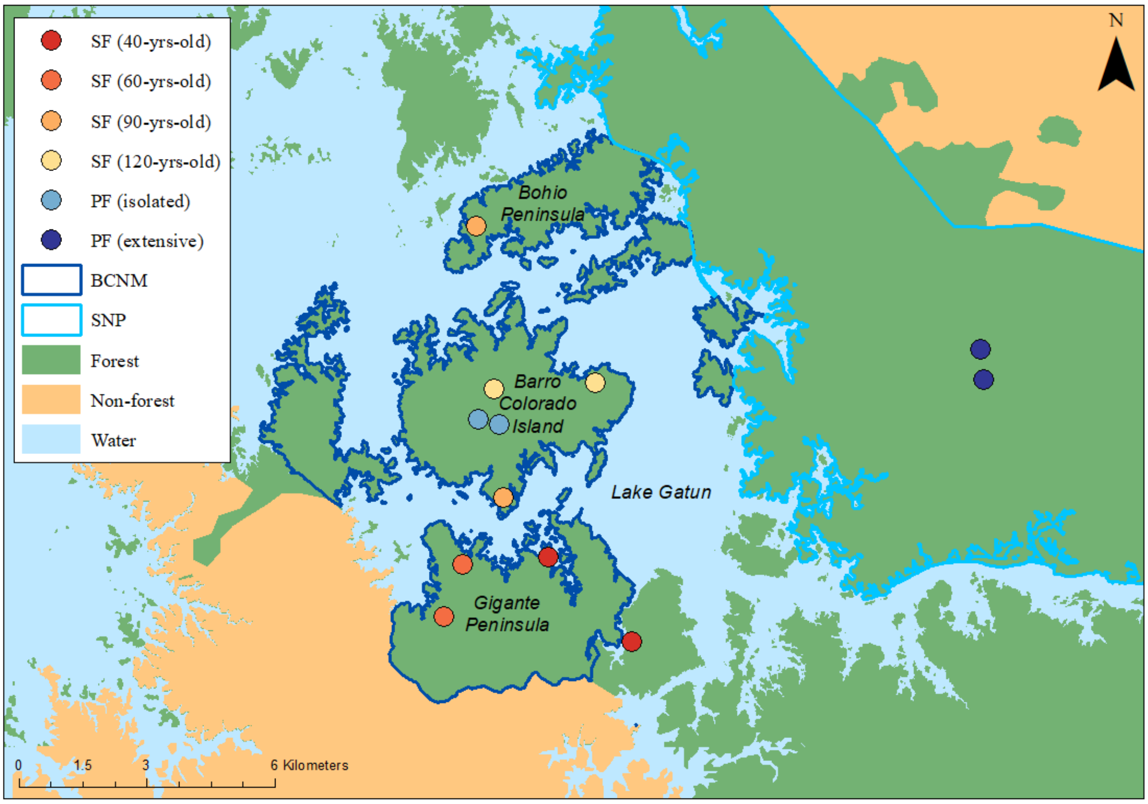

Figure S4.1: Map of study sites

Map of the 12 study sites in central Panama. Sites are colour-coded by forest age (PF = primary forest; SF = secondary forest). This area of central Panama is composed of a mosaic of contiguous different aged forest stands interspersed with a water and agricultural matrix. The main areas in which different aged forest stands are embedded are the Barro Colorado National Monument (BCNM), including Barro Colorado Island (1,560 ha) and Gigante peninsulas (2,600 ha), and Soberania National Park (SNP) and surrounding contiguous forest (22,000 ha).

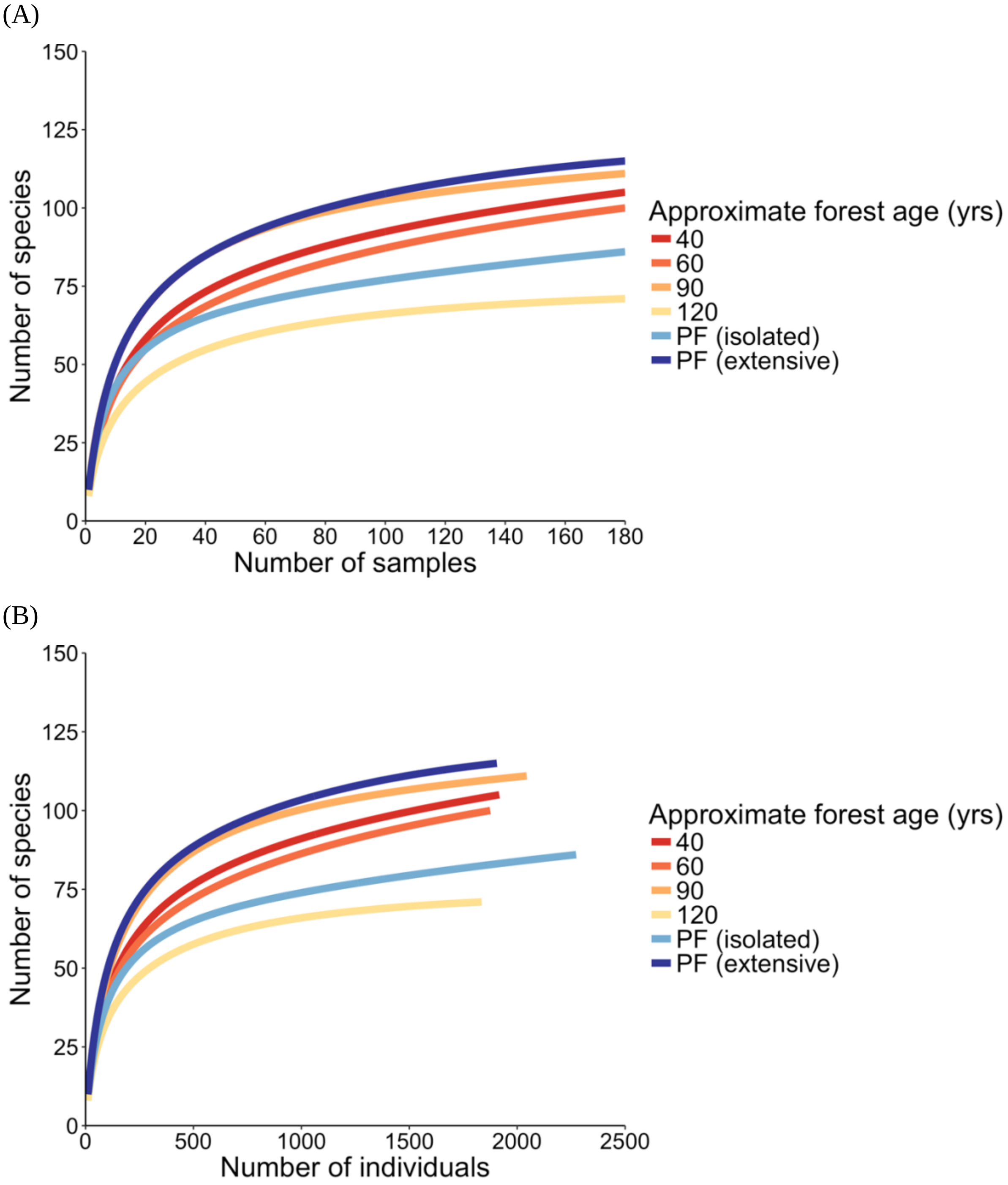

Figure S4.2: Bird species accumulation curves

Species accumulation curves scaled by (A) sample and (B) by number of individual birds detected for bird communities in each of five secondary forest (SF) age categories: 20, 40, 60, 90, 120-yr-old, and isolated primary forest (PF) and extensive PF for all birds.

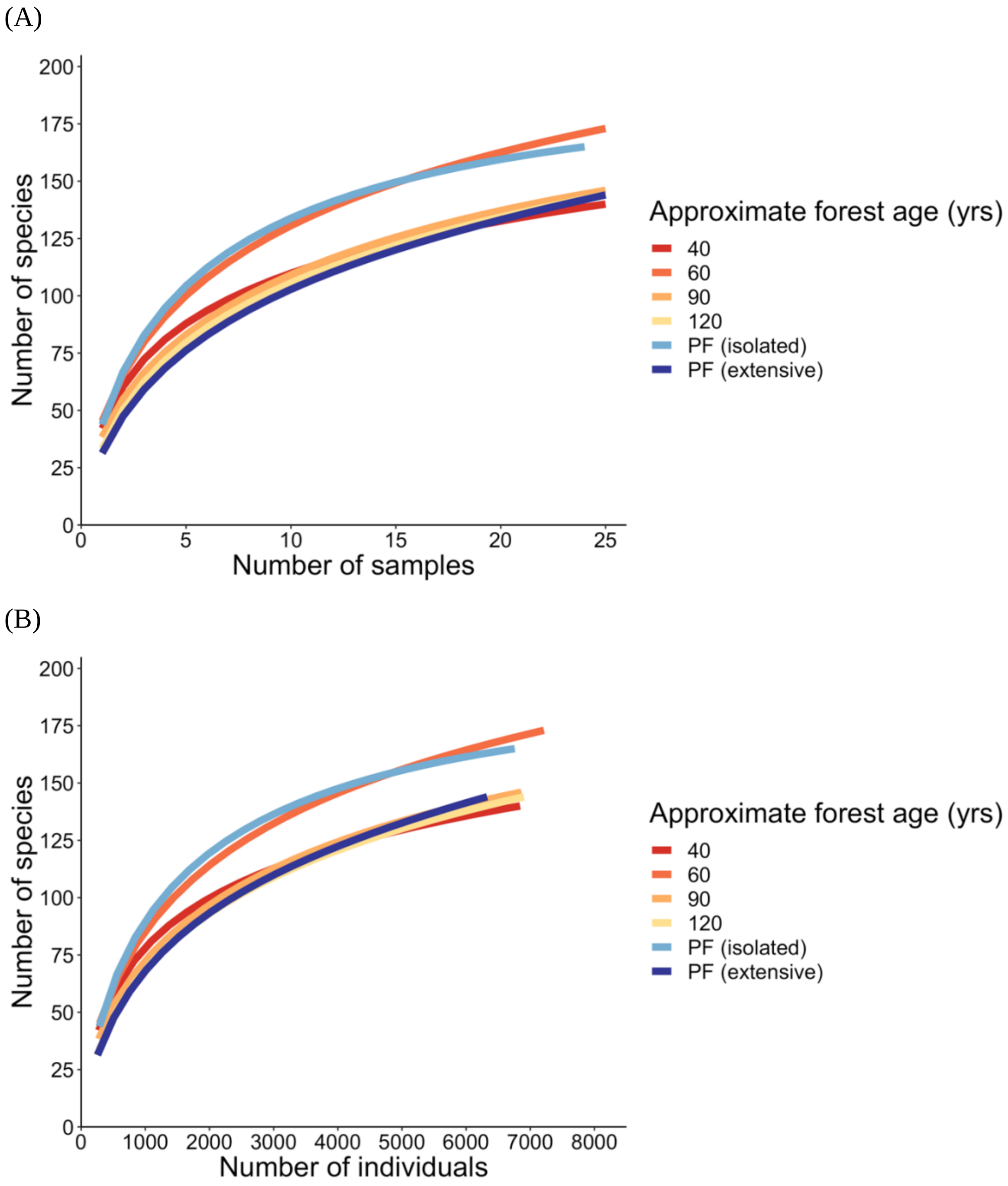

Figure S4.3: Tree species accumulation curves

Species accumulation curves scaled by (A) sample and (B) by number of individual trees at two forest sites in each of four secondary forest age categories: 40, 60, 90, 120-year-old, and isolated primary forest and extensive primary forest for bird communities.

Chapter 5: The influence of avian frugivore-plant interactions on seed-dispersal networks in the Neotropics

D. H. Dent and J. A. Tobias supervised the project, A. Pigot compiled the published seed-dispersal networks, and D. H. Dent commented on draft versions of the chapter.

