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The dispersal of native and introduced seeds by São Tomé forest birds

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Djitu tem ku tem

RESUMO ALARGADO

Com a população mundial a aumentar, os impactos antropogénicos nos ecossistemas naturais vão sendo cada vez mais evidentes. Assistimos actualmente a uma elevada taxa de extinção de espécies, e com elas se perdem as funções e os serviços ecossistémicos que prestam, deixando os ecossistemas mais vulneráveis às pressões humanas. Uma dessas funções, essencial à manutenção da dinâmica florestal, é a dispersão de sementes, que nos trópicos é feita essencialmente através de relações mutualistas entre plantas e animais. A eficácia da dispersão pode variar substancialmente em função da espécie dispersora e depende não só da quantidade de sementes que os animais transportam, mas também da qualidade do tratamento que estes proporcionam às sementes. A perda de um dispersor chave num ecossistema pode portanto comprometer a viabilidade das populações de plantas e alterar a dinâmica da vegetação.

Os efeitos da perda da biodiversidade são particularmente graves nas ilhas, onde se concentra grande parte das espécies, sobretudo endémicas. Aqui, as espécies evoluíram em isolamento, existindo naturalmente uma menor diversidade de espécies e possivelmente uma menor redundância funcional entre espécies. Estas características fazem com que estes ecossistemas sejam mais frágeis, e é nas ilhas que se tem verificado a maioria das extinções de espécies. Uma das principais ameaças identificadas é a introdução de espécies invasoras, que competem com as espécies nativas, acabando por as excluír.

São Tomé é uma pequena ilha oceânica de clima tropical, situada no sistema insular do Golfo da Guiné. Com uma das maiores concentrações de endemismos de todo o mundo, São Tomé está a sofrer as consequências dos impactos humanos, estando a sua biodiversidade bastante ameaçada.

Este trabalho tem então como objectivo perceber de que forma as aves estão a contribuir para a dispersão de sementes, uma função ecossistémica essencial para as florestas ricas em endemismos de São Tomé. Para tal, foram definidos três objectivos específicos: (1) avaliar a rede de dispersão de sementes por aves do sub-bosque em floresta de montanha, através da análise dos excrementos de aves capturadas com redes verticais; (2) avaliar a contribuição específica dos pombos como potenciais dispersores de sementes em São Tomé, através da análise de conteúdos de papos de pombos caçados; (3) caracterizar a dispersão de sementes na floresta de montanha, unindo os dados provenientes dos pontos anteriores, ponderados com a abundância relativa das aves. As redes de dispersão de sementes foram construídas analisando as matrizes de interação com o ‘package’ *bipartite* do programa R. A frequência de interação foi quantificada como o número de excrementos ou papos de cada espécie de ave contendo pelo menos uma semente intacta de cada espécie de planta.

Foram capturadas 15 espécies de aves com redes verticais no sub-bosque em floresta de montanha, todas elas endémicas. Confirmámos dispersão de sementes por seis destas espécies, de destacar a contribuição do Olho-grosso (*Speirops lugubris*), responsável por 88% da frequência de interação. As espécies de plantas nativas dominam esta rede (14 espécies, 70% das espécies identificadas), incluindo algumas espécies endémicas ameaçadas, enquanto que poucas são as espécies introduzidas incorporadas na rede de dispersão (seis espécies, 20% das espécies identificadas). Através de curvas de acumulação de espécies, é possível afirmar que o esforço de captura foi bastante elevado, tendo-se conseguido capturar 71% das espécies de aves que ocorrem na área de estudo e 65% das plantas a serem dispersas. A comparação entre as redes de dispersão de sementes da floresta primária (obô) e da floresta secundária (capoeira) revelou poucas diferenças, o que pode estar relacionado com a proximidade geográfica das áreas de amostragem. Estes resultados sugerem ainda que os dispersores

se movem entre os dois tipos de floresta, contribuindo para a disseminação das sementes entre habitats, o que vai facilitar tanto a invasão por espécies introduzidas, como a regeneração de espécies nativas em zonas de floresta degradada.

A análise da rede de dispersão de sementes por pombos em São Tomé permitiu verificar a importância das três espécies endémicas caçadas como potenciais dispersores de sementes. Em especial a Rola (*Columba malherbii*) e o Cécia (*Treron sanctithomae*), tanto por serem as mais abundantes, como por serem as que mais frequentemente continham sementes no papo. Esta rede é dominada por sementes nativas (53 % da frequência de ocorrência) e apenas uma pequena percentagem de introduzidas (21% da frequência de ocorrência), sendo que uma destas (*Cecropia peltata*) está incluída na lista das 100 piores espécies invasoras do mundo. Já o Pombo-do-mato (*Columba thomensis*) é uma espécie mais rara, tendo a sua população vindo a decrescer maioritariamente devido à pressão de caça. É necessária alguma cautela ao analisar estes resultados, uma vez que as sementes nos papos dos pombos teriam ainda de passar por todo o processo de digestão, podendo levar à sua destruição antes de serem depositadas. No entanto, mesmo que poucas sementes resistam à passagem pelo trato digestivo da ave, a probabilidade destas serem dispersas a longa distância é elevada, dada a grande capacidade de voo dos pombos quando comparada com as das restantes aves existentes na ilha.

A dispersão de sementes nas florestas de montanha de São Tomé é suportada exclusivamente por aves endémicas, um resultado surpreendente mesmo no contexto de ilhas oceânicas. A grande importância do Olho-grosso como dispersor de sementes resulta não só da frequência com que as dispersa, mas também da sua elevada abundância nestas florestas. Apesar do método utilizado ser dirigido a aves do sub-bosque, foi possível capturar também alguns indivíduos de espécies mais associadas à copa das árvores, como o Neto-de-olho-grosso (*Zosterops feae*). Foi também possível comprovar que o Pardal (*Serinus rufobrunneus*) é sobretudo um predador de sementes, já que apenas uma reduzida proporção dos dejectos continha sementes intactas. Os pombos parecem ser quantitativamente pouco relevantes, sobretudo devido à sua abundância reduzida, mas podem constituir importantes dispersores a longa distância e de sementes de maiores dimensões. Foi ainda detetada alguma complementariedade entre os vários dispersores, já que apenas o Tordo (*Turdus olivaceofuscus*) e o Papafigos (*Oriolus crassirostris*) foram encontrados a dispersar as sementes maiores (8-10mm). Estes dois dispersores, de maiores dimensões, possuem uma garganta mais larga que lhes permite engolir sementes maiores. A elevada ‘species strength’ destes dispersores reflete isso mesmo: uma grande dependência deles por parte das plantas com sementes maiores, já que estas aves são as únicas capazes de dispersar as suas sementes. O Tchin-tchin-txoló (*Ploceus sanctithomae*), a Camussela (*Ploceus grandis*) e o Pastro (*Onycognathus fulgidus*) já foram observados a consumir frutos e sementes, mas permanecem indicados apenas como potenciais dispersores, pois não foi possível comprovar que desempenhem esta função.

Dos nove dispersores de sementes encontrados neste estudo, seis estão ameaçados de extinção, segundo os critérios da IUCN. Este é um facto preocupante, uma vez que a extinção de qualquer um destes dispersores irá ter um impacto negativo na dispersão de sementes, com consequências desconhecidas para a estabilidade do ecossistema.

Apesar da importância da dispersão de sementes para a dinâmica florestal, muito pouco se sabe sobre esta função do ecossistema em São Tomé. Este é um trabalho pioneiro nesta área, na medida em que foram dados os primeiros passos para compreender como funciona esta importante função do ecossistema nesta ilha. No entanto ainda há muito por perceber. É preciso uniformizar a metodologia de amostragem e aplicá-la a todos os dispersores e também potenciais dispersores, estendendo a

amostragem no espaço e no tempo. É ainda necessário compreender a qualidade do tratamento que cada dispersor dá a cada espécie de planta, inibindo ou aumentando a sua taxa e velocidade de germinação. Para além das aves, focadas neste trabalho, outros grupos de animais terão certamente um papel relevante na dispersão de sementes, nomeadamente os invertebrados, os morcegos frugívoros e alguns dos mamíferos introduzidos, como a Lagaia (*Civettictis civetta*) e o Macaco (*Cercopithecus mona*). É também necessário avaliar até que ponto as espécies de plantas introduzidas se comportam como invasoras e de que forma competem com as nativas, diminuindo as suas probabilidades de recrutamento. Finalmente, o transporte das sementes, mesmo que viáveis, não se traduz necessariamente no recrutamento de novos indivíduos: a qualidade do local de deposição é um factor crucial no contributo das aves para a dinâmica populacional dessa planta, e no conjunto, para a dinâmica florestal.

Em resumo, esta tese fornece a primeira caracterização da rede de dispersão de sementes de São Tomé, abrindo as portas para um conhecimento mais detalhado e abrangente das interacções biológicas que sustêm as comunidades biológicas nestes ecossistemas.

Palavras chave: Dispersão de sementes; Endemismos insulares; Redes ecológicas; Pombos; Florestas de montanha; Speirops.

ABSTRACT

The island of São Tomé, in the Gulf of Guinea, is a biodiversity hotspot with a remarkable number of endemic species and unique forest ecosystems. Much of its biodiversity is currently threatened by the increasing human population and associated habitat change, which is simultaneously threatening ecosystem functions and services. Seed dispersal is one of such key ecosystem services, essential for forest regeneration. The goal of this work is to understand how forest birds are contributing to the dispersal of both native and introduced seeds in São Tomé, providing the first community-level assessment of species interactions in maintaining ecosystem functions in the island.

We collected droppings from mist netted birds and analysed the crop contents of hunted pigeons. All 18 sampled bird species were endemic and nine of them were dispersing seeds. The São Tomé Speirops played a central role as seed disperser. The seed dispersal network is dominated by native plant species, with only a few introduced species being dispersed in the forest. We corrected the frequency of occurrence of seeds in the droppings with independent estimates of bird abundance, and showed that this correction is key to understand disperser contribution to the overall network.

Birds are therefore playing a double role, facilitating the dispersal of introduced species but also spreading the native flora. These results highlight a difficult conservation dilemma, since birds might be simultaneously contributing to forest regeneration and to biological invasion.

Keywords: Seed dispersal; Island Endemism; Ecological Networks; Pigeons; Montane forests; Speirops.

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1. INTRODUCTION

There are about 7.4 billion people on Earth (World Population Data Sheet, 2016). Estimates suggest that up to half of the emerged land surface has already been transformed by human action (Vitousek *et al.*, 1997), while human population continues to grow at a steady pace and is projected to approach *ca.* 10 billion by 2050 (United Nations, 2015). This rapid human population growth is threatening natural ecosystems and biodiversity, through the overexploitation of natural resources, together with habitat loss and degradation, introduction of invasive alien species and climate change (Beumer and Martens, 2013; IUCN, 2016b). As a result of the combined action of all these threats, we are currently facing a biodiversity crisis, with species extinction rates exceeding the natural rate by up to a 1000 times (IUCN, 2016b). Almost 1000 species have been estimated to have been lost in the past 500 years, and about 17000 plant and animal species are currently threatened with extinction (IUCN, 2016b). More worryingly, species diversity ensures ecosystem stability and resilience, providing humans with vital ecosystem functions and services that ultimately sustain human populations (Oliver *et al.*, 2015). It is thus urgent to understand how biodiversity loss affects the resilience of biological communities and the services we derive from them.

Ecological networks provide great tools to explore the relationship between the structure and functioning of biological communities. They are used to quantify the highly complex interactions within ecosystems, allowing to evaluate patterns of energy flow, detect indirect interactions, identify keystone species and simulate the consequences of extinctions. Through network analysis it is possible to characterize and compare emergent patterns between different communities. Furthermore, these studies are useful to access changes in mutualistic networks following the introduction of alien species (Henneman and Memmott, 2001; Memmott and Waser, 2002; Bartomeus *et al.*, 2008), and are essential to monitor ecological restoration and guide further conservation effort (Forup *et al.*, 2008).

