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**Response of avian and mammal seed dispersal networks, to
human induced forest edges in a sub-humid tropical forest**

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Sylvia Plath, *The Bell Jar*

Resumo Alargado

A destruição florestal de origem antropogénica e a perda de habitat são as principais ameaças à biodiversidade na actual crise de extinção do Antropoceno. Quando consideramos esse impacto em ecossistemas ricos em espécies como as florestas tropicais, a perda de grandes frugívoros leva à diminuição do serviço de dispersão, a alteração de padrões de recrutamento de árvores e abundância relativa de espécies. Estas paisagens têm sido continuamente convertidas em zonas de pastoreio e cultivo, resultando em manchas reduzidas de floresta intercaladas por sistemas modificados.

A dispersão de sementes é uma função dos ecossistemas criticamente importante, sendo essencial para lidar com a fragmentação de paisagens, sobre-exploração de recursos, invasões biológicas e até alterações climáticas. Este serviço depende em grande parte das relações entre plantas e animais frugívoros, que funcionam como uma rede de dispersão. As ferramentas derivadas da teoria de rede têm permitido compreender estes padrões de interação entre espécies, providenciando uma perspetiva abrangente do funcionamento da comunidade.

Em África as redes de dispersão são ainda pouco estudadas, constituindo um facto alarmante devido à defaunação contínua por todo o continente. A Guiné-Bissau possui uma das últimas florestas primárias sub-húmidas de África, onde está incluído o Parque Nacional de Cantanhez. A área do parque tem sofrido alterações ao longo dos anos, vindo assim a sua floresta já naturalmente fragmentada sujeita a aumentos de pressão de actividades antropogénicas, com conversão de terrenos para agricultura.

Este trabalho tem como principal objectivo explorar as consequências da indução antropogénica de margens de floresta, através da comparação de redes de dispersão entre floresta madura e orla, em duas manchas de floresta integradas no Parque Nacional de Cantanhez. Pretende-se também compreender o papel de cada espécie na rede, e como estas poderão afectar o serviço de dispersão providenciado às plantas. Adicionalmente, espera-se compreender se existe influência do tipo de habitat e disponibilidade de frutos na riqueza e abundância de frugívoros e plantas.

Para tal realizaram-se observações focais de árvores ao longo de transectos na floresta madura e nas orlas das manchas de floresta de Lauchande e Madina. Foram identificados frugívoros e registados os eventos de consumo ou transporte de frutos. Adicionalmente registou-se o número de árvores com frutos maduros ao longo dos transectos. As redes de dispersão foram posteriormente construídas através da análise de matrizes de interação, considerando o número de eventos de consumo de frutos por cada espécie de frugívoro.

Foram identificadas mais interações na floresta madura, sendo que os frutos mais consumidos pertenciam a *Ficus sp.*, *Antiaris toxicaria* e *Strombosia pustulata*, enquanto na margem as *Ficus sp.* foram o recurso mais amplamente preferido. Os maiores consumidores na floresta madura foram *Ceratogymna elata*, *Treron calvus* e *Cercopithecus mona*, enquanto na orla foram os *Ploceus sp.*, *Pycnonotus barbatus* e *Cercopithecus mona*. Grandes frugívoros como calaus e primatas foram mais comuns na floresta madura, e a rede neste habitat estava mais ligada, com maior equitabilidade de interações e maior robustez a extinções tanto de plantas como de frugívoros.

A estrutura de rede foi similar entre habitats, com o mesmo número de espécies de plantas, e apenas mais um frugívoro na floresta madura. Para ambos, foram detectados baixos valores de aninhamento, conectividade, especialização (H_2') e modularidade, em contrapartida a equitabilidade das interações foi elevada. A sobreposição de nicho foi baixa e a robustez elevada para as plantas e frugívoros das duas redes. No que diz respeito à importância das espécies de um nível da rede para as espécies no nível oposto, *C. elata*, *C. mona* e *Pan troglodytes* foram as mais importantes, enquanto as espécies de árvores foram a *A. toxicaria*, *Ficus sp.*, e *S. pustulata*. Para a rede da orla, as espécies de árvores mais

importantes coincidiram com as da floresta madura e os frugívoros mais importantes foram *Ploceus sp.*, *P. barbatus* e *C. mona*. Métricas como o K_{risk} , permitiram a criação de uma hierarquia do risco e vulnerabilidade da rede à perda individual de espécies, sendo que *A. toxicaria* e *Ficus sp.*, foram respetivamente as mais preocupantes para a floresta madura e a margem. Todas as espécies de frugívoros e plantas nas duas redes, foram consideradas periféricas em relação ao papel que desempenham na rede, à exceção de *Parinari excelsa* e *A. toxicaria*, identificadas como conectoras de diferentes comunidades para a floresta madura e a orla respectivamente. A disponibilidade de frutos foi superior na floresta madura, mas a abundância e riqueza de frugívoros foi superior na orla.

O facto de a floresta madura apresentar maior conectividade e maior equitabilidade de interação, poderá ser explicado pela maior presença de grandes frugívoros neste habitat. Para além disso, os baixos níveis de especialização e equitabilidade de interação resultam em elevada robustez para ambas as redes devido a redundância na rede, que providencia vias alternativas para a persistência da rede aquando a extinção de uma espécie. Dos vários módulos que compõe as redes, alguns incluíam aves de grande porte como calaus, e primatas. É possível que estes módulos sejam formados por espécies com limitações morfológicas e funcionais semelhantes, como a abertura do bico e o tamanho dos frutos. Árvores como *A. toxicaria* e *P. excelsa*, possíveis conectoras, com sementes grandes, foram consumidas por uma vasta gama de frugívoros de diferentes tamanhos, sendo que a forma de tratamento dos mesmos difere. Os frugívoros mais pequenos tendem a extrair a polpa e a deixar cair as sementes debaixo da planta-mãe, enquanto os primatas as transportam para longe nas suas bochechas. Outras árvores como *Ficus sp.* e *S. pustulata* possuem elevada importância para os frugívoros, sendo que as primeiras são consideradas recursos chave em florestas tropicais e consumidas por quase todos os frugívoros no estudo, enquanto a última parece estar mais associada à dieta de grandes frugívoros.

Calaus e primatas apresentaram maior importância na floresta madura, sendo que o seu papel como dispersores já está amplamente documentado. Os seus grandes *home ranges*, a sua capacidade de se deslocarem entre manchas de habitat e atravessarem zonas degradadas, e a capacidade de voo no caso dos calaus, e a sua capacidade de consumirem grandes frutos, resulta num aumento da sua importância para a dispersão e restauração de zonas degradadas. Nas margens, esse papel recai sobre *Ploceus sp.* e *P. barbatus*, sendo que o papel de dispersão para o primeiro não está muito estudado, enquanto o último é considerado um importante dispersor para uma espécie de pequeno tamanho. A maior abundância de potenciais dispersores na orla poderá dever-se ao maior número de visitantes da floresta aí registados. Esta maior ocorrência na margem pode também dever-se à baixa heterogeneidade da vegetação, árvores amplamente visíveis e elevada abundância de frugívoros nas áreas de cultivo circundantes.

A dispersão de sementes é um importante condutor da regeneração de várias espécies de plantas. Estudos como este são relevantes porque permitem aceder à estrutura e funcionamento desta função ecológica numa perspetiva integrativa de rede. Para além disso, a identificação de árvores e potenciais dispersores mais importantes, permite propor medidas específicas, como a de plantação de determinadas espécies em zonas de forma a atrair frugívoros e as sementes que transportam. A identificação de potenciais dispersores permite ainda acompanhar o estado das suas populações e propor medidas direccionadas para a sua conservação.

Em suma, medidas de conservação para o PNC, devem ter em conta os papéis de todos os componentes da rede de dispersão e os comportamentos das espécies que as compõem, procurando uma abordagem que tenha em conta o contexto regional e cultural do parque.

Palavras-chaves: Interações planta-frugívoro; Degradação de floresta, Análise de rede; Aves; Mamíferos.

Summary

Human induced forest destruction and habitat loss are the current main threats to biodiversity. Impacts on species rich ecosystems such as tropical forests are considered, along with the abundance of mutualistic relationships they include, the loss of a species, may have unpredictable and deleterious consequences in the continuity of these ecological processes. Most tropical plant species rely on animals to disperse their seeds, thus studying the disruption of mutualistic networks becomes urgent in fragmentation scenarios. In the last couple of decades ecologists have been using the network theory as a tool to understand the pattern of mutualistic interactions. However, few are the studies that use this tool to compare populations in different types of strata or habitat.

In Africa, seed dispersal networks are poorly studied, which is alarming considering the increasing defaunation in the continent. Guinea-Bissau contains one of the last primary sub-humid forest in Africa, where the National Park of Cantanhez (CNP) is included. The area of the park has been continuously converted for agriculture practices and the forest increasingly fragmented.

The goal of this work is to explore the consequences of induced forest edges, by comparing seed dispersal networks between mature forest and forest edge, in two forest patches within the CNP. Additionally, I aim to understand the role of each species within the network, and how they may affect the seed dispersal service provided to plants.

Focal tree observations were carried along transects at the edge and mature forest in two forest remnants of the Cantanhez National Forest (Guinea Bissau) for 39 days, and fruit consumption events were registered. Additionally, trees along each transect were inspected for ripe fruits to test the influence of fruit availability on the frugivore community.

Fruit availability was higher at the mature forest whereas frugivore abundance and richness was higher at the forest edge, mostly due to an increase in forest visitors. The structure of plant frugivore networks was quite similar in the two habitats, with low nestedness, connectance, specialization (H2') and modularity. Interaction evenness was quite high for both. Niche overlap was low, and robustness was high for frugivore level and plant level in both networks. Regarding species roles, most species were peripheral, with only one connector detected for each habitat. In the mature forest there was a prevalence of large bodied frugivores, whereas small bodied frugivores were more abundant at the edge. Species such as the Yellow casqued hornbill, the Bark cloth tree and the Guinea Plum, pose the highest risk for the cohesion of the network of interactions if they go extinct for the mature forest, whereas Weaver, Fig trees and the Bark cloth tree bear the same roles at the forest edge.

These results suggest that the dispersal by large bodied frugivores may be hindered at the forest edges. Moreover, mature forest had higher interaction evenness, slightly higher connectance and higher robustness for plants and frugivores, which may be explained by the increase in the importance of large bodied frugivores. Nevertheless, both networks had low to moderate nestedness, modularity and specialization, resulting in functional redundancy and network robustness in both habitats. These results are positive, but there is still a need for more information on how seed dispersers are moving between the two habitats, and how effectively is the service being provided.