5.1 Abstract

In tropical forests, frugivorous birds play a key role in dispersing seeds of fleshy-fruited plants. Understanding the relationship between frugivores and their food plants is key to comprehending how changes in bird communities may impact seed-dispersal networks following forest disturbance. Here we investigate seed-dispersal networks in the Neotropics using new data from an avian frugivore-plant network in Panama, integrated with 12 previously published avian frugivore-plant networks from the Neotropics, along with corresponding bird and plant functional trait datasets. We examine which avian functional traits best predict the seeds that birds consume, and identify the distinguishing traits of bird species that disperse large-seeded tree species (i.e. with seeds > 10 mm diameter). Gape width was the best predictor of seed sizes consumed by birds; specifically, species with larger gape-widths consumed larger seeds. In addition, large-gaped birds consumed a wider variety of seed-sizes than small-gaped birds, and small-seeded trees attracted a greater number of bird species than large-seeded trees. Species with a primarily frugivorous diet also tended to have a higher degree of specialisation, feeding on plant species rarely visited by other bird species. Only 11 of the 134 bird species from the 13 study networks dispersed large seeds. There was no distinct set of traits displayed by these 11 species, although they all had large gape-widths and above average body mass. These results imply high levels of redundancy among small-gaped avian frugivores and small-seeded plant species, suggesting that habitat disturbance will have minimal impacts on seed-dispersal of small-seeded plants. However, low levels of redundancy among large-seeded plant species and their avian dispersers, renders these plants at risk of dispersal limitation following losses in avian frugivore assemblages.

5.2 Introduction

In the Neotropics more than 75 percent of plants are dispersed by frugivorous vertebrates, with birds and bats responsible for the majority of long-distance seed-dispersal (Howe & Smallwood 1982, Wenny *et al.* 2016). However, habitat disturbance, such as expanding urban areas, intensifying agriculture, and forest clearance, causes the loss and degradation of primary forest (PF) habitats (Laurance 2015), precipitating declines in the abundance and diversity of animal species (Newbold *et al.* 2015). This defaunation impacts seed dispersal along with many other ecological interactions, with a range of functional consequences (Brose & Hillebrand 2016, Hooper *et al.* 2005). Species are not lost randomly with increasing disturbance; instead the probability of loss usually depends on species' functional and life-history traits, and sensitivity to habitat change. For example, large-bodied frugivores are often the most susceptible to habitat disturbance, either directly as a result of hunting, or due to the loss of suitable habitats for nesting and foraging (Dirzo *et al.* 2014). The loss of large frugivorous birds is predicted to disproportionately reduce the dispersal of large-seeded plant species compared to small-seeded plant species (Cramer *et al.* 2007), as many large-seeded plant species are thought to be obligately dependent on large birds for seed-dispersal. Thus the of loss of large birds may inhibit the recruitment of large-seeded plant species, resulting in long-term shifts in the composition of future tree communities (Wotton & Kelly 2011). Such disruptions to seed-dispersal networks may have subtle and pervasive impacts on ecosystem functioning, and understanding these network interactions is critical to predicting the effect of disturbance on tropical forest habitats. Frugivores determine how seeds are distributed in space (in terms of where and how far they deposit seeds), therefore influencing the distribution of the adults of many plant species (Howe 1989, Nathan & Muller-Landau 2000). Thus, frugivore-plant interactions can have consequences for plants at the individual, population and community levels (Jordano *et al.* 2007).

Successful seed dispersal is dependent on first, whether a bird feeds on fruit from a particular plant species; second, whether it consumes seeds whilst feeding on the fruit and third, whether it subsequently disperses or destroys the seeds (Moran *et al.* 2004). Fruit selection by frugivorous birds is generally associated with morphological traits, such as gape width, which determines the maximum size of fruit or seed that can be swallowed (Wheelwright 1985). However, birds can also consume fruit in a piecemeal fashion without ingesting the seeds (Jordano 2014), or if they ingest the seeds along with the fruit, they might crush and destroy the seeds during feeding thus providing no seed dispersal (e.g. some parrots; Janzen 1981). The efficacy of a bird species' seed dispersal service is also affected by the relative abundance of individuals, and how frequently they consume fruit from plant species (Schupp 1993).

Frugivore-plant networks regularly involve hundreds of fleshy-fruited plant species, and almost as many frugivores that may or may not consume the fruits of these plants (Corlett 1998, Moran & Catterall 2010). Detailed information about these interactions is frequently difficult to obtain from field studies; ripe fruiting trees are often temporally and spatially widely distributed, and locating them may be a time-consuming process. In addition, the majority of frugivores' fruit consumption takes place high in the canopy, so that interactions are hard to observe. To overcome these fieldwork-related difficulties, functional traits are often used as proxies for species' ecological roles (Dehling *et al.* 2016, Moran & Catterall 2010). Functional traits are generally easier to obtain than detailed dietary information (e.g. del Hoyo *et al.* 2017, Wilman *et al.* 2014), and include morphological or behavioural attributes that shape a species' ecological role and determine how they interact with their environment and other species (Diaz & Cabido 2001). However, the link between morphological and behavioural traits, and a species' functional role in ecological communities is still not fully understood (Ricklefs 2012).

Previous studies have highlighted various functional trait constraints that limit the number of potential frugivore-plant interactions (Chen & Moles 2015, Dehling *et al.* 2016, Moran & Catterall 2010, Pigot *et al.* 2016a, Sebastian-Gonzalez 2017). For example, gape-width dictates the size of seed that a bird can swallow (Wheelwright 1985). Bird species with large gape-widths should be able to consume a greater diversity of plant species than small-gaped bird species. Likewise, small-seeded plant species are predicted to attract a greater number of species, as more birds are physically capable of consuming their seeds, while large-seeded plant species will attract fewer species. Consequently, some bird species interact with multiple plant species (and vice versa), whilst others have highly restricted interactions. For example, at one site in Panama, seed dispersal of *Virola surinamensis* was found to be limited to only six bird species, with one toucan (*Ramphastos ambiguus*) accounting for almost half the interactions (Howe & Kerckhove 1981). These uneven interactions suggest that not all bird or plant species are of equal importance in the maintenance of frugivore-plant networks (Jordano *et al.* 2007, Mello *et al.* 2015) .

The proportion of fruit in a bird's diet (degree of frugivory) will affect how much fruit a bird species consumes, which will determine how important a disperser this species is within the seed-dispersal network (i.e. how many seeds they disperse; Moran *et al.*

2004). The diversity of plants a bird feeds on (degree of specialisation) determines how likely and often bird species visit specific plant species, and thus how important a role that species plays in the maintenance of the seed-dispersal service (Mello *et al.* 2015). Birds that visit a wide range of plant species are fundamental to the maintenance of the entire seed-dispersal network, but bird species that consistently visit a restricted number of plants species are critical to the effective dispersal of these host plants. Furthermore, dispersal ability (i.e. how far a species can fly) will also affect seed-dispersal (Tobias 2015), with the potential to impact spatial patterns of plant regeneration.

Due to the difficulty in collecting detailed information on avian frugivore-plant networks, and the inherently small sample sizes involved, quantitative relationships matching frugivore traits to seed traits have only recently been elucidated. This is particularly the case when examining the functional traits of bird species that disperse large seeds. Greater understanding of these interactions has important consequences for the population-level responses of large-seeded plant species to habitat disturbance. Given large-seeded plant species' predicted reliance on large-gaped birds for seed-dispersal, and the sensitivity of large frugivores to habitat disturbance, these findings have important conservation implications (Dirzo *et al.* 2014, Wotton & Kelly 2011).

The aim of this study was to examine which avian functional traits best predict the seed-sizes consumed, and to identify the defining traits of bird species that disperse large-seeded (> 10 mm) tree species. We observed 17 species of fruiting trees in Panama, recording birds that visited and consumed fruit. We combined these data with datasets from 12 published Neotropical frugivore-plant networks, and a corresponding bird and plant functional trait dataset to investigate seed-dispersal networks in the Neotropics. We test four specific hypotheses; 1) there is a positive correlation between size of plant seed consumed and bird gape width, 2) large-gaped birds ingest a greater diversity of seed sizes than small-gaped birds, 3) small-seeded plant species attract a greater number of bird species than large-seeded plant species, and 4) bird species that ingest large seeds will have a diet that is primarily frugivorous, a high dispersal ability, and be more specialised.

5.3 Methods

A dataset of avian frugivore feeding networks from the Neotropics was collated from field observations in the Barro Colorado Nature Monument, Panama, and from data extracted from published studies.

Study site and bird surveys

Field surveys were conducted within the 50-ha Forest Dynamic Plot on Barro Colorado Island (1560 ha, 9°9’ N, 79°51’ W) in the Barro Colorado Nature Monument, Panama. The plot consists of lowland, moist, tropical primary forest, and elevation ranges from 120 to 155 m a.s.l. (Croat 1978, Leigh *et al.* 1982). Based on phenology data from Wright *et al.* (1999), and tree composition information from the 50-ha plot (Condit 1998, Hubbell 1999, Hubbell *et al.* 2005), we identified seventeen potential bird-dispersed tree species with fleshy-fruits. Surveys of birds visitations and feeding events on fruiting trees took place between February and April 2015 to coincide with the peak fruiting on Barro Colorado Island (Wright *et al.* 1999). Locations of individual trees within the forest plot, and suitable vantage points for observing the canopy of these trees were identified prior to the start of surveys. Fruiting tree species were surveyed with a mean of two individuals per species (n = 35 individual trees). Trees were monitored regularly to ascertain when fruit ripened. Surveys (n = 60) were conducted between 06:30 and 12:00, and between 14:30 and 17:30 to coincide with peak feeding activity of birds and lasted on average 2 hours and 11 mins, but were dependent on frugivore activity. If no activity was detected after 30 mins then the survey was stopped in favour of moving on to a different fruiting tree. The observer was located on the ground below the fruiting tree, at a suitable vantage point to view the canopy. Individual birds visiting a fruiting tree were identified to species level using binoculars and a telescope. Time of arrival, departure and, where possible, feeding behaviour (i.e. consuming the whole fruit, eating it piecemeal, seed crushing, or dropping the fruit) were recorded. All surveys were carried out by one observer who was experienced in local avian ID (including bird calls). The final dataset comprised avian species that had been observed either eating fruit whole, or in a piecemeal fashion; this included 32 bird species, 10 fruiting plant species and 323 unique feeding events. We hereafter refer to this network as MAYH.

Additional avian frugivore networks

An additional database of lowland Neotropical avian frugivore-plant networks, describing visitation and feeding events between birds and fruiting plants, was compiled from published literature. We obtained 12 additional networks, from six studies (Table S5.1). Ten networks recorded quantitative data (i.e. number of individual birds visiting each plant species), whilst the other two recorded only the presence or the absence of interactions.

Bird functional traits

We collected biometric trait data for all avian species recorded in the 13 networks (n = 134 species) from bird specimens in museum collections. Most specimens were housed at the Natural History Museum, Tring, UK, and the Smithsonian Tropical Research Institute, Panama. We took six functional measurements from each specimen: beak length, width and depth, gape width, wing length, and Kipp's distance (the distance between the tip of the longest primary/wing tip and the first secondary feather measured on the folded wing). These six traits were selected as they provide information relating to resource use and feeding preferences (beak morphology) and dispersal information (calculated from Kipp's distance and wing length to produce the hand-wing index; Claramunt *et al.* 2012, Pigot *et al.* 2016b, Wheelwright 1985).

The three beak measurements were taken from the anterior edge of the nostrils: 1) length to the tip of the beak, 2) width and 3) depth (as vertical height). Gape width was measured at commensurate points at the base of the bill, where the mandible and maxilla join. Wing length was the distance between the carpal joint and the wing tip of the unflattened wing. Kipp's distance was measured from the tip of the first secondary to the tip of the longest primary on the closed wing. All measurements were taken with digital callipers to the nearest 0.01 mm, apart from wing length, which were measured using an end-ruler to the nearest mm. We measured 857 specimens, a mean of 6.4 ± 4.2 per species. We aimed to measure a minimum of two males and two females per species, although for 137 specimens we were unable to ID the sex and these specimens were recorded as unsexed (mean number of specimens per species: 2.9 ± 1.7 males; 2.5 ± 1.4 females and 1.0 ± 3.0 unsexed). We generated a mean value for each functional trait by averaging data across all specimens (male, female and unsexed) for each species.

We also collated published estimates of mean species' body mass (g), and the percentage contribution of fruit, seeds, nectar, 'other plant material', invertebrates, vertebrates and carrion to the species' diet (Wilman *et al.* 2014). Species were assigned a primary habitat based on habitat preferences in Stotz *et al.* (1996), and a conservation status from the IUCN's Red List (IUCN 2017).

Tree functional traits

Fruits were collected from the trees on Barro Colorado Island where the bird surveys took place, and the length and width of fruits and seeds were measured with digital callipers to the nearest 0.01 mm (n = 20 per species). Seed sizes for plant species from other networks were collated from published literature, and online databases, such as the Smithsonian Tropical Research Institute's Herbarium.