One of such mutualisms is the function of seed dispersal, essential for vegetation dynamics and forest regeneration (Traveset *et al.*, 2014). Seeds are frequently the only mobile stage in a plant's life cycle and their dispersal allows the colonization of new sites and increases the success of plant recruitment by promoting the deposition of seeds in favourable micro-habitats (Connell, 1971; Janzen, 1971; Howe and Smallwood, 1982). There are several types of seed dispersal mechanisms, depending on the strategy of each plant species. Seeds may be dispersed by abiotic vectors, like water (hydrochory), or wind (anemochory), rely on intrinsic plant mechanisms such as "explosive" structures (balistochory), or on mutualisms with animal dispersers (zoochory; Traveset and Rodríguez-Pérez, 2008). Some plants may even rely on several of these mechanisms and others do not have any specialized dispersal strategy. Regarding zoochory, reptiles, birds and mammals are the major dispersal agents, although fish, ants and other invertebrates may also be relevant dispersers for some species. Regarding biotic dispersal, seeds may be transported externally by adhesion on animal's fur, hairs or skin (exozoochory), or internally in the animal's digestive tract after ingestion of nutritious fleshy fruits (endozoochory). When a particular seed is dispersed by two or more dispersal vectors, this is called diplochory or secondary seed dispersal (Vander Wall ans Longland 2004; Nogales *et al.*, 2007).

In the tropics, most tree and shrub species (>90%) developed fleshy fruits adapted to internal animal dispersal (Frankie *et al.*, 1974; Opler *et al.*, 1980; Howe and Smallwood, 1982), relying on mutualistic interactions with frugivorous vertebrates for the dispersal of their seeds (Terborgh *et al.*, 1990). Animals are particularly good dispersers, as they can considerably increase the dispersal distance (Traveset and Rodríguez-Pérez, 2008), enhance seed germination by the treatment offered to digested seeds - scarification (Verdú and Traveset, 2004), transport seeds to particularly favourable recruitment sites such as forest openings – direct dispersal (Wenny and Levey, 1998), and provide the seed with a highly favourable micro-site for germination – faeces (Sánchez de la Vega and Godínez-Alvarez, 2010).

However, not all dispersed seeds will germinate and result in recruitment. The net contribution of a disperser to plant fitness is known as seed dispersal effectiveness, and depends on both the quantity of seeds dispersed (number of visits made to the plant by a disperser and number of seeds dispersed per visit) and the quality of the treatment offered by the disperser (quality of digestive treatment and the quality of seed deposition; Schupp 1993, Schupp *et al.* 2010). Disperses differ considerably in their effectiveness (Côrtes *et al.*, 2009; McKey, 1975; Howe and Estabrook, 1977; Snow, 1981; Wheelwright and Orians 1982; Levey, 1987). For example, larger birds often have greater gut retention times, which increases both the potential for long distance dispersal (Levey 1987) and seed scarification (Traveset *et al.*, 2001). However, greater seed retention times can also increase seed mortality on some plant species, resulting in lower germination (Murray *et al.*, 1994). Therefore, the diversity of dispersers moving the seeds of a specific plant can be a very important adaptive strategy to spread germination events both in time and in space, increasing the likelihood at least some seeds will successfully recruit into the next generation (More, 2001; Traveset *et al.*, 2001).

The loss or decrease of key frugivores that contribute to seed dispersal may lead to the disruption of this important ecosystem function (Bond and Slingsby, 1984; Böhning-Gaese *et al.*, 1999; Traveset and Richardson, 2006), changing the abundance of plant populations and their extinction probability (Bond, 1995). In the long term, it can alter the structure and dynamics of forest ecosystems (Bleher and Böhning-Gaese, 2001) and compromise the stability of the whole ecosystem (Lawton and Brown, 1993; Traveset and Rodríguez-Pérez, 2008; Blüthgen and Klein, 2011).

The disruptive effects of biodiversity loss are particularly alarming on the simplified ecosystems of oceanic islands, where much of the world's threatened biodiversity is concentrated. Despite comprising only *ca.* 5% of the Earth's emerged land surface, over 15% of all plant and animal species are restricted to islands (Fernández-Palacios, 2010; Whittaker and Fernández-Palacios, 2007). Islands are especially vulnerable to species extinction due to the low species redundancy (Kaiser-bunbury *et al.*, 2010b), and also especially vulnerable to invasions due to their evolution in the absence of strong competition (Whittaker and Fernández-Palacios, 2007; Traveset *et al.*, 2016). It is no surprise that the majority of recorded extinctions (80%) occurred on islands (Groombridge, 1992). Animals are the most affected: there have been 116 insular bird species extinct since 1500 (de Lima, 2012). Although islands plants have suffered comparatively less (Sax *et al.*, 2002), in some places they are under a lot of pressure, i.e. 50% of the plant species are at risk of extinction in Hawaii (Sakai *et al.*, 2002) and 82% in Mauritius (Kaiser-bunbury *et al.*, 2010b).

In oceanic islands, where terrestrial mammals are nearly always absent due to the filtering effect of the ocean to colonization (Whittaker and Fernandez-Palacios, 2007), birds and reptiles tend to be the most important or even the only relevant seed dispersers (Whittaker and Fernández-Palacios, 2007; Valido and Olesen, 2007; Traveset *et al.,* 2014), as they are both highly mobile and incorporate a large fraction of fruits into their diets. Within island birds, columbid and passerine frugivores are the most frequent seed dispersers (Kaiser-bunbury *et al.*, 2010b). Although some specific interactions may exist, most mutualisms are formed between generalist species, meaning that each plant tends to be dispersed by a variety of dispersers, and that each disperser tends to feed on several plant species (Cox *et al.*, 1991; Meehan *et al.*, 2002). This characteristic confers resilience against species extinctions

(Kaiser-bunbury *et al.*, 2010a, Lever *et al.*, 2014), but also facilitates the invasion by introduced plants and animals (Richardson *et al.*, 2000).

Biological invasions are indeed a key threat to island ecosystems (Millennium ecosystem assessment, 2005). The disruption of seed dispersal through biodiversity loss and biological invasions has been recorded in a number of island systems, such as Tonga (Meehan *et al.*, 2002; McConkey and Drake, 2006), Mauritius (Baider and Florens, 2006; Hansen *et al.*, 2008), Pitcairn Island (Kingston and Waldren, 2005, the Balearic islands (Traveset and Riera, 2005), the Canary islands (Nogales *et al.* 2005; López-Darias and Nogales, 2008) and Hawaii (Chimera and Drake, 2010), but even the most basic information is missing from many island systems worldwide, including the Gulf of Guinea islands.

The island of São Tomé is part of the Gulf of Guinea island system. There are three major ecological regions: montane, at higher altitudes; south, which includes the lowlands with high rainfall; and north, which includes the dry lowlands, all with tropical climate. Millions of years of isolation, together with the proximity to the biodiversity-rich Congo rainforests and an extremely diverse mosaic of landscapes, led to the evolution of an exceptional number of endemic species, throughout all taxonomic groups (Melo and Ryan, 2012). The island hosts more than 1000 species of plants, about 100 of which are endemic. Families such as the Orchidaceae, Rubiaceae, Euphorbiaceae, Melastomataceae and Begoniaceae are represented by multiple species, a high percentage of which are endemics (Figueiredo *et al.*, 2011). Animals also present a high number of endemic species, with birds standing out. In fact, São Tomé holds the world's highest density of endemic birds (Melo, 2007).

São Tomé is also suffering with current biodiversity crisis. 31 of its plant species are listed as threatened, a relatively small number considering the high diversity of plants in the island. However, the threat status for many of its plant species remains unassessed, lacking crucial information on abundance, distribution and reproduction. Animals have been better studied, and almost all of its endemic bird species have been assessed for the IUCN red list. 45 % of São Tomé's endemic birds are threatened of extinction (IUCN, 2016a), which is alarming at all accounts, and particularly in that we know nearly nothing about their functional importance in these ecosystems, including as potential seed dispersers.

Even though the island has only been occupied by humans since the 16th century, rapid population growth has caused severe habitat changes, mostly due to overexploitation of forest resources and deforestation (de Lima *et al.*, 2013; Jones and Tye, 2006). Some original old-growth forests have been able to persist only in the most remote parts of the island, most of which are included in the recently established Obô Natural Park (Albuquerque and Cesarini, 2009). These forests are surrounded by secondary forest, deriving from old abandoned crops, which in turn have agricultural field in the proximities (de Lima *et al.*, 2013).

1.1. AIMS

The main goal of this thesis is to gain a better understanding of the role of birds as dispersers of native and introduced seeds in the forests of São Tomé. To do so, we implement a network approach that will allow evaluating the contribution of each bird species as a disperser for each plant species, while simultaneously detecting patterns at the level of pairwise species interactions and evaluate emergent community-level patterns. We have three specific objectives:

1) Evaluate the structure of seed dispersal networks by montane forest understorey birds, comparing interaction patterns in old-growth and secondary forest;
2) Evaluate the specific contribution of pigeons species as potential seed dispersers across the whole island;
3) Characterize overall bird seed dispersal network in São Tomé montane forests.

This work will contribute towards a better understanding of bird-plant interactions in São Tomé. We will discuss potential implications to forest dynamics, identifying the most relevant dispersers, thereby contributing to inform long-term conservation strategies for these important ecosystems.

2. METHODS

2.1. STUDY SITE

São Tomé is an 857 km² oceanic island located in the Gulf of Guinea, central Africa. It belongs to the Democratic Republic of São Tomé and Príncipe. The island is part of the Cameroon volcanic line, with its oldest emerged land surface dated 13 MY old (Lee *et al.*, 1994).

São Tomé has a rugged terrain, reaching 2,024 m above the sea level (a.s.l.). The mountains intercept the prevailing southwest winds, causing high precipitation in the south and a rain shadow in the north. This originates a steep rainfall gradient across the island, from over 7,000 mm in the southwest to less than 700 mm in the northeast (Bredero *et al.,* 1977). Despite its proximity to the equator, it is possible to distinguish two main seasons in São Tomé: the dry season (gravana), between June and August, and a rainy season, from September to May. There is also a smaller dry season (gravanito), in December and January. The average temperature is fairly constant, decreasing with rainfall, altitude and in the dry season.

Three main ecological regions can be distinguished: (1) montane, between 800 and 1,400 m a.s.l., (2) north, up to 800 m a.s.l. and less than 2,000 mm of annual rainfall, and (3) south, up to 800 m a.s.l. and more than 2,000 mm of annual rainfall (Fig. 2.1; Exell, 1944; de Lima *et al.*, 2013).

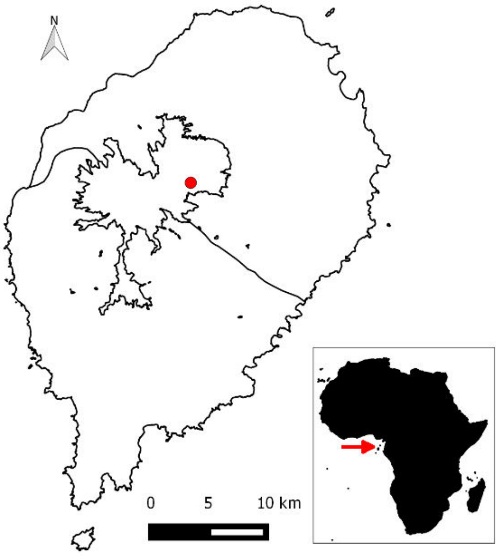

FIGURE 2.1 – Map of São Tomé Island. The red arrow in the inset indicates the location of São Tomé, in relation to mainland Africa. The red dot in the main figure shows the location of Macambrará, the main field site, along with the main ecological regions of the island: montane (centre), north and south (adapted from de Lima *et al*., 2013).

