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The role of avian seed dispersal in forest regeneration on degraded areas of a sub-humid forest in Guinea-Bissau (West Africa)

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RESUMO ALARGADO

As florestas tropicais albergam grande parte da biodiversidade terrestre, no entanto, a sua área de ocupação está a diminuir a um ritmo acelerado e preocupante. Resultado de uma crescente pressão antropogénica, o abate de manchas de floresta nativa e da sua conversão em terrenos agrícolas é recorrente. Simultaneamente, as terras anteriormente cultivadas começaram a ter períodos de pousio mais curtos, inviabilizando a regeneração natural da fertilidade dos solos. Desta forma, a sucessão natural da floresta nas áreas degradadas dá-se de uma forma lenta e depende em grande escala dos movimentos de animais frugívoros, tais como as aves, para a dispersão de sementes provenientes do interior da floresta.

Diferentes espécies de frugívoros podem diferir drasticamente na sua capacidade de dispersão, dependendo do seu grupo taxonómico, de traços ligados à sua história de vida, da sua morfologia ou do seu comportamento de alimentação. Para além disso, a estrutura da paisagem tem um papel fundamental na atracção dos dispersores. A disponibilidade de poisos, a complexidade estrutural da vegetação e a presença de recursos alimentares, especialmente de frutos, são exemplos de características relevantes que podem aumentar o número de visitas por frugívoros, facilitando a recolonização e a regeneração das áreas degradadas. Por outro lado, a eficácia da dispersão de sementes por animais pode ser limitada pelo grau de isolamento à fonte de sementes, pela ausência de dispersores na região, pelo tamanho das sementes ou mesmo pela predação das próprias sementes pelo dispersor. A disrupção da relação mutualista entre plantas e animais dispersores de sementes, em consequência da degradação da floresta e das alterações no uso do solo pelo Homem, pode condicionar o futuro das florestas tropicais.

Uma longa história de ocupação humana do continente Africano levou a um ritmo alarmante de perda de floresta e, particularmente na Guiné-Bissau, a agricultura familiar e a conversão de floresta em plantações de caju têm vindo a transformar a vegetação do país. Actualmente, é possível encontrar pequenas manchas residuais de floresta sub-húmida e seca semi-decídua em razoável estado de conservação na região sudoeste da Guiné-Bissau, no Parque Nacional de Cantanhez (PNC). Identificar e compreender os mecanismos pelos quais a floresta poderá regenerar naturalmente nas áreas degradadas, nomeadamente através da dispersão de sementes por aves, são tópicos chave de conservação não só para as florestas do PNC, como também para a generalidade das florestas de África Ocidental.

Este estudo tem como principal objectivo contribuir para o conhecimento do papel da dispersão de sementes por aves nas áreas degradadas do PNC e propor medidas de gestão que promovam a presença de aves dispersoras, nestes locais, de forma a que a regeneração natural e a conservação das florestas seja potenciada.

Para concretizar estes objectivos, identificaram-se as espécies de plantas que estão a ser dispersadas desde o interior da floresta, até às áreas degradadas. Para isso, foram montadas 120 armadilhas de sementes, em 24 talhões, nas áreas degradadas circundantes de duas manchas de floresta madura (Lauchande e Madina), de forma a recolher excrementos e a identificar as espécies de plantas das sementes neles contidas. Registaram-se, adicionalmente, as características da vegetação presente em cada talhão e para cada armadilha de sementes, de forma a perceber os factores que poderão influenciar a deposição de sementes nestes locais. Para averiguar a viabilidade das sementes que chegam a estas áreas e perceber se podem potenciar a regeneração da floresta, realizaram-se testes de germinação em laboratório. Para além disso, identificaram-se e quantificaram-se as aves potenciais dispersoras de sementes presentes nas mesmas áreas, através da realização de 64 pontos de observação. Foram realizadas observações ao amanhecer e ao entardecer, num total de 149.5 horas, em árvores de diferentes famílias e em áreas abertas. Em cada ponto de observação foram registadas as características da árvore

e da paisagem, de forma a identificar as características destas áreas que poderão influenciar a presença das diferentes espécies de potenciais dispersores nestes locais.

No total, foram recolhidos 166 excrementos, sendo que cerca de 28% continham sementes. A altura das árvores, por baixo das quais se montaram as armadilhas, revelou ter uma importante influência na deposição de excrementos e de sementes, sendo que árvores mais altas apresentaram maiores abundâncias de ambos. Árvores mais altas deverão ser pousos importantes para as aves, uma vez que oferecerem uma maior proteção contra predadores e também melhores oportunidades de alimentação. Para além disso, foi encontrada uma relação positiva entre a abundância de excrementos e talhões com uma maior complexidade da vegetação, implicando também um maior número de árvores médias e altas no local. Reforçando este resultado, as árvores da família Bombacaceae, que são tipicamente árvores altas e com grandes copas, parecem favorecer a deposição de excrementos em áreas degradadas. Por outro lado, a relação positiva entre a abundância de excrementos e árvores da família Moraceae pode ser explicada pelo facto destas árvores possuírem frutos que atraem uma grande diversidade de dispersores, o que sugere que as árvores de fruto são importantes focos de recrutamento de sementes.

Foram contabilizadas um total de 4747 sementes e confirmada a dispersão de, pelo menos, 225 das mesmas. Foram encontrados 12 morfotipos diferentes, em que se identificaram três espécies ou géneros de árvores pertencentes ao interior da floresta, nomeadamente *Ficus* sp., *Strombosia pustulata* e *Zanthozylum* sp. A maior parte das sementes que está a ser depositada nas áreas degradadas são pequenas sementes e cerca de 73% das mesmas pertencem ao género *Ficus*. Isto pode ser justificado pelo facto de espécies de plantas pioneiras, possuírem geralmente sementes mais pequenas. Para além disso, as sementes maiores têm restrições acrescidas na sua dispersão, dependendo de aves com um maior tamanho corporal e maior abertura do bico, ou seja, da presença de uma maior diversidade de dispersores nas áreas degradadas. No final dos testes de germinação, apenas as sementes do género *Ficus* germinaram. Este resultado era esperado, uma vez que muitas aves conseguem dispersar as suas sementes de forma viável e não implica que, dadas as condições favoráveis no seu habitat natural, as restantes sementes não tivessem capacidade de germinar e revelar potencial de regeneração.

Quanto aos potenciais dispersores de sementes, foram identificadas 21 espécies ou géneros de aves nas áreas degradadas do PNC. As espécies mais abundantes foram os tecelões (*Ploceus* sp.), os pombos-verdes-africanos (*Treron calvus*) e as rolas (*Streptopelia* sp.). No entanto, estes não deverão ser os dispersores mais eficientes, uma vez que são considerados predadores de sementes e, provavelmente, apenas uma pequena percentagem de sementes por eles ingeridas poderão ser excretadas de forma viável. Assim sendo, os bulbuls (Pycnonotidae), os estorninhos-de-dorso-violeta (*Cinnyricinclus leucogaster*) e os calaus (Bucerotidae), surgem como os potenciais dispersores de qualidade mais abundantes nas áreas degradadas do PNC. Tendo em conta que os calaus são mais dependentes de floresta não perturbada, poderão ter um papel mais importante enquanto dispersores junto à orla da floresta. Por outro lado, os bulbuls e os estorninhos-de-dorso-violeta visitam regularmente o interior da floresta, no entanto, não dependem dela totalmente, o que poderá fazer com que tenham um papel importante na dispersão de sementes do seu interior para as áreas degradadas.

Mais uma vez, árvores altas parecem favorecer a presença de potenciais dispersores importantes nas áreas degradadas do PNC, tais como os bulbuls, os estorninhos-de-dorso-violeta e espécies especialistas de floresta, tais como os calaus e os turacos (Musophagidae). Para além disso, as árvores da família Moraceae, tais como as figueiras (*Ficus* sp.) e o pó-de-bicho (*Antiaris toxicaria*), favorecem uma maior riqueza de espécies e uma maior abundância de aves de maior porte nas áreas degradadas, talvez por possuírem frutos considerados valiosos para uma grande diversidade de frugívoros. Assim sendo, é importante que as comunidades locais sejam encorajadas a deixar estas e outras árvores de fruto nativas nas áreas degradadas, na eventualidade de existirem novos cortes de vegetação. Em áreas severamente

degradadas, poderá ser necessária uma plantação direta de algumas árvores de fruto nativas que sejam interessantes para as aves, tais como as acima mencionadas. No entanto, isto deve ser feito de forma cautelosa, uma vez que as árvores de fruto que são normalmente plantadas nestes locais pertencem à família Anacardiaceae, que não parecem ter uma influência positiva na generalidade dos dispersores.

Por fim, este estudo fornece uma importante visão geral de uma função-chave do ecossistema nas florestas do PNC: a dispersão de sementes pelas aves. Este primeiro passo para a compreensão de mecanismos que podem promover a regeneração natural das florestas, é importante não só para as florestas da Guiné-Bissau, mas também para as florestas da África Ocidental em geral, onde os fatores antropogénicos que afetam as florestas são semelhantes.

Palavras-chave: Frugivoria; Aves; Dispersão de sementes; Regeneração florestal.

ABSTRACT

Human action has been shaping the landscape of tropical regions with increasing deforestation rates and conversion of forest patches into agricultural land. Natural forest succession in degraded areas is slow and depends largely on the movements of fruit eating animals, such as birds, which disperse seeds from the forest interior. However, forest fragmentation and isolation limit the process of seed dispersal and the reduced number of dispersers present in degraded areas can abridge the future of tropical forests. In Guinea-Bissau, slash-and-burn agriculture and the conversion of forest into cashew tree orchards are the main threats to this country's forests. In the present days, mature sub-humid forest can only be found in the south-western region of the country, in Cantanhez National Park (CNP).

The main goal of this study is to understand the role of seed dispersal by birds in degraded areas of CNP and to contribute with management measures that promote their presence in these areas, so that natural regeneration and conservation of forests is improved.

To achieve this, I aimed to determine which plant species are being dispersed from mature forest to degraded areas and understand whether dispersed seeds are viable and can potentiate forest regeneration. Seed traps were assembled in degraded areas to collect bird droppings and seeds. After identification, seeds were subjected to germination trials in the lab. In order to identify potential avian seed dispersers and the landscape elements that attract different dispersers to these areas, focal points were conducted at dawn and dusk, in trees of different species and in open fields. Landscape and tree elements that may influence the presence of birds in these areas were measured and registered.

Twenty-one bird species were identified as potential seed dispersers. Weavers (*Ploceus* sp.), the African Green-pigeon (*Treron calvus*) and doves (*Streptopelia* sp.) were the most abundant, even if probably not the most efficient. Recognized as good dispersers and also abundant in the area, were Bulbuls, Violet-backed starlings and Hornbills. The first two are considered forest visitors, seeming to benefit from taller trees. Tree height, is also an important driver of faeces and seed deposition and tall trees offer better predator lookouts, foraging opportunities. Hornbills are known to disperse a wide variety of seeds, including large ones, but seem to have a greater impact on forest regeneration near forest edges.

Active management actions to promote forest regeneration in degraded areas should encourage that scattered native trees or small patches of trees are left in the degraded areas. Tall and large trees such as trees belonging to the Bombacaceae family should be favoured, but the presence of any perch has been proven to be beneficial to attract seed dispersers and increase seed deposition. The presence of native fruit trees, such as Fig trees (*Ficus* sp.) and Bark Cloth trees (*Antiaris toxicaria*), and a higher vegetation complexity also seem to attract a wider diversity of dispersers and increase faeces and seed deposition and should thus be promoted. These management actions should enhance seed dispersal functions and contribute for the regeneration and conservation of forests of the CNP and elsewhere in West Africa.

Keywords: Frugivory; Birds; Seed dispersal; Forest regeneration.

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1. INTRODUCTION

1.1. General background information

Tropical forests sustain the largest biodiversity reservoir on Earth and provide crucial ecosystem services, playing a major role in the carbon and hydrological cycles, as well as providing essential resources for human communities (Fearnside 2000; Foley et al. 2005). Unfortunately, these forests are facing unprecedented pressures and degraded tropical landscapes are expanding as deforestation and changes in land-use increase due to anthropogenic pressure (Parrotta et al. 1997; Geist & Lambin 2002; Mayaux et al. 2005). With the expansion and growth of human populations in these areas, there is an increasing demand for agricultural land, a greater intensification of farmland production and overexploitation of natural resources (Foley et al. 2005; Laurance et al. 2014; Malhi et al. 2014). As a result, we have increasingly fragmented natural ecosystems consisting of smaller, isolated forest fragments separated by a mosaic of human-altered land (Haddad et al. 2015).

Traditional agricultural practices contributed for the maintenance and sustainability of agricultural fields, which were often left fallow to recover nutrients and potential production quality, allowing the natural succession of native vegetation after agricultural fields were abandoned (Brown & Lugo 1994). However, with increasing intensification of agriculture, the resources needed for forest regeneration and succession, such as seed banks, are often depleted (Brown & Lugo 1994; Duncan & Chapman 1999). Thus, after agricultural surrender the process of natural forest regeneration occurs more slowly and depends largely on the arrival of seeds from the forest interior, which are disseminated to these degraded areas either by frugivorous animals or by the wind (Brown & Lugo 1994; Nepstad et al. 1996; Duncan & Chapman 1999).

Seed dispersal is a fundamental process for the natural regeneration and restoration of forests (Wunderle Jr 1997), such that plants have adapted seed structures in several ways to both abiotic and biotic dispersal (van der Pijl 1982). In tropical regions, about 80% of tree species depend on mutualistic interactions with frugivorous animals to disperse their seeds (Howe & Smallwood 1982). These seeds are generally adapted to internal (endozoochory) or external (epizoochory) animal dispersal (van der Pijl 1982). In these regions, birds are recognized as one of the predominant animal vectors for seed dispersal of pioneer tree species, playing an important role in seed recruitment and establishment (Peña-Domene et al. 2014).