Data analyses

Two datasets were analysed; one included all recorded interactions between birds and fruiting plants (hereafter known as 'all data'), the second excluded data where plant seed width was greater than bird gape width (hereafter known as 'subset data'). Whilst interaction events are not necessarily synonymous with seed-dispersal events, the removal of interactions where plant seed width was greater than bird gape width ensures that we focused on those species most likely to be functioning as seed-dispersers. The final database included 2617 unique interactions between 134 bird species and 193 species of fruiting plants for all data, and 1588 interactions between 115 bird species and 77 fruiting plant species for the subset data. Bird-fruit interactions of species in the family Psittacidae (n = 3 species) were included, since they may both disperse and predate seeds (Jordano *et al.* 2009). These interactions represent a small proportion of the total (1% of all data, and 1.86% of the subset data). For analyses that utilised all 13 networks, quantitative data was converted to binary data so that analyses were carried out solely on presence/absence information to help mitigate differences in survey methodology and effort among studies. All analyses were carried out in R version 3.4.1 (R Core Team 2017).

Relationship between plant seed size and bird functional traits

Using linear mixed-effects models, we examined the relationship between seed sizes consumed by birds and several avian functional traits proposed to influence frugivore-plant interactions (including: gape width, body mass, percentage of fruit in diet and dispersal ability). As random effects, we included 'network', to account for differences in sampling strategy and effort among networks, and 'bird family' to incorporate phylogenetic relatedness of species. All models were fitted using the R package 'lme4' (Bates *et al.* 2015). Seed width, gape width, body mass and dispersal ability were normalised using $\log^{10}$ transformations. Gape width and body mass were highly correlated (Pearson correlation $r > 0.8$), so these were modelled separately. Residuals were checked for normality and homoscedasticity. We used AIC model comparisons to assess predictor terms (Burnham *et al.* 2011), and likelihood ratio tests to compare our final models against a null model that included only intercept terms, and ‘network’ and ‘bird family’ as random effects. This analysis was performed on both all data and the subset data.

Large-gaped birds ingest a greater diversity of seed sizes than small-gaped birds

To assess if large-gaped birds consume a greater diversity of seed sizes than small-gaped birds we used a Fligner-Killeen test to assess for homogeneity of variance of gape width when plotted against seed width. This is a non-parametric test that is robust against departures from normality. We also divided the data into three gape width categories (less than 10 mm, 10-20 mm, and greater than 20 mm), and calculated the coefficient of variation (the ratio of the standard deviation to the mean) for each category. This gave a measure of the dispersion around the mean for each gape width category and was performed for all data and the subset data.

Small-seeded plant species attract a greater number of bird species than large-seeded plant species

In order to investigate whether small-seeded plants attracted more bird species than large-seeded plants, the number of bird species consuming each plant species was calculated for each network individually. This was then modelled using linear mixed-effect models (including ‘network’ and ‘plant family’ as random effects), following the methods outlined above.

Frugivore-plant interaction diagrams were created using the R package ‘bipartite’ (Dormann *et al.* 2009) to examine how gape-width and seed-size determine bird-plant interactions. Visualising these networks allowed us to establish both the range of seed sizes consumed by bird species with varying gape-widths, and the frequency with which they are consumed. These analyses were conducted for networks with 10 or more plant species, and 50 or more unique binary frugivore-plant interactions, as these provided the most robust information on species interactions.

Quantifying bird species frugivory specialisation

Degree of specialisation (d’) was calculated for bird species in each quantitative network that had more than 150 frugivore-plant interactions, and included more than one plant family. Specialisation of bird species, in terms of specialisation on specific fruiting plants, was calculated using standardised Kullback-Leiber distance for each individual network (Blüthgen *et al.* 2006), producing a metric which varies from 0 (generalist) to 1 (specialist). The total number of frugivore interactions with each plant species was used as a measure of plant availability as independent measures of plant abundances were not available. Blüthgen *et al.* (2006) note the actual number of interactions more often reflects resource availability and consumer activity, rather than an independent measure of plant species abundance, as the local abundance of a plant species does not always reflect differences in resource quality and/or quantity. Thus, this metric accounts for differences in visitation rates; frugivores that deviate from a random feeding pattern of available fruiting plants by preferentially selecting plants of low availability are deemed to be more specialised.

Linear mixed-effects models were used to investigate the relationship between d' and other bird functional traits, following the methods outlined above.

5.4 Results

Relationship between plant seed size and bird functional traits

Large-gaped birds tended to consume larger seeds than small-gaped birds, as demonstrated by the positive relationship between plant seed width and bird gape width (Fig. 5.1A; $\chi^2(1) = 20.794$, $p = < 0.001$; Table S5.2). This relationship was more significant when only including interactions where seed width was smaller than bird gape width (Fig. 5.1B; $\chi^2(1) = 32.827$, $p = < 0.001$, Table S5.3). Bird gape width alone was the best predictor of seed size consumed, and other bird functional traits (such as, body mass, bird dispersal ability, and percentage of fruit in diet) did not improve model fit (Table S5.2). Although gape width was the best predictor of seed size consumed, body mass was also significantly different from the null model ($\chi^2(1) = 7.564$, $p = < 0.01$), suggesting that body mass could be used as a surrogate for gape width in the absence of more detailed morphological data.

For the dataset restricted to interactions where seed width was smaller than bird's gape width, body mass appeared to be an even more reliable predictor of seed size consumed ($\chi^2(1) = 13.939$, $p = < 0.001$) and there was no significant difference between the gape width and body mass models ($\chi^2(0) = 0$, $p = 1$; Table S5.3).

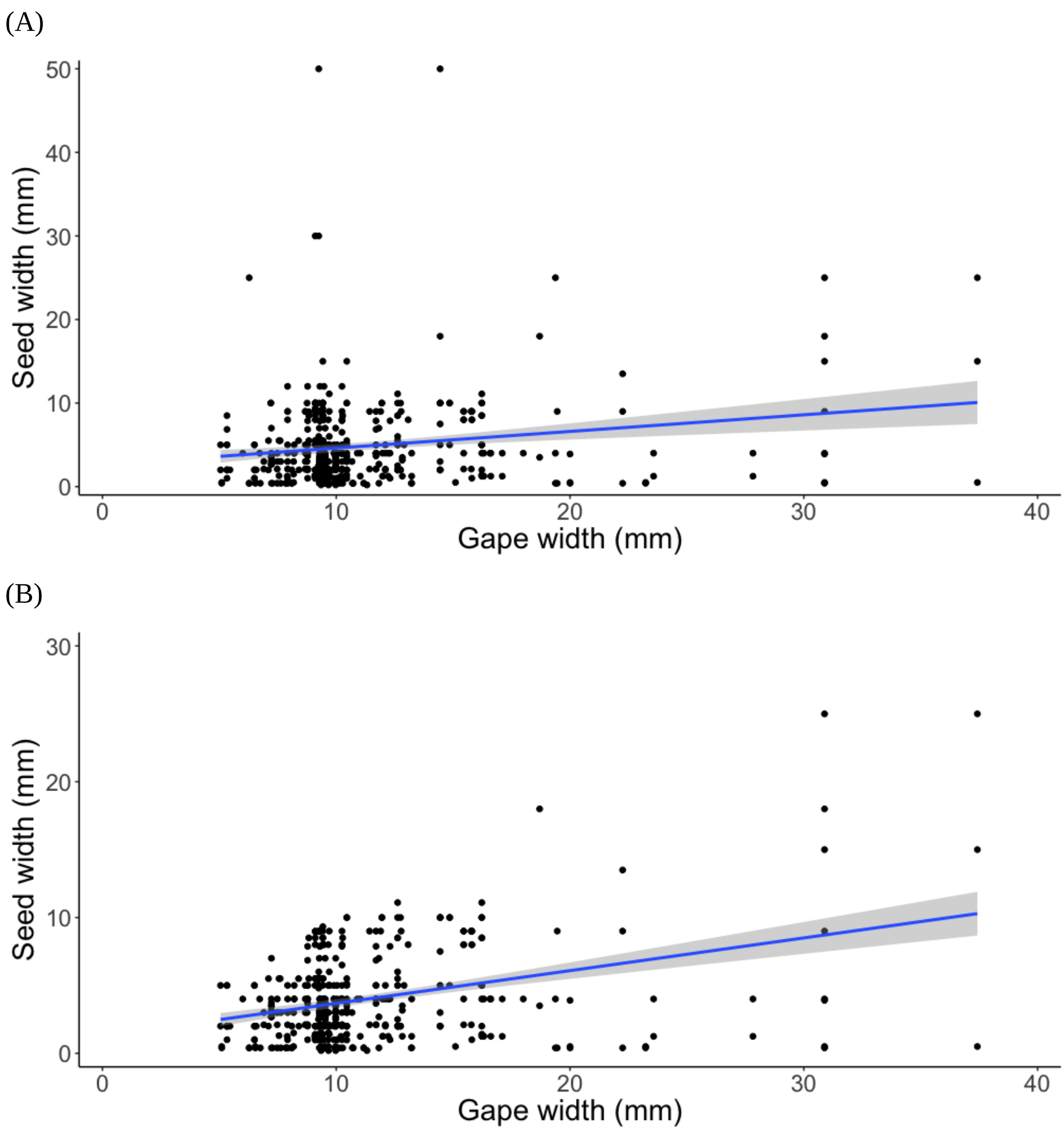

Figure 5.1: Relationship between bird gape width and tree seed width

Relationship between bird gape width and plant seed width across 13 frugivore networks from the lowland Neotropics for (A) all data, and (B) dataset restricted to interactions where seed width is smaller than bird gape width. Regression lines are plotted with 95% confidence intervals.

Large-gaped birds ingest a greater diversity of seed sizes than small-gaped birds

Variation in size of seed consumed was greater for large-gaped than small-gaped birds (Fig 5.1A and 5.1B), indicating that large-gaped birds consume a greater diversity of seed sizes than small-gaped birds. Fligner-Killeen tests (used to assess for homogeneity in the data), confirmed that there was a difference in the variances among bird gape widths and the seed sizes they consume, and that both datasets were heteroscedastic (All data: med$\chi^2(102) = 145.41$, p = < 0.01; Subset data: med$\chi^2(101) = 154.13$, p = < 0.001). Coefficients of variation (a measure of the dispersion around the mean) also indicated that larger-gaped birds consumed a greater diversity of seed sizes than small-gaped birds, and this relationship was more pronounced when the dataset was restricted to interactions where seed width was smaller than bird's gape width (Table 5.1).

Table 5.1: Coefficient of variation for gape width and seed size

Coefficient of variation values for three bird gape width categories for all data, and a subset of data where seeds wider than the birds' gape width were removed.

Dataset	Bird gape width (mm)		
	< 10	10 - 20	> 20
All Data	107	101	118
Subset Data	69	72	118

Small-seeded plant species attract a greater number of bird species than large-seeded plant species

Small-seeded plant species attracted more bird species than large-seeded plant species, although this result was not significant (Fig. 5.2A; $\chi^2(1) = 1.702$, p = 0.192; Table S5.4). This was expected as data distributions illustrate that there are more small-seeded plant species and small-gaped birds and fewer large-seeded plant species and large-gaped birds (Fig. S5.1 and S5.2). A clearer pattern was seen when the dataset was restricted to interactions where seed width was smaller than the bird's gape width, although again this relationship was not significant (Fig. 5.2B, $\chi^2(1) = 3.466$, p = 0.063; Table S5.4). Plants with seeds > 10 mm diameter interacted with fewer birds (3.668 ± 0.344 birds; mean ± standard error) than small-seeded plant species (< 10 mm; 5 ± 1.452 birds). Results were very similar when data were restricted to interactions where seed width is smaller than bird gape width (seeds > 10mm diameter: 3.632 ± 0.361 birds; seeds < 10 mm diameter: 5 ± 1.394 birds).

Frugivore-plant interaction diagrams produced for three individual networks with ≥ 10 plant species, and ≥ 50 unique frugivore-plant interactions (CACI, GEN2 and MAYH, see Table S5.1) reveal the diverse range of seed sizes consumed by birds (Fig. 5.3A, 5.4A and 5.5A). For the CACI and GEN2 networks, there was no clear pattern among the interactions (Fig 5.3A and 5.4A). These two networks highlight that many bird species consume fruit with seeds that are larger than their gape width, and that large-gaped bird species tend to consume fruits with both small seeds and large seeds. The MAYH network was dominated by *Miconia argentea*, a trees species with small seeds (0.4mm width; Fig. 5.5A); almost every bird species in the network interacted with this small-seeded species, whereas plants with larger seed widths (such as *Virola surinamensis* with a seed width of 25 mm) interacted with a smaller number of bird species. Across the three networks, smaller-seeded plants attracted more bird species than large-seeded plant species (Fig. 5.3B, 5.4B and 5.5B), confirming the general pattern observed when data from all networks were combined.