This study focused in the montane forest, where temperatures can reach 30ºC but, unlike what happens in the lowlands, they can also drop below 15ºC (Carvalho *et al*., 2004). Humidity and cloud cover are high throughout the year. The two major forest ecosystems in the montane region are old-growth and secondary forests. The old-growth forest, locally known as *obô*, is rich in endemic species and has a dense canopy, with many trees exceeding 30 m of height and emergent trees surpassing 50 m. Lianas are abundant, as are epiphytic plants like mosses, ferns and orchids (Monod, 1960; Figueiredo *et al*., 2011). This forests remained very little disturbed until late 19th century, when significant areas were cleared to plant coffee, cocoa and quinine. Subsequent agricultural abandonment, as well as logging, led to the development of secondary forests, locally known as *capoeira* (Tenreiro, 1961). These have a higher proportion of introduced species, a lower canopy, less biomass, and a denser understorey when compared to native forests (Monod, 1960; Figueiredo *et al*., 2011). There is also another forested ecosystem, not considered in this study, known as shaded plantation, in which cocoa or coffee are grown, shaded by large tree species such as the introduced coral trees *Erythina* sp. and breadfruit trees *Artocarpus altilis* (Diniz *et al*., 2002; de Lima *et al*., 2014).

2.2. DATA COLLECTION

2.2.1. SEED DISPERSAL BY MONTANE FOREST UNDERSTOREY BIRDS

The study took place in the forests near Macambrará, at approximately 1,300 m a.s.l. (Fig. 2.1 and Fig. 2.2). Their location and configuration offer ideal conditions for this work, with a relatively accessible and extensive block of old-growth forest surrounded by secondary forest. Data was collected from two 0.5 ha plots in each of these forest types (Fig. 2.2), between October and November 2015.

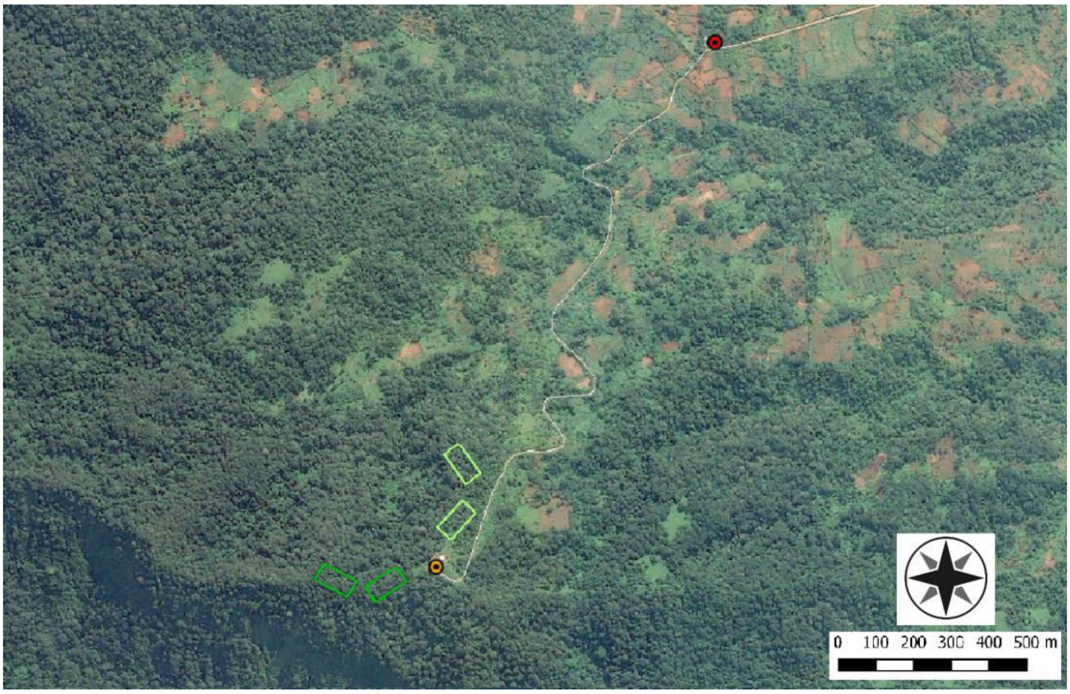

FIGURE 2.2 – Location of sampling plots, at Macambrará. The four 0.5 ha plots are coloured in green (dark green: old-growth forest; light green: secondary forest). Yellow dot indicates the base camp at the radio antenna (0º16’33’’N 6º36’19’’E), accessible through the road to the Botanical Garden of Bom Sucesso (Red dot). In the figure it is visible the agricultural areas surrounded by secondary forests (*capoeira*) and some less accessible areas with well preserved forest (old-growth forest: *obô*).

Seed dispersal was assessed by detecting intact seeds in the droppings of mist netted birds. Birds were captured using mist nets operated at ground level, opened before sunrise and left opened while climate conditions were favourable (i.e. no heavy rain, wind or fog). Effort in each plot was standardized to 3,000 hours x meter. Captured birds were identified to the species level (Jones and Tye, 2006) and left for up to 1 h in a disposable paper bag. Fecal samples collected from the bags were analyzed under a dissecting microscope and all intact seeds were extracted. These seeds were then identified to the species level using a seed reference collection. This collection was constructed with seeds from ripe fruits gathered in the study area. The seeds were extracted, cleaned, dried at room temperature, photographed, identified to the species level following Figueiredo *et al.* (2011) and stored. Unidentified seeds were further compared with specimens of the herbaria collections of the Tropical Research Institute (LISC) and the University of Coimbra (COI).

The frequency of frugivorous visits is often considered the best predictor of dispersal ability of a given vertebrate (Schupp, 1993, Vázquez *et al*., 2005). Hence, we quantified interaction frequency as the number of droppings from each bird species containing at least one intact seed of each plant species (frequency of occurrence, see Heleno *et al*., 2013b; Correia *et al*. 2016).

To assess the completeness of the sampling effort, we calculated the proportion of detected species in relation to those estimated to occur in the study area, using sample-based rarefaction curves (Gotelli and Colwell, 2001) and the Chao estimator (Chao, 1987), via function *specpool* from the package *vegan* (Oksanen *et al*., 2016) for R 3.2.5 (R core team, 2016).

2.2.2. PIGEON SEED DISPERSAL

Seed dispersal by pigeons was assessed through the analysis of crop contents of hunted pigeons, captured across the island between 2011 and 2013 (Palmeirim *et al.*, 2013). Every two weeks, birds were obtained from local hunters and their crop content analyzed. These animals had been killed for commercial purposes and were subsequently sold to restaurants, to avoid creating an incentive for hunting.

We considered a seed dispersal interaction only when intact seeds were present in the crop, although leaves, flowers and pulp were also detected. We used the presence of intact seeds in the crops as a proxy for seed dispersal, even if we could not confirm if all seeds remained viable until defecated. Interaction frequency was quantified as the number of crops from each pigeon species containing at least one intact seed of each plant species (frequency of occurrence, see Heleno *et al.*, 2013b; Correia *et al.*, 2016).

2.2.3. MONTANE FOREST SEED DISPERSAL NETWORK

To assess the overall seed dispersal network in montane forests, we merged the data from the understorey birds mist netted at Macambrará with that of the pigeons hunted in montane forest. This allows for a better understanding of the whole bird seed dispersal network, since pigeons tend to use the tree canopy and were not captured in the mist nets.

In this analysis we used abundance-corrected interaction frequency, to incorporate the two datasets as a way to avoid potential biases arising from different species' capture likelihood associated with the different sampling techniques (Heleno *et al.*, 2013b). For each species, we divided the abovementioned interaction frequencies by the number of captured individuals, and then multiplied it by their relative abundance in montane forest. Relative abundance was extracted from a previous independent study (de Lima *et al.*, 2013), obtained through point counts in old-growth and secondary forests in montane region.

2.3. NETWORK ANALYSES

The obtained interactions were compiled into bipartite interaction matrices, quantifying all the recorded interactions between each seed species and their respective disperser species. These matrices were then used to visualize seed dispersal networks by representing disperser birds in the higher level and dispersed plants in the lower level (Fig. 2.3; Jordano *et al.,* 2003; Heleno et *al*., 2013a). In these networks, the relative importance of each pairwise interaction, between a plant species and a bird species, is weighed by their interaction frequency.

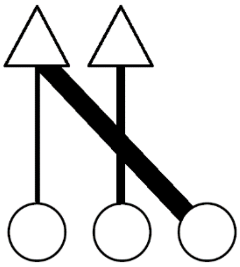

FIGURE 2.3 - Visualization of a theoretical seed dispersal network where nodes are bird species (top) represented by triangles and plant species (bottom) represented by circles. Lines connecting plants and animals reflect their pairwise interactions and the width of lines is proportional to the relative frequency of each interaction, i.e. the number of droppings of bird *i* containing seeds of plant *j*.

The emerging structure of the interactions between animals and plants can be described by several metrics that reflect different attributes of the network. These metrics can be divided into two main groups: those that describe emergent properties of the whole network, network-level descriptors, and those that describe properties of each interaction node, species-level descriptors (Dormann *et al.*, 2008). To evaluate how each plant and bird species integrate into seed dispersal networks, we calculated three key species-level descriptors: (1) disperser linkage level, which is the number of seed species dispersed by each bird species; (2) disperser species strength, reflecting the importance of each disperser species to the whole plant community, and mathematically defined as the sum of all the dependencies of the plants relying on each animal (Bascompte *et al.*, 2006); (3) disperser specialization (d'), a selectivity index reflecting the deviation of the observed interaction frequencies of each species regarding a random selection of partners, where resources (i.e. plants) are used in proportion to their availability (Blüthgen *et al.*, 2006). Species level descriptors were calculated using package *bipartite* 1.16 (Dormann *et al.*, 2008) for R 3.2.5 (R core team, 2016).

3. RESULTS

3.1. SEED DISPERSAL BY MONTANE FOREST UNDERSTOREY BIRDS

During 21 sampling days, we captured 743 birds of 15 species, including 148 recaptures, all of which were endemic to the Gulf of Guinea (Table 7.1 – Supplementary information). These birds produced 228 droppings with entire seeds (Table 7.2 - Supplementary information). A total of 4828 intact seeds from 43 plant species was retrieved, corresponding to 433 dispersal events (i.e. occurrences of seed species in droppings) by six disperser species (Fig. 3.1).

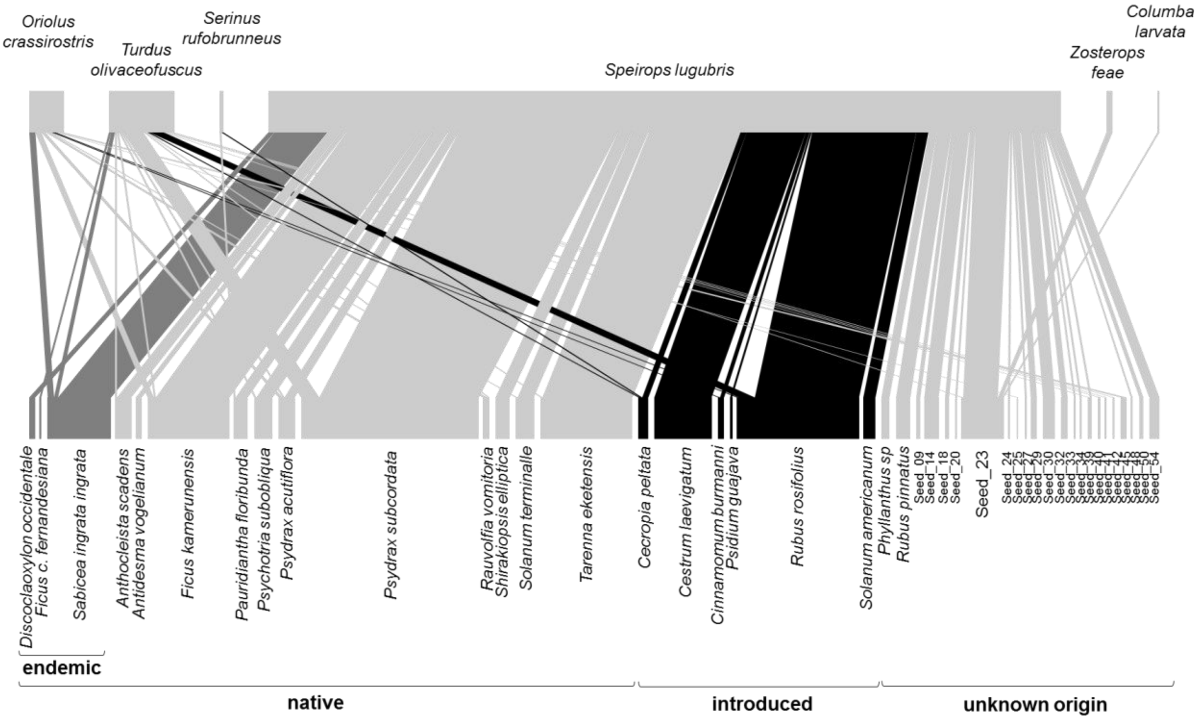

FIGURE 3.1 - Visualization of the seed dispersal network by understorey birds of São Tomé montane forests. Upper boxes represent bird species whereas lower boxes represent plant species. The width of the lines connecting two species is proportional to the interaction frequency between each bird and plant species. Introduced plant species are coloured in black and endemic in dark grey. All dispersers are endemic.