Keywords: Plant-frugivore interactions; Network analysis; Forest degradation; Birds; Mammals.

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1. INTRODUCTION

1.1 Habitat loss and forest fragmentation

In the last 500 years humans have been impacting ecosystems, triggering an extinction wave with a rate and magnitude similar to previous events of mass extinction on Earth (Barnosky et al. 2011, Dirzo et al. 2014). Species extinctions may lead to the loss of different functional roles (Fahrig 2003, Hagen et al. 2012, Dirzo et al. 2014, Emer et al. 2018), which in turn has worrying consequences for ecological processes and functions, and ecosystem services they provide (Bello et al. 2015, Haddad et al. 2015, Emer et al. 2018). Although extinctions are of great importance, declines in abundance and changes in species composition tend to have immediate impacts in ecosystem functions (IUCN 2007, Galetti et al. 2013, Dirzo et al. 2014).

Human induced habitat loss and forest destruction are two of the main threats to biodiversity under the current extinction crisis of the Anthropocene (Ceballos et al. 2015). If we consider impacts on species rich ecosystems such as tropical forests (Turner 1996, Laurance 1999, Hill & Curran 2003), studies have shown that when depleted of large frugivores, this habitats tends to experience a decrease in seed dispersal, altered patterns of tree recruitment and relative species abundance (Terborgh et al. 2001, Peres et al. 2002, Andresen 2007, Stoner et al. 2007, Wright et al. 2007a). These landscapes have been continuously converted to pasture or cultivated land (Brown & Lugo 1994), resulting in forest fragmentation, which leads to smaller forest patches imbedded in a matrix of modified habitats (Sala et al. 2000, Laurance et al. 2014). Consequences of fragmentation and habitat loss occur both at the landscape and patch level (Turner 1996), affect biodiversity (Findlay & Houlihan 1997, Gurd et al. 2001, Schmiegelow & Mönkkönen 2002, Lande 1987, Venier & Fahrig 1996, Gibbs 1998, Hargis et al. 1999, Guthery et al. 2001) and also changing habitat characteristics (Robinson et al. 1995, Boulinier et al. 2001, Fahrig 2003).

A common feature of forest fragmentation is the increase of edge habitats, transitional areas between forested and non-forested habitats, with their relative importance increasing as patch size decreases (Murcia 1995, Turner 1996). This leaves populations of plants and animals not only reduced and sub-divided, but also exposed to ecological changes associated with edges to which they may not be adapted (Wilcove et al. 1986, Laurance & Yensen 1991). Moreover, the impacts of such edges, may differ according to the size of the resulting patch, with small forest patches containing fewer species, as fragmentation typically triggers local extinctions (MacArthur & Wilson. 1968, Laurance 1997, Cordeiro & Howe 2003). Although remnant patches are able to sustain a significant fraction of biodiversity (Morante-Filho et al. 2016, Sfair et al. 2016, Beca et al. 2017), the long term persistence of viable populations require connectivity between patches (Hanski 1998, Leibold et al. 2004). The extensive fragmentation and habitat loss will ultimately isolate populations and may reduce their persistence, not only by physical isolation but also through barriers to gene flow. This process will eventually lead to lower genetic diversity and consequently low effective population sizes (Darvill et al. 2006, Ellis et al. 2006, Vanbergen 2014). Tropical forests are rich in mutualistic relationships, as those found between plants and their pollinators and seed dispersers, thus the loss species may have unpredictable and deleterious effects on the continuity of these ecological processes (Howe 1977, Tewksbury et al. 2002, Cordeiro & Howe 2003).

1.2. Seed dispersal

Seed dispersal is an essential stage in the life cycle of plants, corresponding to the mobile stage of this cycle, often requiring a vector for the transport of seeds (Janzen 1971, Howe & Smallwood 1982, Nathan et al. 2008), and is an important process for ecosystem functioning. It allows plants to evade intraspecific competition and avoid high mortality rates due to higher levels of predation and frequency of fungi attacks near the parental plant (Janzen 1970, Stiles 1992, Poulsen et al. 2002). It also allows plants to reach and colonize new areas (Howe & Smallwood 1982, Traveset et al. 2014, Correia et al. 2017). Plants have different strategies of seed dispersal that can either require an abiotic vector, e.g. water (hydrochory) or wind (anemochory), a biotic vector, such as the mutualistic animal dispersers (zoochory), or just an intrinsic mechanism, such as explosive structures (balistochory) (Howe & Smallwood 1982). Regarding zoochory, or animal-mediated seed dispersal, seeds can be transported externally through fur, hair and/or skin adhesion (exozoochory), or internally in the digestive tract of an animal after ingestion of fleshy fruits (endozoochory) (Howe & Smallwood 1982). Animals are important dispersal vectors, and up to 80% of the vascular plants in the tropics depend of them to some extent (Howe & Smallwood 1982). Animals actively remove seeds away from the parental plants, influencing dispersal patterns from short distance dispersal events (< 25m) to long distance dispersal events (> 10 km) (Traveset et al. 2014), transporting seeds to locations with favorable conditions for recruitment such as forest openings (Wenny & Levey 1998), enhancing germination through scarification (Verdú & Traveset 2004) and providing with their feces a micro-site with conditions favorable to germination (Sánchez de la Vega & Godínez-Alvarez 2010). The efficiency of seed dispersal depends on several factors, including the number of seeds carried, the quality of the gut treatment when being dispersed, the distance of dispersal, and the conditions of the dropping area for germination and recruitment (Schupp et al. 2010, Correia et al. 2017). Knowledge on seed dispersal has become critically important to deal with the ongoing landscape fragmentation, overharvesting, biological invasions, and even climate change (McConkey et al. 2012, Reid et al. 2015, Stone et al. 2017).

1.3 Mutualistic networks

It is widely accepted that the loss of biodiversity has the potential to disrupt ecosystems and their functioning (Kaiser-Bunbury et al. 2017), especially if we consider that a diverse assemblage of dispersers is essential to maintain long-term vegetation dynamics and forest regeneration (Terborgh 2013, Heleno et al. 2014, Correia et al. 2017). It has also become evident, that habitat restoration should not focus solely on the recovery of diversity, flagship species and physiognomic vegetation traits, but also in the complex interactions that are involved in providing ecosystem functions and sustaining its communities, which may as a whole, perpetuate our conservation efforts by natural processes (Group 2004, Palmer et al. 2006, Rodrigues et al. 2009, Heleno et al. 2010b, Devoto et al. 2012, Ribeiro da Silva et al. 2015, Correia et al. 2017). A network perspective can be used to study the interactions patterns of interdependencies between plant and frugivores. In the last couple of decades ecologists have used network theory and tools derived from it, to understand these patterns of interactions, which allows a community-wide perspective (Solé & Montoya 2001, Bascompte & Jordano 2007), while simultaneously aiming to explore the role of individual species within these networks (Olesen et al. 2007). Such tools have been applied in multiple contexts (Memmott et al. 2004, Tylianakis et al. 2007, Memmott 2009, Mello et al. 2011a) and have provided useful information for species conservation (Tylianakis et al. 2010, Gray et al. 2014, Kaiser-Bunbury & Blüthgen 2015). Initially, network studies

used binary networks (Hall & Raffaelli 1993), with interaction being recorded as present or absent. However, interactions between species are not equally important (Paine 1980, Benke & Wallace 1997, Ings et al. 2009), and such acknowledgment has resulted in an increased effort to use quantitative data on species interactions.

The structure of such networks can be assessed through metrics that consider the diversity and distribution of interactions, and also the importance of each species within them (Donatti et al. 2011, Saavedra et al. 2014). The increasing research effort on how these networks are structured has started to uncover similar patterns and contrasting differences across different types of interactions (Bascompte et al. 2003, Lewinsohn et al. 2006, Thebault & Fontaine 2010, Stouffer 2012). Recent studies have shown that interactions tend to be asymmetric in terms of degree (number of links of a species) and interaction strength, in mutualistic and antagonistic networks (Bascompte et al. 2003, 2006, Vázquez & Aizen 2004, Vázquez et al. 2005, Guimarães et al. 2006). Regarding their structure, mutualistic networks tend to have a nested pattern, in which less connected species (specialists) tend to interact strongly with a subset of highly connected species (generalists), which form a core of highly connected generalist species (Bascompte & Jordano 2007). This introduces functional redundancy in the system, offering different routes for network persistence and conferring robustness against species extinctions cascades (Bascompte & Jordano 2007, Blüthgen et al. 2007). This contrasts with antagonistic networks, such as plant-herbivore, which are less nested and more modular, and are characterized by the existence of well-defined groups of tightly interacting species (modules), with many intragroup links and fewer intergroups links (Dicks et al. 2002, Guimarães et al. 2007, Olesen et al. 2007, Bascompte 2010, Thebault & Fontaine 2010). These contrasting architectures are thought to be what allows the persistence of species on both network types (Thebault & Fontaine 2010). However, they are not mutually exclusive (Fortuna, et al. 2010), rather reflect complementarity and convergence phenomenon's, related to co-evolution and trait-matching between interacting species within a network (Nuismer et al. 1999, Thompson 2005, Jordano et al. 2007, Santamaria & Rodriguez-Gironés 2007, Vázquez et al. 2009, Fortuna et al. 2010, Guimarães Jr et al. 2011). Mutualistic networks define the nexus of ecosystem functions (Ings et al. 2009), and allow important insights about the robustness of a network, and its susceptibility to a cascade of secondary extinctions following the extinction of a specific species (Bascompte & Jordano 2007, Bastolla et al. 2009, García-Algarra et al. 2017). Previous works with both pollination networks and food webs, have shown that systems with skewed link distributions, are more robust to the loss of random and less connected species. On the other hand, the loss of generalist species (highly connected), may be of greater risk for the networks (Dunne et al. 2002, Memmott et al. 2004). Important work has also been done regarding species roles in the network, to further identify key species and prevent the collapse of the whole system. Such roles explore the position of a species within modules and in relation to species in other modules: peripheral species have few links within their module and seldom to others, a connector has multiple links to other modules, being extremely relevant to the cohesion of the network. A module hub on the other hand is paramount for the consistency of its own module, and finally a network hub acts as both a connector and a module hub, and is a key node for the coherence of both its module and the network (Guimerà & Amaral 2005a, 2005b, Guimerà et al. 2005, Olesen et al. 2007).