Characteristics of bird species that ingest large seeds

Only 11 bird species, from five of the 13 frugivore networks, visited plants with seed widths > 10 mm and had gape widths greater than the seed consumed (Table 5.2). Ten of the eleven species were classified as forest specialists (Stotz *et al.* 1996), with two of the forest specialists listed as species Near Threatened, all other species were listed as Least Concern (IUCN 2017). Species came from a range of families, with the two most common being *Ramphastidae* and *Tyrannidae*. Ten of the 11 bird species' body mass was higher than the median for all recorded species (median = 31g), and eight species had a higher dispersal ability than the median (median hand-wing index = 19). However, there was a wide range of dispersal abilities (as indicated by the hand-wing index), and degree of specialisation (*d'*), as well as percentage of fruit in diet (range = 10 – 80%); only five species were classed as frugivores (≥ 40% fruit in diet), five were insectivores and one was an omnivore (Wilman *et al.* 2014).

Across all quantitative networks, the degree of frugivore specialisation (*d'*) increased significantly with percentage of fruit in diet ($\chi^2(1) = 6.710$, $p = < 0.01$), as well as body mass ($\chi^2(1) = 16.831$, $p = < 0.001$) and gape width ($\chi^2(1) = 3.917$, $p = < 0.05$; Table S5.5). This suggests that large-bodied, specialist frugivores act as key dispersers for a subset of plant species within the seed-dispersal network.

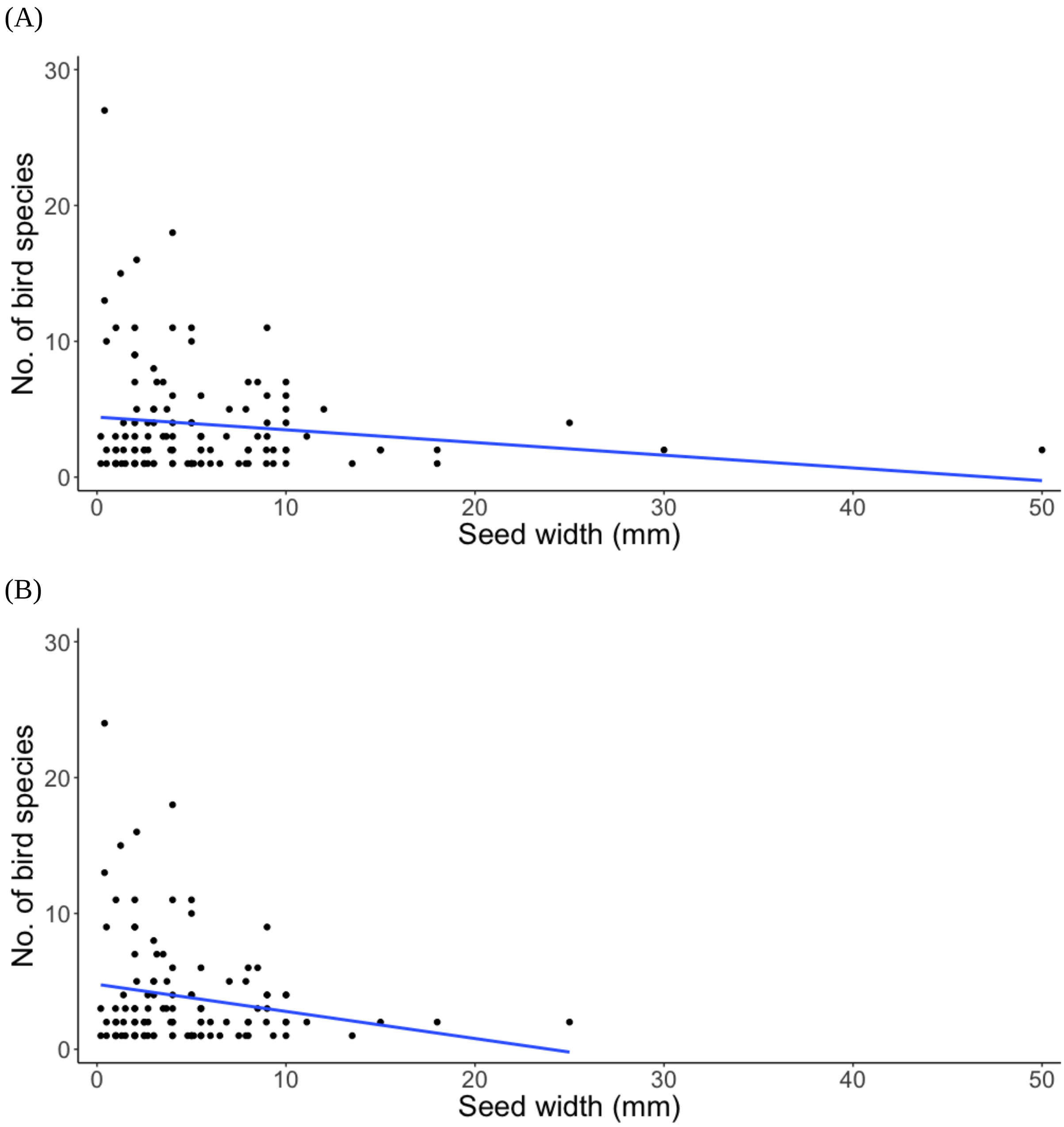

Figure 5.2: Relationship between number of bird species and seed width

Relationship between number of bird species observed feeding on different sizes of seeds across 13 frugivore networks from the lowland Neotropics for (A) all data, and (B) dataset restricted to interactions where seed width is smaller than bird gape width. Each data point represents the number of bird species per plant species per network. Regression lines are plotted.

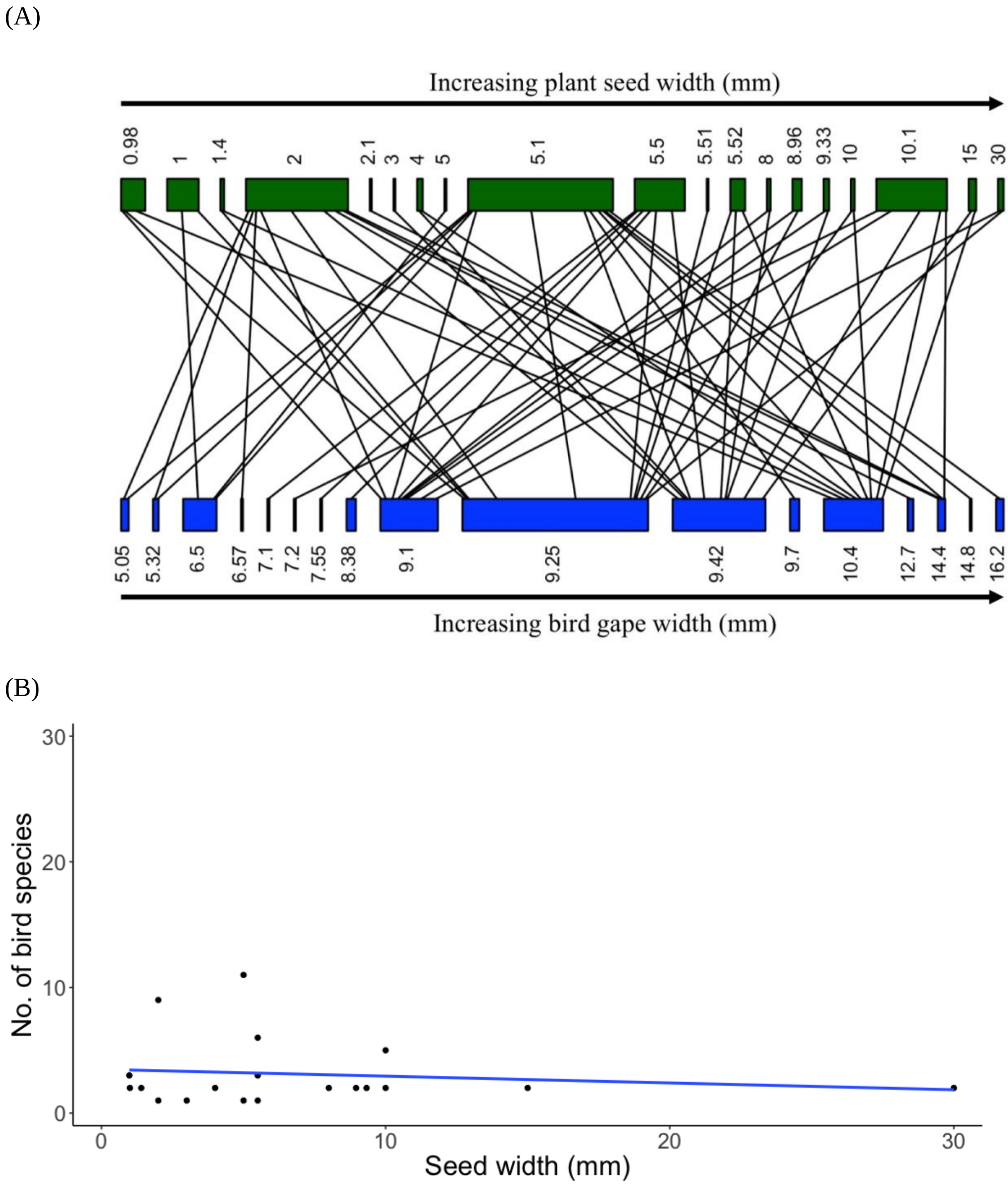

Figure 5.3: CACI frugivore network

CACI frugivore network displaying (A) plant and frugivore interactions (plants in green and ordered by increasing seed size, and birds in blue ordered by increasing gape width. Bar width is proportional to total number of interactions; wider bars indicate a greater number of interactions have been observed), and (B) the relationship between number of birds observed feeding on different sizes of seeds with regression line plotted.

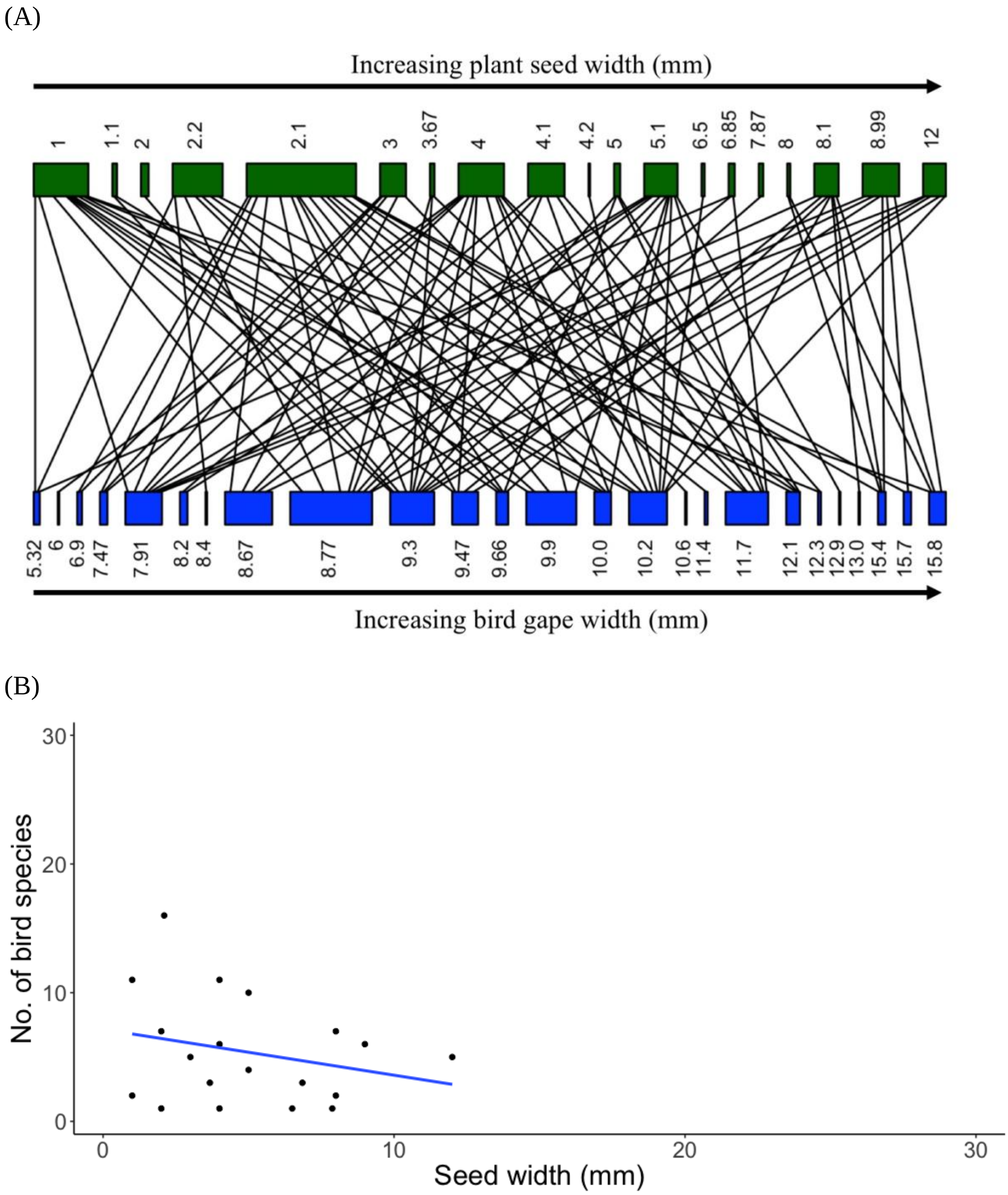

Figure 5.4: GEN2 frugivore network

GEN2 frugivore network displaying (A) plant and frugivore interactions (plants in green and ordered by increasing seed size, and birds in blue ordered by increasing gape width. Bar width is proportional to total number of interactions; wider bars indicate a greater number of interactions have been observed), and (B) the relationship between number of birds observed feeding on different sizes of seeds with regression line plotted.