Speirops lugubris was, by far, the most frequent disperser. It was responsible for 88% of the interaction frequency, dispersing 4274 intact seeds of 36 species, and producing 84% of all droppings with seeds (Table 7.2 - Supplementary information). *Turdus olivaceofuscus* and *Oriolus crassirostris*, contributed respectively with 9% and 5% of all droppings with seeds, and dispersed 16 and nine plant species, respectively. The remaining three dispersers were *Zosterops feae*, *Serinus rufobunneus* and *Columba larvata*, together responsible for only 2% of the droppings with seeds.

Among the 43 plant species dispersed, 14 were native (59% of interaction frequency), including three endemics (8% of interaction frequency), six were introduced (23% of interaction frequency), and 23 were of unknown origin (18% of interaction frequency), either because they could not be identified or because it is not clear if they are native or introduced (Table 7.3 - Supplementary information).

The most commonly dispersed species is the native tree *Psydrax subcordata* (Rubiaceae; 263 seeds present in 85 droppings), followed by the invasive shrub *Rubus rosifolius* (Rosaceae; 1929 seeds in 58 droppings; Table 7.3 - Supplementary information). Together with *Tarenna eketensis* (Rubiaceae), *Ficus kamerunensis* (Moraceae), *Sabicea ingrata* (Rubiaceae), *Cestrum laevigatum* (Solanaceae) and one unidentified seed (morphotype Seed_23), they represent about 70% of the interaction frequency.

Species accumulation curves estimated that our sampling captured 71% of the total bird species present in the region (captured species=15; Chao estimator=20.7). Similarly, sampling completeness of seeds was estimated at 65% (observed species=43; Chao estimator=66.3; Fig. 7.1 - Supplementary information).

The seed dispersal networks reconstructed for the old-growth forest (*obô*) and secondary forests (*capoeira*) were remarkably similar (Fig. 3.2). Both had the same number of dispersed plant species (33 species), and only one extra disperser in the secondary forest (*C. larvata*). Overall, the seed dispersal network was slightly larger in the secondary forests, including more interactions (250 *vs* 183 interactions). A significant proportion of the seed species retrieved could not be identified (interaction frequency of 51% in old-growth forest and 39% in secondary forest). Based on those that could, old-growth forest had slightly fewer introduced species (25% of identified species; n=4) than secondary forests (30% of identified species; n=6).

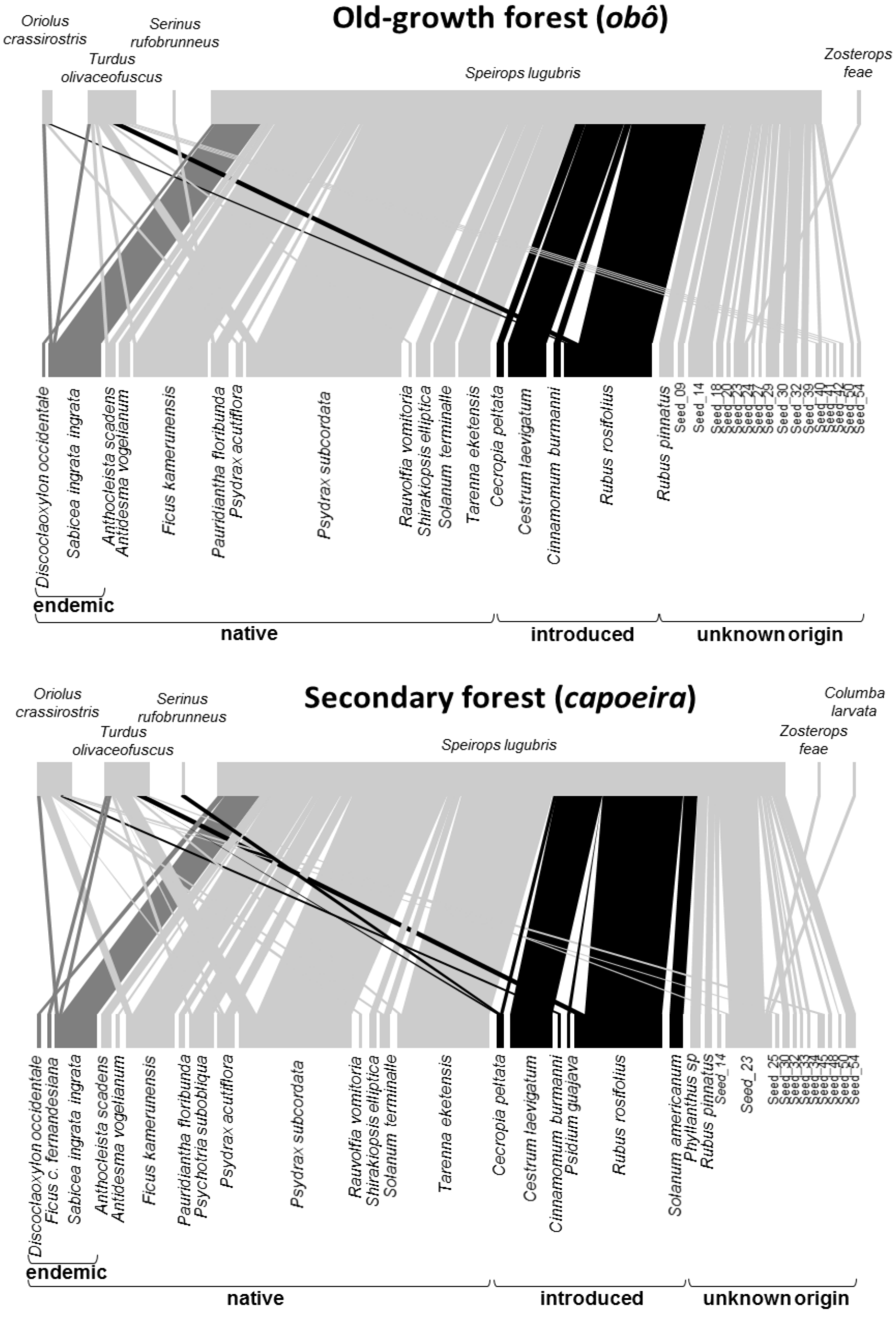

FIGURE 3.2 - Visualization of the seed dispersal network by understorey birds of São Tomé's main montane habitats: old-growth forest (*obô*) and secondary forest (*capoeira*). Upper boxes represent bird species whereas lower boxes represent plant species. The width of lines is proportional to the interaction frequency between each bird and plant species. Introduced species are coloured in black and endemic in dark grey. All dispersers are endemic.

3.2. PIGEON SEED DISPERSAL

Overall, 1077 crops from three pigeon species (*Columba malherbii, C. thomensis* and *Treron sanctithomae*) were collected by local hunters and inspected for seeds (Table 7.4 - Supplementary information). Among these, 58% (n=620) contained seeds corresponding to a total of 778 dispersal events, between the three disperser species and 46 dispersed plant species (Fig. 3.3).

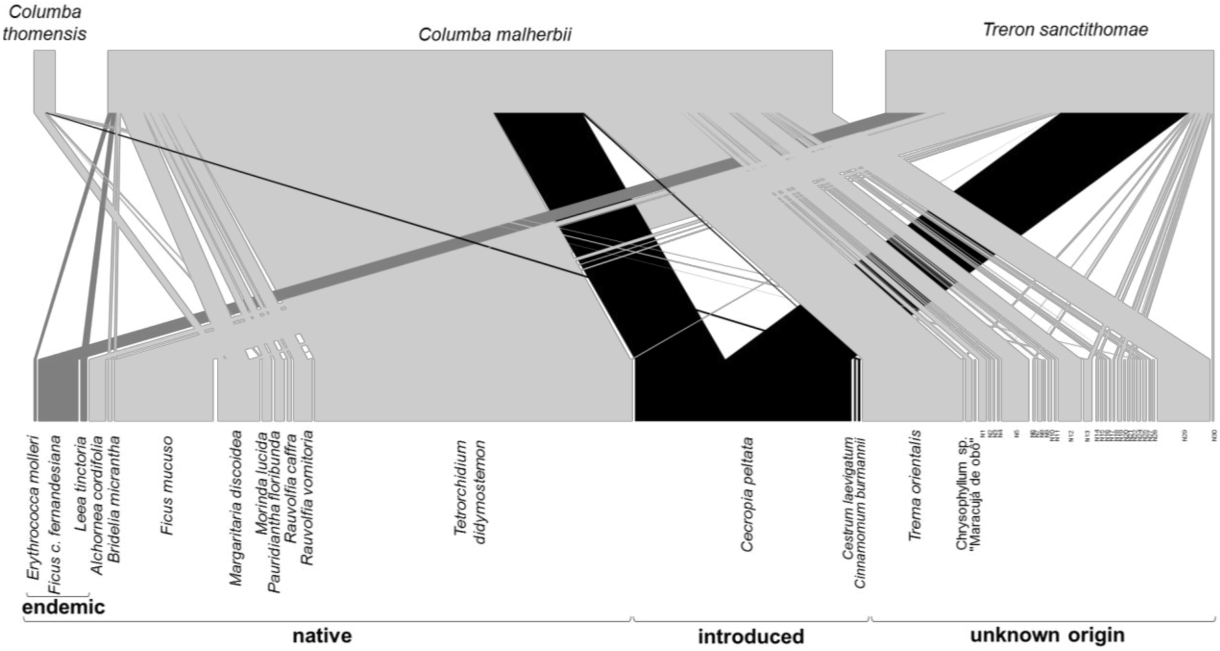

FIGURE 3.3 - Visualization of the São Tomé Island seed dispersal network of pigeons across the island. Upper boxes represent bird species whereas lower boxes represent plant species. The width of lines is proportional to the interaction frequency between each bird and plant species. Introduced species are coloured in black and endemic in dark grey. The three dispersers are endemic.

C. malherbii was the major contributor, with 64% of the dispersing individuals (n=395), followed by *T. sanctithomae*, with 34% of the dispersing individuals (n=212; Table 7.4 – Supplementary information). *C. thomensis* was captured less frequently (only 3% of the individuals), and therefore represented a small fraction of the crops with seeds (2%; n=13).

Out of the 46 plant species being dispersed, 12 are native (representing 53% of interaction frequency), including three endemics (4.5% of interaction frequency), three are introduced (21% of interaction frequency) and the remaining 31 are of unknown origin (26% of interaction frequency). The most commonly dispersed species is the native tree *Tetrorchidium didymostemon* (Euphorbiaceae; 230 crops; 30% of interaction frequency) followed by the introduced *Cecropia peltata* (Moraceae; 158 crops; 20% of interaction frequency; Table 7.5 - Supplementary information). Together with the native *Ficus mucoso* (Moraceae) and *Trema orientalis* (Ulmaceae; uncertain origin) they represent 69% of the interaction frequency.