Network approaches are thus important as they offer a community wide perspective that addresses issues such as ecosystem resilience and functional performance of the community (Rodrigues et al. 2009, Devoto et al. 2012, Walker 2013, Kaiser-Bunbury et al. 2017), which have been proven useful to test the efficiency of conservation efforts and restoration programs (Ribeiro da Silva et al. 2015, Correia et al. 2017, Kaiser-Bunbury et al. 2017). Furthermore, a network approach seems to be useful to promote guidelines for conservation, as it allows the characterization of a species role within

its network and their importance for the landscape scale, which in turn may help accelerate network reconstruction and combat effects of habitat fragmentation (Ribeiro da Silva et al. 2015).

1.4 The case study of Cantanhez National Forest

African seed dispersal networks have so far been poorly studied, which is alarming in face of the defaunation occurring across the continent, where key dispersers such as primates, birds and bats are becoming critically endangered (Vanthomme et al. 2010, Campos-Arceiz & Blake 2011, Schleuning et al. 2011), and forests are lost (Rudel & Roper 1996). The community wide effects of the extinction of such species depends on the structure of mutualistic networks and ecological correlates (Bascompte & Jordano 2007), thus more studies on this issue are of paramount urgency. Guinea-Bissau contains one of Africa's remaining sub-humid forest (Oom et al. 2009), and has been identified by World Wide Fund for Nature as one of the 200 most important ecoregions in the world. This recognition resulted in large swaths of forest being included in the Cantanhez Forest National Park (CNP). The CNP was created in February 2011 and encompasses an area of 1067.67 km². As in most parts of the world, this forest has been changing considerably due to human encroachment, and consequent human activities. In this area, activities consist mainly of slash and burn agriculture to allow the cultivation of staple food such as rice (*Oryza* spp.) and cassava (*Manihot esculenta*), along with the conversion of forests into cashew (*Anacardium occidentale*) plantations (Hockings & Sousa 2013). Conversion of the forest land into scrubland and cultivation areas, has resulted in forest degradation and habitat fragmentation. The result of land use changes has been the depletion of the natural landscapes of resources that are essential for its regeneration and forest succession through animal seed dispersal (da Silva et al. 1996, Nepstad et al. 1996). Thus, understanding the structure and function of the seed animal-dispersal network in forest fragments of the CNP will add to the knowledge about this system, which is essential to inform conservation strategies that aim to enhance the forest's natural regeneration through animal conservation directives.

1.5 Main Goals

My main goal was to explore the consequences of induced forest edges, by comparing seed dispersal networks between mature forest and forest edge, in two forest patches within the CNP. Furthermore, I aimed to understand the role of each species within the network, and how they may affect the seed dispersal service provided to plants. To this end the objectives of the present work were three-fold:

1. Characterize the plant-frugivore interactions of the forests of CNP, and how they differ between mature forest and forest edge.
2. Identify the role of the different species in the plant-frugivore networks.
3. Assess the influence of resource availability, i.e. fruit availability, on parameters such as frugivores' species richness and frugivores' abundance.

2. Methods

2.1 Study area and sampling design

Field work was conducted from January to March 2018, in the CNP (Fig. 2.1) located in the southwestern region of Guinea-Bissau and the Tombali Administrative region (10°55'–12°45' N, 13°37'–16°43' W). With a tropical semi-humid climate, the CNP experiences a long dry season from November to May, and a rainy season from June to October (Catarino 2004). In this region, rainfall may reach up to 2,400 mm each year and the average temperature ranges from 28° to 31° C. The CNP is composed of a patchy mosaic of forest, savanna and mangroves (Gippoliti & Dell'Omo 2003, Catarino 2004) supporting a large proportion of the West Africa's remaining sub-humid forest (Oom et al. 2009). In 2008, Cantanhez was declared National Park due to the recognized need of conservation of the local biodiversity and the promise of development of ecotourism ideas that would financially benefit the local communities (Gippoliti et al. 2003). In the last three decades, the intensification of anthropogenic pressures, mainly crop production, led to an annual rate of deforestation of 1,17%, increased habitat fragmentation, and a shift from closed to open forest and savanna-woodland mosaic (Oom et al. 2009).

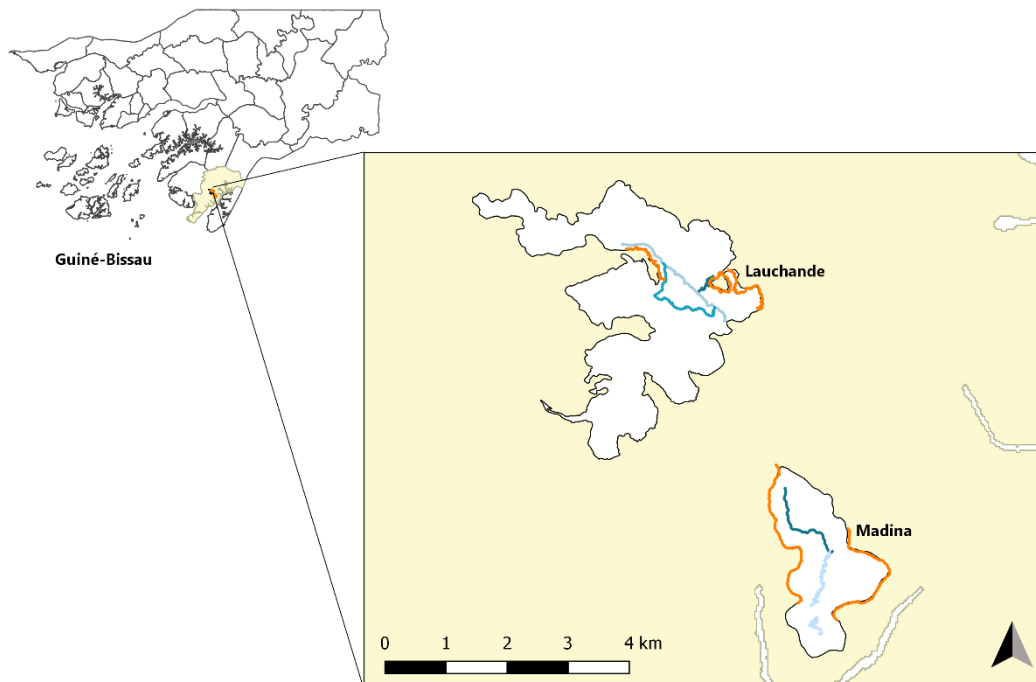


Figure 2.1 Location of the two forest remnants (Lauchande and Madina) located within the PNC (coloured in light yellow) in Guinea Bissau. The squared frame shows the transects made within both forest remnants. The orange lines represent the edge transects while the lines in different blue shades corresponds to mature forest transects.

Two forest remnants, Lauchande and Madina, were selected as study sites within the CNP. At each site, two forested habitats were sampled: mature forest, starting ca 200m from the edge, and forest edge, the transition area from mature forest to deforested areas, with multiple soil uses mainly for agricultural purposes. Madina was surrounded by mangroves and farmlands on opposite sides of the forest, while Lauchande was mainly delimited by abandoned or cultivated fields. To control for the edge effect, which usually includes proliferation of shade intolerant vegetation along fragment's edges as

well as changes in the microclimate and light regimes (Laurance & Yensen 1991), a strip of ca 25m in the transition between the two types of forest was not considered.

Within each forest habitat, I selected transects ranging from 2-3 km and mapped the location of fleshy fruit trees present along the transects. All mapped fleshy fruit trees were registered only when found within 7 meters to the left or right of the main path. At Madina, two transects were chosen for each habitat, and at Lauchande three, making a total of 5 edge and 5 mature forest transects. Each transect was sampled at least three times, alternating between forest remnants for 39 days. All transects were mapped using the Runkeeper app (available at <https://runkeeper.com/>).

2.2 Plant-Frugivore interactions

Plant-frugivore interactions, as in fruit-consuming events by each frugivore species, were recorded along each transect by focal observation, with the assistance of binoculars, and performed at all fruiting trees with good visibility. These transects were covered during two four-hour periods, one starting at sunrise and one late in the afternoon until the sunset. To facilitate focal tree observations in both forest remnants, the edge trees were observed from the deforested areas looking in. Observation sessions at focal trees started when a tree with ripe fruits was located and lasted up to 1h. Every new arrival or departure of a frugivore restarted the clock. If no activity was detected for a period of 15 minutes, the session would end before reaching the 1h limit. On the second half of the day, the observation sessions were repeated for the same trees. In total I performed 138 hours of observations. All animals visiting the focal trees were recorded, and the frugivore identified to the lowest taxonomic level possible, resorting to published field guides (Borrow & Demey 2001, Kingdom 2016). The duration of animal visits and the number of fruits removed (either by swallowing on the spot or carrying it away) were also registered. When birds visited the focal tree in flocks, and simultaneous observations were impossible, foraging behavior was recorded for visible randomly chosen individuals (Saavedra et al. 2014). At the end of each session tree height was estimated and its GPS coordinates registered. To maximize data collection and the number of interactions, whenever a frugivore was spotted on a tree between observation periods, that was registered as occasional.

2.3 Networks analysis

To analyze the pattern of interactions between plant species and their potential seed dispersal animal species, a network of interactions was compiled for each forest habitat. Interaction frequency was defined as the number of fruit-eating events of each animal species to the different plant species, or if an animal left the focal tree carrying fruits. Interactions were then organized in a matrix with animals as columns and plants as rows.

Networks were characterized by calculating several commonly used network descriptors to evaluate the distribution of interactions across the network and its overall structure:

1) Network specialization (H^2), which measures the degree of niche complementarity between species, integrating species-level specialization across the entire community, and reflecting the functional niche of frugivore species relative to the available fruit resources (Blüthgen et al. 2006, Albrecht et al. 2013, Chama et al. 2013).

2) Weighted connectance, that estimates the proportion links that are actually observed in the networks (Jordano 1987).

3) Interaction evenness, which estimates how homogenous is the distribution of interactions between all species in the network (Tylianakis et al. 2007).

4) Vulnerability, which is the weighted mean of species in the frugivore level of the network per species in the plant level (Tylianakis et al 2007). It indicates the mean number of frugivores per plant species. Vulnerability is commonly calculated alongside its analogue network descriptor - generality, which quantifies the mean number of plants species per frugivore in the network (Schoener 1989).