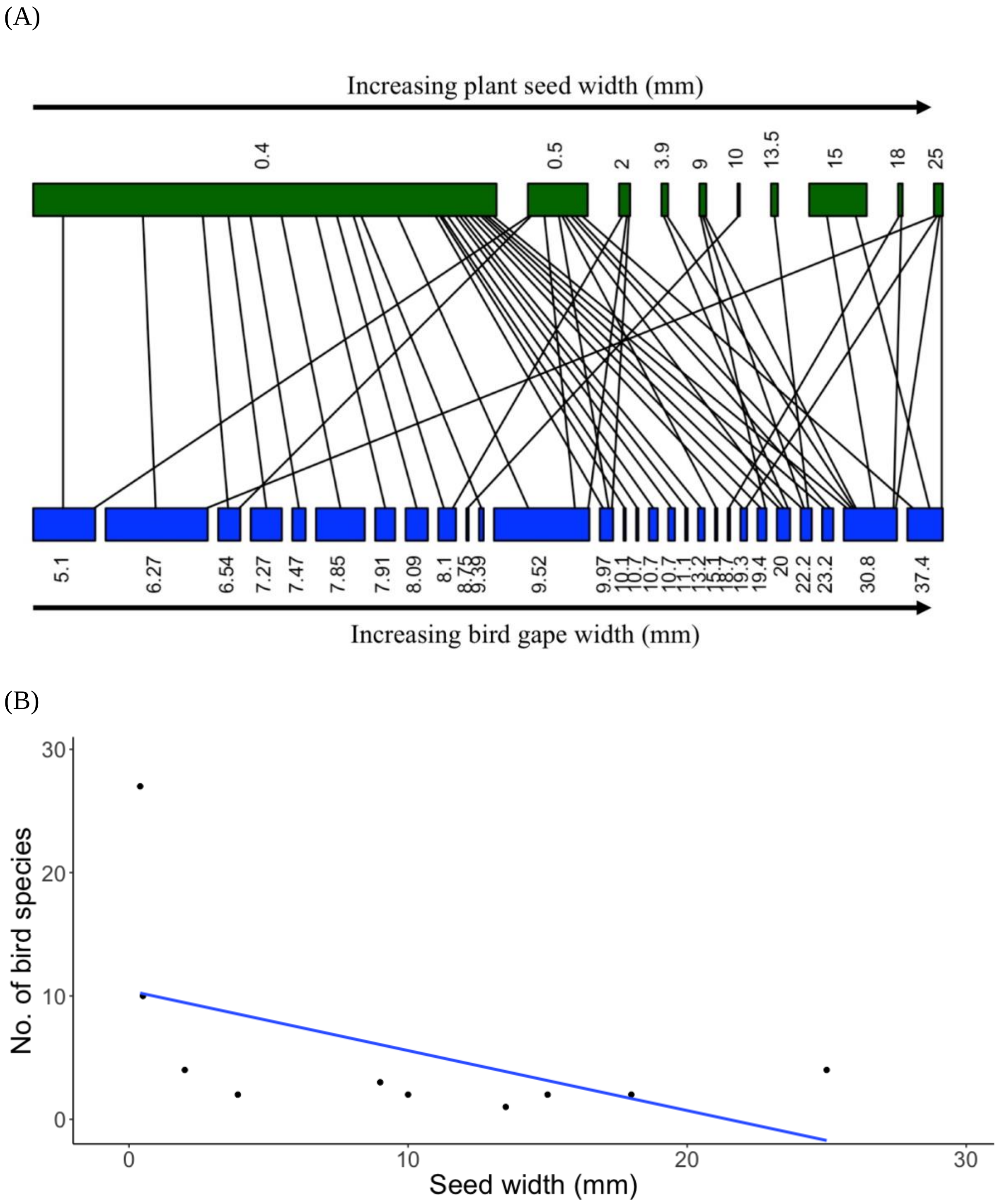

Figure 5.5: MAYH frugivore network

MAYH frugivore network displaying (A) plant and frugivore interactions (plants in green and ordered by increasing seed size, and birds in blue ordered by increasing gape width. Bar width is proportional to total number of interactions; wider bars indicate a greater number of interactions have been observed), and (B) the relationship between number of birds observed feeding on different sizes of seeds with regression line plotted.

Table 5.2: Bird species that disperse large seeds

Bird species that disperse seeds > 10mm diameter, and whose gape width is > 10mm (thus capable of dispersing seeds that are > 10mm diameter), in 13 frugivore networks in the lowland Neotropics.

Family	Scientific Name	Status[1]	Primary Habitat[2]	Dietary Guild[3]	% Fruit[4]	Body Mass (g)	Hand-wing Index[5]	d' range[6]
Trogonidae	*Trogon violaceus*	LC	Forest	F	80	46.5	35.77	0.874 (n = 1)
Ramphastidae	*Ramphastos ambiguus*	NT	Forest	F	60	651.68	8.36	0.578 (n = 1)
Ramphastidae	*Ramphastos sulfuratus*	LC	Forest	F	60	409.69	14.75	0.530 (n = 1)
Picidae	*Melanerpes portoricensis*	LC	Forest	I	10	59.86	25.12	0 (n = 1)
Psittacidae	*Amazona farinosa*	NT	Forest	F	50	625.99	26.81	0.667 (n = 1)
Tyrannidae	*Myiarchus antillarum*	LC	Forest	I	10	23.4	15.99	0 - 0.126 (n = 2)
Tyrannidae	*Tyrannus caudifasciatus*	LC	Forest	I	10	42.36	24.32	0.260 - 0.271 (n = 2)
Tyrannidae	*Tyrannus dominicensis*	LC	Forest	I	30	46.5	31.50	0.248 - 0.410 (n = 2)
Turdidae	*Turdus plumbeus*	LC	Forest	O	30	75.3	22.01	0.193 - 0.373 (n = 2)
Mimidae	*Margarops fuscatus*	LC	Scrub	F	40	98.43	19.91	0.117 - 0.298 (n = 3)
Thraupidae	*Nesospingus speculiferus*	LC	Forest	I	10	35.2	18.99	0.419 (n = 1)

[1] Status: LC = Least Concern; NT = Near Threatened (IUCN 2017).

[2] Primary Habitat: classed as ‘Forest’ species if a forest habitat (either F1 ‘evergreen forest’, F4 ‘montane forest’, or F7 ‘deciduous forest’) was listed as its primary habitat (Stotz *et al.* 1996).

[3] Dietary Guild: F = Frugivore, I = Insectivore, O = Omnivore (Wilman *et al.* 2014).

[4] Percentage of diet composed of fruit (Wilman *et al.* 2014).

[5] Hand-wing Index: An indication of bird dispersal ability, with higher values signifying greater dispersal and gap-crossing ability (Claramunt *et al.* 2012).

[6] *d'* range: Degree of specialisation (*d'*) of each frugivore (Blüthgen *et al.* 2006). The index varies from 0 (generalist) to 1 (specialist). This is calculated per Network, therefore a range is presented for those species that occur in more than one Network.

5.5 Discussion

Seed consumption is determined by bird gape width

In the Neotropics, the relationship between frugivorous bird species and the seeds they consume is strongly related to bird gape width. We found a positive relationship between gape width and seed size, which adds support to previous tropical studies that suggest deterministic factors structure seed dispersal networks in the tropics (Moran & Catterall 2010, Wheelwright 1985). In contrast, studies from temperate systems suggest that stochastic variation, rather than deterministic factors, structure frugivore-plant interactions (Burns 2006, 2013, Fuentes 1995). However, the lack of strong interspecific differences in the sizes of fruits and frugivores in temperate studies may preclude more specific associations between particular fruit and bird species (Burns 2006). In contrast to previous tropical studies that found degree of frugivory was a significant factor in predicting patterns in fruit consumption (Moran & Catterall 2010, Sebastian-Gonzalez 2017), we found that additional bird functional traits (degree of frugivory and dispersal ability) did not help to explain variation in fruit consumption.

Body mass was highly correlated with gape width, since larger birds tend to have larger gape widths, and we found that body mass could adequately predict the size of seeds consumed by bird species. Body mass is generally a more widely available functional trait than gape width (e.g. Wilman *et al.* 2014) and so it may be useful as a surrogate measure of bird species' plant consumption patterns. For example, the presence of large-bodied frugivorous birds in forest fragments, regenerating forest or degraded habitats suggest that the avian dispersers of large-seeded tree species are present and that seed dispersal of these trees will persist.

Large-gaped birds ingest a greater diversity of seed sizes than small-gaped birds

Large-gaped bird species consume a wider variety of seed sizes than small-gaped birds, and act as important dispersers of both small- and large-seeded plant species in seed-dispersal networks. Optimal foraging theory predicts that frugivorous birds should preferentially select fruits at the upper size limit of what they can consume in order to maximise energy yields and minimise time spent locating and handling fruits (Martin 1985a). Thus large-gaped bird species might be expected to focus their foraging efforts on large fruits, and Moran & Catterall (2010) reported this pattern for Australian avian frugivores, which predominantly consumed fruits at the upper limit of their handling capacity. However, we found that large-gaped birds consumed many small-seeded fruits as well as larger-seeded fruits, suggesting that frugivores in the Neotropics may be more opportunistic in their foraging. Alternatively, the strong seasonal variability of fruits at some of the sites in the present study (Wright *et al.* 1999) may oblige species to alter their foraging strategies to adapt to food resources available at different times of the year. Many large-seeded tree species have highly seasonal fruiting patterns (e.g. *Virola* species), so although frugivores may optimise foraging on larger fruits when available, they may have to feed on smaller fruits outside this fruiting season.

Plant species have a diverse range of fruit morphology and traits, which may affect their attractiveness to frugivores. For example, large fruits can contain many small seeds or fewer large seeds, and fruits containing a higher pulp to seed ratio may be more attractive to frugivores. The energy content and nutritional value of fruit can also be a major determinant for how many bird species are attracted to a fruiting plant (Sebastian-Gonzalez, 2017). For example, some studies have suggested that birds with a high degree of frugivory typically consume fruits with greater protein and lipid rather than sugar content (Moermond & Denslow 1985, Snow 1981), although this pattern is not always consistent (Fuentes 1994, Witmer & Soest 1998). Therefore, when frugivorous birds are foraging, a wide range of factors affect how they select fruits, and this selection process has obvious implications for seed dispersal, as whether a frugivore consumes the seed of a plant is the first step in the plant's dispersal and regeneration prospects.

Small-seeded plant species attract more bird species

Small-seeded plant species occupy a more central position in seed-dispersal networks than large-seeded plant species (Sebastian-Gonzalez 2017), and represent the bulk of fruit available to frugivorous birds. We found that small-seeded plant species attracted a greater number of bird species than large-seeded plant species, suggesting that small-seeded plant species provide food for a wide range of frugivorous bird species. As both small- and large-gaped bird species are capable of consuming small-seeded plant species (Wheelwright 1985), there are high levels of redundancy in the dispersal of small seeds, suggesting that these interactions are most robust to habitat disturbance. Moreover, a more diverse frugivore community can produce higher seed-dispersal fitness as a consequence of more varied foraging patterns (and thus, dispersal outcomes) from different frugivores (Sebastian-Gonzalez 2017). Conversely, large-seeded plant species were obligately dispersed by only a small number of bird species with large gape-widths. Such species-specific interactions are likely to be at greater risk of disruption following habitat disturbance.