3.3. MONTANE FOREST SEED DISPERSAL NETWORK

The overall montane seed dispersal network results from crossing the two previously described datasets, filtering for the pigeons captured in the montane region. We analyzed a total of 1020 individual birds from 18 species in the montane region, all endemic to the Gulf of Guinea (Table 3.1). From these we obtained 228 droppings (understorey birds) and 171 crops (pigeons) containing at least one entire seed, and quantified a total of 626 dispersal events between nine bird species and 58 plant species (Fig. 3.4).

TABLE 3.1 – Seed dispersal by bird species captured in montane forest. Species are ordered by decreasing number of captured birds. Relative abundance is extracted from de Lima *et al.* (2013). Interaction frequency is corrected for abundance. The percentages refer to the proportion of the total across all species.

Species	Relative abundance	Captured birds (%)	Crops or droppings with seeds (%)	Frequency of occurrence (%)	Corrected interaction frequency %	Dispersed plant species (%)
Speirops lugubris	211	261 (25.6)	192 (48.1)	381 (60.9)	74.1	36 (62.1)
Treron sanctithomae	17	240 (23.5)	149 (37.3)	166 (26.5)	2.8	15 (25.9)
Anabathmis newtoni	121	109 (10.7)	0	0	0	0
Turdus olivaceofuscus	51	86 (8.4)	20 (5.0)	31 (5.0)	4.4	16 (27.6)
Serinus rufobrunneus	54	82 (8.0)	2 (0.5)	2 (0.3)	0.3	2 (3.4)
Terpsiphone atrochalybeia	28	81 (7.9)	0	0	0	0
Prinia molleri	103	40 (3.9)	0	0	0	0
Ploceus sanctithomae	17	33 (3.2)	0	0	0	0
Columba malherbii	5	23 (2.3)	17 (4.3)	19 (3.0)	1.0	8 (13.8)
Dreptes thomensis	1	18 (1.8)	0	0	0	0
Columba thomensis	1	14 (1.4)	5 (1.3)	7 (1.1)	0.1	5 (8.6)
Oriolus crassirostris	29	13 (1.3)	11 (2.8)	17 (2.7)	9.1	9 (15.5)
Columba larvata	34	12 (1.2)	1 (0.3)	1 (0.2)	0.7	1 (1.7)
Zosterops feae	62	4 (0.4)	2 (0.5)	2 (0.3)	7.5	1 (1.7)
Otus hartlaubii	1	1 (0.1)	0	0	0	0
Zoonavena thomensis	2	1 (0.1)	0	0	0	0
Chrysococcyx cupreus	-	1 (0.1)	0	0	0	0
Onychognathus fulgidus	4	1 (0.1)	0	0	0	0
TOTAL		1020	399	626	100	58

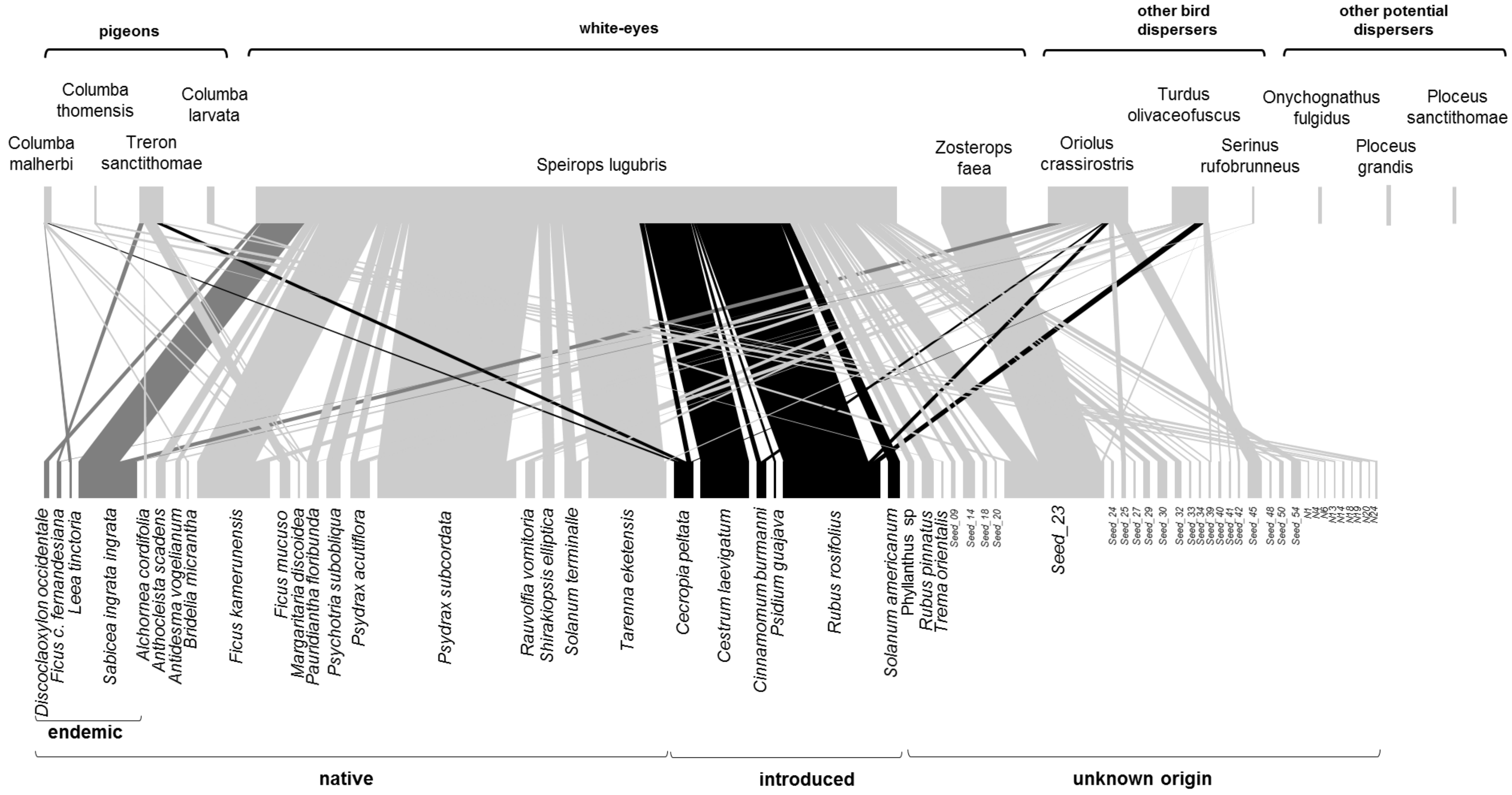

FIGURE 3.4 – Visualization of the montane forest bird seed dispersal network of the montane region. Upper boxes represent bird species whereas lower boxes represent plant species. The width of lines is the interaction frequency between each bird and plant species corrected for relative bird abundance. Potential dispersers have no interaction frequency, and where included only to allow a qualitative discussion of their potential importance. Introduced species are coloured in black and endemic in dark grey. All dispersers are endemic.

Speirops lugubris was responsible for most dispersal events (60.9% of the frequency of occurrence). Being the most abundant species in montane forest (Table 3.1), it represents 74% of the bird dispersal for the corrected network and has the highest species strength (Table 3.2). *Treron sanctithomae* was responsible for 26% of the frequency of occurrence and had the second highest species strength (Table 3.2). However, due to its low abundance (Table 3.1), it had a relatively small contribution for bird dispersal in the corrected network (2.8% of corrected interaction frequency).

TABLE 3.2 – Main species-level descriptors, characterizing the interaction patterns of the seed dispersers of the montane forests of São Tomé: (1) disperser linkage level is the number of plant species dispersed by each disperser; (2) disperser species strength reflects the relative importance of each disperser to the whole plant community (Bascompte *et al.*, 2006); (3) disperser specialization (d') is a measure of the selectivity of dispersers taking into account plant availability (Blüthgen *et al.*, 2006).

Species	English name	Linkage level	Species strength	specialization (d')
Speirops lugubris	São Tomé Speirops	36	31.7	1
Treron sanctithomae	São Tomé Green Pigeon	14	9.0	1.4
Turdus olivaceofuscus	São Tomé Thrush	16	4.4	1.1
Serinus rufobrunneus thomensis	Príncipe Seedeater	2	0.2	1.4
Columba malherbii	Bronze-naped Pigeon	8	5.3	1.5
Columba thomensis	Marron Pigeon	5	2.0	1.5
Oriolus crassirostris	São Tomé Oriole	9	4.7	1.6
Columba larvata simplex	Lemon Dove	1	0.1	1.6
Zosterops feae	Príncipe White Eye	1	0.7	1.6

Out of the 58 plant species being dispersed, 19 are native (55% of corrected interaction frequency), including four endemics (8% of corrected interaction frequency), six are introduced (21% of corrected interaction frequency), and 33 are of unknown origin (24% of corrected interaction frequency). The most dispersed species is the native tree *Psydrax subcordata* (16% of corrected interaction frequency), followed by the unidentified Seed_23 (11% of corrected interaction frequency) and the introduced shrub *Rubus rosifolius* (11% of corrected interaction frequency; Table 7.6 - Supplementary information). Together with *Tarenna eketensis*, *Ficus kamerunensis*, *Sabicea ingrata* and *Cestrum laevigatum* they represent 68.5% of the corrected network.

4. DISCUSSION

This work revealed that, out of 18 bird species analyzed, at least nine disperse entire seeds. For six of these bird species, it is the first time they are described as seed dispersers. All birds captured during this study are endemic to the Gulf of Guinea islands. Since oceanic islands have relatively low animal diversity, plants tend to rely on a reduced number of seed dispersers (Kaiser-Bunbury *et al.*, 2010b). Nevertheless, the proportion of birds involved in seed dispersal is considerably lower than that reported for other oceanic islands. For example in the Azores 7 out of 9 common forest birds species disperse seeds (Heleno *et al.,* 2013b) and in the Galápagos 15 out of 18 sampled bird species also produced droppings with seeds (Heleno *et al.,* 2013a). The low involvement of birds in the seed dispersal of São Tomé's flora may be explained by the island's wide resource availability, which may have allowed birds to retain their ancestrors' broad feeding niche.

33 seed morphotypes could not be identified (24% of total interaction frequency), reflecting the difficulty in assembling a comprehensive reference collection for the highly diverse montane forest of São Tomé. However, it is still clear that the seed dispersal in montane forests is dominated by native plant species (76% of identified species are native *vs* 24% that are introduced) revealing an overall positive conservation status of the dispersal networks. Regarding interaction frequency, native bird-plant interactions are definitely the most common (55% of total interaction frequency), whereas a smaller part are interactions between native birds and introduced plants (21% of total interaction frequency). Despite its apparent low involvement in the network, three of these introduced species are aggressive invaders (Global Invasive Species Database, 2016), highlighting the vulnerability of these ecosystems.

Seed dispersal by montane forest understorey birds

Species accumulation curves estimate that our sampling effort detected 71% of the bird species and 65% of the dispersed plant species in the study area. While some of these unsampled interactions likely correspond to "true absences", others are forbidden interactions that can never occur due to phenologically, spatial or morphologically mismatches between species (González-Varo and Traveset, 2016; Olesen *et al.*, 2011). Species interactions networks are inevitably incomplete representations of the reality (Heleno *et al.*, 2014), as rare interactions require highly intensive sampling (Olesen *et al.*, 2011). However, these rare interactions are likely less relevant from the community point of view, particularly as highly specialized seed dispersal interactions are rare (Bascompte *et al.*, 2003). Our sampling effort is higher than that of similar community level studies (e.g. Chacoff *et al.*, 2012) and, since the detection of both animal and plant species is clearly approaching an asymptote (Fig. 7.1), it is considered adequate to identify broad community patterns (Gonzales and Loiselle, in press; Costa *et al.*, 2016).