Birds can disperse seeds to favourable recruitment sites (Howe & Smallwood 1982; Wenny & Levey 1998), allowing the colonization of new areas. This increases the success of seedling establishment and growth by avoiding intraspecific competition near the parent plant and high mortality rates due to predation and acquisition of pathogens (Janzen 1971; Howe & Smallwood 1982). Furthermore, seed dispersers may also improve the germination and survival of seeds they defecate, regurgitate or bury (Howe & Smallwood 1982; Heleno et al. 2011; Lenz et al. 2011), through scarification, depending on the way they handle fruits and their gut passage time (Traveset 1998). Recolonization of degraded areas is thus facilitated by the action of these vector species, and plant diversity can potentially be slowly restored (Wunderle Jr 1997; Bleher & Böhning-Gaese 2001). However, it is important to highlight that not all dispersed seeds result in recruitment (Schupp 1993). Some bird species are considered seed predators since they may destroy most of the seeds they ingest (Janzen 1971; Traveset 1998). Moreover, even if seeds arrive to a favourable site, these can be predated by insects, rodents or other species (Nepstad et al. 1996; Holl & Lulow 1997).

Efficient seed dispersers must be able to cover large distances after visiting forested habitats and cross degraded areas that separate forest fragments (Lenz et al. 2011). However, different frugivores may drastically differ in their dispersal ability, depending on their morphology, life history traits, flight capacity or even foraging behaviour (Spiegel & Nathan 2007). For instance, larger birds are expected to move and forage over larger areas, having greater home-ranges (Jetz et al. 2004) and holding potential for long distance dispersal (Levey 1987). In addition, different species hold different levels of dependency upon relatively undisturbed forest (Bennun et al. 1996). Forest specialists rarely visit the outside of undisturbed forests and hence offer limited dispersion services to these areas, whereas forest generalists frequently move between different habitat patches, becoming more interesting dispersers in degraded areas (Wunderle Jr 1997).

Some landscape structures play a crucial role in attracting dispersers. Seed dispersers are generally not attracted to degraded areas since these usually provide few perches for resting, and offer no protection from predators and poor foraging opportunities, having low fruit diversity and availability (Da Silva et al. 1996; Wunderle Jr 1997). This way, the effectivity of the mutualistic relation between plants and animal seed dispersers can be disrupted, as a consequence of human land-use changes that cause deforestation, forest degradation and fragmentation (Cordeiro & Howe 2003). This can further constrain the future of tropical forests, altering their community structure and dynamics (Bleher & Böhning-Gaese 2001), decreasing habitat heterogeneity and slowing ecological succession processes (Terborgh et al. 2008; Markl et al. 2012; Peña-Domene et al. 2014).

During the formation of an agricultural field, native vegetation is generally cut down and burned. However, some trees of large size are frequently left in the fields as they are more difficult to remove, provide shade to crops and sometimes hold an economical or cultural value for local human communities (Lawson 1966). These trees in degraded areas can act as important seed recruitment foci, enhancing forest succession (McDonnell & Stiles 1983; Guevara et al. 1986; Holl et al. 2000, 2013). Likewise, other landscape elements may have an equally attractive effect for dispersers and it is important to identify them to create efficient management strategies, that may use natural mechanisms to provide a faster regeneration of forests. Despite the fast rate of deforestation in the tropics, there are still large areas of degraded land that hold recovery potential, making it urgent to take management measures to restore biodiversity of these areas and, in this way, preventing the loss of important ecological functions (Lamb et al. 2005).

1.2. The sub-humid forests of Guinea-Bissau

A long history of human occupation in the African continent, has led to an alarming rate of forest loss (Poorter et al. 2004). In Guinea-Bissau, the slash-and-burn agriculture and the conversion of forest into cashew tree (*Anacardium occidentale* L.) orchards in the last decades have been modelling vegetation cover, leaving primary or old secondary forest restricted to residual patches (Catarino et al. 2001, 2008; Oom et al. 2009). It is in the south-western region of Guinea-Bissau, in Cantanhez National Park (CNP), that remnants of sub-humid and dry semi-deciduous forests in reasonable state of preservation can be found (Catarino et al. 2001). However, prior to the declaration of Cantanhez as a National Park in 2008, there was also a marked trend of deforestation and forest degradation with the transition of closed to open forest (Oom et al. 2009).

Historically, the forest patches in this region have been protected and conserved largely due to the presence of ethnicities that limited the access to the densest forests as well as low population densities (Temudo 2009). As the human population grows and the demand for food increases, larger areas of native forest are being converted to farmland, while previously farmed lands have shorter fallow periods

and natural regeneration of soil fertility is not allowed (Catarino et al. 2001). Moreover, economic instability and the “land laws” that emerged in the 1980s generated insecurity regarding land ownership, which has led to an increased pressure on the forest. Deforestation for the plantation of fruiting trees, emerged as a strategy to claim individual property rights to land (Temudo 2009; Sousa et al. 2015) and cashew trees were widely used due to their favourable characteristics, such as easy propagation, rapid growth and production of fruits with market demand (Temudo 2009). Monocultures of this species have been dramatically increasing over the years, replacing what were former patches of forest and fallow land (Oom et al. 2009; Catarino et al. 2015; Sousa et al. 2015). Although it is recognised that these orchards can potentially conserve viable seed banks for forest recovery (Sousa et al. 2015), the management actions of these cultures imply the annual cutting of lower vegetation layers, which can eventually lead to exhaustion of seed banks (Catarino et al. 2015). Consequently, there is a gradual reduction in exploitation sustainability of forested ecosystems.

Identifying and understanding the natural mechanisms through which forests can naturally regenerate, namely seed dispersal by animals, are key issues to their conservation, not only for Cantanhez National Park forests, but also for West African forests in general. Up to date, in Guinea-Bissau, studies focused on frugivory have been biased towards the diet of primates (Bessa et al. 2015), however no data on seed dispersal have been collected so far. This highlights the urgency of studying the role of bird seed dispersal in native forest regeneration in these degraded areas.

1.3. Aims

Restoring forested habitats in degraded areas by natural processes, like seed dispersal, may depend on the appropriate management of areas that were once forested and were later converted into farmlands, orchards and occasionally left fallow or abandoned. To achieve this, we need to understand (1) the potential importance of seed dispersal by birds in the natural regeneration of forests in degraded areas and (2) how some manageable landscape features may promote seed dispersal by birds into these areas.

In order to meet this general objective, this study encompasses three specific objectives:

- (1) Determine which plant species are being dispersed from mature forest patches to degraded areas and understand if the dispersed seeds are viable and can efficiently contribute to forest regeneration;
- (2) Identify bird species that venture out of the forest to degraded areas and that can be potential seed dispersers;
- (3) Identify the landscape elements that can attract different dispersers to degraded areas.

My ultimate aim was to integrate the results and provide recommendations for the best management practices in degraded areas of Cantanhez National Park. These recommendations should promote the presence of avian dispersers in degraded areas and potentiate natural regeneration and conservation of forests.

2. METHODS

2.1. Study area

The study area, Cantanhez National Park (CNP), is located in the administrative region of Tombali (Latitude 10°55'–12°45' N and Longitude 13°37'–16°43' W), sector of Bedanda, in south-western Guinea-Bissau, West Africa, and comprises an area of 1067.67 Km². The climate in this region is characterized by two distinct seasons, the dry season, which begins in November and lasts until May, and the rainy season, from the end of May or early June to October. Annual rainfall varies between 2200 and 2600 mm (Tassin 1988) and the mean annual temperature is 26.5°C. The mean annual relative humidity varies, accordingly to the rain regime, from 69 to 79% (Catarino et al. 2008).

Although soils are poor in Guinea-Bissau, the most complex vegetation formations can be found in the ferralsols of CNP, where patches of Guinean sub-humid mature forest remains (Catarino et al. 2001). These forests are threatened and their area has been decreasing (Oom et al. 2009) mainly due to slash-and-burn agriculture and the conversion of forested areas into cashew plantations (Catarino et al. 2001).

The fieldwork was conducted during the dry season, between January and March of 2018. Degraded areas or, in other words, areas that were forested in the past and were converted into farmland and orchards and sometimes abandoned, were sampled in the surrounding areas of two forest patches, namely Lauchande and Madina (Fig. 2.1 and Fig. 2.2).

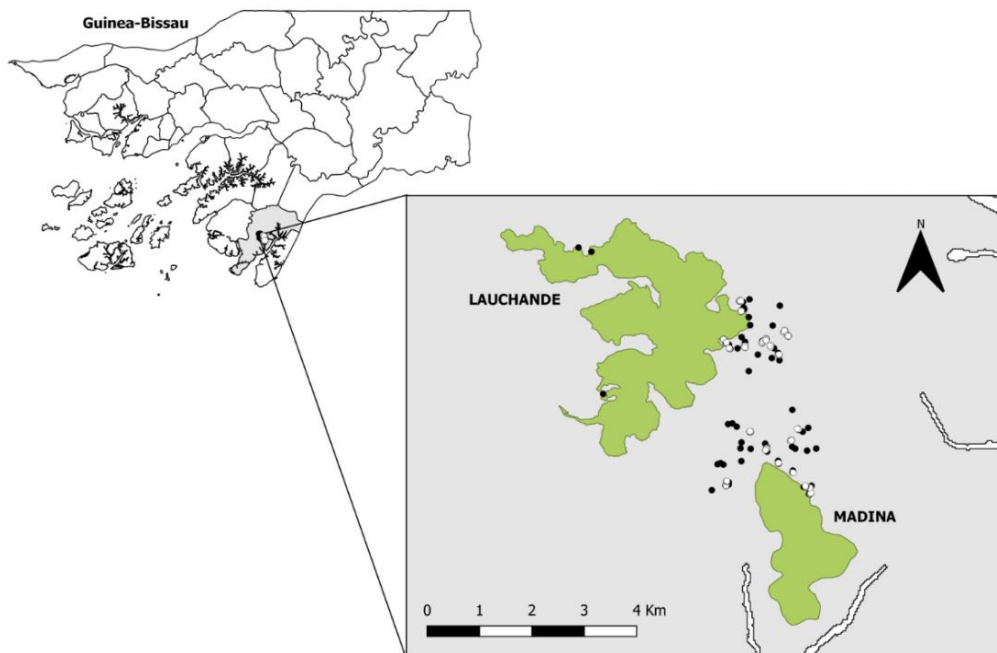


Figure 2.1 - Map of the study area. Cantanhez National Park is highlighted with a grey colour, Lauchande and Madina forest patches are highlighted in green and observation focal points and seed trap locations are identified by black and white dots, respectively.

2.2. Data collection

2.2.1. Reference seed collection

Numerous herbarium samples have been collected and preserved for CNP forests, yet a reference seed collection is still missing to this day. In the interest of comparing seeds of tree species fruiting at the time of the study in the forest interior, with those arriving at degraded areas, a seed reference collection was built. To this aim, paths were walked in the interior of the two forest patches to collect specimens. Along the paths, fruiting trees were located and identified five meters to each side of the path. Samples which included stems, leaves and fruits (or flowers) were carefully collected. Additionally, every individual was photographed to facilitate its future identification and to record the colour of specimens, which fades over time in the herbarium after the drying process.

Collected specimens were dried inside newspaper sheets, alternated with corrugated cardboard sheets that worked as ventilators. Then these were kept inside a metal press and tightened with straps. In order to accelerate the drying process, the press was regularly placed under sunlight or, when available, inside a cloth funnel connected to a fan heater. Bulky items, such as fleshy fruits, were also dried according to this process, after which the dried fruits were placed inside paper envelopes within plastic containers filled with silica gel (Heithaus et al. 1975).



Figure 2.2 – Image representing the forest edge of Lauchande and adjacent degraded areas.

2.2.2. Seed dispersal

To determine which plant species are being dispersed from mature forest to degraded areas, seed traps were used to sample the seed rain within several degraded areas. These were located up to a maximum distance of 1km from the edge of the forested areas of Lauchande and Madina (Fig. 2.1).

Twenty-four plots were defined, equally divided between the degraded area surrounding each forested area. Each plot had approximately 50x50m and were located at different distances to the closest forest edge. Five seed traps were placed haphazardly inside each plot (Duncan & Chapman 1999; Stone et al. 2017), making a total of 120 seed traps deployed. Seed traps consisted of a polyester cloth, with a

collection area of 0.75m² (1m x 0.75m) (Stone et al. 2017) and were elevated in wooden poles 0.8m tall to reduce seed predation (Chapman & Chapman 1999).

The outlines of the forest patches of Lauchande and Madina were defined using a satellite image in QGIS software version 2.14.0, and the minimum distance from each seed trap to the nearest forest patch was measured using the Nearest Neighbour Join (NNJoin) plugin in the same software. In addition to distance, the habitat in each plot was thoroughly characterized according to vegetation structure and composition (percentages and mean height of herbaceous and shrub stratum, and percentage of bare soil), tree height and tree phenology (Gautier-Hion & Michaloud 1989; Bleher et al. 2003; Watson et al. 2004). These notes were used to develop a vegetation complexity index (check section 2.3.1).

Moreover, to distinguish fruits and seeds handled by birds from those that fell from the parent plant (Gorchov et al. 1993), each seed trap was individually characterized by the presence or absence of tree canopy directly above the trap, tree species, tree height, tree phenology and distance to other trees. The description of variables used for the characterization of plots and seed traps is summarized in Table 2.1.

Table 2.1 - List of variables used for seed trap and plot characterization.

Acronym	Variable Description	Type	Range	Source
Traps				
Closest_edge	Distance from each seed trap to the closest forest edge	Continuous	0 – 851 (m)	GIS data
PA_tree	Presence or absence of tree above the seed trap	Binary	0 – 1	Field data
TreeHeight	Height of the tree above the seed trap	Continuous	0 – 40 (m)	Field data
Fam	Family of each tree above the seed trap	Categorical	AA: Empty fields Anac: Anacardiaceae Apoc: Apocynaceae Arec: Arecaceae Bomb: Bombacaceae Chry: Chrysobalanaceae Gent: Gentinaceae Mora: Moraceae	Field data
Closest_dist	Distance from each seed trap to the closest tree	Continuous	0 – 50 (m)	Field data
Plots				
SpFrut	Presence or absence of fruiting trees in the plot	Binary	0 – 1	Field data
SpFlow	Presence or absence of flowering trees in the plot	Binary	0 – 1	Field data
IndVeg	Vegetation Complexity Index in the plot	Continuous	-1.3 – 0.9	See section 2.3.1.

The seed traps were set up in two different periods, each one lasting between 24 and 26 days, making a total of 50 sampling days. Traps were monitored every two days, alternating between sampling areas (Duncan & Chapman 1999), to collect faecal samples and prevent seed removal by ants and rodents.