Bird species that disperse large seeds

Large seeds can only be dispersed if the gape width of the bird is large enough to consume the seed, thus large-seeded plant species have fewer potential interacting partners (Wheelwright 1985). Seeds with a diameter > 10 mm appeared to be most at risk from disruption to seed-dispersal networks, as they had a small number of avian consumers. In our dataset, only 11 of the 134 bird species across the 13 networks dispersed these large seeds. There was no clear set of traits for bird species that consumed seeds > 10 mm. Although, these species tended to have the higher body mass associated with the large gape-widths and over half had a greater than average dispersal ability. However, no other traits were consistently associated with this group.

The realised extent of seed-dispersal by a given frugivore species will be influenced by their degree of frugivory. Yet only five of the species (*Trogon violaceus, Ramphastos ambiguus, Ramphastos sulfuratus, Amazona farinosa* and *Margarops fuscatus*) that consumed seeds > 10 mm diameter were classed as frugivores (i.e. had ≥ 40% fruit in their diet; Wilman *et al.* 2014), and could therefore be relied upon to regularly consume fruit and provide subsequent seed-dispersal functions. Fruit was only a small component of the diet (< 40%) for the other six species, likely limiting the role they play in seed-dispersal.

Specialisation in frugivorous birds

Bird species with a high degree of frugivory tended to be more specialised, (i.e. with higher *d'*), indicating that they deviated from a random feeding pattern of available plant species and frequented specific plant species more often. In consequence, species that are more important dispersers (i.e. highly frugivorous) are potentially of particular importance for the seed-dispersal of a small subset of plant species in the network. Other studies have also reported that body mass increased significantly with specialisation (Pigot *et al*. 2016a). In combination, these findings suggest that if the diversity and abundance of large-gaped, specialised bird species are affected by forest disturbance, then the dispersal of large-seeded plant species would also be affected, with long-term implications for plant community composition. However, another recent study from both temperate and tropical regions found conflicting patterns, where birds with a high degree of frugivory interacted with a wider variety of plant species in order to fulfil their nutritional requirements (Sebastian-Gonzalez 2017). A lack of specialisation in frugivorous birds has also been found in community-level studies focused solely on temperate regions (Burns 2006, 2013, Fuentes 1995). This suggests that there may be a community-level difference in the strength of fruit preferences exhibited by bird species between tropical and temperate zones.

Implications for seed-dispersal functions

Habitat disturbance and fragmentation have negatively affected the diversity and composition of Neotropical bird communities (Cleary *et al.* 2007, Lees & Peres 2006, Tscharntke *et al.* 2008). Small-seeded plant species and small birds account for the majority of interactions in seed-dispersal networks in the Neotropics, and are likely to be the most robust in the face of ecosystem disturbance. In contrast, large-bodied, long-lived, non-migratory, and primarily frugivorous forest specialists are often absent from disturbed habitats, or present in low densities (Newbold *et al.* 2013, Owens & Bennett 2000, Sekercioğlu 2007). In contrast to large-gaped frugivorous birds, the small bird species that survive habitat disturbances are generally unable to disperse large-seeded plant species and thus are unlikely to compensate for the loss of large frugivores following forest disturbance (Kitamura *et al.* 2002).

Frugivores from other taxonomic groups also play a role in the dispersal of large-seeded plant species. However, studies have shown that dietary overlap among large-gaped frugivorous birds and other large-bodied frugivores is often minimal. For example, hornbill and primate species in Cameroon were shown to have dissimilar diets, and are therefore not redundant as seed dispersers (Poulsen *et al.* 2002).

The loss of large-bodied frugivores may have important knock-on effects for large-seeded plant species (Wotton & Kelly 2011). In extreme cases, dispersal failure could prevent the regeneration of large-seeded plants (Janzen 1986), eventually leading to the successional replacement of mature forests with small-seeded plant species. In tropical Asian forests, many of the plant species that are reliant on large birds and other large frugivores for seed-dispersal now display reduced ranges and densities, as hunting pressure has reduced the abundance of their seed-dispersers (Corlett 1998, Kitamura *et al.* 2002). In the Neotropics, defaunation has reduced seed removal from *Virola flexuosa* in Ecuador following declines in large seed-dispersers, such as large primates and toucans, due to hunting (Holbrook & Loiselle 2009). This had led to dispersal limitation, with seeds reaching fewer recruitment sites than expected (Holbrook & Loiselle 2009). Other Neotropical studies have reported a range of negative impacts on forest plants communities due to the loss of large-bodied frugivores, including reduced seed removal and density of seedlings (Donatti *et al.* 2009), reduced species richness and density of large-seeded trees (Nuñez-Iturri & Howe 2007), and increased richness and diversity of small-seeded and abiotically dispersed plant species (Nuñez-Iturri & Howe 2007, Wright *et al.* 2007a).

Caveats

While the seed-dispersal networks analysed here represent the largest Neotropical dataset available, there are some limitations. There is a notable lack of large-bodied bird species in many of the seed-dispersal networks analysed in this study. This low frequency of large-bodied bird species may be a consequence of the natural predominance of small-bodied bird species and low-abundance of large-bodied birds in natural communities (Vidal *et al.* 2013). Equally, the absence of larger bird species from most networks may also suggest that defaunation processes have already affected these networks. In addition, many studies did not collect data over a full annual cycle, potentially missing some frugivore-plant interactions. Finally, data were obtained using different sampling methods, which may influence the species observed and their densities. To minimize the impacts of different sampling methods, we largely used presence/absence interactions to standardise data from different networks for our analyses, and the in-depth analyses, such as degree of specialisation, were restricted to the most robust qualitative networks.

Conclusions

The collection of detailed, species-specific dietary information for frugivorous birds is time-consuming and difficult, particularly in species-rich tropical ecosystems. Bird functional traits can be used as a substitute for these data, enabling a systematic, general approach to identifying relationships among frugivores and plants that can be applied across the tropics (Dehling *et al.* 2016, Moran & Catterall 2010). Our results imply high levels of redundancy between small-gaped avian frugivores and small-seeded plant species, suggesting that habitat disturbance may not affect these sections of seed-dispersal networks. Bird species that disperse large-seeded plant species tend to have large gape widths and high body mass, along with a high degree of frugivory and specialisation in their diet. The much lower levels of redundancy among large-seeded plant species and their dispersers leaves them at greater risk of dispersal failure following any change in avian frugivore assemblages resulting from habitat degradation and disturbance.

5.6 Acknowledgments

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5.7 Supplementary Information

Table S5.1: Details of bird-plant networks

Details of networks (n = 13) analysed in the current study.

Source	Network	n bird species	n plant species	n interactions	Interaction type [1]	Location	Altitude (a.s.l.)
Carlo *et al.* (2003)	CACG	15	25	230	Q	Caguana, Puerto Rico	430m
Carlo *et al.* (2003)	CACI	20	34	478	Q	Cialitos, Puerto Rico	650m
Carlo *et al.* (2003)	CACO	13	25	122	Q	Cordillera, Puerto Rico	250m
Carlo *et al.* (2003)	CAFR	15	21	118	Q	Fronton, Puerto Rico	300m
Galetti and Pizo (1996)	GEN1	18	7	150	Q	Santa Genebra Reserve T1, Brazil	640m
Galetti and Pizo (1996)	GEN2	29	35	397	Q	Santa Genebra Reserve T2, Brazil	640m
Gorchov *et al.* (1995)	GORCH1	7	37	154	Q	Loreto, Peru	130m
Gorchov *et al.* (1995)	GORCH2	6	6	29	Q	Loreto, Peru	130m
Kantak (1979)	KANT	25	5	83	B	Campeche State, Mexico	260m
Poulin *et al.* (1999)	POULI1	19	4	200	Q	Soberania National Park, Panama	85m
Poulin *et al.* (1999)	POULI2	11	13	292	Q	Soberania National Park, Panama	85m
Sarmento *et al.* (2014)	SARM	8	28	41	B	Atlantic Forest, Brazil	500 – 600m
Own data	MAYH	32	10	323	Q	Barro Colorado Island, Panama	140m

[1] Interaction type: Q = quantitative data; B = binary data

Table S5.2: GLMMs examining bird traits and seed width

Results of linear mixed-effects models (GLMM) examining the relationship between seed width and bird functional traits for all data, for 13 frugivore networks from the lowland Neotropics. 'Network' and 'bird family' were included as random effects.

Fixed effects	Estimate	Standard Error	t value
Seed Width ~ Gape Width (AIC = 392.227)			
Gape Width	0.7267	0.1315	5.526
Seed Width ~ Gape Width + % Fruit (AIC = 394.016)			
Gape Width	0.7318	0.1317	5.553
% Fruit	-0.0003	0.0007	-0.466
Seed Width ~ Gape Width + Dispersal Ability (AIC = 394.115)			
Gape Width	0.7183	0.1338	5.366
Dispersal Ability	-0.0456	0.1361	-0.335
Seed Width ~ Gape Width + Dispersal Ability + % Fruit (AIC = 395.910)			
Gape Width	0.7239	0.1341	5.366
Dispersal Ability	-0.0432	0.1361	-0.318
% Fruit	-0.0003	0.0007	-0.453
Seed Width ~ Body Mass (AIC = 405.457)			
Body Mass	0.1695	0.0572	2.961
Seed Width ~ Body Mass + Dispersal Ability (AIC = 406.786)			
Body Mass	0.166	0.0564	2.942
Dispersal Ability	-0.1233	0.1471	-0.838
Seed Width ~ Body Mass + % Fruit (AIC = 407.374)			
Body Mass	0.1712	0.0574	2.98
% Fruit	-0.0002	0.0008	-0.289
Seed Width ~ Body Mass + Dispersal Ability + % Fruit (AIC = 408.746)			
Body Mass	0.1674	0.0567	2.951
Dispersal Ability	-0.1201	0.148	-0.812
% Fruit	-0.0001	0.0008	-0.201

Table S5.3: GLMMs for bird species dispersing large seeds

Results from linear mixed-effects models (GLMM) examining the relationship between seed width and bird functional traits for a subset of data, where seed widths that were greater than bird's gape widths were removed, for 13 frugivore networks from the lowland Neotropics. 'Network' and 'bird family' were included as random effects.

Fixed effects	Estimate	Standard Error	t value
Seed Width ~ Gape Width (AIC = 265.742)			
Gape Width	0.9306	0.1629	7.936
Seed Width ~ Gape Width + Dispersal Ability (AIC = 267.225)			
Gape Width	0.9161	0.1189	7.702
Dispersal Ability	-0.088	0.1222	-0.72
Seed Width ~ Gape Width + % Fruit (AIC = 267.702)			
Gape Width	0.9313	0.117	7.961
% Fruit	0.0001	0.0007	0.207
Seed Width ~ Gape Width + Dispersal Ability + % Fruit (AIC = 269.183)			
Gape Width	0.9166	0.1187	7.723
Dispersal Ability	-0.088	0.1219	-0.721
% Fruit	0.0001	0.0007	0.21
Seed Width ~ Body Mass (AIC = 284.629)			
Body Mass	0.2357	0.0562	4.19
Seed Width ~ Body Mass + Dispersal Ability (AIC = 285.107)			
Body Mass	0.2303	0.055	4.19
Dispersal Ability	-0.1756	0.1391	-1.262
Seed Width ~ Body Mass + % Fruit (AIC = 286.576)			
Body Mass	0.2366	0.0565	4.185
% Fruit	-0.0002	0.0008	-0.232
Seed Width ~ Body Mass + Dispersal Ability + % Fruit (AIC = 287.1043)			
Body Mass	0.2306	0.0553	4.173
Dispersal Ability	-0.1745	0.1402	-1.245
% Fruit	-0.00004	0.0008	-0.053

Table S5.4: GLMMs for number of bird species and seed width

Linear mixed-effects model (GLMM) results examining the relationship between number of bird species consuming seeds and seed width for 13 frugivore networks from the lowland Neotropics. ‘Network’ and ‘plant family’ were included as random effects.