Most of the dispersal events (88% of interaction frequency) where promoted by a single bird species: the *Speirops lugubris*. Half of the dispersers captured belonged to this species, and a high percentage of them (74%; n=261) were transporting seeds. Although *Speirops lugubris* has been described as mainly insectivorous, it is known to feed also on fruits (Atkinson *et al.*, 1991). Its considerable body size (*ca.* 16.2g; n=261) allows the species to include a wider diversity of fruit in its diet than the other Zosteropidae in the island, the *Zosterops feae* (Melo *et al.*, 2011).

The native plant species dominate this network (70% of identified species; 60% of total interaction frequency), the native *Psydrax subcordata* being the most dispersed species. Three of the native species are endemic to the Gulf of Guinea, including the Near Threatened *Leea tinctoria* (Leeaceae) and the Vulnerable *Discoclaoxylon occidentale* (Euphorbiaceae; IUCN, 2016a). The conservation status for most of these species has not yet been evaluated or is in need of updating (IUCN, 2016a). The second plant species most commonly dispersed is the introduced *Rubus rosifolius*, representing 13% of interaction frequency. This is particularly worrying given that its high invasibility has made it an important weed in many islands, such as Saint Helena, New Caledonia, Reunion, Hawaii and French Polynesia (Meyer, 2004; Global Invasive Species Database, 2016).

Contrary to our expectations, the networks from old-growth and secondary montane forests were extremely similar (Fig. 3.2). This similarity suggests that this habitat border might not be as relevant for the movement of dispersers as initially perceived. Indeed, our results show that birds move between these forest types. During the course of this work we detected at least five individuals of *Serinus rufobrunneus* and three of *Speirops lugubris* moving between both forest types, likely contributing to the dissemination of seeds and most likely also to the dissipation of the habitat interface. Some non-disperser bird species were also detected moving between forest types, namely two *Anabathmis newtoni*, one *Dreptes thomensis* and one *Terpsiphone atrochalybeia*. As animals are responsible for several other ecosystem functions, such as nutrient cycling and pollination, it is likely that this blurred border also affects these and other functions.

Regarding the conservation of the São Tomé old-growth forests, these results are concerning as bird seed dispersal is likely to be promoting the transport of invasive introduced plant species. On the other hand, it also represents good news for the regeneration of native species in the disturbed forest patches, since the seed dispersal network is clearly dominated by native species. Due to logistic constraints, the four sampling sites were located next to each other and near the forest edge, being influenced by edge effects that might not be persistent further away from the habitat interface.

Seed dispersal by pigeons

While the seed dispersal potential of montane forests has been estimated by the presence of entire seeds in bird droppings, the importance of pigeons was estimated based on the presence of entire seeds in the crops of hunted animals. This means that these seeds would still have to pass through the entire digestive tract before being ejected by the bird, and could still be destroyed during that process (Traveset, 1998). Furthermore, some pigeon species contain muscular gizzards with grit, that destroy fruits and also most of the small seeds (Cowles and Goodwin, 1958). Although there is little information on São Tomé pigeons' biology, it is likely that pigeons are dispersing seeds, as at least some of those seeds are able to survive gut passage and germinate (Lambert, 1989). Importantly, those seeds that are defecated or regurgitated intact, are likely to be dispersed over long-distances, given that most pigeons are able to flight long distances, making them important and ubiquitous long distance dispersers (Corlett, 2009; Lambert, 1989).

Of the six species of pigeons (Family: *Columbidae*) present in the island of São Tomé, four are forest species: *Columba larvata*, *Treron sanctithomae*, *Columba thomensis* and *Columba malherbii*; Atkinson *et al.*, 1991; Dallimer *et al.*, 2009; de Lima, 2012). All of them are endemic to the Gulf of Guinea and the latter three species are regularly hunted for human consumption (Carvalho *et al.*, 2015). The high contribution of *Treron sanctithomae* and *Columba malherbii* stands out, while the *Columba thomensis* contributes poorly to the number and diversity of seeds dispersed (Fig. 3.3). The apparent low importance of *Columba thomensis* as a seed disperser is largely due to its lower abundance, as its population is declining fast due to hunting pressure (Atkinson *et al.*, 1991; Carvalho *et al.*, 2015). This is a frugivorous species (Atkinson *et al.*, 1991; Jones and Tye, 2006) with twice the weight of the second largest pigeon species in São Tomé (*Columba thomensis* mass=415 g, n=1, *vs. Treron sanctithomae* mass=206 g, n=4; Martim Melo, pers. comm.), presenting a large potential for seed dispersal and namely for specialized dispersal of larger seeds.

The plant most commonly found from pigeon crops is the native tree *Tetrorchidium didymostemon*. While the vast majority of the seeds dispersed by pigeons are native (80% of the identified species;

53% of total interaction frequency), three are introduced species, one of which, *Cecropia peltata,* represents 20% of the whole pigeons' network (Fig. 3.3). This species is highly invasive, listed in the 100 World's Worst Invasive Alien Species (Global Invasive Species Database, 2016), and pigeons are likely facilitating its spread into the old-growth forest.

Several biases are likely to affect the current estimates of pigeons' contribute to seed dispersal, requiring caution in the interpretation of these results. First, hunters tend to explore accessible secondary forests and hunt under popular fruiting tree species, thus influencing the species of pigeon captured and the seeds present in their crops (Palmeirim *et al.*, 2013). Secondly, the circumstances of death, particularly, the time of the day and birds activity, are likely to affect the diversity and the abundance of seeds found in the crops, and these are also affected by how these samples were obtained.

Overall seed dispersal in montane forests

Seed dispersal in the montane forests of São Tomé is exclusively sustained by birds endemic to the Gulf of Guinea. In this sense this is the "most endemic" seed dispersal network ever described, highlighting the urgency to understand how this important function has been structured by natural selection in isolation, before it gets significantly disturbed. *Speirops lugubris* is, at least quantitatively, the most important seed disperser in the montane forests of São Tomé. This importance results not only from its high abundance, but also from the high frequency at which it consumes fruit and disperses seeds. Other confirmed dispersers, such as the *Zosterops feae*, *Serinus rufobrunneus*, *Turdus olivaceofuscus*, *Oriolus crassirostris* and *Columba larvata* are also present in relatively high abundances in montane forests forest (Dallimer *et al.*, 2009; de Lima *et al.*, 2013; Olmos and Turshak, 2010).

We also captured some bird species that are more characteristic of the high canopy, such as *Zosterops feae* (Melo *et al.*, 2011). Two out of the four individuals of this species contained intact seeds in their droppings, therefore, although they represent only a small fraction of the overall number of dispersed seeds, the potential importance of *Zosterops feae* becomes more evident when correcting interaction frequency for bird abundance. Although their feeding habits have been poorly studied, it was already known that they complement their mostly insectivorous diet with small fruits (Atkinson *et al.*, 1991; Jones and Tye, 2006; Leventis and Olmos, 2009). Other species were extensively sampled but produced a low number of intact seeds. Such was the case of *Serinus rufobrunneus*, for which only two birds produced intact seeds, out of the 82 individuals captured. This result suggests that *Serinus rufobrunneus* is mostly a seed predator, destroying most ingested seeds and only occasionally dispersing intact seeds, as it has been described for other frugivorous species (Heleno *et al.*, 2011; Williams and Karl, 1996).

Finally, in the case of pigeons, corrected interaction frequencies reduce their overall relevance in the seed dispersal network, comprising only 5% of corrected interaction frequency. This is mainly because most pigeons are not very common in the montane forest (de Lima *et al.*, 2013). The above results highlight the importance of correcting the frequency of occurrence of seeds in the droppings, by estimated species abundance. Although this correction is unanimously recognized to be very important in estimating real functional role of species, it is still rarely implemented, as it requires independent estimates of species abundances and their proportional contribution to overall bird abundance (Heleno *et al.* 2013b).

On average each pigeon only transported one type of seed in the crop (mean of the three pigeon species = 1.10 seeds per crop; n=171), suggesting that they are more restricted in each feeding than *Speirops lugubris*, which feeds on several species at a time (mean = 1.98 seeds per droppings; n=192). This is in line with field observations, where pigeons are usually observed spending intensive periods feeding on a single fruiting tree, whereas *Speirops lugubris* forages on the move (pers. obs.). However, some care must be taken when comparing crop and dropping content analyses, as some seeds might be destroyed during gut passage. It would therefore be expected to find more seeds in the crops, so the differences observed in our study between the amount of seeds in crops and droppings seem legitimate.

Importantly, most of the larger seeds found in the droppings, such as those of *Rauvolfia vomitoria* (10 mm) and some large unidentified seeds of similar size (8-10 mm), were dispersed by *Turdus olivaceofuscus* or *Oriolus crassirostris*, but not by the white-eyes (*Speirops lugubris* and *Zosterops feae*), which dispersed more that 60% of all plant species (including unidentified morphotypes). Most frugivores tend to swallow whole fruits and can only swallow fruits that are smaller than their maximum gape size, thus limiting birds' choices (Wheelwright, 1985; Zaret, 1980). It is known that larger birds tend to consume more species as they can include larger seeds in their diets (Wheelwright, 1985). In our networks, *Turdus olivaceofuscus* and *Oriolus crassirostris* have indeed greater gape size and can swallow larger fruits than the other most common dispersers, the white-eyes (*Oriolus crassirostris* gape=11.2 mm, n=12; *Turdus olivaceofuscus*=8.2 mm, n=155; *Speirops lugubris*=5.1 mm, n=329; *Zosterops feae*=4.0 mm, n=24; Martim Melo, pers. comm.). Therefore these two larger species have a complementary function regarding the smaller dispersers and their functional role for the dispersal of larger fruited species is particularly relevant. Although they disperse a relatively modest diversity of seeds, those that are dispersed by these larger birds, such as *Rauvolfia vomitoria* and the morphospecies Seed_25, Seed_40, Seed_41 and Seed_45 tend to rely heavily on them, and that is reflected in their relatively high species strength. Our results suggest the existence of a functional complementarity between these bird species of different sizes. Other groups of species, even amongst those with overall smaller contributions to overall seed dispersal, might perform additional complementary functions, as in the case of pigeons with long-distance dispersal. Therefore, the interpretation of the seed dispersal network should take into consideration not only the overall contribution of each animal, but also the level of functional complementarity between dispersers.

Three additional bird species might be relevant seed dispersers in the study area: *Onychognathus fulgidus*, *Ploceus sanctithomae*, and *Ploceus grandis* (represented in Fig. 3.4). These three species are known to incorporate some fruit in their diets (Jones and Tye, 2006) and can likely disperse some viable seeds in montane forests. Unfortunately they were captured in small numbers or not captured at all, making it difficult to evaluate their role in seed dispersal. *Onychognathus fulgidus*, for instance, was only captured once and was not carrying any seeds. This might be a particularly relevant disperser as it is known to swallow large seeds (Jones and Tye, 2006; Leventis and Olmos, 2009), and it has a large gape size (9.4 mm; Martim Melo, pers. comm.).

Three out of the nine seed dispersers in São Tomé are currently listed as threatened, and two others are classified as Near Threatened (IUCN, 2016a; Table 7.1 - Supplementary information). This is particularly worrying as we have found little functional redundancy among the few dispersers in São Tomé, indicating that the loss of any of these threatened dispersers could cause a substantial loss in seed dispersal service available to plants, with unknown consequences for ecosystem stability. Fortunately, so far no extinction has been recorded in São Tomé, and important conservation work is currently in place to prevent species loss. On a positive note, the main seed disperser in montane forest, *Speirops lugubris*, is not threatened, ensuring the regeneration of a great part of the plant species in a context of species extinction.

Future avenues of research

Seed dispersal is critical for long term vegetation dynamics, however very little is known about the structure, the function or the conservation status of seed dispersal interactions in São Tomé, a place that has been systematically identified as a global priority for conservation, due to the high number of endemic species. Our work constitutes an important first step to understand animal seed dispersal in São Tomé, but there are several important knowledge gaps that should be addressed in the future in order to provide a more comprehensive picture of this important ecosystem function.