5) Nestedness, measures how strongly interactions of a network conform to a nested pattern. This pattern is characterized by little connected species (specialists) interacting with others that are a subset of species interacting with highly connected ones (generalists) (Bascompte et al. 2003).

6) Modularity, which estimates the extent to which species form groups of tightly connected species-modules, interacting more often with each other than with species in other modules (Guimerà & Amaral 2005b).

7) Network robustness, quantifies the degree to which a network can withstand a cascade of secondary extinctions of plant species following the random loss of their animal dispersers (Memmott et al. 2004, Burgos et al. 2007).

8) Niche overlap, which determines the closeness in interaction patterns between species that share the same trophic level (Krebs 1989).

To test if the empirical network parameters were not a mere result of stochastic processes, I resorted to null models, i.e. generation of randomized data sets (Gotelli 2000). There are several types of null models, but their foundation consists on randomly reassigning pairs of interacting species from the observed interaction matrix to obtain simulated networks (Gotelli 2000, Vázquez & Aizen 2003, Blüthgen et al. 2008, Ribeiro da Silva et al. 2015). I used the *vaznull* model, based on the algorithm by Vázquez et al 2007, which is a conservative model that preserves the original structure of the network and considers the original species richness, interaction frequency and connectance (Dorman et al 2008). Finally 1000 null networks were produced, to which observed networks were compared using a z-score test to check if the observed scores were significantly different from random expectations (Ribeiro da Silva et al. 2015).

2.4 Network species' roles

To investigate the potential importance of animal species to the seed dispersal service provided to plants species level metrics were also calculated, such as:

1) Species' degree, which quantifies the number of links of each species (Bascompte et al. 2003).

2) Species' strength, which quantifies the importance of each frugivore species for the set of plant species and vice versa. It is defined as the sum of the dependencies of species from one level of the network to the species on the other level (Bascompte et al. 2006).

3) Species' roles: the modules obtained in modularity analyses allow the classification of nodes (species) into different roles, such as peripheral, connectors, module and network hubs (Olesen et al.

2007). These roles are described by two parameters: z , i.e., standardized number of links to other species in the same module, and c , i.e., the level to which the species is connected to species in other modules (Guimerà & Amaral 2005a, Olesen et al. 2007). A peripheral species has both a low z (≤ 2.5) and a low c (≤ 0.62), it has a few links inside its own module and rarely any to other modules. A connector species has a low z (≤ 2.5) and a high c (> 0.62), connecting different modules and is thus important to network cohesion. A module hub has a high z (> 2.5) and a low c (≤ 0.62) and has an important role to the consistency of its own module. A network hub has both a high z (> 2.5) and a high c (> 0.62) and is thus important to the coherence of both the network and its own module (Guimerà & Amaral 2005a, 2005b, Guimerà et al. 2005).

4) K_{risk} was estimated to assess how vulnerable the network is to the loss of a particular species, allowing the identification of a species whose disappearance poses a greater risk to the entire network (García-Algarra et al. 2017).

All network and species-level metrics were calculated using the *bipartite* package (Dormann et al. 2008, 2009) in R software (version 3.5) (The R Development Core team 2008), except for K_{risk} , which was estimated with the package *kcorebip* (García-Algarra et al. 2017) also in R environment.

2.5 Influence of fruit availability and habitat type

Fruit availability was estimated by counting all ripe fruiting trees along all the transects, including trees that did not hold the adequate visibility conditions for focal observations. During this stage, tree samples were collected from both Lauchande and Madina, for later identification. Plants were photographed and other information such as habitat, vegetation type and GPS coordinates were registered. All plant samples were pressed and dried at room temperature or under the sun. Fruits and seeds were also collected and stored in porous coin envelopes with silica gel.

To account for effects of habitat type on fruit availability, generalized linear mixed models (GLMMs) were performed. Habitat type (forest edge and mature forest) was included as a fixed effect, whereas forest remnant (Lauchande and Madina) and sampling date were included as random effects.

GLMMs were also fitted to assess the effects of habitat type and fruit availability on frugivore abundance and richness considering interactions, i. e. fruit consumption event by an individual on a tree. For fixed effects, habitat type (forest edge and mature forest) was considered once more, along with fruit availability, and for random effects, again forest remnant (Lauchande and Madina) and sampling date.

All independent variables were subject to a graphical exploratory analysis and checked for collinearity using a Spearman correlation matrix. Variables with correlation values > 0.7 were excluded from the analysis; such was the case of the variable “fruit availability” that was excluded as it was correlated with habitat type, in the models of frugivore abundance. All GLMMs assumptions were tested beforehand and different models of the same dataset were compared using the Akaike Information Criteria for small samples (AICc) (Burnham & Anderson 2014). Some species were not included in the modelling procedure, because they were only present in one of the habitat types. All models were analyzed with a Poisson distribution with the R package *lme4* (Bates et al. 2015).

The average size of all potential disperser species observed was estimated using data obtained from published literature (Zihlman & Cramer 1978, Smith & Jungers 1997, Glenn & Bensen 1998, Nowak 1999, Borrow & Demey 2001).

3. Results

During the sampling period, 1540 animal visitors (visits with and without fruit consumption) were recorded at the focal trees, of which 77 frugivores were observed feeding on fruits. Nine tree taxa were considered for observation: Fig trees (*Ficus sp.*), Bark cloth tree (*Antiaris toxicaria*, Lesch.), White silk-cotton tree (*Ceiba pentrandia*, L., Gaertn), Velvet tamarind (*Dialium guineense*, Willd.) African oil palm (*Elaeis guineensis*, Jacq.), Guinea Plum (*Parinari excelsa*, Sabine) and African nutmeg (*Pycnanthus angolensis*, Welw.), *Anthostema senegalense* (A. Juss) and *Sterculia sp.*

Regarding the selected forest habitat, mature forest had 900 registered visitors while the edge had 640. In both forest remnants, trees in the mature forest received more visitors than the edge, and the frugivore species richness followed the same trend with 29 species in the interior versus 19 in the edge. Twenty-six bird species, 5 primates and at least 2 species of squirrels were detected. Trees attracting the highest number of visitors were Fig trees (n=734), Bark cloth tree (n=201), White silk-cotton tree (n=197) and *S. pustulata* (n=175). At the mature forest, African Green pigeons (*Treron calvus*) (n=238), Common bulbuls (*Pycnonotus barbatus*) (n=106), Western piping hornbills (*Bycanistes fistulator*) (n=78) and Great blue turacos (*Corythaeola cristata*) (n=68) were the most frequent visitors to fruiting trees, while in the forest edge these were replaced by Weavers (*Ploceus sp.*) (n=143), Violet-backed starlings (*Cinnyricinclus leucogaster*) (n=108), Commons bulbuls (n=97) and African green pigeons (n=85). The median weight of frugivores was higher at the mature forest, mostly due to the presence of large bodied species such as all primates and bird species such as hornbills and turacos (Fig. 3.1).

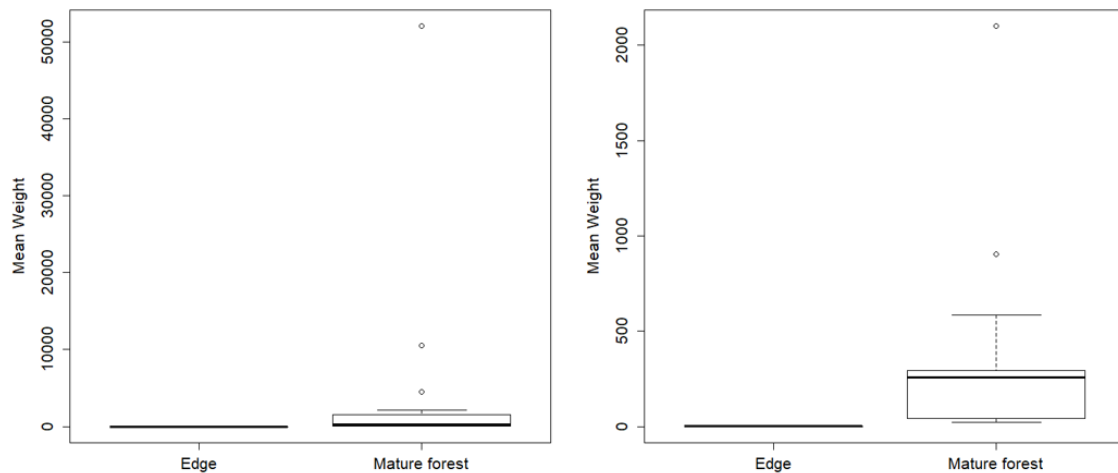


Figure 3.1 - Differences in median weight of frugivores at the forest edge and mature forest forest. Boxplot on the left, includes mammals and birds, and the right only birds are compared.

3.1 Plant-Frugivore networks

When considering fruit consumption events, fewer interactions (36) were detected in the edge in relation to the mature forest habitat (41). At the forest edge, fruits of Fig trees (n=19) were the most consumed, whereas at the mature forest the most consumed were Bark cloth trees (n=13), Fig trees (n=9) and *Strombosia pustulata* (Oliv.) (n=9) (Fig. 3.1). At the mature forest, the most significant consumers were Yellow-casqued Hornbills (*Ceratogymna elata*) (17.1%), African green-pigeons (17.1%) and

Mona monkeys (*Cercopithecus mona*) (17.1%), while at the edge the most significant were Weavers (*Ploceus sp.*) (16.7%) and Common bulbuls (*Pycnonotus barbatus*) (16.7%) (Fig. 3.2).