All faecal samples were kept separate and stored in individually labelled porous paper envelopes, which were placed under sunlight or, when available, inside a cloth funnel connected to a fan heater, to start the drying process. Afterwards, the paper envelopes were placed inside waterproof plastic containers filled with silica gel (Heithaus et al. 1975). Seed identification in the lab, was made using the seed

reference collection, specific bibliography (e.g. Catarino *et al.* 2008) and the herbaria collections of the former Tropical Research Institute (LISC, Lisbon University).

After seed identification, germination trials were carried out on seeds collected from the faeces, to confirm their viability and regeneration potential (Compton *et al.* 1996). Seed surface was sterilized using a treatment of ethanol 70% for two minutes and then Sodium hypochlorite (NaOCl) 2.5% for five minutes. Seeds were rinsed with distilled water between and at the end of these treatments (A. Silva pers. comm.). The trials were carried out in a greenhouse (25°C during the day and 18°C during the night period) and the seeds were placed in Petri dishes with filter paper and kept moist with distilled water (Compton *et al.* 1996; Galindo-González *et al.* 2000). The fungi development was closely monitored to ensure that seeds were transferred to a new Petri dish as soon as contamination was detected, avoiding seed mortality. Seed germination dates were determined by the emergence of a rootlet (Spiegel & Nathan 2007).

2.2.3. Dispersal agents

To identify bird species and quantify the frugivore activity on degraded areas, observations were made at point locations haphazardly distributed within 1km of the forest edges of Lauchande and Madina.

Focal point observations were performed, rather than transects, to minimize disturbance and avoid affecting animal behaviour. To evaluate which landscape elements could potentially attract dispersers to degraded areas, a tree was chosen for observation in each focal point. For each tree, its coordinates were registered, along with the variables summarized in Table 2.2. Fifty-six isolated trees from twelve species and eight different empty fields were selected for the focal point observations, totalling 64 different locations. To simplify data analysis and reduce the total number of classes, tree species were grouped in their seven families: Anacardiaceae, Apocynaceae, Arecaceae, Bombacaceae, Chrysobalanaceae, Leguminosae (Fabaceae) – subfamily Mimosoideae and Moraceae (Tab. 2.3).

Table 2.2 - List of variables used for the characterization of focal points for the observation of potential seed dispersers.

Acronym	Variable Description	Type	Range	Source
TreeHeight	Tree height	Continuous	0-40 (m)	Field data
Fam	Tree families	Categorical	See Table 2.3	Field data
Frutif	Fructification state	Categorical	0: Not fruiting nor flowering 1: Flowering 2: Fruiting	Field data
Closest_edge	Distance to the closest forest edge	Continuous	0-1114 (m)	GIS data
Closest_dist	Distance to the closest tree	Continuous	0-45 (m)	Field data
Closest_height	Height of the closest tree	Continuous	3-40 (m)	Field data
Max_height	Height of the tallest tree nearby	Continuous	10-40 (m)	Field data

Each tree was watched at approximately the same distance by the observer, guaranteeing an unobstructed view of the tree and all birds that flew over or perched on it. Bird species (or genus), as well as group size and behaviour were recorded (Compton *et al.* 1996; Borrow & Demey 2014).

Focal points were carried out during two distinct periods, corresponding to birds' peaks of activity. The first period started shortly after dawn (7-11 am.) and the second period of observation comprised the three hours preceding sunset (4-7 pm.) (Chapman & Chapman 1999). Thirty minutes were spent at each

focal point. Birds were observed using binoculars and the point counts only started a few minutes after arrival, to minimize possible disturbance after the observer's arrival to the site on bird behaviour.

Four focal points were carried out each day and the points made during the morning period were repeated in the afternoon, totalling 149.5 hours of observations. In addition, a total of 64 different focal points was sampled and repeated throughout all sampling period (Table 2.3), between the 27th of January and the 17th of March, aiming to follow the evolution of the flowering and fruiting state of each tree.

Table 2.3 – Tree species and families sampled during focal points and number of times each family was sampled during field work. Vernacular names are presented in Creole. The table also summarizes species' origin in Guinea-Bissau.

Acronym	Tree Family	Tree Species	Common Name	Vernacular Name	Origin	Nr of Samples
AA	-	-	Empty fields	-	-	19.5
Anac	Anacardiaceae	<i>Anacardium occidentale</i> L.	Cashew tree	Cadjú	Introduced	29
		<i>Mangifera indica</i> L.	Mango tree	Mango	Introduced	
Apoc	Apocynaceae	<i>Alstonia boonei</i> De Wild.	Alstonia	Tagara	Native	14.5
Arec	Arecaceae	<i>Elaeis guineensis</i> Jacq.	African Oil Palm	Palmera	Native	17
Bomb	Bombacaceae	<i>Ceiba pentandra</i> (L.) Gaertn.	Kapok tree	Poilão	Native	21
Chry	Chrysobalanaceae	<i>Parinari excelsa</i> Sabine	Guinea Plum	Mampatás	Native	12
Mimo	Leguminosae (Fabaceae) – Mimosoideae	<i>Albizia adianthifolia</i> (Schumach)	Flat-crown Albizia	Farroba-de-lala	Native	15
Mora	Moraceae	W. F. Wight <i>Antiaris toxicaria</i> Lesch.	Bark Cloth tree	Pó-de-bicho	Native	21.5
		<i>Ficus dicranostyla</i> Mildbr.	Fig tree	Pó-de-leite	Native	
		<i>Ficus elasticoides</i> De Wild.	Fig tree		Native	
		<i>Ficus glumosa</i> Delile	Fig tree		Native	
		<i>Ficus polita</i> Vahl	Fig tree		Native	

2.3. Data analysis

2.3.1. Seed dispersal

In order to evaluate which variables better explain the arrival of faecal samples to each seed trap, an analysis using Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution and a log link function, was carried out. The number of seeds per seed trap was too small to carry out an analysis at this level, thus, careful considerations were made based on the spearman correlations between the number of seeds and all predictor variables, also considering the consistency of these results with the results for the faecal samples models. In addition, the relation between faecal samples or seed abundance and each tree family was evaluated using an analysis of variance (ANOVA) with a Tukey post-hoc test.

The vegetation complexity index, one of the variables considered in these models, was obtained using a data ordination technique named Detrended Component Analysis (DCA), which allowed to extract patterns of variation and thus find a gradient of complexity in the data (Hill & Gauch 1980; Skowno & Bond 2003). Variables considered for this ordination analysis were the percentage of bare soil, the

percentage and average height of herbaceous vegetation and shrubs, the number and average height of small and medium trees and the number and average height of tall trees, which were then used to ordinate seed traps' plots from lowest to highest vegetation complexity. The index was created choosing the eigenvalues and the axis of the resulting plot which better explained the data. In this case, a lower value of complexity index is associated with the percentage of bare soil, while a higher complexity index is linked to the average height of medium and tall trees, and to height of the tallest tree (Fig. S1.1). The DCA analysis was conducted with the “*vegan*” package in R software (Oksanen et al. 2018).

After verifying the data distribution of the predictor variables with a graphical analysis, variables which did not follow a normal distribution were transformed, namely distance from each seed trap to the closest forest edge (*Closest_edge*) and distance from each seed trap to the closest tree (*Closest_dist*). The transformation which performed best among these variables was the square root. A spearman correlation matrix was generated to verify the existence of collinearity (i.e. correlation >0.7) (Tabachnick & Fidell 2014) and all descriptors revealed correlation values below the established level, with the exception of presence/absence of tree above each seed trap (*PA_tree*) and tree height (*TreeHeight*) (Tab. S2.1). Tree height was chosen to be included in the models, since it contained more information.

To exclude variables with a p-value > 0.3 and reduce the number of variables in the multivariate models, a univariate model analysis was performed. For the multivariate analysis, the closest forest patch (Lauchande and Madina) and the average sampling date were used as crossed random factors. The offset parameter, used to correct the number of events of a population size estimate, was included as the number of days each seed trap was left in the field, accounting for sampling effort. An intercept of zero was forced in all models to guarantee positive fits, since the type of data considered in this study (number of faecal samples present in each seed trap) can not take negative values. Models were obtained using “*lme4*” package in R software (Bates et al. 2015).

The most parsimonious models were selected using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). To verify if the assumptions of normality and homoscedasticity were violated, model residuals were explored using a graphical analysis with Q-Q plots. Multicollinearity of predictor variables was further investigated by computing variance inflated factors (VIF) with the “*car*” package in R software (Fox & Weisberg 2011). All analyses were conducted in R v3.5.1 software (R Core Team 2018).

2.3.2. *Dispersal agents*

To identify the landscape characteristics that can act as an element of attraction for the dispersers to visit the degraded areas, a Generalised Linear Mixed Model (GLMM) analysis was performed considering total species abundance and individual species abundance, species richness and an analysis at the guild level, grouping species with similar eco-morphological traits which are known to affect seed dispersal. Explanatory variables included in the models are summarised in Table 2.2.

Species richness was estimated by calculating the non-parametric and abundance-based Chao1 richness estimator, using EstimateS 9.1.0 (Gotelli & Colwell 2011). Given that there is not an adequate richness estimator for every situation or for specific taxa, the Chao1 richness estimator was chosen due to its performance, especially in presence of reduced sample sizes, being considered as a precise and robust estimator of minimum richness (Walther & Martin 2001; Waltert et al. 2005).

For each bird species, a general model was generated. For species with lower number of contacts two separate models were adjusted: one based on tree characteristics – tree model, and another one on the

landscape characteristics – landscape model. Moreover, species which still presented an insufficient number of observations to be modelled individually, were grouped in families.

The different guild levels modelled followed the classification made by Bennun et al. (1996), who gathered information concerning habitat requirements of forest birds from Eastern Africa (Kenya and Uganda). The authors classified bird species' habitat requirements in three different levels according to the different levels of human disturbance and impact on the forest structure:

- 1) “Forest specialists (FF)”: species typical of the interior of undisturbed forest, which may also prevail in secondary forest, provided their ecological requirements are met. Uncommon far from forest interior and rare in non-forested areas.
- 2) “Forest generalists (F)”: species which are probably more common in secondary forest than in undisturbed forest, although they might also occur there. Often found in forest strips, edges and gaps.
- 3) “Forest visitors (f)”: species which are not entirely reliant on forests. More common in non-forested areas, but often recorded inside forests.

In this study a fourth guild was added: Non-forest bird species (Nf), which include species that are more dependent on savannah and farmland habitats but may regularly visit forest edges. This guild was not modelled, taken that 99% of the individuals present on the guild are Weavers, for which a model was obtained. Forest specialists revealed an insufficient number of individuals to analyse using GLMMs, thus, careful considerations were made based on the spearman correlations between forest specialists and different predictor variables.

Model assumptions were verified according to section 2.3.1. (Tab. S2.2). After verifying the data distribution of the predictor variables with a graphical analysis, every continuous variable was transformed with the square root, except for tree height.

GLMMs were fit with a Poisson error distribution and a log link function. The closest forest patch (Lauchande and Madina) and average sampling date were used as crossed random factors. The offset parameter was included as the number of times each focal point was sampled. An intercept of zero was also forced in all models, since the type of data considered (bird counts in each focal point) can not take negative values. Models were obtained using “*lme4*” package in R software (Bates et al. 2015).

Model selection and validation of the assumptions of normality and homoscedasticity were also completed following the procedure described in section 2.3.1. A thorough analysis for the detection of outliers was performed for models in which these assumptions were not respected. In the presence of outliers, new models were developed without them.

Multicollinearity of predictor variables was further investigated by computing variance inflated factors (VIF) with the “*car*” package in R software (Fox & Weisberg 2011). Variables with a VIF value < 10 were considered for the analysis, following the recommendations of several authors (Graham 2003; Kutner et al. 2004; Chatterjee & Hadi 2006), due to the fact that VIF values are less sensitive in the presence of categorical variables and a higher tolerance was needed. All analyses were conducted in R v3.5.1 software (R Core Team 2018).

3. RESULTS

3.1. Seed dispersal

In the 120 assembled seed traps, 58 had faecal samples. A total of 166 faecal samples were collected in these seed traps, 47 of which contained seeds (approximately 28%). The faecal samples that presented seeds were distributed by only 18 of the 58 seed traps, with a total of 4747 seeds. Seeds were found to belong to 12 different morphotypes, of which three taxa were identified: *Ficus* sp., *Strombosia pustulata* and *Zanthoxylum* sp. (Tab. 3.1). The remaining nine morphotypes were assumed to correspond to nine different plant species. Seed size ranged between 1-2mm – for *Ficus* sp. – and 10-12mm – for *S. pustulata*. When possible, seeds belonging to the same taxa of the tree above each seed trap were removed from the analysis. Thus, a total of 225 seeds, of which 73% belonged to *Ficus* genus, were considered for the analysis.

Table 3.1 – Abundance of plant taxa identified in faecal samples and their origin in Guinea-Bissau. Vernacular names are presented in Creole.

	Identified morphotypes			Unidentified morphotypes								
	<i>Ficus</i> sp.	<i>Strombosia pustulata</i> Oliv.	<i>Zanthoxylum</i> sp.	1	2	3	4	5	6	7	8	9
Number of seeds	165	2	2	5	33	10	1	2	2	1	1	1
Tree family	Moraceae	Olacaceae	Rutaceae	-	-	-	-	-	-	-	-	-
Common name	Fig tree	-	-	-	-	-	-	-	-	-	-	-
Vernacular name	Pó-de-leite	Osso-de-dari	-	-	-	-	-	-	-	-	-	-
Origin	Native	Native	Native	-	-	-	-	-	-	-	-	-

The model adjusted for the number of faecal samples revealed that distance from each seed trap to the closest forest edge, tree height above the seed trap and the index of vegetation complexity positively affected the number of faecal samples present in the traps ($p < 0.01$, Tab. 3.2). Concerning the main drivers of seed capture, a significant positive correlation was found between the number of captured seeds and tree height (Spearman $r = 0.29$) (Tab. S2.1, Fig. S2.1). Moreover, abundance of faecal samples is significantly affected by different tree families (ANOVA, $Df = 7$, $F = 3.8$, $p < 0.001$), with higher abundances under trees from Moraceae (Tukey's HSD test, $p = 0.002$) and Bombacaceae (Tukey's HSD test, $p = 0.009$) families and lower abundances in empty fields (Fig. 3.1). Seed abundance revealed no significant differences between tree families (ANOVA, $Df = 7$, $F = 0.4$, $p = 0.885$).