Future studies should try to elucidate the relative importance of bird seed dispersal to forest dynamics, by improving our understanding about the contrasting effects of native and introduced plant dissemination. Namely they should try to assess the role of species that were undersampled, the distance at which birds can disperse seeds and the differences in seasonality. Furthermore, bird seed dispersal should be quantified in a wider variety of ecosystems across the island, sampling core areas to exclude edge effects.

Our work has focused on seed dispersal by birds. Birds are among the most important disperser groups, particularly on islands due to the absence of large mammals (Traveset *et al.*, 2014; Whittaker and Fernández-Palacios, 2007). Nevertheless, seed dispersal in São Tomé is certainly not entirely restricted to birds. Other potentially important seed dispersers include native fruit bats, at least one of them able to eject viable seeds (Ana Rainho, pers. comm.), ants and other invertebrates. More importantly, introduced mammals, such as the feral pig (*Sus scrofa*) and the monkey (*Cercopithecus mona*), are also likely to consume fruits and disperse their seeds. Most of these species are common in São Tomé forests and it is critical to understand how their role as seed dispersers can affect natural plant recruitment patterns.

Although quantitatively less frequent than primary dispersal, there is also the potential for secondary seed dispersal in São Tomé. This process is known to be ecologically relevant in the Canaries, as a mechanism of transport of seeds to favourable microhabitats, and increasing substantially the dispersal distance (Nogales *et al.*, 2002; 2007). In São Tomé *Milvus migrans parasitus*, which occasionally feeds on lizards, birds, bats or other animal carcasses (Jones and Tye, 2006), may potentially act as a secondary dispersal agent for the seeds in their prey's guts (Vander Wall and Longland, 2004). Other predators such as nocturnal birds of prey, snakes and the introduced feral cat (*Felix catus*), weasel (*Mustela nivalis*) and african civet (*Civettictis civetta*) may also act as secondary seed dispersers, to a lesser extent.

We detected birds dispersing three widely recognized invasive species: *Cecropia peltata*, *Rubus rosifolius* and *Psidium guajava*. Although there is no published information on the invasiveness of these species in São Tomé, their invasive behavior elsewhere, together with the fact that they have successfully been incorporated in birds feeding habits, is enough to raise concern. As both native and introduced plants are being dispersed throughout the forest, it is likely that they will arrive simultaneously to a forest gap. While most tropical species are gap-dependent, requiring high levels of light to reproduce and grow (Denslow, 1987), introduced species, particularly invasive ones, usually respond better to canopy opening, as they have higher spread and population growth rates (Sakai *et al.*, 2001). Invasive species may thus outcompete natives when the forest is cleared, displacing and eliminating them, with implications for the functioning of the ecosystem (Simberloff, 2013). However, not all introduced species become invasive: in the Seychelles, for example, no more than 6 to 12% of exotic shrubs and trees are considered invasive (Rocamora and Henriette, 2015). It is not clear if the other three introduced species, *Cestrum laevigatum*, *Cinnamomum burmannii* and *Solanum americanum*, have an invasive behaviour or not, but dispersers seem to assist their dispersal in the island. Furthermore, even native species might outcompete their native counterparts in a context of forest clearing, leading to significant changes in forest structure and functions (Meyer, 2004). In the current context of land use intensification in São Tomé, as elsewhere across the globe, it is also key to understand how bird seed dispersal might determine the characteristics of regenerating forests.

Finally, while we considered the presence of macroscopically unharmed seeds in the droppings as an evidence of seed dispersal, we did not check if they where viable. Although viability or germination tests should ideally be performed to confirm that intact seeds are still viable (Schupp *et al.*, 2010), studies which took that approach generally found that the visual inspection of seeds provides a good surrogate of interaction strength and the resulting estimate of dependence of a plant on its animal mutualists (Vázquez *et al.*, 2005). Furthermore, other studies have shown that species similar to those found dispersing in São Tomé act as legitimate seed dispersers: white-eyes (Larosa *et al.*, 1985), pigeons (Lambert, 1989; Corlett, 2009) and thrushes (Côrtes *et al.*, 2009). In the future, it would be highly informative to perform germination tests under natural conditions, to evaluate the quality of seed dispersal by each of the dispersers, in the distinct ecosystems, and compared to seeds that have not been digested by birds, to understand if birds are only transporting seeds or also altering their viability. Even if seeds are still viable after digestion, the transport of the seeds does not necessarily translate to recruitment (Traveset and Rodríguez-Pérez, 2008), as the quality of seed deposition is also a crucial requirement not only to germination but also to seedling establishment and subsequent survival and growth (Christian, 2001; Schuup *et al.*, 2010). It would therefore be ideal to assess plant recruitment of the different plant species being dispersed by birds, in the different ecosystems to fully understand how birds might affect forest vegetation dynamics through seed dispersal.

Concluding remarks

This thesis is the first quantitative study on seed dispersal in São Tomé. The seed dispersal network is dominated by native plant species, including some endemics, and not that many introduced plant species seem to have found their way into the old-growth forests. However, knowing that introduced species are among the major threats to biodiversity, further studies will allow a better understanding of this topic, and specifically if their effects can be stopped and mitigated in São Tomé.

We encountered a relatively low enrollment of birds in seed dispersal, when compared to other oceanic islands. However, this is the most endemic-rich seed dispersal network ever described, with all dispersers being endemic to the region. We described for the first time the seed dispersal service that birds provide to plants in São Tomé. While one of the few species that are not endangered, the *Speirops lugubris*, plays an unequivocally central role in bird seed dispersal in the island, five of the other important dispersers are threatened species. This is a concerning result, since the loss, or decline of these species might disrupt the seed dispersal function and subsequently threaten plant species that rely on this service.

This thesis is an important first step to characterize animal seed dispersal in São Tomé. However, rather than providing a definitive seed dispersal network for the island, it has served to show that there is still much to be done in order to understand how seed dispersal shapes the long-term dynamics of São Tomé forests. In particular, it has served to highlight how these dynamics can be affected by current threats associated with land-use changes and invasive species. These results pose a pressing conservation dilemma, since birds are simultaneously contributing to forest regeneration and invasion. They should be taken in consideration in the management of the Obô Natural Park, recognising that the complex threat of invasive plant species may go far beyond those of direct human impact.

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7. SUPPLEMENTARY INFORMATION

TABLE 7.1 – Details on bird species mentioned in the text. ST refers to São Tomé, P to Príncipe and A to Annobón. The conservation status according to the IUCN Red List (IUCN, 2016a) categories: Not evaluated (NE), Least Concern (LC), Nearly Threatened (NT) and Vulnerable (VU). *species described by (Melo *et al.*, 2011).

Species	English name	Local name	Family	Distribution	Conservation status
Speirops lugubris (Hartlaub, 1848)	São Tomé Speirops	Olho-grosso	Zosteropidae	ST endemic species	LC
Treron sanctithomae (Gmelin, 1789)	São Tomé Green Pigeon	Cécia	Columbidae	ST endemic species	VU
Anabathmis newtoni (Bocage, 1887)	Newton's Sunbird	Selêlê	Nectariniidae	ST endemic species	LC
Turdus olivaceofuscus (Hartlaub, 1852)	São Tomé Thrush	Tordo	Turdidae	ST endemic species	NT
Serinus rufobrunneus thomensis (Gray GR, 1862)	Príncipe Seedeater	Pardal	Fringillidae	STP endemic species, ST endemic subspecies	LC
Terpsiphone atrochalybeia (Thomson, 1842)	São Tomé Paradise Flycatcher	Jegue-jegue	Monarchidae	ST endemic species	LC
Prinia molleri (Bocage, 1887)	São Tomé Prinia	Truqui-sum-Dessu	Cisticolidae	ST endemic species	LC
Ploceus sanctithomae (Hartlaub, 1848)	São Tomé Weaver	Tchin-tchin-txoló	Ploceidae	ST endemic species	LC
*Columba malherbii (*Verreaux and Verreaux, 1851)	São Tomé Bronze-naped Pigeon	Rola	Columbidae	STPA endemic species	NT
*Dreptes thomensis (*Bocage, 1889)	Giant Sunbird	Selêlê-mangotchi	Nectariniidae	ST endemic species	VU
*Columba thomensis (*Bocage, 1888)	Maroon Pigeon	Pombo-do-mato	Columbidae	ST endemic species	EN
*Oriolus crassirostris (*Hartlaub, 1857)	São Tomé Oriole	Papafigos	Oriolidae	ST endemic species	VU
*Columba larvata simplex (*Temminck, 1809)	Lemon Dove	Mucanha	Columbidae	ST endemic subspecies	LC
Zosterops feae (*Hartlaub, 1866)	Príncipe White Eye	Neto-de-olho-grosso	Zosteropidae	ST endemic species	NE
Otus hartlaubii (Giebel, 1849)	São Tomé Scops-owl	Kitóli	Strigidae	ST endemic species	VU
Zoonavena thomensis (Hartert, 1900)	São Tomé Spinetail	Andorinha	Apodidae	STP endemic species	LC
Chrysococcyx cupreus insularum (Shaw, 1792)	Eemerald Cuckoo	Ossobó	Cuculidae	STPA endemic subspecies	LC

Onychognathus fulgidus fulgidus Hartlaub, 1849	Chestnut-winged Starling	Pastro	Sturnidae	ST endemic subspecies	LC
Ploceus grandis (Gray 1849)	Giant Weaver	Camussela	Ploceidae	ST endemic subspecies	LC

TABLE 7.2 – Bird species captured with mist nets. Percentages refer to the relative proportion to the total for each column.

Species	Captured birds (%)	Droppings with intact seeds (%)	Interaction frequency (%)	Dispersed plant species (%)
Speirops lugubris	261 (35)	192 (84)	380 (88)	36 (84)
Anabathmis newtoni	109 (15)	0	0	0
Turdus olivaceofuscus	86 (12)	20 (9)	31 (7)	16 (37)
Serinus rufobrunneus thomensis	82 (11)	2 (1)	2 (<1)	2 (5)
Terpsiphone atrochalybeia	81 (11)	0	0	0
Prinia molleri	40 (5)	0	0	0
Ploceus sanctithomae	33 (4)	0	0	0
Dreptes thomensis	18 (2)	0	0	0
Oriolus crassirostris	13 (2)	11 (5)	17 (4)	9 (21)
Columba larvata simplex	12 (2)	1 (<1)	1 (<1)	1 (2)
Zosterops feae	4 (1)	2 (1)	2 (<1)	1 (2)
Otus hartlaubii	1 (<1)	0	0	0
Zoonavena thomensis	1 (<1)	0	0	0
Chrysococcyx cupreus insularum	1 (<1)	0	0	0
Onychognathus fulgidus fulgidus	1 (<1)	0	0	0
TOTAL	743	228	433	43

TABLE 7.3 – Complete list of plant species retrieved from the droppings of mist netted birds. Interaction frequency of each species is given by the number of droppings where it was present. Origin in São Tomé is based on Figueiredo *et al.* (2011) and Estrela Figueiredo pers. comm.. ST = São Tomé, P = Príncipe; Percentages refer to the relative proportion to the total for each column *likely introduced species.