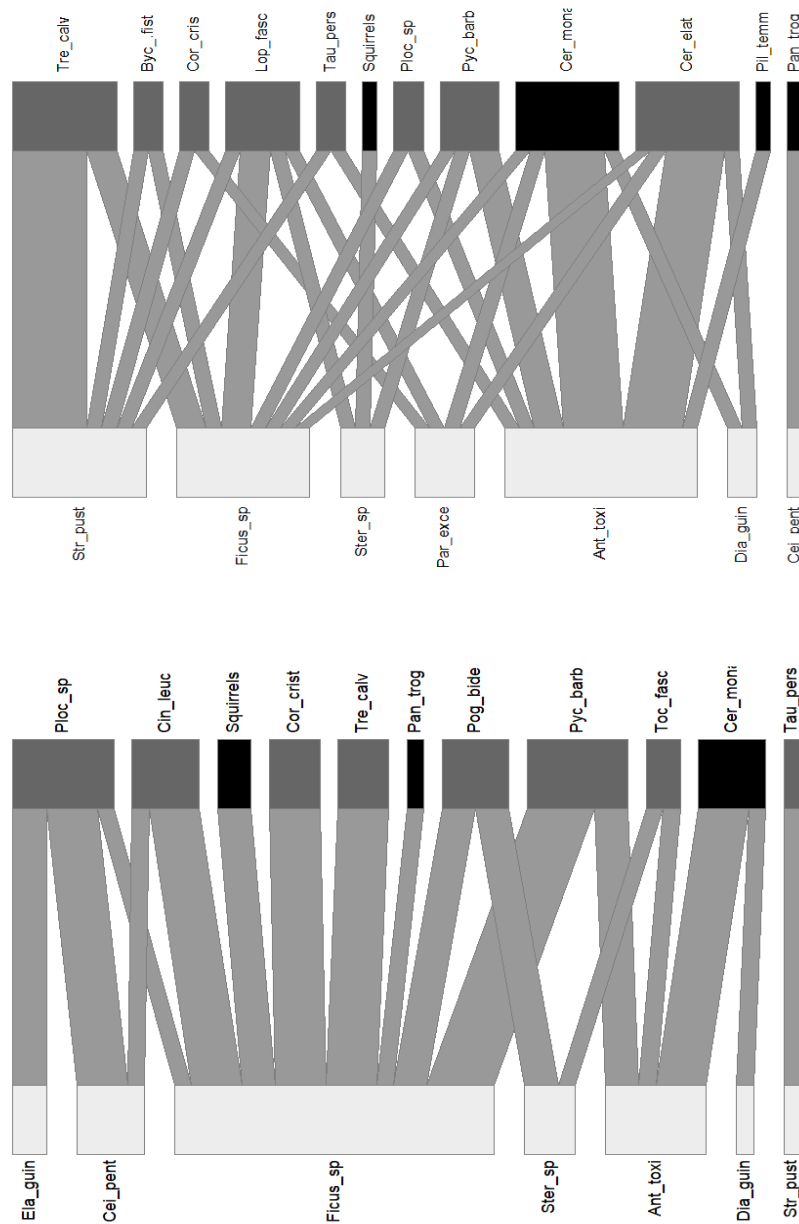


Figure 3.2 - Quantitative plant-frugivore network of the mature forest (top) and forest edge (bottom) in the Cantanhez National Park, Guinea-Bissau. The upper boxes represent frugivore species, whereas the lower boxes represent plant species. Box width corresponds to the relative fraction of interactions contributed by each species to the networks. Line width is proportional to the interaction frequency between each frugivore and plant species. At the upper level, black rectangles are mammals and grey are bird dispersers. Species names may be found in Table 3.3.

The structure of the plant-frugivore networks from both types of forest was very similar, having the same number of plant species (7 species) and differing by one in the number of frugivore species (11 for the edge, 12 for the mature forest) (Fig. 3.2). Nestedness and interaction evenness of the secondary forest network were the only descriptors that significantly differed from random expectations, and both were lower than expected by null model. Nestedness showed the most noticeable difference between forest types, with the forest edge showing a much higher value of nestedness than the mature

forest. Connectance was relatively low and slightly higher in mature forest. Interaction evenness was high, with the mature forest exhibiting the highest scores. Mature forest had higher generality, while the edge showed higher vulnerability (Tab. 3.1). Both habitats showed moderate levels of modularity and network specialization, with the forest edge being more modular and more specialized. Five modules were found at the mature forest, whereas at the forest edge 6 modules were detected.

Niche overlap for the frugivore level was slightly higher for the forest edge, whereas the niche overlap for the plant level showed an opposite trend. Robustness for both levels was high, with the mature forest exhibiting the highest scores for the frugivore and plant levels (Tab. 3.1).

Table 3.1 - Network level descriptors calculated for mature forest (Mature_F) and forest edge (Edge F). The observed values are presented for each descriptor, along with the significance results of a z-score test used to compare the observed values with that of the mean of 1000 randomly regenerated networks.

Metrics	Mature_F	z score	p value	Edge_F	z score	p value
Weighted nestedness	0.065	-2.058	0.039	0,403	-0.083	0.933
Weighted connectance	0.189	-1.613	0.107	0,182	0.098	0.922
Interaction evenness	0,692	-2.897	0.004	0,639	1.647	0.099
Specialization (H2')	0.308	0.885	0.376	0,476	0.065	0.948
Niche Overlap HL	0.323	-0.809	0.419	0,395	0.042	0.967
Niches Overlap LL	0.255	-0.709	0.478	0,119	-0.767	0.443
Robustness HL	0.783	0.624	0.533	0,653	-0.294	0.769
Robustness LL	0.696	0.605	0.545	0,587	-1.195	0.232
Generality	2.594	-1.215	0.224	1,774	-0.284	0.777
Vulnerability	4.570	-1.079	0.280	4,768	0.148	0.883
Modularity	0.382	0.631	0.375	0.463	0.923	0.357

3.2 Network species' roles

For mature forest, species strength, ranged from 1.17 to 0.08 for frugivores, whereas that of plants on frugivores ranged from 3.64 to 0.29. The most important frugivores were Yellow casqued hornbills, Mona monkeys and Chimpanzees (*Pan troglodytes*). Additionally, trees with the highest strength were Bark cloth tree, Fig tree and *S. pustulata*. For forest edge, species strength of frugivores on trees ranged from 1.80 to 0.05 whereas that of plants on frugivores ranged from 6.0 to 0.25. Weavers, Common bulbuls and Mona monkeys had the strongest impact, and as for tree species, Fig tree, Bark cloth trees and *S. pustulata* had the highest scores (Tab. 3.2).

Using K_{risk} analyses I was able to identify species whose loss poses a greater risk to network cohesion. For mature forest the frugivore species posing the highest risk were Yellow casqued hornbill followed by African green pigeon, Mona monkeys and Congo pied hornbill (*Lophoceros fasciatus*) whereas for tree species were Bark cloth tree, Fig tree and *S. pustulata*. For forest edge the riskiest to lose frugivores, were Weavers, followed by Common bulbuls and Mona monkeys, whereas the tree species were Fig tree, Bark cloth tree, and *S. pustulata*. If we look at the system without differentiating groups, the species whose loss poses a greater risk for the mature forest was the bark cloth tree whereas for the forest edge was the Fig tree (Tab. 3.2).

Regarding species roles in the networks, in mature forest all frugivore species were peripheral, with four out of the twelve species having no links outside their own module. Most of the plant species (5) were peripheral, with three species showing no links outside their own module. Guinea Plum was identified as possible connector. For forest edge, all frugivore species were peripheral, with six having no links to species outside their own module. All six plants species were peripherals except for the Bark cloth tree which was a connector (Tab. 3.2, Fig. 3.3).

Table 3.2 - Species level descriptors calculated for mature forest (left) and forest edge (right). The observed values are presented for each frugivore and plant species.

Mature Forest Species		<i>c</i>	<i>z</i>	Species strength	Krisk	Forest Edge Species		<i>c</i>	<i>z</i>	Species strength	Krisk	
Frugivores	<i>C. elata</i>	0.172	0.577	1.169	0.02	Frugivores	<i>Ploceus. sp</i>	0.057	0.000	1.803	1.020	
	<i>T. calvus</i>	0.408	1.500	0.778	0.02		<i>P. barbatus</i>	0.475	1.291	1.500	0.020	
	<i>C. mona</i>	0.172	0.577	1.169	0.02		<i>C. mona</i>	0.000	0.000	1.000	0.010	
	<i>L. fasciatus</i>	0.544	1.265	0.917	0.02		<i>C. leucogaster</i>	0.475	0.323	0.772	0.020	
	<i>P. barbatus</i>	0.382	0.316	0.598	0.02		<i>P. bidentatus</i>	0.236	0.707	0.544	0.020	
	<i>B. fistulator</i>	0.500	-0.500	0.222	0.02		<i>C. cristata</i>	0.000	0.323	0.500	0.010	
	<i>C. cristata</i>	0.426	-0.500	0.361	0.02		<i>T. calvus</i>	0.000	0.323	0.408	0.010	
	<i>Ploceus sp.</i>	0.483	-0.949	0.188	0.02		<i>Squirrels</i>	0.000	-0.645	0.158	0.010	
	<i>T. persa</i>	0.483	-0.500	0.188	0.02		<i>L. fasciatus</i>	0.444	-0.707	0.158	0.020	
	<i>Squirrels</i>	0.000	-0.632	0.333	0.01		<i>P. troglodytes</i>	0.000	-1.614	0.105	0.010	
	<i>P. troglodytes</i>	0.000	0.000	1.000	0.01		<i>T. persa</i>	0.000	0.000	0.053	0.010	
	<i>P. temminckii</i>	0.000	-1.155	0.077	0.01		Plants	<i>Ficus sp.</i>	0.200	0.000	6.083	4.020
	Plants	<i>A. toxicaria</i>	0.559	1.155	3.643			1.02	<i>A. toxicaria</i>	0.632	0.707	1.583
<i>S. pustulata</i>		0.152	0.707	2.414	0.02	<i>C. pentrandia</i>		0.444	0.707	0.750	0.020	
<i>Ficus sp.</i>		0.590	0.707	2.223	0.02	<i>Sterculia sp.</i>		0.000	0.000	1.000	0.020	
<i>Sterculia sp.</i>		0.000	-0.707	1.450	0.02	<i>E. guineensis</i>		0.000	-0.707	0.333	0.010	
<i>C. pentrandia</i>		0.000	0.000	1.000	1.02	<i>D. guineense</i>		0.000	-0.707	0.250	0.010	
<i>P. excelsa</i>		0.618	-0.577	0.986	0.02	<i>S. pustulata</i>	0.000	0.000	1.000	0.010		
<i>D. guineense</i>	0.000	-0.577	0.286	0.01								