Table 3.2 – Best model for the number of faecal samples collected in the seed traps. Variables' acronyms can be found in Table 2.1. Results include Akaike's Information Criterion for small samples (AICc) and variance inflated factors (VIF). Significance codes: '****' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

	Estimate	Std. Error	z value	Pr (> z)	AICc	VIF
Number of faecal samples						
General model					354.6	
Closest_edge	0.096	0.023	4.314	1.60e-05 ***		1.011
TreeHeight	0.489	0.065	7.530	5.09e-14 ***		1.245
IndVeg	0.511	0.179	2.853	0.00433 **		1.243

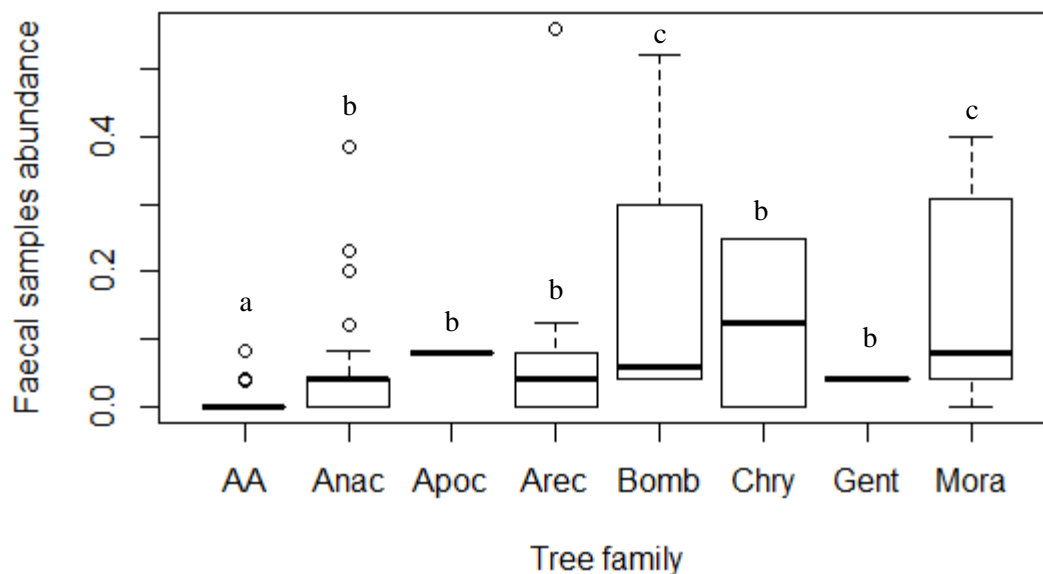


Figure 3.1 - Boxplot representing the abundance of faecal samples found in seed traps under trees from seven families and empty fields (AA). Significant differences between tree families are represented with letters from 'a' to 'c'. Tree family acronyms are described in Table 2.1.

At the end of seed germination trials, the only taxon that revealed germination signs was *Ficus* sp., in which small rootlets emerged within less than 15 days. After two months *Strombosia pustulata* and *Zanthoxylum* sp. revealed no signs of germination.

3.2. Dispersal agents

A total of 9341 bird visitors were observed in the 64 focal points located in degraded areas, during the sampling period. Twenty-one species or genus of potential seed dispersers were identified (Tab. 3.3), leaving a small percentage of individuals not identified (7.4%). The most common bird species were Weavers (*Ploceus* sp.), followed by the African Green-pigeon (*Treron calvus*) and Doves (*Streptopelia* sp.). One of the identified species, the Yellow-casqued Hornbill (*Ceratogymna elata*), holds a global Vulnerable conservation status, according to the IUCN Red List (BirdLife International 2016).

Thirteen genus and species were grouped into six groups, according to bird families: **Weavers** (Ploceidae), which comprise *Ploceus* sp. and *Ploceus cucullatus*, due to the low number of weavers identified to the species level; **Hornbills** (Bucerotidae), including *Lophoceros semifasciatus*, *Bycanistes fistulator* and *Ceratogymna elata*; **Turacos** (Musophagidae), including *Tauraco persa*, *Corythaeola cristata* and *Crinifer piscator*; **Bulbuls** (Pycnonotidae), including *Pycnonotus barbatus* and *Chlorocichla simplex*; **Glossy Starlings** (*Lamprotornis* sp.), since not all individuals were identified with certainty to species level; **Doves**, which include *Streptopelia* sp. and a small number of individuals identified as *Streptopelia semitorquata*.

All the models that best summarize the roles that different intrinsic characteristics of observed trees and landscape elements have on abundance and richness of potential seed dispersers in degraded areas, are compiled in Table 3.4. Most models show a good adjustment to the data, except the models for

Gypohierax angolensis and Turacos. Careful considerations should be made regarding the results for these species and family.

Table 3.3 - List of bird species identified as potential seed dispersers in the degraded areas and guild-level assignment for each species. Guild levels were attributed based on Bennun et al. (1996) classification, described in section 2.3.2. and new classifications are marked with symbol ‘*’.

Bird Species	Common name	N	Guild Habitat
<i>Ploceus</i> sp.	Weavers	4274	Nf*
<i>Treron calvus</i> (Temminck, 1808)	African Green-pigeon	1203	F
<i>Streptopelia</i> sp.	Doves	1133	f
<i>Pycnonotus barbatus</i> (Desfontaine, 1789)	Common Bulbul	738	f
<i>Cinnyricinclus leucogaster</i> (Boddaert, 1783)	Violet-backed Starling	622	f
<i>Streptopelia semitorquata</i> Rüppell, 1837	Red-eyed Dove	165	f
<i>Lamprotornis</i> sp.	Glossy Starlings	135	F
<i>Turtur afer</i> (Linnaeus, 1766)	Blue-spotted Wood-dove	119	f
<i>Lophoceros semifasciatus</i> (Hartlaub, 1855)	West African Pied Hornbill	115	F
<i>Ploceus cucullatus</i> (Müller, 1776)	Village Weaver	36	Nf*
<i>Gypohierax angolensis</i> (Gmelin, 1788)	Palm-nut Vulture	31	Nf*
<i>Bycanistes fistulator</i> (Cassin, 1852)	Western Piping Hornbill	26	FF
<i>Chlorocichla simplex</i> (Hartlaub, 1855)	Simple Greenbul	7	f*
<i>Poicephalus senegalus</i> (Linnaeus, 1766)	Senegal Parrot	7	Nf*
<i>Turtur tympanistria</i> (Temminck, 1809)	Tambourine Dove	7	F
<i>Tauraco persa</i> (Linnaeus, 1758)	Green Turaco	7	FF*
<i>Corythaëola cristata</i> (Vieillot, 1816)	Great Blue Turaco	5	FF*
<i>Crinifer piscator</i> (Boddaert, 1783)	Western Plantain-eater	5	Nf*
<i>Pogonornis bidentatus</i> (Shaw, 1789)	Double-toothed Barbet	5	FF*
<i>Ceratogymna elata</i> (Temminck, 1831)	Yellow-casqued Hornbill	4	FF*
<i>Nicator chloris</i> (Valenciennes, 1826)	Western Nicator	3	F

Overall, models show that tree height and distance to the closest forest edge are the most influential variables, having a significant effect on the abundance of most potential seed dispersers. Tree height had a significant positive effect in Bulbuls, Turacos, Doves and Forest visitors, and a negative effect on African Green-pigeons, Blue-spotted Wood-doves, Weavers and Forest generalists (Tab. 3.4). Distance to the closest forest edge positively affects the abundance of the total number of potential seed dispersers, Weavers, Doves and Forest visitors. On the other hand, it negatively affects the abundance of African Green-pigeons, Hornbills and Forest generalists (Tab. 3.4).

There appears to be no generalized pattern for tree families that attract most of the potential seed dispersers, however they seem to be less attracted by trees of Anacardiaceae and Chrysobalanaceae families (Tab. 3.4). Notwithstanding, the model for species richness seems to highlight a higher species richness in trees belonging to the Moraceae family (Tab. 3.4, Fig. 3.2).

Weavers are the predominant species of the guild Non-forest bird species, so both models show a positive relation with distance to the closest forest edge ($p < 0.001$) and height of the nearby tallest tree ($p < 0.001$) (Tab. 3.3, Fig. 3.3A and 3.3B). In addition, their abundance revealed a negative relation with tree height ($p < 0.05$, Tab. 3.4, Fig. 3.3C), being more abundant in trees belonging to Arecaceae family. Trees from Anacardiaceae and Chrysobalanaceae families seem to have a less positive impact on the abundance of these individuals (Tab. 3.4, Fig. 3.3D).

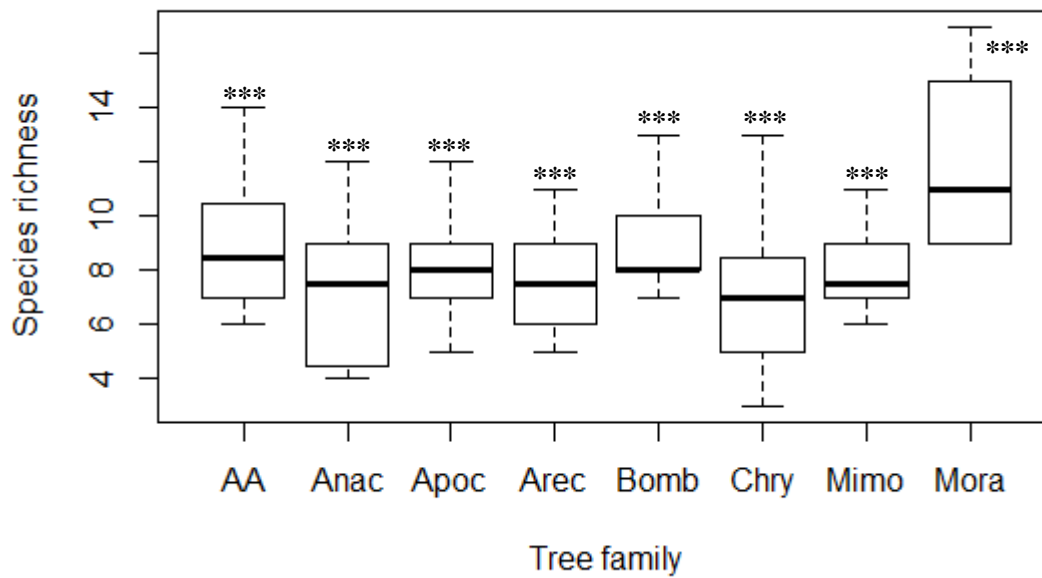


Figure 3.2 - Boxplot representing species richness of potential seed dispersers in seven tree families and empty fields (AA). Tree family acronyms are described in Table 2.3. Significance codes: ‘***’ $p < 0.001$, ‘**’ $p < 0.01$, ‘*’ $p < 0.05$.

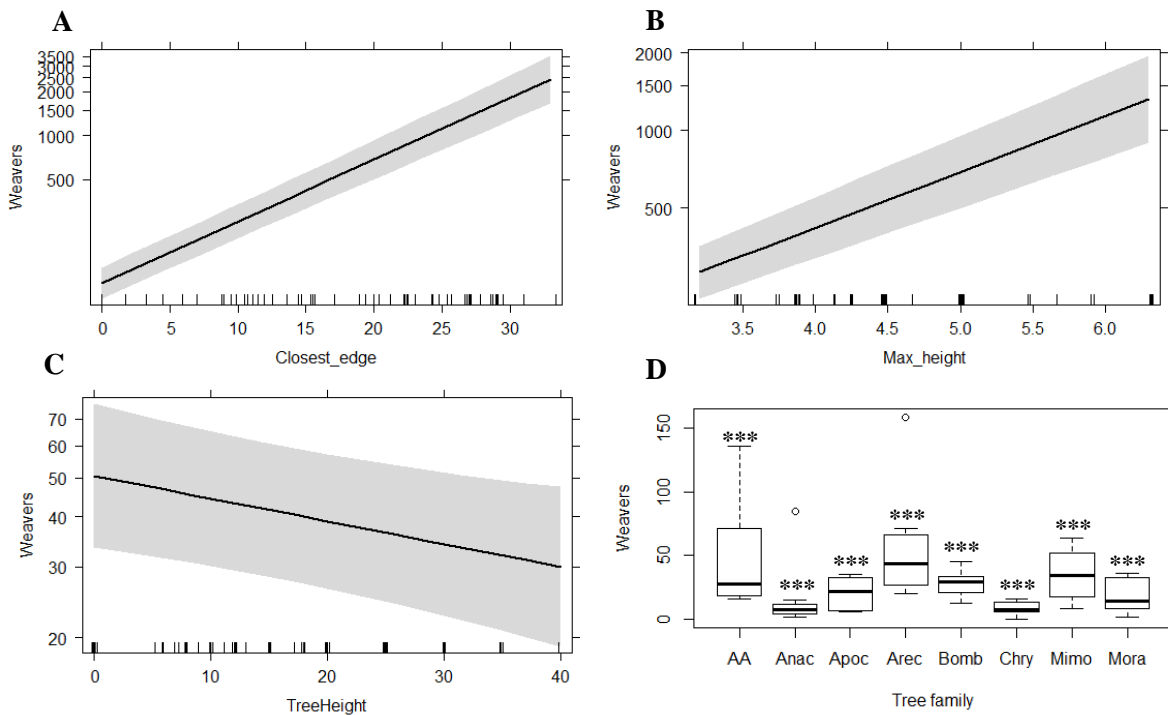


Figure 3.3 - Plots of the effect of distance to the closest forest edge (A), height of the tallest tree nearby (B) and tree height (C) on Weaver’s abundance, with 95% confidence intervals. Bird abundance is represented with a logarithmic scale. Boxplot D shows the effect of different tree families on Weaver’s abundance. Tree family acronyms are described in Table 2.3. Significance codes: ‘***’ $p < 0.001$, ‘**’ $p < 0.01$, ‘*’ $p < 0.05$.