Species	Origin in ST	Interaction frequency (%)	Number of dispersers
Anthocleista scadens	Native	7 (1.6)	2
Antidesma vogelianum	Native	3 (0.7)	1
Cecropia peltata	Introduced	5 (1.2)	3
Cestrum laevigatum	Introduced	28 (6.5)	1
Cinnamomum burmanni	Introduced	3 (0.7)	2
Discoclaoxylon occidentale	STP endemic species	3 (0.7)	1
Ficus chlamydocarpa fernandesiana	ST endemic subspecies	1 (0.2)	1
Ficus kamerunensis	Native	39 (9.0)	3
Pauridiantha floribunda	Native	7 (1.6)	2
Phyllanthus sp.	Unknown	4 (0.9)	1
Psidium guajava	Introduced	1 (0.2)	1
Psychotria subobliqua	Native	9 (2.1)	2
Psydrax acutiflora	Native	8 (1.8)	3
Psydrax subcordata	Native	85 (19.6)	2
Rauvolfia vomitoria	Native	3 (0.7)	2
Rubus pinnatus	Unknown*	7 (1.6)	1
Rubus rosifolius	Introduced	58 (13.4)	3
Sabicea ingrata ingrata	ST endemic subspecies	30 (6.9)	3
Seed_09	Unknown	2 (0.5)	1
Seed_14	Unknown	7 (1.6)	1
Seed_18	Unknown	2 (0.5)	1
Seed_20	Unknown	1 (0.2)	1
Seed_23	Unknown	20 (4.6)	4
Seed_24	Unknown	1 (0.2)	1
Seed_25	Unknown	1 (0.2)	1
Seed_27	Unknown	1 (0.2)	1
Seed_29	Unknown	3 (0.7)	1
Seed_30	Unknown	6 (1.4)	1
Seed_32	Unknown	3 (0.7)	1
Seed_33	Unknown	1 (0.2)	1
Seed_34	Unknown	1 (0.2)	1
Seed_39	Unknown	2 (0.5)	2
Seed_40	Unknown	1 (0.2)	1
Seed_41	Unknown	1 (0.2)	1
Seed_42	Unknown	1 (0.2)	1
Seed_45	Unknown	3 (0.7)	1
Seed_48	Unknown	1 (0.2)	1
Seed_50	Unknown	2 (0.5)	1
Seed_54	Unknown	5 (1.2)	1
Shirakiopsis elliptica	Native	7 (1.6)	1

Solanum americanum	Introduced	6 (1.4)	1
Solanum terminalle	Native	9 (2.1)	2
Tarenna eketensis	Native	45 (10.4)	2
TOTAL		433	6

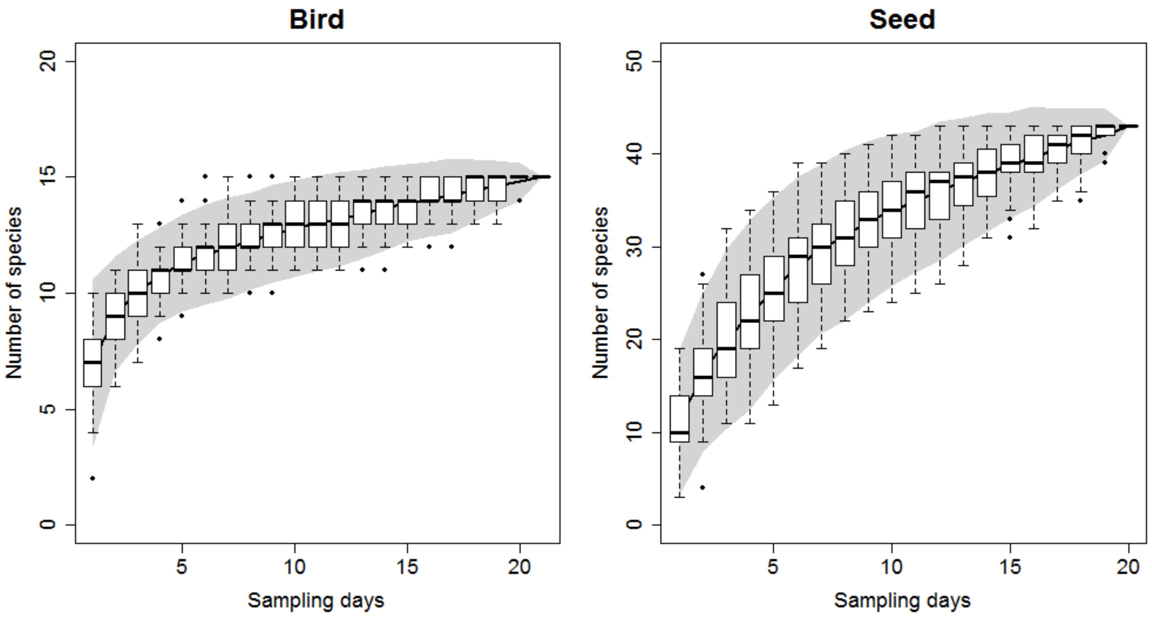

FIGURE 7.1 – Bird and plant species accumulation curves. Boxplots show the 25, 50 (median) and 75 percentiles, whiskers represent the minimum and maximum values, and black dots signal the outliers. The Chao estimator indicates the total estimated species richness of 21 birds and 66 plants.

TABLE 7.4 – Hunted pigeon species used in this study. Percentages refer to the relative proportion to the total for each column.

Species	Captured birds (%)	Crops with seeds (%)	Interaction frequency (%)	Dispersed plant species (%)
Columba thomensis	38 (3)	13 (2)	15 (2)	7 (15)
Columba malherbii	611 (57)	395 (64)	525 (67)	35 (76)
Treron sanctithomae	428 (40)	212 (34)	238 (31)	21 (46)
TOTAL	1077	620	778	46

TABLE 7.5 - Complete list of plant species retrieved from the crops of hunted pigeons. Interaction frequency of each species is given by the number of crops where it was present. Origin is based on Figueiredo *et al.* (2011) and Estrela Figueiredo pers. comm.. ST = São Tomé, P = Príncipe. Percentages refer to the relative proportion to the total for each column. *likely introduced species.

Species	Origin	Interaction frequancy (%)	Number of Dispersers
Alchornea cordifolia	Native	12 (1.5)	1
Bridelia micrantha	Native	2 (0.3)	2
Cecropia peltata	Introduced	158 (20.3)	2
Cestrum laevigatum	Introduced	1 (0.1)	1
Chrysophyllum sp.	Unknown	4 (0.5)	1
Cinnamomum burmannii	Introduced	1 (0.1)	1
Erythrococca molleri	Endemic species	2 (0.3)	1
Ficus chlamydocarpa fernandesiana	Endemic subspecies	29 (3.7)	1
Ficus mucuso	Native	73 (9.4)	2
Leea tinctoria	Endemic species	4 (0.5)	1
"Maracujá-de-obô"	Unknown	1 (0.1)	1
Margaritaria discoidea	Native	31 (4.0)	3
Morinda lucida	Native	7 (0.9)	2
N1	Unknown	6 (0.8)	1
N2	Unknown	2 (0.3)	1
N3	Unknown	1 (0.1)	1
N4	Unknown	2 (0.3)	2
N5	Unknown	20 (2.6)	2
N6	Unknown	2 (0.3)	2
N7	Unknown	1 (0.1)	1
N8	Unknown	1 (0.1)	1
N9	Unknown	1 (0.1)	1
N10	Unknown	2 (0.3)	1
N11	Unknown	2 (0.3)	1
N12	Unknown	17 (2.2)	1
N13	Unknown	6 (0.8)	2
N14	Unknown	2 (0.3)	1
N15	Unknown	1 (0.1)	1
N16	Unknown	2 (0.3)	1
N17	Unknown	1 (0.1)	1
N18	Unknown	1 (0.1)	1
N19	Unknown	4 (0.5)	2
N20	Unknown	1 (0.1)	1
N21	Unknown	1 (0.1)	1
N22	Unknown	1 (0.1)	1
N24	Unknown	3 (0.4)	2
N25	Unknown	3 (0.4)	1
N27	Unknown	1 (0.1)	1
N28	Unknown	1 (0.1)	1

N29	Unknown	39 (5.0)	1
N30	Unknown	1 (0.1)	1
Pauridiantha floribunda	Native	8 (1.0)	3
Rauvolfia caffra	Native	3 (0.4)	1
Rauvolfia vomitoria	Native	14 (1.8)	2
Tetrorchidium didymostemon	Native	230 (29.6)	2
Trema orientalis	Unknown*	73 (9.4)	2
TOTAL		778	3

TABLE 7.6 - Complete list of plant species retrieved from the droppings of mist netted birds and hunted pigeon crops. Interaction frequency of each species is corrected for bird abundance. Origin in São Tomé is based on Figueiredo *et al.* (2011) and Estrela Figueiredo pers. comm.. Percentages refer to the relative proportion to the total for each column.*likely introduced species

Species/morphotype	Origin in São Tomé	Frequency of occurrence (%)	Corrected interaction frequency %	Number of Dispersers
Alchornea cordifolia	Native	12 (1.9)	0.2	1
Anthocleista scadens	Native	7 (1.1)	1.3	2
Antidesma vogelianum	Native	3 (0.5)	0.6	1
Bridelia micrantha	Native	2 (0.3)	0.1	2
Cecropia peltata	Introduced	61 (9.7)	2.2	5
Cestrum laevigatum	Introduced	28 (4.5)	5.4	1
Cinnamomum burmanni	Introduced	4 (0.6)	0.9	3
Discoclaoxylon occidentale	Endemic species	3 (0.5)	0.6	1
Ficus chlamydocarpa fernandesiana	Endemic sub-species	21 (3.4)	0.5	2
Ficus kamerunensis	Native	39 (6.2)	8.6	3
Ficus mucuso	Native	71 (11.3)	1.2	2
Leea tinctoria	Endemic species	2 (0.3)	0.1	1
Margaritaria discoidea	Native	4 (0.6)	0.1	2
N1	Unknown	2 (0.3)	0.1	1
N4	Unknown	1 (0.2)	<0.1	1
N6	Unknown	2 (0.3)	<0.1	2
N13	Unknown	6 (1.0)	0.1	2
N14	Unknown	2 (0.3)	<0.1	1
N18	Unknown	1 (0.2)	<0.1	1
N19	Unknown	1 (0.2)	0.1	1
N20	Unknown	1 (0.2)	<0.1	1
N24	Unknown	1 (0.2)	<0.1	1
Pauridiantha floribunda	Native	10 (1.6)	1.4	4
Phyllanthus sp	Unknown	4 (0.6)	0.8	1
Psidium guajava	Introduced	1 (0.2)	0.2	1
Psychotria subobliqua	Native	9 (1.4)	1.7	2
Psydrax acutiflora	Native	8 (1.3)	2.2	3
Psydrax subcordata	Native	85 (13.6)	16.1	2
Rauvolfia vomitoria	Native	3 (0.5)	1.2	2
Rubus pinnatus	Unknown *	7 (1.1)	1.4	1
Rubus rosifolius	Introduced	58 (9.3)	11.3	3
Sabicea ingrata ingrata	Endemic sub-species	30 (4.8)	6.8	3
Seed_09	Unknown	2 (0.3)	0.4	1
Seed_14	Unknown	7 (1.1)	1.4	1
Seed_18	Unknown	2 (0.3)	0.4	1
Seed_20	Unknown	1 (0.2)	0.2	1
Seed_23	Unknown	20 (3.2)	11.4	4
Seed_24	Unknown	1 (0.2)	0.2	1
Seed_25	Unknown	1 (0.2)	0.5	1
Seed_27	Unknown	1 (0.2)	0.2	1

Seed_29	Unknown	3 (0.5)	0.6	1
Seed_30	Unknown	6 (1.0)	1.2	1
Seed_32	Unknown	3 (0.5)	0.6	1
Seed_33	Unknown	1 (0.2)	0.2	1
Seed_34	Unknown	1 (0.2)	0.2	1
Seed_39	Unknown	2 (0.3)	0.3	2
Seed_40	Unknown	1 (0.2)	0.1	1
Seed_41	Unknown	1 (0.2)	0.1	1
Seed_42	Unknown	1 (0.2)	0.1	1
Seed_45	Unknown	3 (0.5)	1.6	1
Seed_48	Unknown	1 (0.2)	0.2	1
Seed_50	Unknown	2 (0.3)	0.4	1
Seed_54	Unknown	5 (0.8)	1.0	1
Shirakiopsis elliptica	Native	7 (1.1)	1.4	1
Solanum americanum	Introduced	6 (1.0)	1.2	1
Solanum terminalle	Native	9 (1.4)	2.1	2
Tarenna eketensis	Native	46 (7.3)	8.9	2
Trema orientalis	Unknown*	4 (0.6)	0.1	2
TOTAL		626	100	9