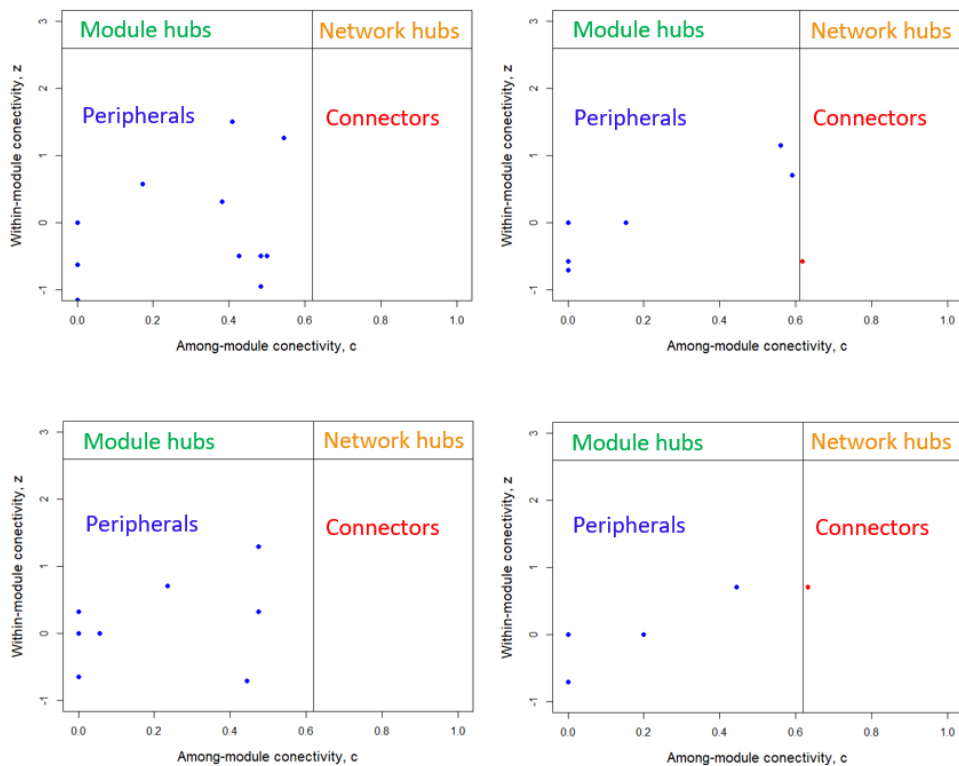


Figure 3.3 Distribution of frugivore and plant species according to their network role. Each dot represents a species, and each small pane shows the role distribution of selected group of species. Upper panes are of the mature forest, and lower panes of the forest edge. From left to right, frugivore and plant graphs.

3.3 Habitat type and fruit availability

There was an overall effect of habitat type on fruit availability with mature forest displaying the highest availability (Mature forest with 440 trees and the edge with 114). Concerning individual species, White silk-cotton tree, *Sterculia* sp. and Velvet tamarind showed a significantly higher abundance at the forest edge. Some species were not included in the model because they were only present in one of the forest types: the African nutmeg registered only in the mature forest and *A. senegalense* and African oil palm in the forest edge (Tab. 3.3).

Frugivore abundance and richness differed significantly between habitats and was slightly higher at the forest edge. Habitat type affected several frugivores: African pied hornbill, Mona monkeys, Green turacos (*Tauraco persa*) and African green pigeons consumed more fruits at the mature forest, whereas Squirrels, Great blue turacos, Chimpanzees and Weavers seemed to prefer to forage at the forest edge. Common bulbuls showed no significant effects on either habitat type or fruit availability. Some animal species were not modelled because they were observed in only one of the habitats: African pied hornbills, Yellow-casqued hornbills and Temminck's Red Colobus (*Ptilocolobus badius temminckii*), at the mature forest, whereas Violet backed-starlings and the Double-toothed barbets (*Pogonornis bidentatus*) were recorded exclusively at the edge (Tab. 3.4).

Table 3.3 - Selected models regarding the influence of habitat type on fruit availability.

	Estimate	Std. error	Z value	Pr(> z)	
<i>D. guineense</i>	0.6931	0.1543	4.492	<0.001	***
Mature forest	0.7985	0.1581	5.050	<0.001	***
Forest edge					
<i>Ficus</i> sp.					
Mature forest	-0.164	0.266	-0.616	0.538	
Forest edge	0.219	0.247	0.887	0.375	
<i>S. pustulata</i>					
Mature forest	1.654	1.018	1.625	0.104	
Forest edge	-2.066	1.076	-1.921	0.055	
<i>P. excelsa</i>					
Mature forest	-1.579	1.406	-1.123	0.261	
Forest edge	-3.095	1.652	-1.873	0.061	
<i>C. pentrandia</i>					
Mature forest	-3.527	1.342	-2.628	0.009	**
Forest edge	-0.050	0.936	-0.054	0.957	
<i>A. toxicaria</i>					
Mature forest	-1.328	1.040	-1.278	0.201	
Forest edge	-1.649	1.065	-1.548	0.122	
<i>Sterculia</i> sp.					
Mature forest	-3.045	1.000	-3.045	0.002	**
Forest edge	-2.197	0.707	-3.107	0.002	**
Abundance					
Mature forest	2.559	0.599	4.266	<0.001	***
Forest edge	1.315	0.605	2.172	0.0298	*

Table 3.4 - Selected models regarding the influence of habitat type and fruit availability on frugivores.

	Estimate	Std. error	Z value	Pr(> z)	
<i>C. mona</i>					
Mature Forest	-5.778	2.315	-2.496	0.013	*
Forest edge	-6.059	2.428	-2.495	0.013	*
<i>T. fasciatus</i>					
Mature Forest	-1.163	0.447	-2.601	0.009	**
Forest Edge	-1.872	0.7071	-2.647	0.008	**
<i>T. calvus</i>					
Mature Forest	-1.449	0.730	-1.984	0.047	*
Forest Edge	-2.117	0.924	-2.293	0.022	*
<i>C. cristata</i>					
Mature Forest	-7.135	3.123	-2.278	<0.001	***
Forest Edge	-6.137	2.910	-2.109	0.035	*
Squirrels					
Mature Forest	-7.178	3.539	-2.028	0.043	*
Forest Edge	-6.813	3.576	-1.905	0.057	
<i>P. troglodytes</i>					
Mature Forest	-5.221	2.567	-2.026	0.043	*
Forest Edge	-3.659	1.227	-2.983	0.003	**
<i>Ploceus sp.</i>					
Mature forest	-3.226	1.524	-2.116	0.034	*
Forest edge	-1.698	1.095	-1.551	0.121	
<i>P. barbatus</i>					
Mature forest	-3.861	2.180	-1.771	0.077	
Forest edge	-3.104	2.077	-1.495	0.135	
<i>T. persa</i>					
Mature Forest	-1.698	0.832	-2.041	0.041	*
Forest Edge	-2.853	1.001	-2.850	0.004	**
Frug. Abundance					
Mature forest	0.683	0.215	3.172	0.002	**
Forest edge	0.916	0.221	4.150	<0.001	***
Frug. Richness					
Mature forest	0.486	0.196	2.476	0.013	*
Forest edge	0.571	0.209	2.736	0.006	**

4. Discussion

In the present work I was able to assess how the process of seed dispersal might be affected by deforestation of the native forest in the CNP, by looking at differences between the structure of plant-frugivore interaction networks, and the role of species in this process. Network structure was quite similar in mature forest and forest edge, with low nestedness, connectance, specialization and modularity. Interaction evenness was high for both networks. Furthermore, niche overlap for plants and frugivores was low, while robustness was quite high. Generality and vulnerability were low, and similar in both networks. The results also show that both networks, probably due to their size, are composed of mostly peripheral species, having few links and mostly within their module. Some species are of greater importance to the network: in the mature forest, frugivores such as Yellow casqued hornbills and trees such as the Bark cloth trees possess the most connections and represent the highest risk for the network if they go extinct. For the forest edge, those roles fall to Weavers, for the frugivore level, whereas Fig trees seem to be the most important plant species. Frugivore abundance and richness were higher at the forest edge, while fruit availability was higher at the mature forest. Fruit availability was highly correlated with habitat type, so no isolated significant effects were detected on frugivore abundance and richness.

Regarding limitations or possible biases, it is important to consider the observation conditions in each habitat. The characteristics of the two study sites, only allowed observations of the edge from outside the forest remnant. This context may have benefited focal observations by allowing a picture of the whole tree, providing greater visibility. On the other hand, it should be taken into account, that

the greater visibility also meant more exposure of the observer, due to the absence of camouflaging vegetation such as trees in those surrounding open areas. In this study, fruit availability was established as the number of ripe fruit trees along the transects. This approach may be over/under estimating the fruit availability for both habitats, and ultimately the importance of tree species for frugivores and the network as a whole. Finally, the number of frugivore visits was significantly higher than the registered number of fruit consuming events. Although this may signal an underestimation of the number of frugivores consuming fruits, I consider that this information is important, and that the effort should be directed towards improving and using techniques that allow this type of data collection, such as camera traps in tree canopies.

4.1 Plant-Frugivore networks

The structure of the plant-frugivore networks was quite similar between the two habitat types considered, although some differences should be emphasized. The network at the edge was more nested, and this may be related to differences in the frugivore community, considering, that there was a significant overlap between plant species present in both habitats. Menke et al., (2012), found the same pattern, with nestedness increasing strongly from mature forest to forest edge. The less nested pattern seen at the mature forest seems to underline that frugivores are not all equivalent at dispersing seeds in regards to their abundance (Blüthgen 2010, Fortuna et al. 2010, Correia et al. 2017). Moreover, a higher prevalence of large bodied frugivores at the mature forest was detected, with some consuming fruits exclusively there. Previous studies reported that specialist frugivores are often large species (>250g) that rely on fruits as a critical resource and live in small groups (Howe 1993, Cramer et al. 2007). The presence of large bodied frugivores along with small bodied ones at the mature forest, contrasts with the edge, where the most important frugivores are small bodied birds. Although network specialization ($H2'$) is slightly higher at the edge, both networks show medium to low scores, which are expected for networks in sub-tropical and tropical ecosystems (Blüthgen & Klein 2011, Schleuning et al. 2011, 2012, Ribeiro da Silva et al. 2015). In the case of the Cantanhez forest, it's possible that the low network specialization is a consequence of the distance between fruiting trees and the low number of trees producing fruits simultaneously, which limits the fruit choice and concentrates fruit consumption in a smaller number of species. With low specialization, the high interaction evenness for both networks comes with no surprise. A more homogenous distribution of the interactions may have impacts on seed dispersal services not accessed by fruit consuming events. Frugivores may be consuming mostly the same plant species and, although niche overlap was low, their roles as dispersal agents might still be complementary (Fleming & Estrada 1993, Schleuning et al. 2011). Seed dispersal for both habitats might differ not by the distribution of frugivores but by their behavior, such as the use of micro-habitats, the distance travelled before seed release, home range size and habitat preferences (Bascompte & Jordano 2007, Schleuning et al. 2011, Morales et al. 2013, Saavedra et al. 2014). An even contribution of species with different morphologies in the mature forest may in the end contribute to a higher quantity and quality of seed dispersal (Saavedra et al. 2014).