Forest visitors, such as Doves and Bulbuls, are positively affected by tree height ($p < 0.001$, $p < 0.01$ and $p < 0.001$, respectively) (Tab. 3.4, Fig. 3.4A) and height of the closest tree ($p < 0.001$, Tab. 3.4). Conversely, Blue-spotted Wood-doves (*Turtur afer*) show a negative relation with tree height ($p < 0.05$, Tab. 3.4, Fig. 3.4B). Species belonging to this guild are more common in empty fields and in the presence of trees from Mimosoideae subfamily (Tab.3.4, Fig. 3.4D). Trees from the Chrysobalanaceae family seem to have a less positive impact on forest visitor's abundance (Tab. 3.4, Fig. 3.4C). Forest visitors also revealed a positive relation with distance to the closest forest edge ($p < 0.05$, Tab. 3.4, Fig. 3.4C) and distance to the closest tree ($p < 0.01$, Tab. 3.4).

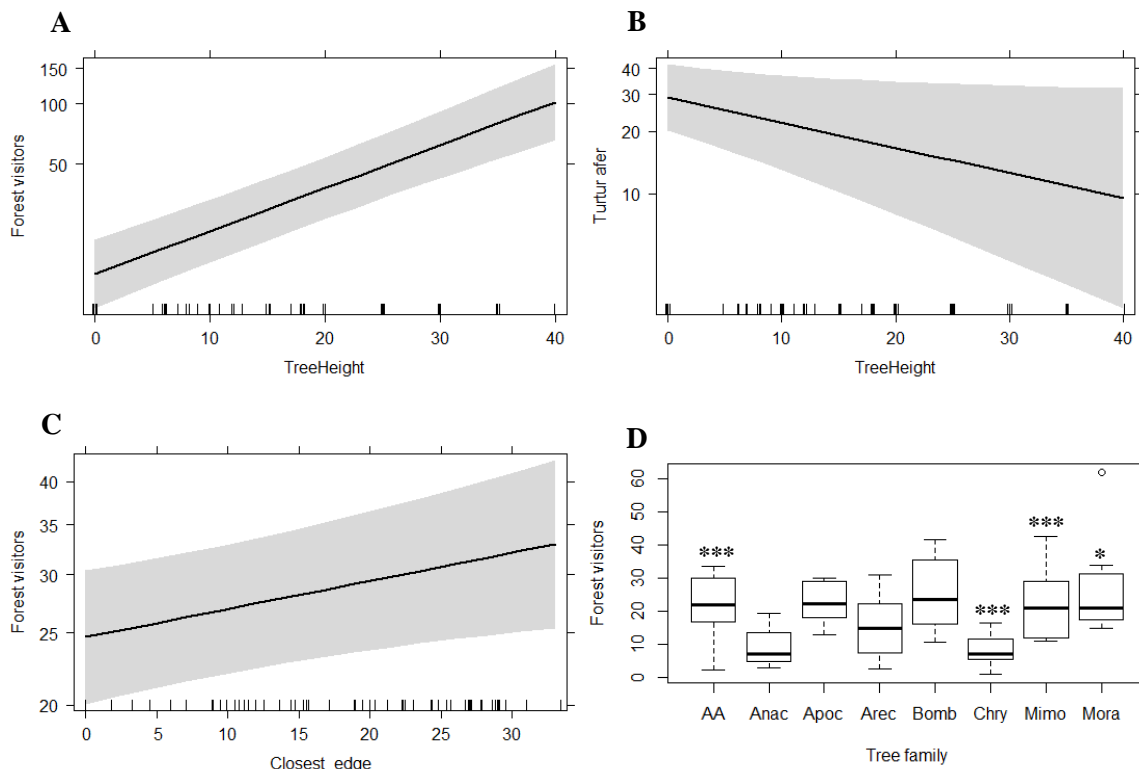


Figure 3.4 - Plots of the effect of tree height on Forest visitors' (A) and Blue-spotted Wood-doves' (B) abundance, with 95% confidence intervals. Bird abundance is represented with a logarithmic scale. Plot C shows the effect of distance to the closest forest edge and Boxplot D the effect of tree families on Forest visitors' abundance. Tree family acronyms are described in Table 2.3. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

Forest generalists, such as the African Green-pigeon, show a negative relation with distance to the closest forest edge ($p < 0.001$, Tab. 3.4, Fig. 3.5A). Glossy starlings, on the other hand, seem to be more abundant further away from forest edges ($p < 0.001$, Tab. 3.4). Tree height revealed to affect species in this guild negatively ($p < 0.01$, Tab. 3.4, Fig. 3.5B). Moreover, these species appear to be positively affected by trees from Apocynaceae, Chrysobalanaceae and Moraceae families (Tab. 3.4, Fig. 3.5C).

Turacos and Hornbills seem to be, respectively, positively driven by an increase in tree height ($p < 0.01$) and negatively by distance to the closest forest edge ($p < 0.001$) (Tab. 3.4, Fig. 3.6A), being more abundant close to forest patches. Even though it was not possible to obtain models for Forest specialists, which comprise two turaco species, two hornbill species and one African Barbet species (Tab. 3.4), results from Spearman correlations show that all height variables (tree height (Spearman $r = 0.39$), height of the closest tree (Spearman $r = 0.31$) and height of the tallest and closest tree (Spearman $r = 0.28$))

have a positive and significant effect on Forest specialist species (Tab. 3.4, Fig. S2.2). Additionally, Forest specialists seem to be positively affected, even if not significantly, by trees from the Moraceae family (Fig. 3.6B).

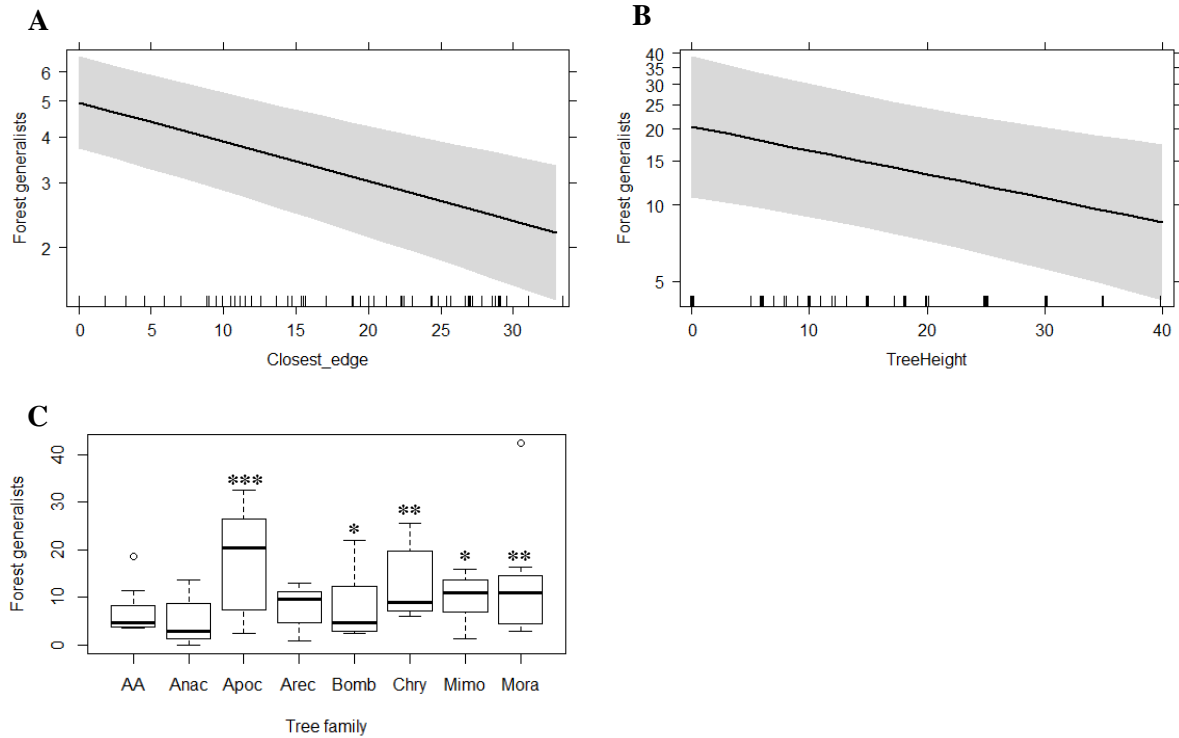


Figure 3.5 - Plots of the effect of distance to the closest forest edge (A) and tree height (B) on Forest generalists' abundance, with 95% confidence intervals. Bird abundance is represented with a logarithmic scale. Boxplot C shows the effect of tree families on Forest generalists' abundance. Tree family acronyms are described in Table 2.3. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

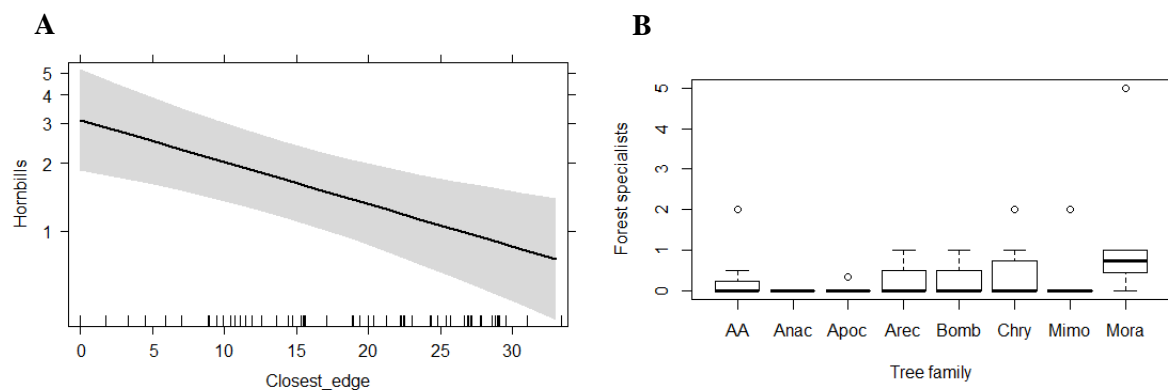


Figure 3.6 - Plot A represents the effect of distance to the closest forest edge on Hornbills' abundance, with 95% confidence intervals. Bird abundance is represented with a logarithmic scale. Boxplot B shows the effect of different tree families on Forest specialists' abundance. Tree family acronyms are described in Table 2.3.

Table 3.4 - Summary of the best models for potential dispersers' abundance, species richness, species, families and guild levels. Variables' acronyms can be found in Table 2.2 and species included in each guild level can be found in Table 3.3. In species with smaller sample sizes a Tree model and a Vegetation model are presented, instead of a General model. Results include Akaike's Information Criterion for small samples (AICc) and variance inflated factors (VIF). Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$.

	Estimate	Std. Error	z value	Pr (> z)	AICc	VIF
1. Total of potential dispersers						
Tree model					1647.2	
Fam: AA	2.582	0.147	17.52	<2e-16 ***		n/a
Anac	1.767	0.149	11.84	<2e-16 ***		
Apoc	2.380	0.149	15.94	<2e-16 ***		
Arec	2.657	0.148	18.01	<2e-16 ***		
Bomb	2.634	0.148	17.77	<2e-16 ***		
Chry	1.917	0.154	12.44	<2e-16 ***		
Mimo	2.688	0.150	17.98	<2e-16 ***		
Mora	2.430	0.156	15.61	<2e-16 ***		
Landscape model					1746.3	
Closest_edge	0.037	0.002	16.814	<2e-16 ***		1.022
Closest_dist	0.034	0.008	3.952	7.75e-05 ***		1.558
Closest_height	0.043	0.015	2.845	0.00444 **		1.131
Max_height	0.221	0.024	9.308	<2e-16 ***		1.550
2. Species richness						
General model					321.6	
Fam: AA	2.197	0.118	18.64	<2e-16 ***		n/a
Anac	1.969	0.108	18.26	<2e-16 ***		
Apoc	2.100	0.150	14.70	<2e-16 ***		
Arec	2.031	0.128	15.87	<2e-16 ***		
Bomb	2.208	0.105	21.07	<2e-16 ***		
Chry	1.966	0.141	13.90	<2e-16 ***		
Mimo	2.079	0.144	14.41	<2e-16 ***		
Mora	2.497	0.109	23.02	<2e-16 ***		
Guild						
3. Weavers (<i>Ploceus</i> sp.) = Non-forest bird species (Nf)						
Tree model					1760.9	
TreeHeight	-0.013	0.005	-2.517	0.011846 *		7.297
Fam: AA	1.910	0.200	9.570	<2e-16 ***		7.297
Anac	0.947	0.206	4.585	4.54e-06 ***		
Apoc	1.383	0.226	6.120	9.38e-10 ***		
Arec	2.290	0.214	10.680	<2e-16 ***		
Bomb	2.088	0.234	8.926	<2e-16 ***		
Chry	0.965	0.258	3.734	0.000189 ***		
Mimo	2.153	0.211	10.204	<2e-16 ***		
Mora	1.107	0.254	4.354	1.27e-05 ***		
Landscape model					1550.5	
Closest_edge	0.097	0.004	25.33	<2e-16 ***		1.026
Max_height	0.499	0.028	17.78	<2e-16 ***		1.026