Data Subset	Fixed effects	Estimate	Standard Error	t value
All Data	Seed Width	-0.1176	0.0894	-1.315
Subset Data [1]	Seed Width	-0.1856	0.0982	-1.892

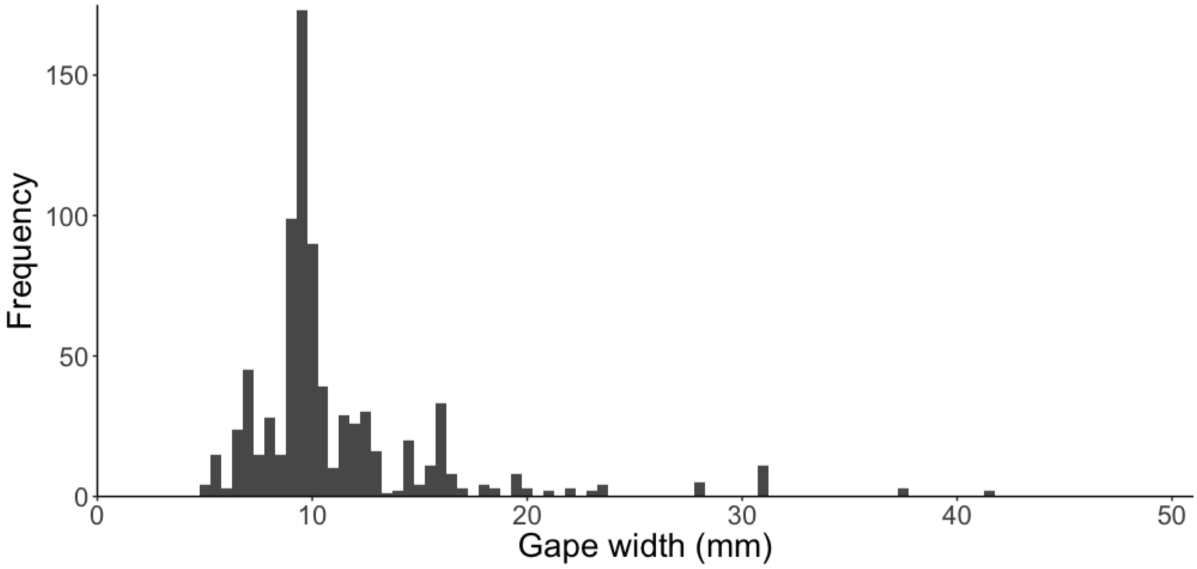
[1] Subset Data: data where plant seed width was greater than bird gape width removed

Table S5.5: GLMMs for specialisation and seed width

Linear mixed-effect model (GLMM) results examining the relationship between degree of specialisation (*d’*) and other bird functional traits for seven lowland Neotropical frugivore Networks (CACG, CACI, CACO, CAFR, GEN1, GEN2, and MAYH). ‘Network’ and ‘bird family’ were included as random effects.

Fixed effects	Estimate	Standard Error	t value
d' ~ Body Mass (AIC = -482.715)			
Body Mass	0.18	0.0411	4.375
d' ~ % Fruit (AIC = -472.593)			
% Fruit	0.001	0.0003	2.658
d' ~ Gape Width (AIC = -469.8)			
Gape Width	0.2263	0.1045	2.166

(A)



(B)

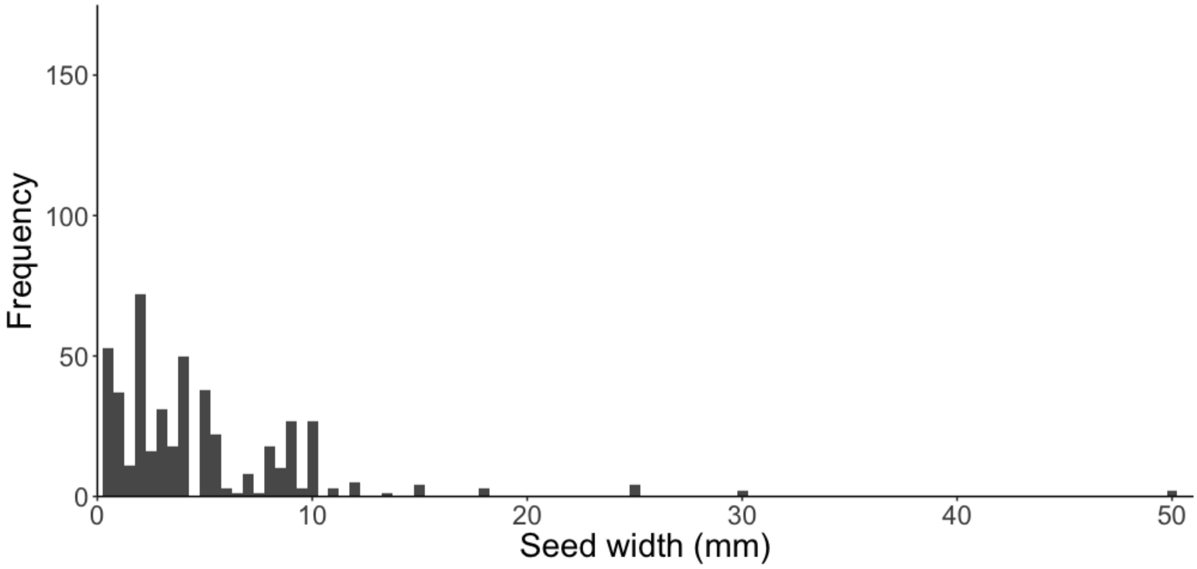


Figure S5.1: Histograms of bird gape width and tree seed width data

Distribution of (A) bird gape width data and (B) plant seed width data for 13 frugivore networks in lowland Neotropics.

Chapter 6: General Discussion

6.1 Overview of thesis

The continued loss of tropical primary forest (PF) habitats has the potential to cause catastrophic species extinctions (Dent & Wright 2009, Wright & Muller-Landau 2006a). However, the ongoing expansion of secondary forest (SF) habitats is reducing the net loss of forest cover in the tropics (FAO 2015), and could potentially provide new habitats for many PF taxa. There is a growing literature documenting the ability of tropical SF to host biodiversity, yet conservation biologists are still divided over the extent to which expanding areas of SF will be able to offset the loss of various taxonomic groups from PF deforestation and degradation (e.g. Barlow *et al.* 2007, Chazdon *et al.* 2009, Dent & Wright 2009, Gibson *et al.* 2011). Thus, there is a critical need to assess whether regenerating SF can support species typically found in PF, and so inform efforts to prevent extinctions and maintain ecosystem services. The research presented in this thesis helps to elucidate the conservation potential of SF for tropical bird communities and the ecosystem services they provide.

We use point count surveys in central Panama to compare tropical forest bird communities in 20 – 120-yr-old SF with varying levels of isolation and connectivity to extensive PF. In Chapter 2 we show that SF supports high levels of avian species diversity, and similar community composition to PF. We found that connectivity to extensive PF was more important than forest age in determining compositional similarity to PF, with 20-year-old SF that was well connected to PF showing higher levels of compositional similarity than isolated 120-year-old SF. In Chapter 3 we use morphological traits to demonstrate that the functional diversity and composition of bird communities does not change across the successional and isolation gradient present at our study site. However, we did find inter-guild differences: trophic traits of insectivores varied with forest isolation, while dispersal traits of frugivores differed with isolation. In Chapter 4 we show that there are high levels of similarity in the response of bird and tree species composition to forest succession and isolation, but that isolation appears to have a stronger effect on bird communities. We also found that bird species diversity and community composition is closely related to forest structure, with more diverse bird communities associated with the greater structural complexity present in older tropical forest. Finally, in Chapter 5 we examine avian seed-dispersal networks in the Neotropics, using functional traits of birds and plants to elucidate species interactions. We identify bird gape width as the key predictor of seed size consumed, although body mass was also significant. We found that large-gaped birds consume a wider variety of seed-sizes than small-gaped birds, and small-seeded trees attract a greater number of bird species than large-seeded trees. These results imply high levels of redundancy among small-gaped avian frugivores and small-seeded plant species, suggesting that habitat disturbance will have minimal impacts on seed-dispersal of small-seeded plants. However, low levels of redundancy among large-seeded plant species and their avian dispersers, renders these plants at risk of dispersal failure following changes in avian frugivore assemblages.

6.2 The conservation value of secondary forests in Central Panama

Our results demonstrate the importance of landscape context for evaluating the conservation value of SF for bird communities. Landscape configuration is recognised as playing a key role in shaping avian communities in tropical forests (Barlow *et al*. 2006, Lees & Peres 2009, Wolfe *et al*. 2015). Factors such as forest fragment size and the hostility of the surrounding landscape matrix (including isolation and connectivity to extensive PF) dictate the rates of SF colonisation and occupancy for many bird species. The open waters of Lake Gatun in our study area create a hard barrier to dispersal for many forest species between island, peninsula and mainland sites. The distance between Barro Colorado Island and Soberania National Park on the mainland, where extensive PF is situated, ranges from 0.6 - 3.5km, but we found that even this relatively short distance has major impacts on species diversity and composition.

It is often assumed that because birds are highly vagile species, they are perhaps not as sensitive to habitat fragmentation and isolation as other taxa (Ambuel & Temple 1983). However, tropical forest species tend to be closely associated with closed canopy forest and unwilling to cross gaps created by water, roads or pasture (Develey & Stouffer 2001, Grubb & Doherty 1999, Moore *et al*. 2008, Tobias *et al*. 2013). This extreme dispersal limitation of many forest species could be explained by the naturally low rates of dispersal displayed by many birds (Greenwood & Harvey 1982), a higher perceived predation risk in open areas (Lima & Dill 1990), or a limited perceptual range within which birds can detect and identify other forest patches (Lima & Zollner 1996). Whatever the underlying cause, the result is that many species seem unable to colonise isolated forest patches.

Forest fragment size is closely related to connectivity to PF in determining avian community assembly in tropical forests. A forest-dependent species with large area requirements will only be able to survive in a small forest fragment if resources within the patch can be supplemented from neighbouring and accessible forest patches (Lees & Peres 2009). Barro Colorado Island is a relatively large forest fragment (1560 ha), and yet many bird species have been extirpated since the island was isolated a century ago (Chapman 1938, Eisenmann 1952, Karr 1990, 1982, Robinson 1999, Willis & Eisenmann 1979); 65 species have been lost from the island, including 30 forest species and 35 edge species (Robinson 1999). Bird species may struggle to persist in small forest fragments due to smaller and less diverse food supplies (Burke & Nol 1998), elevated predation levels (Andren 1992), and increased exposure to extreme environmental conditions along forest edges (Murcia 1995). When forest fragments are bounded by a hostile landscape matrix, such as is the case with Barro Colorado Island, the effects of isolation-related extirpations cannot be ameliorated by populations from neighbouring forest patches. Thus, populations of species susceptible to dispersal limitation may be subject to isolation-related effects, even in relatively large forest fragments.

Forest age played a small role in determining the composition of bird communities across the studied successional gradient. This small role was especially evident when comparing our isolated SF to isolated PF, where there was a clear trajectory of increasing similarity in species composition with increasing SF age when compared to isolated PF. This is likely attributable to the close relationship between forest age and increasing forest structural complexity (DeWalt *et al.* 2003), which creates more diverse ways to exploit resources and so allows for more specialist species (Casas *et al.* 2016, MacArthur & MacArthur 1961, Tews *et al.* 2004).

The variation in bird species diversity and composition found across our successional and isolation gradients is not reflected in functional diversity or composition of bird communities, which vary little across our sites. This implies that there is functional redundancy among species in PF and that ecosystem services, such as seed dispersal and insect herbivore predation, are maintained in SF despite changes in bird assemblages. Our results support other studies that suggest SF can support provision of ecosystem functions, including pollination and seed dispersal, with older SF having increased functional redundancy (Sayer *et al.* 2017).

Differences detected in the trait structure of bird communities across the successional and isolation gradient highlighted the previously well-documented loss of understorey insectivores from our isolated sites (Chapman 1938, Eisenmann 1952, Karr 1990, 1982, Robinson 1999, Willis & Eisenmann 1979). In addition, our results shed new light on the loss of frugivorous species with limited dispersal, but also showed that all other traits for frugivores (trophic, locomotory and body size) remained unchanged across the gradient. We identified gape-width and body-size as key predictors of seed size consumption in avian frugivores. Therefore, given that body-size and trophic traits did not vary across sites, we can infer that large-seeded plant species are being effectively dispersed in both SF and isolated sites. This is important given that a reduction in avian frugivores in tropical forest habitats has the potential to impede tree regeneration. Many large-seeded plant species are obligately dependent on large birds for seed dispersal (Wheelwright 1985, Wotton & Kelly 2011), and loss of these bird species may result in long-term shifts in tree community composition (Galindo-González *et al*. 2008, Sethi & Howe 2009, Terborgh *et al*. 2008).