Connectance is a network descriptor closely related to specialization, being sometimes interpreted as the degree of generalization or redundancy of the network (May 1972, Dunne et al. 2002, Estrada 2007, Blüthgen et al. 2008). This descriptor follows the same trend as specialization in this study and is slightly higher at the mature forest. Modularity was moderate for both networks, but slightly higher for forest edge. Modularity is an important descriptor when it comes to providing information about network robustness (Schleuning et al. 2011). Modular networks are connected not only by hubs, i.e., species with many interactions, but also by connectors, i.e., species connecting different modules,

so their structure is more sensitive to the removal of species (Schleuning et al. 2011). In this study, low levels of connectance were also detected for both networks, which may be concurrent with the data provided by Fortuna et al., (2010), stating that communities with low connectance will have equal values of modularity and nestedness. These results point to the communities at least at the edge being moderately nested and modular at same time (Fortuna et al. 2010). This pattern has been observed in pollination networks, with the overall network being modular and a nested pattern being detected within its modules (Olesen et al. 2007).

Vulnerability and generality are analogous indices and provide complementary information, regarding the two different levels of the network (Bersier et al. 2002). It is important to consider that these metrics were initially used for plant-parasite networks, with more parasites per plant, resulting in higher network vulnerability (Tylianakis et al. 2007). In the case of plant-frugivore networks, its interpretation is the opposite, with higher vulnerability meaning a higher number of animals providing a dispersal service to each plant. In this case, these results are quite concurrent with low specialization and high interaction evenness found for both networks, but we should take caution in inferring about network vulnerability considering the small network size (Dormann et al. 2009).

Robustness for both frugivores and plants was quite high in the two habitats, although slightly higher at mature forest. High robustness is a common characteristic of various mutualistic networks (Memmott et al. 2004, Mello et al. 2011a), and is usually associated with more nested networks, which allow for different paths for network persistence when a species is removed (Memmott et al. 2004, Bascompte et al. 2006, Bastolla et al. 2009, Thebault & Fontaine 2010, Ribeiro da Silva et al. 2015). High network robustness is also associated with low specialization, due to functional redundancy (different frugivores consuming most of the same fruits) and low modularity (Whitney et al. 1998), which we also detected in this study. It is possible that these results may be associated with the higher fruit availability, higher interaction evenness and generality (mean plant species available per frugivore) that once associated with the differences in the frugivore community and species-specific roles may provide different paths for network persistence in the mature forest.

In conclusion, both networks had low to moderate scores of nestedness, modularity and specialization, and high scores of interaction evenness and robustness to extinctions. Moreover, mature forest had slightly more connectance and interaction evenness, which may be explained by the increase importance of large bodied frugivores. In the future, studies should evaluate the effectiveness of dispersal to open areas, and how it may be impacted by the absence of species that disperse large seeded plant species.

4.2 Network species' roles

The ecological role of a species within a network, is a direct result of its interactions with other species (Luczkovich et al. 2003, Olesen et al. 2007, Allesina & Pascual 2009, Stouffer 2012). The consequences of species extinctions for a network, depend on their role, e.g. an extinction of a module hub may cause its module to fragment with no relevant consequences or cascading impacts on other modules (Prado & Lewinsohn 2004, Stouffer 2012), whereas the extinction of connectors may fragment the networks into isolated modules (Olesen et al. 2007). Regarding module structure, all frugivore species were peripheral, and only the Guinea plum for mature forest and Bark cloth tree for forest edge were found to be connectors, thus connecting distinct parts of the network. The bark cloth tree fruits are >13mm of diameter and fruit mass is >1 gram (Taylor 1960, Hall & Swaine 1981, Kankam & Odoro

2009), and is consumed by a wide range of frugivores from primates to birds (Irvine 1961, Kankam & Oduro 2009). At forest edge, this species was consumed by one of its most relevant frugivores, the common bulbul, and by two large-bodied frugivores also common to the mature forest: Mona monkey and African pied hornbill. Kankam et al., (2009) showed that these three species may handle Bark cloth tree fruits differently: for example, the Common bulbul was registered extracting the pulp and letting the seed fall beneath the parent tree, while turacos such as the Violet turaco (*Musophaga violacea*) seem to be able to ingest the whole fruit (Kankam & Oduro 2009). Primates such as the Campbell's monkey (*Cercopithecus campbelli*), were also recorded consuming fruits of this tree, by storing them in their cheek-pouches and releasing the seed in big amounts in one place few meters away from the parent tree (Kankam & Oduro 2009), and the same behavior has been registered for other primates (Howe 1980, Russo & Augspurger 2004). The Guinea plum is mostly consumed by large bodied frugivores, specially mammals (Campos-Arceiz & Blake 2011, Gross-Camp & Kaplin 2011, Beaune 2012). The Guinea plum's fruits are ellipsoid with 2.5-6cm x 2-4 cm (Catarino et al. 2006) and in this study they were only consumed at mature forest. Previous studies have shown that primates such as Bonobos and Chimpanzees, often remove the mesocarp of this fruit, chew the wedges and spit the seed (Gross-Camp & Kaplin 2011, Beaune 2012). They may walk several meters from the parent tree before spitting the seed. In our study, the Yellow casqued hornbills and the great blue turacos were both recorded consuming fruits from this species. To my knowledge, such event has not been recorded previously, although the Great blue turaco has previously been recorded consuming flowers of this tree (Sun & Moermond 1997). Further studies should explore if these bird species are of relevance for seed dispersal of this tree species. Jordano (1987) postulated that networks are composed of subsets of phylogenetic related species which have similar ecological roles. Mello et al., (2011) found that birds and bats seem to occupy different modules possibly due to differences in their phylogenetic history. That might be the case for some groups, but in this study, both at the mature forest and at the forest edge, I found modules that included both primates and bird species, such as the Yellow casqued hornbills, Mona monkeys and the Temminck's red colobus. Other studies argue that interactions between plants and dispersers are not limited by their phylogenetic history, but rather by morphological and functional limitations (trait-matching), such as their gape width and fruit size (Mello et al. 2014). Probably due to the low richness of fruiting trees observed in these forests, the Bark cloth tree and Guinea plum fruits appear as preferred by many frugivores in these communities, and thus have the ability to connect different modules of these networks.

The relevance of a frugivore for the set of plants and vice versa, varied strongly between habitats, and the only common important species seems to be the Mona monkeys. Regarding plants species, the ones with most impact for frugivores, were bark cloth tree, Fig trees and *S. pustulata* for both habitats. *Ficus* is the most globally diverse woody plant genus (Corner 1988, Berg 1989, Shanahan et al. 2001) and is considered a key resource in tropical forests, sustaining frugivores in periods of low fruit availability (Shanahan et al. 2001). Studies have shown that hornbills and turacos eat this fruit and defecate its seeds intact (Compton et al. 1996, Barlow & Wacher 1997, Whitney & Smith 1998), along with Chimpanzees and monkeys from the *Cercopithecus* genus (Whitney & Smith 1998, Newton-Fisher 1999, Gross-Camp & Kaplin 2011). Bulbuls are also known to regurgitate or defecate them still viable in pellets (Shanahan et al. 2001). In this study, African green pigeons, usually seed predators, were recorded consuming these fruits. Nevertheless, some seeds may survive gut passage even in this species (Lambert 1988), and thus considering their flight ability, seed dispersal services may benefit from their intervention. This adds to studies reporting the dispersal of seeds by species assumed not to be seed dispersers (e.g. seed predators, insectivorous), thus possibly effectively contributing to this process (Heleno et al. 2010a, Cruz et al. 2013, Timóteo et al. 2016, Genrich et al. 2017).

S. pustulata is an evergreen tree, that produces ellipsoid fruits with 1-3cm of diameter (Catarino et al. 2006). There are not many records of frugivores consuming these fruits, but the few available, point to Yellow casqued hornbill, Western piping hornbill and some primates species such as Colobus monkeys as possible dispersers (Whitney et al. 1998, Holbrook et al. 2002). During the sampling period, I found Chimp dung filled with these fruits, and observed birds such as Green turacos and African green pigeons actively feeding on these trees. My results showed that Madina forest remnant was mainly structured by this tree species. This dominance within the Madina forest remnant should be further explored in the context of the effectiveness of the seed dispersal provided.

In the mature forest, large bodied frugivores had the biggest impact on plant species. The Yellow casqued hornbill was the largest bird frugivore registered consuming fruits, and although there aren't many studies on this species specifically, hornbills are well known as important dispersal agents (Whitney et al. 1998, Holbrook & Smith 2000, Kitamura 2011). Yellow casqued hornbill and the Black casqued hornbill (*Ceratogymna atrata*) usually present higher densities in mature forests (Whitney & Smith 1998), and with their large gape width (consuming fruits 36 – 29 mm), home ranges and their ability to fly over degraded areas (Whitney & Smith 1998) may prove crucial for the maintenance of a seed dispersal network by dispersing a wider range of plant species (Whitney et al. 1998). Mona monkeys and Chimpanzees seem to be as important for the plants in the mature forest. A study in the Bia Biosphere reserve in Ghana, showed that both primates deposited seeds in open forest habitats, which in turn experienced high germination and establishment rates (Wrangham et al. 1994, Chapman 1995, Kankam & Oduro 2009). They postulated that even if only few seeds are deposited in these habitats, considering that one primate defecation can contain in average 22 big seed from almost 3 species (Wrangham et al. 1994, Chapman & Chapman 2009), it may still be relevant for maintenance of some fruit plants. Another study has reported that Chimpanzees effectively move seeds between forest patches in western Uganda (Wrangham et al. 1994, Chapman 1995). Big primates often consume big meals of fruits belonging to different tree species, have large home ranges, and even if they seem to prefer matures forests like what was observed in the present study, they may use different stages of regenerating forests (Wrangham et al. 1994).