(cont.)	Estimate	Std. Error	z value	Pr (> z)	AICc	VIF
4. Forest visitors (f)						
Tree model					780.8	
TreeHeight	0.049	0.006	8.944	<2e-16 ***		5.272
Fam: AA	1.124	0.189	5.942	2.82e-09 ***		5.272
Anac	0.024	0.201	0.118	0.906365		
Apoc	0.358	0.223	1.599	0.109874		
Arec	0.114	0.214	0.531	0.595589		
Bomb	0.392	0.232	1.693	0.090437		
Chry	-0.861	0.259	-3.328	0.000874 ***		
Mimo	1.008	0.203	4.971	6.67e-07 ***		
Mora	0.504	0.245	2.060	0.039445 *		
Landscape model					1060.0	
Closest_edge	0.008	0.004	2.069	0.03850 *		1.021
Closest_dist	0.044	0.015	3.203	0.00136 **		1.131
Closest_height	0.153	0.029	5.203	6.38e-09 ***		1.152
5. Forest generalists (F)						
Tree model					773.9	
TreeHeight	-0.022	0.008	-2.784	0.00536 **		4.908
Fam: AA	0.121	0.320	0.379	0.70480		4.908
Anac	0.165	0.326	0.507	0.61196		
Apoc	1.365	0.350	3.902	9.55e-05 ***		
Arec	0.640	0.341	1.876	0.06063		
Bomb	0.729	0.362	2.012	0.04424 *		
Chry	1.197	0.376	3.183	0.00146 **		
Mimo	0.690	0.334	2.065	0.03895 *		
Mora	1.088	0.387	2.815	0.00487 **		
Landscape model					813.6	
Closest_edge	-0.025	0.005	-5.461	4.73e-08 ***		1.003
Closest_height	-0.213	0.043	-4.979	6.39e-07 ***		1.003
Species/Families						
6. African Green-pigeon (<i>Treron calvus</i>)						
Tree model					690.1	
TreeHeight	-0.034	0.009	-3.855	0.000116 ***		4.709
Fam: AA	-0.215	0.362	-0.593	0.552922		4.709
Anac	-0.046	0.370	-0.124	0.901466		
Apoc	1.416	0.395	3.588	0.000333 ***		
Arec	0.451	0.389	1.159	0.246598		
Bomb	0.784	0.408	1.920	0.054846		
Chry	1.126	0.424	2.656	0.007900 **		
Mimo	0.643	0.378	1.702	0.088748		
Mora	1.193	0.433	2.757	0.005836 **		
Landscape model					723.5	
Closest_edge	-0.032	0.005	-6.308	2.82e-10 ***		1.002
Closest_height	-0.274	0.049	-5.539	3.05e-08 ***		1.002

(cont.)	Estimate	Std. Error	z value	Pr (> z)	AICc	VIF
7. Blue-spotted Wood-dove (<i>Turtur afer</i>)						
General model					233.4	
TreeHeight	-0.028	0.013	-2.128	0.0334 *		1.167
Closest_dist	0.360	0.065	5.500	3.81e-08 ***		1.167
8. Palm-nut Vulture (<i>Gypohierax angolensis</i>)						
General model					143.0	
Max_height	-1.228	0.123	-9.994	<2e-16 ***		n/a
9. Bulbuls (<i>Pycnonotus barbatus</i> + <i>Chlorocichla simplex</i>)						
General model					721.5	
TreeHeight	0.033	0.005	6.759	1.39e-11 ***		n/a
10. Hornbills (<i>Lophoceros semifasciatus</i> + <i>Bycanistes fistulator</i> + <i>Ceratogymna elata</i>)						
General model					308.1	
Closest_edge	-0.043	0.013	-3.318	0.000907 ***		1.821
Max_height	-0.268	0.059	-4.564	5.02e-06 ***		1.821
11. Glossy-starlings (<i>Lamprotornis</i> sp.)						
General model					337.6	
Closest_edge	0.062	0.018	3.482	0.000497 ***		n/a
12. Turacos (<i>Tauraco persa</i> + <i>Corythaecola cristata</i> + <i>Crinifer piscator</i>)						
General model					88.3	
TreeHeight	0.111	0.034	3.249	0.00116 **		n/a
13. Doves (<i>Streptopelia</i> sp.)						
Tree model					639.5	
TreeHeight	0.025	0.009	2.885	0.00391 **		5.814
Fam: AA	0.499	0.250	1.999	0.04569 *		5.814
Anac	-0.649	0.268	-2.424	0.01537 *		
Apoc	-0.017	0.315	-0.054	0.95673		
Arec	-0.152	0.287	-0.531	0.59566		
Bomb	0.474	0.321	1.475	0.14015		
Chry	-0.576	0.368	-1.564	0.11789		
Mimo	0.650	0.276	2.356	0.01846 *		
Mora	0.095	0.335	0.285	0.77582		
Landscape model					760.2	
Closest_dist	0.057	0.020	2.984	0.002845 **		1.285
Closest_height	0.104	0.031	3.338	0.000843 ***		1.285

4. DISCUSSION

4.1. Seed dispersal

4.1.1. Major drivers of seed deposition

Distance to the closest forest edge, tree height, vegetation complexity and two different tree families emerged as important variables to explain the deposition of bird faeces and seeds in degraded areas of CNP. Approximately 28% of the faecal samples had seeds and, although the patterns found for the

number of faecal samples may not fully represent the reality of seed dispersal, they reflect the probability of its occurrence.

A positive and significant relation was found between the number of faecal samples and distance to the closest forest edge. Most studies did not find a consistent trend between the number of seeds dispersed to degraded areas and the distance to the forest edge (Guevara et al. 1986; Duncan & Chapman 1999; Slocum & Horvitz 2000; Cole et al. 2010), suggesting that seed deposition may not be strongly dependent on distance to the seed source. The ones that did, found a negative relation (Gorchov et al. 1993; Cubiña & Aide 2001) and suggested that distance may be important in early forest succession. The positive relation found in the present study only accounts for faecal samples and could possibly reflect the greater abundance of birds associated to farmland habitats, savannah woodland and palm groves, which may not visit the forest interior. In addition, even though seeds were trapped between 0 and 700 m from the forest edge, this does not necessarily mean that all those seeds were dispersed from the forest interior, since nine of the 12 trapped morphotypes were not identified and could belong to species occurring elsewhere.

Tree height, which can also be considered a *proxy* of tree presence, was the only variable with a positive and significant relation for both the number of faecal samples and number of seeds. This pattern has emerged in other studies either under artificial perches (McDonnell 1986; Wunderle Jr 1997; Holl 1998) or under isolated trees in pastures or agricultural fields (Guevara et al. 1986; Duncan & Chapman 1999; Slocum & Horvitz 2000). This could suggest that seed deposition and seedling recruitment to degraded areas depends on and begins under isolated trees (Guevara et al. 1986), since birds are more likely to defecate while perching (Charles-Dominique 1986). In addition to tree presence in open fields, the positive relation between tree height and avian seed deposition found in this study is further supported in other studies (for example, Duncan & Chapman 1999; Toh et al. 1999; Guevara et al. 2004). This can be explained by the fact that tall trees offer a better view of potential predators and better foraging opportunities (McDonnell 1986; Duncan & Chapman 1999).

A higher number of faecal samples was collected from areas with greater vegetation complexity, that is, with more medium and tall trees. This result could be explained by an increased number and diversity of avian seed dispersers associated with more complex vegetation (McDonnell & Stiles 1983; Holl 1998). Consequently, this increased abundance of faeces should result in an increased seed deposition in these areas (Shiels & Walker 2003; Reid et al. 2015).

A significantly higher number of faeces was trapped under trees of the families Moraceae (Fig trees) and Bombacaceae (Kapok trees) relative to areas with no trees. Several studies describe a higher abundance and diversity of seeds in plots with fruit trees in comparison with bare soil plots (Uhl 1982; Guevara et al. 1986), supporting the higher abundance of faecal samples found under these trees. The large diversity of dispersers that Fig trees attract is widely documented (Snow 1981; Shanahan et al. 2001), often resulting in greater densities of seeds in traps below Fig trees relative to plots with other fruiting trees (Poulsen et al. 2013; Cottee-Jones et al. 2016). On the other hand, Kapok tree is one of the most frequent remnant trees in felled forests, but their fruits are probably not be the main reason explaining an increased faeces deposition under these trees. Kapok fruits might be interesting for avian frugivores while immature, but after ripening they are filled with fibres which are typically wind dispersed (Dick et al. 2007). It is possible that their flowers, which have fleshy petals, are consumed by and attract birds. The higher faeces deposition observed could also be explained by the fact that trees of the Bombacaceae family are typically large trees (Catarino et al. 2006), providing good perches for birds.

Finally, it is important to bear in mind that trapping success between habitats and plots might be different, for example due to different wind exposure, generally higher in areas without trees, when compared with the ones deployed in cashew or mango tree orchards. In order to counter this effect, in the second set of traps, braided nylon lines were tied from the ground, crossing each seed trap horizontally. The effect of wind could still have biased the number of faecal samples and seeds captured during the study, but we believe that not significantly as no trend of higher faeces or seed captures was found in the sampled orchards.

4.1.2. Dispersed plant species

Seed dispersal and deposition patterns in degraded areas depend not only on fruit availability but also on fruit and seed size, fruit morphology and frugivorous species and movements (Howe & Smallwood 1982). In this study, twelve different seed morphotypes were trapped in degraded areas surrounding the two forest remnants in CNP. Three morphotypes were identified as tree species that are present in the interior of these dense forests, namely *Ficus* sp., *Strombosia pustulata* and *Zanthoxylum* sp., suggesting that these seeds were effectively dispersed from the forest interior to degraded areas.

Apart from *S. pustulata*, all the other captured seeds can be considered small seeds and those belonging to the *Ficus* genus accounted for approximately 73% of the total number of dispersed seeds. This pattern has been observed in other studies which found that there is a prevalence of small seeds being recruited to degraded areas (Chapman & Chapman 1999; Duncan & Chapman 1999; Harvey 2000; Cubiña & Aide 2001; Ingle 2003; Peña-Domene et al. 2014). Smaller seeds generally belong to early successional plants which are usually the first to recolonize degraded areas (Zahawi et al. 2013; Peña-Domene et al. 2014; Reid et al. 2015). Studies show that small seeds have greater probabilities of being ingested in larger quantities and of successfully passing through small bird's guts, this way being dispersed and defecated far away from the parent plant. On the other hand, larger seeds have lower mobility (Wunderle Jr 1997) and are likely to be regurgitated after ingestion, being largely dependent on the bird's gape width and capacity to swallow whole fruits (Levey 1987; Corlett 1998; Norconk et al. 1998).

In addition to fruit and seed size, fruit morphology is known to influence its attractiveness to frugivores and consequently its dispersal. Figs, arillate and drupe fruits are amongst the most attractive fruit types for frugivores (Snow 1981; Bleher et al. 2003). Fig trees are considered keystone species, attracting a wide diversity of avian frugivores, ranging from all body sizes (Snow 1981; Shanahan et al. 2001). Moreover, they are a critical resource for periods of ripe fruit scarcity due to their aseasonal fruiting pattern (Compton et al. 1996). Each fig produces hundreds of seeds (Laman 1996) and their dispersal by birds is widely reported, many of them being able to disperse intact viable seeds (Compton et al. 1996; Shanahan et al. 2001; Corlett 2017).

Two *S. pustulata* seeds were trapped in a cashew tree orchard close to Madina forest remnant. This forest remnant is mainly composed by *S. pustulata* trees, which were fruiting at the time of the study. Thus, it could mean that the two trapped seeds were dispersed from the interior of this forest. *S. pustulata* is an evergreen tree that produces ellipsoid or globose drupaceous fruits (De La Mensbruge 1966), and there are only a few records of birds consuming them and dispersing their seeds. Its fruits have been identified as an important part of the diet of hornbills (Whitney et al. 1998; Holbrook et al. 2002), that can probably ingest and defecate the seeds intact (Whitney et al. 1998). Green turacos and African Green-pigeons were also registered feeding on these fruits in Guinea-Bissau (Chaves 2018). However, several mammals are known to disperse seeds of *S. pustulata* (Maurois et al. 1997; Masi et al. 2015) but

in Guinea-Bissau the only known dispersal vector are primates (Bessa et al. 2015), hence it is possible that these seeds were dispersed by mammals, instead of birds.

Trees from the *Zanthoxylum* genus generally produce arillate or globose folliculate fruits, with seeds almost the size of the fruit (Sanon et al. 2004). There are several records of the genus being consumed and dispersed by birds in the American continent (Skutch 1980; Wheelwright et al. 1984; Dalling et al. 2002), South Africa and Australasia (Snow 1981).

The diversity of seeds dispersed by birds into degraded areas of CNP may be higher than what was found using this methodology. Even though seed traps have been widely used to sample seed rain beneath isolated trees and tree remnants in degraded areas (Cubiña & Aide 2001; Hardesty & Parker 2002), and to trap bird and bat faecal samples (McDonnell & Stiles 1983; Gorchov et al. 1993; Duncan & Chapman 1999; Harvey 2000), some studies complement this method with the assemblage of vertical mist nets (Gorchov et al. 1993; Harvey 2000). The use of this complementary methodology would enable the identification of the link between animal disperser and tree species' dispersed seed, which is one of this study's limitations. However, this was not possible to attain in the scope of this dissertation due to field work time constraints.

4.1.3. Seed viability

Although it was shown that seeds from the forest interior are being dispersed to degraded areas in CNP, this does not imply that the dispersal process was efficient (Schupp 1993). Seeds arriving at a concrete site should be proven to be viable and able to germinate, in order to verify if they have regeneration potential and will result in recruitment.

Seed germination trials in this study confirmed that *Ficus* sp. seeds were viable, with a small rootlet emerging in less than two weeks. This is consistent with what was expected, since many avian frugivores are able to disperse these seeds in a viable way (Compton et al. 1996; Corlett 2017). Even animal species which are considered seed predators, such as the African Green-pigeon, have been shown to disperse a small percentage of the ingested seeds intact (Lambert 1989).

The seeds of *S. pustulata* and *Zanthoxylum* sp. did not germinate, possibly for different reasons. *S. pustulata* is described as having irregular germination periods, varying from two to ten weeks, and would probably benefit from a pre-sowing treatment, due to its large seed size (De La Mensbrughe 1966). Seeds from *Zanthoxylum* genus are reported to have poor germination, probably due to a hard and oily seed coat that might contribute to a state of seed dormancy (Sanon et al. 2004; Bonner 2008; Okeyo et al. 2011). Studies in which *Zanthoxylum* germination trials were carried out, indicate that washing out the oil from the seed coat with a sodium hydroxide solution (NaOH) enhances seed germination rates (Okeyo et al. 2011). This seems to suggest that even though seeds from these two *taxa* did not germinate during lab trials, it does not imply or prove that these are not viable and that they would not germinate given the favourable conditions in their natural environment.

4.2. Dispersal agents

4.2.1. Identification of potential avian seed dispersers

During focal point observations in the surrounding areas of CNP sub-humid forests, twenty-one species or genus of birds were identified as potential seed dispersers. However, not all of them have the same importance and effectiveness playing this role. Dispersal effectiveness is influenced by both the quantity

of dispersed seeds and the quality of the treatment given to a seed by the disperser, including the quality of seed deposition (Schupp 1993).