Taken together, these results suggest that SF > 20 years has the capacity to retain a large proportion of PF species, but that forest isolation impacts on species diversity and composition. Despite this, functional diversity and composition across the successional and isolation gradients remains intact, suggesting that the ecosystem services provided by birds are maintained.

6.3 Regional differences in land-use patterns: implications for secondary forest regeneration

Forest succession is not a linear, irreversible process. Rather deforestation and reforestation are dynamic processes that can occur at any given spatial or temporal scale (Chazdon 2014). In general, young SF is more likely to be cleared than older SF (Helmer *et al*. 2008). In addition to site and landscape factors, variation in regional land-use patterns will affect SF regeneration and hence its value for biodiversity.

Many countries in Central America and the Caribbean (for example, Costa Rica, El Salvador and Puerto Rico) have more forest cover now than they did 20 years ago due to reductions in deforestation and increases in reforestation and forest regeneration (Aide *et al*. 2013, Rudel *et al*. 2005). Such forest transitions have largely been driven by changing socioeconomic factors over the last 100 years (Chazdon 2014). These factors include: rural-urban migration (Aide & Grau 2004); emigration to other countries (Schmook & Radel 2008); abandonment of farming and ranching on marginal lands (Arroyo-Mora *et al*. 2005); and adoption of agroforestry, or the development of forest-friendly land uses, including eco-tourism or ecological reforestation projects (Kull *et al*. 2007, Sloan 2008). In

Panama, forest cover increased from 1992 to 2000, while the proportion of workers employed in agriculture, fishing and hunting declined (Wright & Samaniego 2008). These forest transitions have encouraged SF in the region, allowing SF to persist, expand and mature, offering stable habitats for many forest species.

In contrast, there is still net deforestation in much of South America, despite large areas of reforestation (Aide *et al.* 2013). In Amazonia, a large proportion of SF is part of small-scale agricultural systems (Almeida *et al.* 2010), where forested areas are slashed and burned for crop cultivation and then left to fallow while new agricultural fields are opened (Coomes *et al.* 2000). The agricultural cycle length is variable, with 1–3 years of cultivation, followed by a fallow period of anywhere from two to > 15 years, depending on the farmers' decisions (Jakovac *et al.* 2015). In recent decades however, population pressure and socioeconomic factors are driving agriculture towards intensification in an attempt to increase crop yield per unit of area and time (Coomes *et al.* 2000, Metzger 2002, van Vliet *et al.* 2012). With this shift, there is a growing predominance of shorter fallow periods and an increasing number of cycles; fields that used to be cultivated for up to three fallow cycles now experience many more (Jakovac *et al.* 2015). Increasing the number of fallow cycles can compromise soil fertility and can slow successional recovery following agricultural abandonment (Lawrence 2004). A 10-year time-series of 26 Landsat scenes sampled across the most deforested region of Brazilian Amazonia revealed that SF was almost invariably short-lived, with a mean lifespan of less than 5 years (Neeff *et al.* 2006). Similar patterns were seen in the Brazilian state of Rondônia; in 2003, 65% of SF was estimated to be < 5 years old, whereas only 9.8% was 19-28 years old (Helmer *et al.* 2009). Thus, SF in Amazonia are often short-lived and the majority of regenerating SF patches do not persist for long enough to develop structural complexity and species diversity, limiting the contribution of these forests to conservation.

The clearance of young SF has several potential implications for conservation at the landscape scale (Chazdon 2014). First, the future extent of SF cover within the landscape is reduced, preventing development of potential biological corridors and buffer zones. Second, the average age of SF within the landscape is constrained, and SF patches do not have sufficient time to develop complex structures. Third, older SF and PF patches in the landscape are more likely to become isolated. Finally, long-lived tree species, and animals that require specialised resources usually only present in older SF and PF, are less likely to be found in the landscape. For example, long-term persistence of SF patches is essential for regeneration of long-lived taxa, such as slow-growing canopy trees (Liebsch *et al.* 2008). Thus, the regional differences in land-use across the Neotropics have implications for the spatial and temporal regeneration of SF, and will dictate the conservation value of SF for biodiversity.

6.4 Relative value of secondary forest

Regional differences in history, geography, and the political, social and economic setting will influence the relative conservation value of SF. It is often due to these contextual variables that studies present contrasting results in the role that SF can play in conserving tropical biodiversity. For example, in areas with little or no remnant PF, SF can provide critical refugia for remaining forest species (Chazdon 2014), whereas in areas where large tracts of undisturbed PF exist, SF habitats are less crucial for forest taxa.

Across Central American and Caribbean countries, the historical clearance of PF was dramatic. Today, SF in this region accounts for 51% of total forest cover in Guatemala and 93% of total forest cover in El Salvador (FAO 2010). In Puerto Rico, PF cover had been reduced to less than 10% in the 1930s (Rudel *et al.* 2000). However, the transformation from an agricultural to manufacturing economy led to significant rural-to-urban migration. The subsequent abandonment of sugarcane fields, coffee plantations and pastures led to an increase in forest cover, reaching 42% in 1991, despite continued population growth (Helmer *et al.* 2002, Rudel *et al.* 2000, Yackulic *et al.* 2011). El Salvador presents another context for forest regeneration, where in the Cutumayo basin only 18% of PF cover remained in 1978 (Herrador Valencia *et al.* 2011). However, during the armed conflict in the 1980s, many villagers were forced to abandon their homes and farms, leading to SF regeneration on previously cultivated fields. When the people returned in the 1990s they decided to use their new forest to create a protected natural area, as the basis for economic development of the region; forest cover here reached 61% in 2004 (Herrador Valencia *et al.* 2011).

In contrast, tropical PF accounts for a much higher proportion of total forest cover in South America. Although only 14% of forest cover in Colombia is PF, this figure rises to 93% in Brazil and 95% in French Guiana (FAO 2010). This compares to the situation in Central America, where as little as 2% of forest is PF in El Salvador, or in the Caribbean where the mean PF is only 4.2% (FAO, 2010). Thus, the presence of SF in much of South America is, perhaps currently, less crucial to the persistence of forest species than in Central America and the Caribbean.

An appropriate PF baseline is essential for evaluating the conservation value of SF, with some researchers hypothesising that the lack of such a baseline in many studies accounts for overly positive conclusions concerning SF value (Barlow *et al.* 2007b, Gardner *et al.* 2007). Indeed, in landscapes with large areas of intact PF, such as in parts of the Brazilian Amazon, studies have highlighted the lack of PF-specialist taxa present in SF (Barlow *et al.* 2007b, Gibson *et al.* 2011). However, in regions where extensive PF is limited, or simply no longer exists, the presence of SF is crucial for the survival of remaining forest species, and for overall biodiversity conservation.

6.5 Policy implications

Historically, conservation efforts have focussed on protected areas as the best way to reduce deforestation and limit the loss of biodiversity. Generally, these areas have consisted of natural ecosystems, such as PF (Dudley 2008), which are considered to be irreplaceable for their biodiversity value and ecosystem services (Gibson *et al.* 2011). However, there are limitations to relying exclusively on protected areas: it is rarely possible to designate sufficient areas of land to adequately represent the range of communities found in specific biomes (Cox & Underwood 2011), or support viable populations of many species (Struhsaker *et al.* 2005). Furthermore, biodiversity declines often continue in protected areas due to poaching, forest-product exploitation or habitat disruption (Laurance *et al.* 2012). Thus, it may be unwise to rely solely on protected areas of PF for then conservation of tropical biodiversity and ecosystem services (Sayer *et al.* 2017).

Our results indicate that SF as young as 20 years can provide suitable refugia for many forest bird species, especially when connected to PF source populations. We also found that even when avian species composition of SF diverges from neighbouring PF, the functional composition of bird communities can remain intact, providing important ecosystem services such as seed dispersal and insect herbivore predation. Thus, SF can provide critical biological corridors and buffer zones, as well as ecologically important habitats in their own right. In today’s human-modified landscapes, habitats that can safeguard areas of PF from encroaching anthropogenic demands on land, and that can aid the movement of PF species between patches are essential. Tropical PF should remain a conservation priority as these habitats host greater biodiversity and more rare species than other types of forest (Gibson *et al*. 2011). However, SF must also be integrated into conservation initiatives to support and buffer PF habitats.

The future value of abandoned pastures or unused agricultural lands is rarely considered in conservation planning, and SFs are often unrecognised and underappreciated as valuable ecosystems. However, recent international targets aim to restore more than 15% of degraded forests by 2020 (Secretariat of the Convention on Biological Diversity 2010), while the New York Declaration on Forests proposes to restore 200 million hectares of degraded forests worldwide (United Nations, 2014). These initiatives present opportunities to encourage adoption of strategies at the national level that recognise the potential value of SF. Effective strategies might include encouraging creation and protection of forest habitat corridors, and the establishment of SF buffer zones surrounding existing protected areas. In Panama, the Panama Canal Authority (ACP) already supports schemes designed to encourage landowners to plant and protect forest in cleared areas to limit soil erosion and improve catchment management around the Panama Canal (ACP 2014). The research presented in this thesis adds to a growing body of evidence highlighting the potential conservation value of SF (e.g. Chazdon *et al*. 2009, Dent & Wright 2009, Sayer *et al*. 2017). Together, we hope that this information will help to inform policy makers and management activities.

6.6 Scope for future research

The research presented in this thesis used point count methods to establish the presence of birds in forest habitats. While this method is suitable for detecting species, it does not account for how birds use SF habitats. Some researchers have suggested that in SF adjacent to PF, bird populations may be transitory, with individuals using the SF for foraging and returning to the PF habitat to roost and nest (Stotz *et al*. 1996, Tobias *et al*. 2013). It is also possible that SF may act as a sink for many individuals, and that populations in neighbouring PF maintain SF communities. We cannot rule out this possibility in our 20-year-old SF sites that are contiguous with PF, and more research is needed to clarify population demography and viability in SF. More in-depth behavioural studies of birds would allow us to deduce which bird species are able to complete all aspects of their lifecycles in SF, and how reliant these birds remain on PF resources. Technologies such as radio tracking offer opportunities to elucidate avian behaviours in this context, and the few studies which have employed such labour-intensive methodologies so far highlight important inter-species differences in the use of SF (Gillies & St. Clair 2010, Powell *et al.* 2015c).

To determine the role that individual bird species play in seed-dispersal networks, more information is required on where and how far birds are dispersing seed. The majority of studies, including our own, rely on observations of birds consuming fruit to imply seed dispersal. From these observations, it is usually possible to infer whether the seed is consumed, and from species' ecology we can surmise whether the seed is predated or dispersed, however there is currently very limited information detailing how far bird species are likely to disperse seed. Thus, in our own seed dispersal network, we can only assume that fruit consumption equates to dispersal of seed. Where and how far a bird disperses seed will relate to how bird species use forest patches within human-modified landscapes; their movement patterns are unlikely to be random, but rather strongly influenced by site- and landscape-scale factors (Díaz Vélez *et al.* 2015, Gillies & St. Clair 2010). The little evidence available on avian seed dispersal distances suggests that even small frugivorous birds are capable of dispersing seeds up to 600 m through a fragmented landscape, but this is dependent on the presence of riparian strips to act as habitat corridors (Şekercioğlu *et al.* 2015). Further knowledge on seed dispersal distances and the habitat features that favour bird movements, would allow us to make more accurate predictions as to the consequences of changes in avian frugivore assemblages and habitat change on seed dispersal services, and ultimately on tree communities.

6.7 Conclusions

The conservation value of SF for tropical birds is not only dependent on forest age, but on the surrounding landscape. Ultimately though, the value of SF will depend on the aims of conservation strategies. If the goal is to create and maintain habitat that can support specialist bird species that are restricted to PF, then our results suggest that SF is of limited value and the preservation of PF is essential as avian forest specialists may be absent from SF habitats. However, the richness of forest specialists increases with SF connectivity to PF, and so maintaining PF in the landscape will have associated positive impacts on SF. Alternatively, if conservation strategies are designed to maintain ecosystem functioning, then our results suggest that SF are capable of supporting bird species that will preserve functions such as seed dispersal and insect herbivore predation. However, low levels of redundancy among large-gaped birds and large-seeded trees suggests that these plants may be the most at risk of dispersal failure following any change in avian frugivore assemblages. Maintaining forest habitat connectivity within landscapes, as well as minimising on-going forest disturbance and preventing overhunting, can help to mitigate the loss of these large frugivores and key seed dispersers. Together, these results suggest that SF can play a key role in sustaining the majority of tropical biodiversity, and in maintaining ecosystem services. Our findings emphasise the importance of integrating SF into conservation strategies to support and buffer tropical PF habitats.

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