At the forest edge, weavers and common bulbuls were the most important bird species. Weavers in West Africa and around the world occupy a great variety of habitats and are mostly considered seed predators (Borrow & Demey 2001). Studies have shown that they incorporate fruit in their diet, but there is not enough data regarding their role as potential seed dispersers for trees with small seed such as the figs, which they consumed at the edge in the PNC (Bleher & Böhning-Gaese 2001). Common bulbuls on the other hand have been found to be important dispersers, in two separate studies, one in Kakamega forest in Kenya and the other in South Africa (Compton et al. 1996, Schleuning et al. 2011). This species is associated with a variety of wooded or bushy habitats with usually fluctuating with fruit crop tendencies. Although no relationship was found with fruit availability, they may also occupy forest edges, entering the canopy of primary or old secondary forests according to that availability (Borrow & Demey 2001).

It comes with no surprise that the species with higher K_{risks} scores are somewhat overlapping with the ones found to be the most important for the other level of the network, when using species strength. Bark cloth trees for mature forest had high species strength and present high risks for the network if removed, whereas for the edge, Fig trees seem to be even more important to maintain stability. K_{risk} allows the identification of keys species to preserve most of the giant component, which ultimately is the goal of all conservation strategies (García-Algarra et al. 2017).

4.3 Habitat type and fruit availability

This study showed that induced forest edges affect frugivore species richness, composition and abundance. There was a great overlap in composition of fruit trees between mature forest and edge. However, the number of fruiting trees and fruit availability was higher at the mature forest probably due to the dominance of *S. pustulata* in the Madina mature forest remnant. The frugivore abundance and richness was higher at the forest edge and this pattern has already been found (Menke et al. 2012, Saavedra et al. 2014). However, it contrasts with other findings that partially justified higher frugivore richness and/or abundance with increasing fruit availability (Herrera 1985, Fleming et al. 1987, Bleher et al. 2003, Menke et al. 2012, Chama et al. 2013, Saavedra et al. 2014). The higher presence of frugivores at the edge of the forest may be rather due to the higher permeability this habitat type presents to visiting species more common in opens areas and the farmland surrounding the forest remnants (Menke et al. 2012) and that may in fact be attracted by fruit abundance at the mature forest. As previously observed in the Kakamega forest (Kenya), the three most common bird visitors at the edge in Cantanhez were typical farmland, open woodland and savannah species like weavers (Borrow & Demey 2001, Eshiamwata et al. 2006, Garcia et al. 2010). This pattern may be due to additional factors not accounted for in this study, such as the low vegetation heterogeneity, widely visible trees and even high frugivore diversity in surrounding farmland areas (Galetti et al. 2003, Eshiamwata et al. 2006, Laube et al. 2008, Menke et al. 2012, Saavedra et al. 2014). These results, raise further awareness to the role of forest visitors as seed dispersers along induced forest edges, enhancing the urgency of future studies that explore these patterns (da Silva et al. 1996, Menke et al. 2012).

Regarding frugivore species registered in both habitats, there was an overlap, but the mature forest had more large bodied species and some, such as Yellow casqued hornbill, Western piping hornbill and Temminck's red colobus, fed exclusively on trees from in this habitat. Large bodied frugivores are known to possess large home ranges and long gut passage time (Sun et al. 1997, Yumoto et al. 1999, Holbrook & Smith 2000, Schleuning et al. 2011), to travel long distances, and due to their wider gapes width, consume fruits inaccessible to smaller frugivores (Moran et al. 2004, Cramer et al. 2007). For example, hornbills are among the most important seed dispersers in the tropics, consuming fruits from at least 22% of the existing plant species (Whitney & Smith 1998, Poulsen et al. 2002). As well as hornbills, primates also possess diverse diets and compromise 25% to 40% of the frugivore biomass in tropical forests (Chapman 1995). Although they are more limited in terms of mobility, they possess the dexterity and strength needed to handle different types of fruits (Poulsen et al. 2002). Big dispersers such as these are more susceptible to extinction, considering they are more affected by habitat loss and degradation, and hunting pressures (Corlett 2007, Wright et al. 2007b, Kitamura 2011). Moreover, primates rarely move between fragments especially when those patches are deprived of preferred fruit resources (Schwarzkopf & Rylands 1989, Estrada et al. 1994, Bollen et al. 2004, Ratiarison & Forget 2005, Cramer et al. 2007). Considering this higher prevalence of large bodied frugivores in the mature forest, it is plausible that the quality of the seed dispersal services along the forest edges may be affected due to a reduction in functional diversity of dispersers species and hindering the natural recovery of these areas because they are not attractive to these species (Restrepo et al. 1999, Lehouck et al. 2009, Menke et al. 2012).

4. 4 Implications for Conservation

The results I found for the networks in the CNP, show a lack of large bodied frugivores consuming fruits at the edge of the forest remnants. Moreover, network specialization was low and interaction evenness was high, which points to redundancy and network robustness within forest edge and mature forest. Such characteristics are positive signs for maintenance of plant communities within those habitats, but there is not enough information about how frugivores move from within the mature forest, and how they may act as to help regenerating abandoned fields surrounding the forest remnants.

Previous studies have shown that seed dispersal is a huge driver of the regeneration of several of the studied plants (García et al. 2005, Mendoza et al. 2009, Garcia et al. 2010). In that sense, network studies are useful because they allow access to the whole system, and through their structure reflect how a community is providing the seed dispersal service allowing inferences regarding the redundancy and robustness of those systems (McConkey et al. 2012). Metrics such as nestedness and modularity, reflect how the network is structured, and both are influenced by habitat fragmentation which often leads to lower species abundance (Krishna et al. 2008, Hadley & Betts 2012, Hagen et al. 2012), the extinctions of top frugivores and invasion by hyper-generalists (Aizen et al. 2008). Moreover, metrics such as specialization, niche overlap, and interaction evenness provide information on the redundancy of ecological properties within the network, and although regional temporal fluctuations in resource availability should be considered, they allow inferences on the robustness of networks to extinctions (Chama et al. 2013, Kaiser-Bunbury et al. 2017). Future studies should focus on following changes in these patterns along gradients of fragmentation, to aid in improving the knowledge on how these metrics vary.

However, it is impracticable to propose strategies to preserve or restore forests, without considering the specific roles frugivores play within seed dispersal networks. Especially when considering the continuous anthropogenic pressures acting and changing environmental gradients that affect their behavior (Sanford et al. 2009, Garcia et al. 2010). Although studies have shown that networks are often robust to the loss of frugivores (Jordano et al. 2003, Mello et al. 2011a), little is known about the how efficient is the replacement of ecological roles (McConkey et al. 2012).

The network theory may help identify, hubs and connectors (Donatti et al. 2011, Mello et al. 2011b) as it did for this system. *S. pustulata* and Bark cloth trees are clearly important as connectors, along with fig trees, as highly sought-after fruit resources in both habitats, and thus may be important species to consider in regeneration strategies. As many studies point out, remnant isolated trees in abandoned fields or between once connected forest patches, may act as catalysts for succession, facilitating the re-colonization of the native vegetation (Parrotta 1992, Lugo et al. 1993, Brown & Lugo 1994, Wunderle 1997). Not only they will attract frugivores due to their fruits, they will also attract frugivores that are morphologically different, and thus may have different ecological roles. Moreover, they will influence microclimate and soil fertility, suppressing dominant grasses (Parrotta 1992), potentiating seed dispersal effectiveness. Seed rain seems to be significantly higher below perches comparing to empty sites (Wunderle 1997). In that sense, it would be useful to consider including a tree nursery for species that have the most impact, in a reforestation project for abandoned areas surrounding the PNC forest remnants.

Regarding frugivores, I was able to detect which poses greater risks if extinct, using metrics such as species strength and K_{risk} . These metrics allow inferences on how species composition may alter the seed dispersal services provided. In this study, large bodied frugivores, such as the Yellow casqued hornbill and Mona monkeys, were pivotal frugivores in the mature forest. The network role of large frugivores may shed light on how degraded habitats around the world, are performing or evolving through time in relation to relatively undisturbed habitats. Although there is little understanding on how frugivore species abundance and density may influence their seed dispersal service (Schupp et al. 2010,

McConkey et al. 2012), it may be important to consider performing surveys not only on their mature forest presence, but also on their movements between forest remnants and towards forest edges (García et al. 2010).

Species level metrics are of great importance and should be combine in future studies, in order to better understand ecological roles within the network (species roles – (Olesen et al. 2007, Stouffer 2012)), the impact of a specific species on the other set (species strength – (Bascompte et al. 2006)) and finally by ranking them according to vulnerability to possible extinction scenarios (K_{risk} – (García-Algarra et al. 2017)). Being able to identify the most relevant species for the seed dispersal service, such as *C. elata* and *C. mona.*, allows the elaboration of specific legislation to protect them,

It is important to use behavioral studies and integrate that information in network approaches. Assessing frugivores' home ranges and gut passage times is crucial to understand their impact on this service. Moreover, nocturnal frugivores such as bats should also be accounted for, due to their confirmed importance and role as seed dispersers (Fleming & Heithaus 1981, Gorchov et al. 1993, Galindo-González et al. 2000, Galindo-González & Sosa 2003, Abedi-Lartey et al. 2016). Studies such as this, should lead to follow up research, on the effective role of network frugivores as dispersers, using seed traps or netting to understand who crosses the edges, and what seeds arrive at open and abandoned areas surrounding forest remnants.

Finally, conservation measures and directives should use the knowledge and culture of human communities integrated in natural reserves such as the PNC, and work alongside them to ensure and reinforce sustainable agriculture practices and to find a balance that allows the coexistence and persistence of natural processes. Increased park surveillance and monitoring is still crucial to control hunting practices and guarantee the prevalence of reforestation measures if ever implemented. Several forest and trees in the PNC, such as *S. pustulata*, White silk cotton tree and the Velvet Tamarin, have symbolic or religious meaning (Frazão-Moreira 2001, Sousa & Frazão-Moreira 2010). As for animals, chimpanzees are considered important due to their like human-like appearance, which inhibits hunting by the community (Sousa et al. 2011, Hockings & Sousa 2013). Such information may prove useful and should be assessed in parallel with network studies for the design of forest restoration measures. The best strategy is to add what is known of networks hubs and connectors for plant and frugivore species, to the regional and cultural context of the study site, to propose measures that allow the enhancement of seed dispersal service.

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