The most abundant species detected in degraded areas of CNP were Weavers and African Green-pigeons and Doves, that belong respectively to two different families, Ploceidae and Columbidae. These are mainly recognized as seed predators (Janzen 1971). Despite being considered seed predators, this does not imply that these species are unable to disperse some of the seeds they consume (Lambert 1989; Corlett 1998; Hulme 2002; Mokatjomela et al. 2016). Some authors have even suggested that contrary to the idea that there is a dichotomy between predation and dispersal, there is more often a continuum between these two extremes (Wheelwright & Orians 1982; Hulme 2002; Heleno et al. 2011). African Green-pigeons, particularly, pay frequent visits to the forest interior and are known to take great amounts of fruit while inside (Lambert 1989). High abundance combined with powerful flight capacity, allows them to make large movements between forest remnants (Lambert 1989). These traits combined with the fact that a fraction of the excreted seeds may be viable, can make these seed predators act as seed dispersers and have an important role in the dispersal of some plant species in CNP. However, they can not be considered the most efficient dispersers as only a small percentage of seeds can pass through their guts unharmed (Lambert 1989; Corlett 1998).

The most abundant avian species recognized as quality dispersers, present in these areas, were two forest visitors, Bulbuls and Violet-backed starlings, and Hornbills. Considering that Hornbills are more dependent upon undisturbed forest and thus probably play a more important role in seed dispersal near forest edges, Bulbuls and Violet-backed starlings emerge as important potential dispersers in these areas. Their high abundance in degraded areas, coupled with their frequent visits to the forest interior, assigns them an important role in forest regeneration in these areas.

4.2.2. Major drivers of avian abundance and richness

Tree height and distance to the closest forest edge were the most important variables explaining the abundance of potential avian seed dispersers in degraded areas. These variables influence potential dispersers in different ways and their effect will be more or less important, depending on the ecology of the species of dispersers, that is of their guilds.

No generalized pattern of attraction was found to affect bird abundance in terms of tree families. However, trees from the families Anacardiaceae and Chrysobalanaceae seem to have a general less positive effect on bird abundance. Trees from Anacardiaceae family, namely cashew trees and mango trees, are exotic cultivated trees and were fruiting at the time of the study. However, their fruits were not ripe until the end of the study period and this could have influenced the number of birds visiting these trees. Even though frugivores can not disperse their seeds, these fruits can act as attractants and birds can disperse seeds from the forest interior, to their locations. In the end of the field work period, when cashew fruits had ripened, many Bulbuls and Weavers were seen feeding on these fruits.

Trees of the Chrysobalanaceae family, namely the Guinea Plum, have drupaceous fruits and are potentially attractive to avian frugivores. However, the fact that their pulp is hard and adhering and that their seeds are large, might make them more attractive to large-bodied avian dispersers (Levey 1987; Gross-Camp et al. 2009). Hornbills have been seen feeding on these fruits (Gross-Camp et al. 2009), but most dispersal events in other studies have been registered for large-bodied mammals, squirrels and bats (Dowsett-Lemaire 1988; Gautier-Hion & Michaloud 1989; Chapman & Chapman 1999). A lower abundance of large-bodied birds in degraded areas could explain the less positive effect of this tree

family on general potential dispersers' abundance. In addition, these trees have large and dense canopies, posing an increased difficulty for focal point observations, thus possibly having skewed bird counts.

Nevertheless, bird species richness has been shown to be positively influenced by trees from Moraceae family in degraded areas. This was an expected result, since numerous studies show their importance as attractors and key resources for several frugivores (Snow 1981; Shanahan et al. 2001), and highlight their importance in degraded areas as a focus of seed deposition and recruitment (Poulsen et al. 2013; Cottee-Jones et al. 2016).

Tree fructification state was initially considered a variable with potential importance explaining bird's abundance in degraded areas. However, it was not possible to evaluate it properly during fieldwork, due to the short sampling period.

4.2.3. *Non-forest bird species*

Non-forest bird species are more reliant upon savannah and farmland habitat and represent the most abundant potential dispersers in degraded areas. Weavers represent most individuals in this guild and show a positive relation with distance to the forest edge, which reflects the trait of their ecology mentioned above. Although they are frequently observed visiting forest edges, this does not imply that they are relevant seed dispersers. As mentioned in the general discussion of potential avian dispersers, Weavers are mainly granivorous and considered as seed predators (Snow 1981). Furthermore, for this genus, there is no record of small seeds passing through their guts unharmed (Compton et al. 1996). However, there are records of individuals being able to disperse seeds to a small distance from the parent plant, carrying seeds in their bills (Bleher & Böhning-Gaese 2001). During this study, some individuals were seen carrying palm tree fruits between different close perches in degraded areas.

Height of the tallest tree nearby also revealed to have a positive influence in Weaver's abundance. This could be explained by this species' preference for palm trees, the highest trees in the area. This is reinforced by the positive relation found with trees belonging to the Arecaceae family, namely palm trees, which are known to be important for nest construction and to bear fruits that are an essential part of Weaver's diet (Din 1991).

Among the other species included in this guild, the Western Plantain-eater could have a particularly interesting role as a quality disperser in degraded areas of CNP. However, only 5 individuals were registered, and assumptions should be made carefully. This turaco species typically occupies savannah woodland habitats but has been described as a relevant avian disperser of *Antiaris toxicaria* in Ghana (Kankam & Oduro 2011), a tree species which also occurs in the interior of mature forests of CNP (Catarino et al. 2006) and that bears fruits which are important resources for several frugivores (Kitamura et al. 2008; Kankam & Oduro 2011).

4.2.4. *Forest visitors*

Forest visitors such as Doves, Bulbuls and Violet-backed starlings, visit the forest interior but do not depend upon it entirely and are generally more common in agricultural fields and degraded areas. As expected, species in this guild revealed a significant and positive relation with distance to the closest forest edge. Therefore, as mentioned above, these species could represent important vectors that potentiate seed dispersal from the forest interior and contribute for forest regeneration in degraded areas.

Dranzoa (1998) and Borghesio (2008), have also highlighted the importance of this guild in disturbed habitats and edges of forest fragments.

Tree height and height of the closest tree seems to be major drivers of forest visitors' abundance in degraded areas of CNP, having a positive effect in species such as Doves and Bulbuls and a negative effect in Wood-doves. Doves are known to be mainly granivorous, seed predators and to forage on the ground (Baptista et al. 1997), however they are occasionally seen plucking berries from trees and can disperse some of their seeds (Mokotjomela et al. 2016). Even though they probably do not play an important role in the dispersal of seeds from the forest interior, they seem to benefit from the presence of tall trees in degraded areas, probably not for their foraging activities but as better predator lookouts (McDonnell 1986).

Bulbuls are small-bodied and highly frugivorous, known as high quality seed dispersers in many tropical regions (Graham et al. 1995; Shanahan et al. 2001; Weir & Corlett 2007; Kunz et al. 2008). These individuals are very abundant and adaptable to degraded and humanized areas, being frequently seen visiting open fields (Corlett & Hau 2000; Weir & Corlett 2007). As a result, they are expected to have a great impact on seed dispersal to the degraded areas of CNP, even if their maximum gape width (~14mm) only allows the dispersal of small seeds (Weir & Corlett 2007).

Although none of the tested variables proved to be an important driver of Violet-backed starlings' abundance in degraded areas, it should be mentioned that this species is a potential important seed disperser, being very abundant in degraded areas in CNP. Violet-backed starlings are mainly frugivorous and move in large flocks, having been recorded to disperse seeds over one kilometre away from parent plants (Dowsett-Lemaire 1988).

Forest visitors showed a positive relation with empty fields and trees from the sub-family Mimosoideae. The positive relation between the abundance of these birds and empty fields seems to suggest that they might be good dispersers between forests and degraded areas, even in the absence of perches or other landscape elements that function as attractors in these areas. On the other hand, trees from the Mimosoideae sub-family, namely some *Albizia* species, are common in degraded areas and their seeds' germination is frequently potentiated by fire (van der Pijl 1982). In Guinea-Bissau, agricultural practices, such as slash-and-burn, can favour the regeneration of these species, that seem to favour the presence of potential seed dispersers in degraded areas of CNP. This is probably due to their rapid development and their role as important perches, at least during an initial phase of vegetation recovery in these areas. The species used for focal point observations were young trees of *A. adianthifolia*, a species typically present in the interior of primary and secondary forests (Catarino et al. 2006).

4.2.5. Forest generalists

Being common in secondary forests, gaps and forest edges (Bennun et al. 1996), forest generalists might also be important dispersers of seeds from the forest interior. This study seems to point out that African Green-pigeons could be more important dispersers near forest edges, while Glossy starlings seem to be more abundant further away from forest edges and thus possibly being important dispersers in degraded areas.

As mentioned in the general discussion of potential avian dispersers, African Green-pigeons could play an important role in the seed dispersal of some plant species in CNP, even if they are not very efficient dispersers (Lambert 1989; Corlett 1998). The negative and significant relation found between this species abundance and distance to the closest forest edge could reflect a dependence on increased fruit

availability inside the forest. However, individuals of this species are known to fly large distances searching for greater foraging opportunities (Lambert 1989) and are frequently seen flying over degraded areas. During this study, some individuals were even spotted constructing nests in trees present in these areas.

Contrary to what might have been expected, forest generalists revealed a negative and significant relation with tree height. For instance, Glossy Starlings are known to forage mainly in canopy above 30m (Craig & Feare 2018) and the positive relation found with tree families Apocynaceae, Chrysobalanaceae and Moraceae, highlights a preference for generally taller trees. This result might reflect a higher number of African Green Pigeons flying over the plots, compared with those effectively perching in focal trees, since this species accounts for about 82% of this guild individuals.

Moreover, even though none of the tested variables prove to be important drivers of West African Pied Hornbills, this species should be one of the most important dispersers of seeds from the forest interior of this guild, owing to its ecology traits. These individuals are large-bodied, highly frugivorous and capable of consuming a wide range of fruits (del Hoyo et al. 2018). In addition, the West African Pied Hornbill is one of the most adaptable Hornbill species in the study area (del Hoyo et al. 2018), being frequently observed crossing and perching in degraded areas and secondary forests.

4.2.6. *Forest specialists*

Forest specialist species, grouping Hornbills and Turacos, showed a positive relation with all tree height variables, which comes as no surprise since these species are generally seen feeding on tall trees (Duncan & Chapman 1999). Results for Turacos reinforce this positive relation with tree height. Individuals of this family have not been recorded in large numbers during this study, yet they are generally considered important seed dispersers, since they are highly frugivorous (Compton et al. 1996; Shanahan et al. 2001). However, the genera registered in degraded areas of CNP (*Corythaeola* and *Tauraco*), are known to have weak flight capability (Turner 1997) and should be, in fact, more relevant dispersers within forest patches, since their dispersal movements are estimated to range up to 304m inside the forest (Sun et al. 1997).

Hornbills, on the other hand, are extremely reliable upon large areas of undisturbed forest, but are still able to make large foraging movements, searching for greater foraging opportunities (Rainey & Zuberbühler 2007). Their large home-ranges, adding to the fact that they can ingest a wide spectrum of seed sizes and retain them in their guts for longer periods, make them exceptional dispersers (Holbrook et al. 2002; Graham & Page 2011). The negative relation found between their abundance and distance to the closest forest edge in CNP, does not reflect their inability to cross or visit degraded areas but it could imply that Hornbills are more important dispersers close to forest edges. Wunderle Jr (1997) has even stated that habitat specialists have limited dispersal services outside their preferred habitat type, suggesting that forest specialists are poor dispersers in areas further away from forest edges.

Additionally, forest specialists seem to be positively affected, even if not significantly, by trees from the Moraceae family, including Fig trees and Bark Cloth trees. These trees were fruiting and bore mature fruits during the study period, which could explain a greater abundance of forest specialists visiting these areas. Moreover, fruit trees are known to attract higher bird diversities to degraded areas (Uhl 1982; Guevara et al. 1986; Duncan & Chapman 1999) and should thus be important attractors for forest specialists.

4.3. Implications for conservation and forest regeneration

This study provides an important overview of a key ecosystem service in the forests of Cantanhez National Park: the dispersal of seeds by birds. This first step towards understanding the mechanisms which can promote the natural regeneration of forests, is not only important for the forests of Guinea-Bissau, but also for forests of Western Africa in general, where anthropogenic factors affecting forests are similar.

Overall, with this study's outcomes, it is possible to infer that tall trees are important drivers of the abundance of several bird dispersers in degraded areas, and therefore, of faeces and seed deposition. Taller trees are known to offer better predator lookouts, foraging opportunities and larger shading areas that facilitate growth and survival of seedlings (Nepstad et al. 1996; Duncan & Chapman 1999; Guevara et al. 2004). With the conversion of forests to farmland, some trees are usually left in the fields, either because they are too large and difficult to remove or because they have a significant cultural, religious or economical value (Lawson 1966). For instance, in the surrounding areas of the forests of CNP, examples of this include trees from the families Bombacaceae, Apocynaceae and Arecaceae, such as Kapok trees, *Alstonia* species and Palm trees, respectively (Frazão-Moreira 2001; Casanova et al. 2014).

Isolated tall trees have been proven to favour the presence of important dispersers such as Bulbuls and Violet-backed starlings but are also known to be important for forest specialists, such as Hornbills and Turacos. Tall and large trees, such as Kapok trees, seem to favour faeces deposition and should thus be preserved in these areas. In addition to isolated trees, small tree remnants have been described as important seed recruitment nuclei, favouring a faster vegetation regeneration (Toh et al. 1999). Results found here seem to reinforce this idea, revealing that there is greater faeces deposition associated with an increased vegetation complexity. To increase vegetation complexity in some of the degraded areas of CNP, it should be encouraged that some small shrubs and trees are allowed to prosper, thus promoting visits of a greater diversity of avian dispersers in these areas and, consequently, an increase in the abundance and diversity of dispersed seeds.

The arrival of seeds to degraded areas of CNP seems to be dominated by the recruitment of small seeds and it is crucial that management measures are proposed to promote a diversification of seeds arriving to these locations. This study showed that Moraceae trees, such as Fig trees and Bark Cloth trees (*A. toxicaria*), favour not only a greater potential dispersers' species richness in degraded areas, but also a greater abundance of forest specialists and large-bodied birds, such as Hornbills and Turacos. Large-seeded species depend on larger-bodied frugivores for their dispersal (Levey 1987). Therefore, it is important that local communities are encouraged to leave these and other fruit tree species during vegetation clearing, in degraded areas. In severely degraded areas, direct planting of forest native trees with interesting fruits for frugivores, like the above-mentioned, should be considered in future restoration strategies. However, selection of tree species should be made with caution, since trees which are frequently cultivated in these areas, such as tree species belonging to the Anacardiaceae family, do not seem to have a very positive influence on the general abundance of dispersers.

Forest regeneration does not depend solely on the arrival of seeds to these sites. Seed banks and resprouting species present in these areas, prior to forest cutting, also play an important role in the speed at which vegetation will regenerate. Soil seed banks are typically depleted after a few years of land-use intensification (Brown & Lugo 1994; Duncan & Chapman 1999) and, considering the long-history of land-use changes in Guinea-Bissau, it would be important to evaluate the current situation of seed banks in degraded areas of CNP.

Future studies in these areas should emphasise the use of methodologies that allow the identification of the link between dispersal agent and plant species of each dispersed seed. This way, it would be possible

to apply direct conservation measures to the most vulnerable tree or bird species with an important role in the dispersal of certain plant species. The Yellow-casqued hornbill, for instance, holds a global Vulnerable conservation status (BirdLife International 2016) and it would be important to favour the presence of this species in CNP, so that a bottleneck in the dispersal of some plant species does not occur in the future. In addition, this study focuses on the dispersal of seeds by avian frugivores, which is unquestionably important in tropical regions, but that represents only a fraction of the dispersal services given by vertebrates in this ecosystem. In the future, it would be important to assess the complementary role of several groups of seed dispersers in degraded areas of CNP, like frugivorous bats and non-volant mammals, such as primates and squirrels.

Finally, the role of IBAP (Instituto da Biodiversidade e das Áreas Protegidas) and CNP officers in promoting sustainable practices among local communities is crucial for the conservation of Guinea-Bissau's forests. However, any proposed conservation measures, should be discussed with the local communities who are at the forefront of conservation in CNP. It is of utmost importance to achieve a balance between the socio-economic development of the country and the proposed management measures for the conservation of these forests, while taking advantage of seed dispersal services.

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SUPPLEMENTARY MATERIALS

SECTION 1: Vegetation Complexity Index

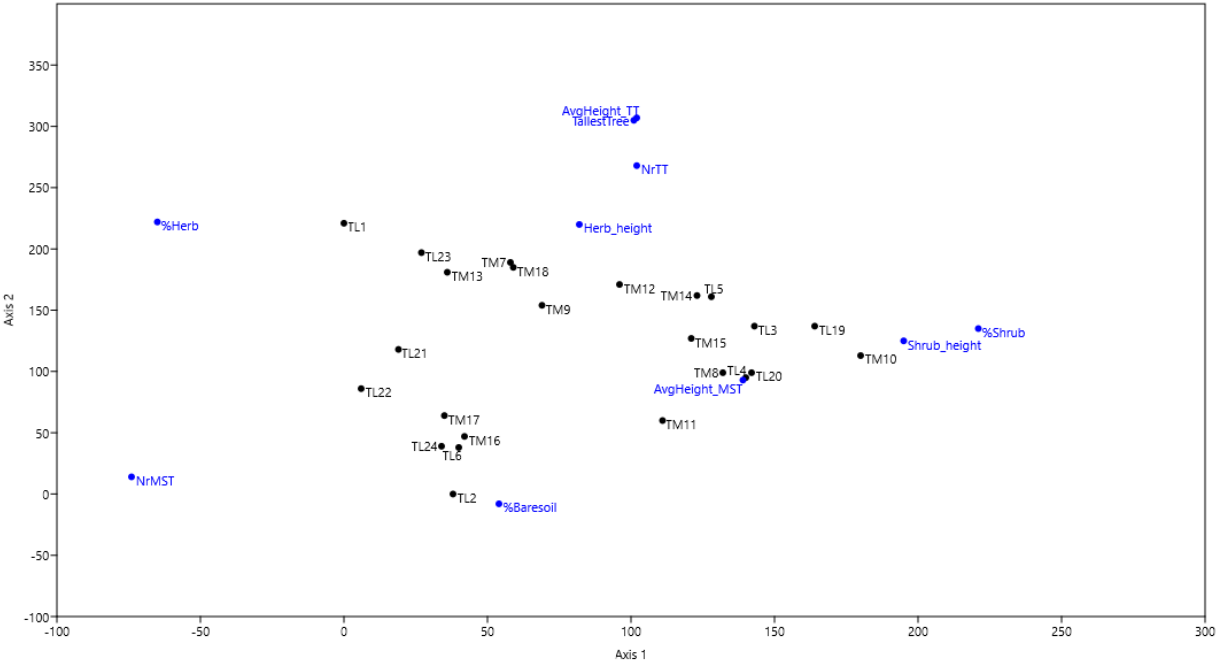


Figure S1.1 - Detrended Correspondence Analysis result. Axis 2 was chosen to ordinate vegetation complexity. Seed traps' plots are represented with "TL" and "TM" initials. The variables considered for this ordination analysis were: percentage of bare soil (%Baresoil), percentage and average height of herbaceous vegetation (%Herb, Herb_height) and shrubs (%Shrub, Shrub_height), number and average height of small and medium trees (NrMST, AvgHeight_MST) and the number and average height of tall trees (NrTT, AvgHeight_TT).

SECTION 2: Spearman correlation results

Table S2.1 – Spearman correlations and respective p-values for the different variables considered in the analysis of seed dispersal and their relation with the number of faecal samples (Nfaecal) and number of seeds (Nseeds). Significant correlations for the number of seeds are presented in bold.

Spearman correlation values (rho)									
	Closest_edge	PA_tree	TreeHeight	Closest_dist	SpFrut	SpFlow	IndVeg	Nfaecal	Nseeds
Closest_edge	1,00	0,31	0,25	-0,12	0,34	0,24	-0,05	0,08	0,07
PA_tree	0,31	1,00	0,8	-0,83	0,56	0,39	-0,18	0,35	0,23
TreeHeight	0,25	0,8	1,00	-0,71	0,47	0,28	-0,05	0,46	0,29
Closest_dist	-0,12	-0,83	-0,71	1,00	-0,51	-0,34	0,12	-0,36	-0,15
SpFrut	0,34	0,56	0,47	-0,51	1,00	0,26	-0,25	0,20	0,08
SpFlow	0,24	0,39	0,28	-0,34	0,26	1,00	-0,30	0,05	0,04
IndVeg	-0,05	-0,18	-0,05	0,12	-0,25	-0,30	1,00	0,02	-0,04
Nfaecal	0,08	0,35	0,46	-0,36	0,20	0,05	0,02	1,00	0,54
Nseeds	0,07	0,23	0,29	-0,15	0,08	0,04	-0,04	0,54	1,00

P-values									
	Closest_edge	PA_tree	TreeHeight	Closest_dist	SpFrut	SpFlow	IndVeg	Nfaecal	Nseeds
Closest_edge		0,001	0,006	0,179	0,000	0,009	0,600	0,400	0,478
PA_tree	0,001		0,000	0,000	0,000	0,000	0,048	0,000	0,013
TreeHeight	0,006	0,000		0,000	0,000	0,002	0,623	0,000	0,001
Closest_dist	0,179	0,000	0,000		0,000	0,000	0,193	0,000	0,112
SpFrut	0,000	0,000	0,000	0,000		0,004	0,012	0,029	0,145
SpFlow	0,009	0,000	0,002	0,000	0,004		0,001	0,589	0,654
IndVeg	0,600	0,048	0,623	0,193	0,012	0,001		0,826	0,634
Nfaecal	0,400	0,000	0,000	0,000	0,029	0,589	0,826		0,000
Nseeds	0,478	0,013	0,001	0,112	0,145	0,654	0,634	0,000	

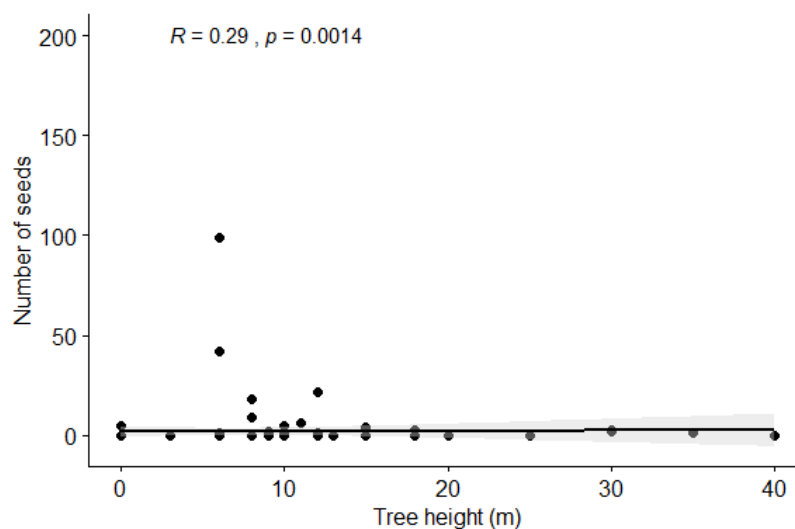


Figure S2.1 – Plot of the significant result of the spearman correlation between the number of seeds and tree height above the seed trap.

Table S2.2 - Spearman correlations and respective p-values for the relation between forest specialists (FF) and the different variables considered in the analysis of dispersal agents. Significant correlations for forest specialists' abundance are presented in bold.

Spearman correlation values (rho)							
	TreeHeight	Frutif	Closest_edge	Closest_dist	Closest_height	Max_height	FF
TreeHeight	1,00	0,38	-0,11	-0,10	0,48	0,29	0,39
Frutif	0,38	1,00	0,01	-0,18	0,03	-0,10	0,07
Closest_edge	-0,11	0,01	1,00	0,14	0,14	-0,06	0,02
Closest_dist	-0,10	-0,18	0,14	1,00	0,36	0,21	0,14
Closest_height	0,48	0,03	0,14	0,36	1,00	0,52	0,31
Max_height	0,29	-0,10	-0,06	0,21	0,52	1,00	0,28
FF	0,39	0,07	0,02	0,14	0,31	0,28	1,00

P-values							
	TreeHeight	Frutif	Closest_edge	Closest_dist	Closest_height	Max_height	FF
TreeHeight		0,002	0,409	0,415	0,000	0,018	0,001
Frutif	0,002		0,945	0,144	0,819	0,429	0,576
Closest_edge	0,409	0,945		0,257	0,257	0,657	0,847
Closest_dist	0,415	0,144	0,257		0,003	0,097	0,270
Closest_height	0,000	0,819	0,257	0,003		0,000	0,012
Max_height	0,018	0,429	0,657	0,097	0,000		0,025
FF	0,001	0,576	0,847	0,270	0,012	0,025	

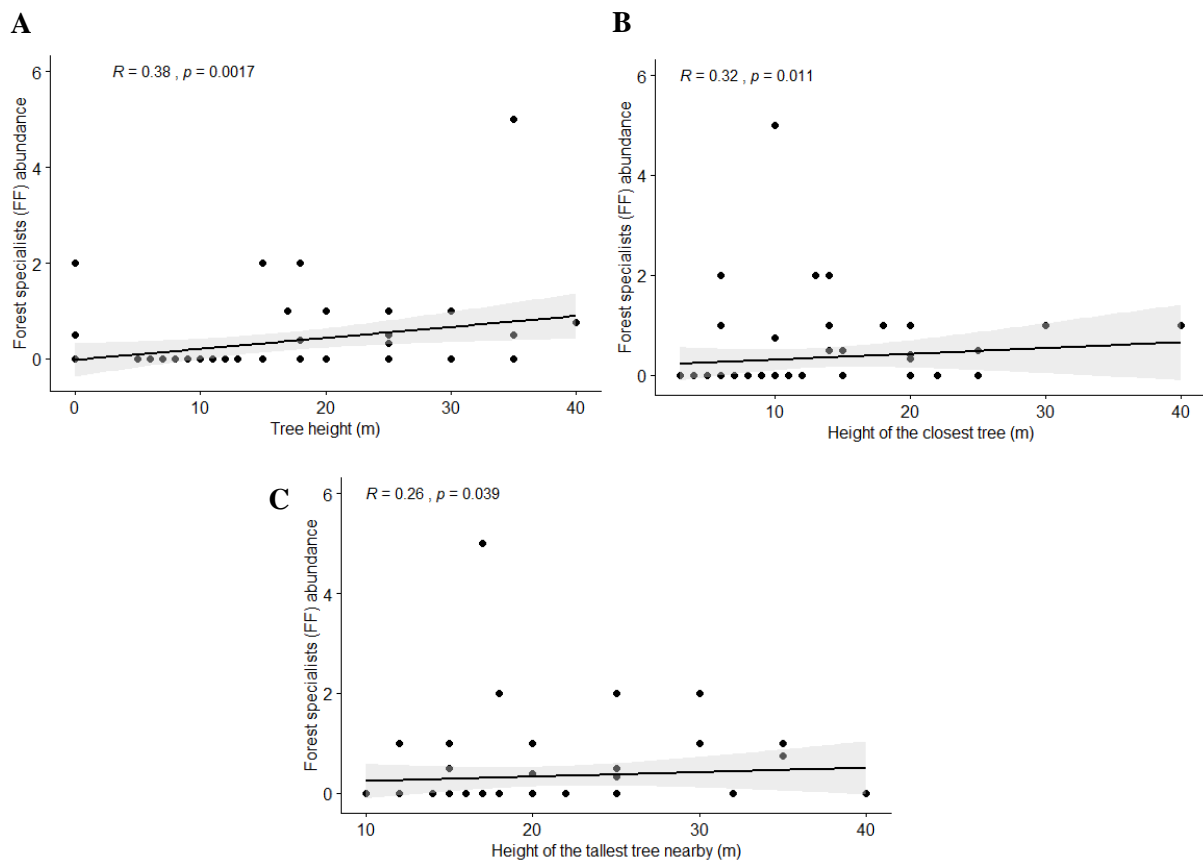


Figure S2.2 - Plots of the significant results of the spearman correlation between forest specialists and tree height (A), height of the closest tree (B) and height of the closest tree nearby (C).