



# Effects of deforestation and forest degradation on the endemism rich bird communities of the Angolan Scarp Forest

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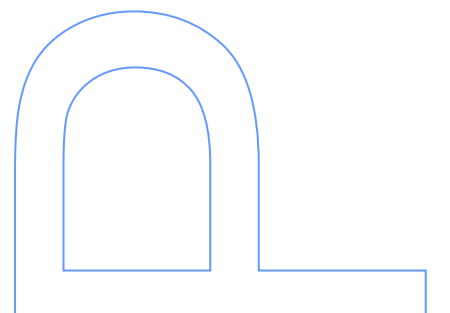
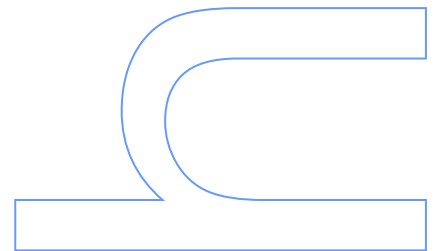
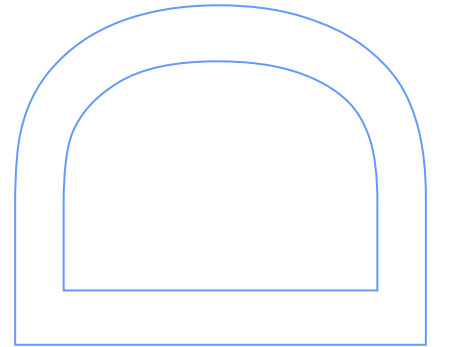
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## Nota prévia

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## Resumo

A perda de habitat provocada por actividades humanas é a principal causa do declínio e extinção de espécies. Isto é particularmente evidente nos trópicos, onde se concentra a maior parte da biodiversidade do planeta e onde os impactos humanos estão a aumentar mais rapidamente. A biodiversidade tropical tende a diminuir com a redução da complexidade da vegetação. No entanto, as respostas às alterações de habitat podem diferir entre espécies e com o contexto da paisagem. Compreender os efeitos das actividades humanas na biodiversidade é crucial para propor medidas que assegurem a sua conservação. No entanto, essa informação não existe para muitas áreas tropicais. Este é o caso de Angola, um país com uma biodiversidade elevada mas muito pouco estudado. Após a guerra da independência, Angola viveu 30 anos de conflitos armados (1974 - 2002) durante os quais praticamente nenhuma investigação foi feita. Além disso, o desenvolvimento económico e o crescimento populacional actuais estão a criar grandes pressões nas áreas naturais. Uma das áreas mais importantes no país para a biodiversidade – e especialmente para as aves – são as florestas da escarpa angolana.

O objectivo principal desta tese foi o de compreender os efeitos da deflorestação e degradação das florestas nas comunidades de aves da floresta da escarpa angolana. Para tal: i) descreveram-se as mudanças históricas no uso de solo e determinou-se o seu efeito nas comunidades de aves; ii) identificaram-se as características do habitat que determinam a riqueza de espécies e a presença de aves endémicas e iii) utilizou-se rádio-telemetria para obter informação detalhada sobre as preferências de habitat e a área vital da ave endémica ameaçada com a área de distribuição mais restrita de Angola, o pisco da Gabela *Sheppardia gabela*. Finalmente, (iv) as taxas de deflorestação e as reservas de carbono foram estimadas para avaliar o potencial de uma iniciativa REDD+ como ferramenta para a conservação da Floresta de Escarpa Angolana.

Os resultados principais deste trabalho mostram que nas últimas duas décadas (1989-2010) a cobertura florestal total não sofreu alterações significativas em Kumbira. No entanto, isto foi conseguido através da substituição de floresta natural por floresta secundária. Esta última é capaz de manter uma comunidade de aves semelhante à da floresta natural. Não obstante, as aves endémicas ameaçadas parecem ser mais dependentes da floresta natural, com uma espécie – o picanço do Amboim *Laniarius amboimensis* – apenas presente neste tipo de habitat.

As características do habitat que influenciaram a diversidade de aves foram a cobertura da copa e a densidade de lianas. A cobertura da copa afectou a riqueza de

espécies e a presença do pisco da Gabela, enquanto a densidade de lianas teve um efeito na presença do Turaco de Angola *Tauraco erythrolophus*. Nenhuma característica de habitat foi identificada como determinante na presença das outras espécies endémicas; isto pode estar relacionado com a baixa detecção de algumas espécies – como o bico-longo de Angola *Macrosphenus pulitzeri* e o picanço de Monteiro *Malaconotus monteiri* – ou com a incapacidade das medidas de vegetação utilizadas em identificar as variáveis que influenciam as espécies - possivelmente o caso para o picanço do Amboim.

O tamanho da área vital do pisco da Gabela foi ligeiramente maior do que para outras espécies do género *Sheppardia* e, curiosamente, o tamanho diminuiu nas áreas com maior perturbação humana. Esta espécie evita claramente o uso de áreas abertas e a floresta é o habitat preferido, embora seja capaz de usar áreas agrícolas e de vegetação secundária. No entanto, esta capacidade parece estar relacionada com o contexto da matriz da paisagem onde persistem fragmentos de floresta natural.

Na última década (2001-2014), com o regresso das populações às zonas rurais após o fim da guerra, a taxa de desflorestação da floresta pode ter atingido os 4% ao ano – o que se traduziu na perda de mais de 1/3 da floresta neste breve intervalo de tempo. Perante esta situação, avaliou-se a aplicabilidade do programa REDD+ como instrumento para parar e inverter esta tendência. O potencial existe pois as reservas de carbono estimadas para Kumbira encontram-se entre os valores estimados para outras florestas de África. No entanto, para que as iniciativas REDD+ sejam uma ferramenta bem-sucedida na conservação da Floresta de Escarpa Angolana, é necessário que sejam dirigidas para programas de desenvolvimento da capacidade das populações locais em implementarem sistemas agro-florestais adequados.

A integração dos resultados desta tese oferece bases sólidas para propor linhas orientadoras para a conservação da floresta da escarpa central. Nomeadamente: i) a criação de uma reserva natural com urgência, e ii) a de minimização dos impactos da agricultura através: ii-a) da introdução de métodos mais amigos do ambiente, tais como a recuperação das plantações abandonadas de café de sombra, ii-b) o uso de práticas agrícolas mais eficientes a fim de evitar o abate e queima de mais floresta natural e ii-c) a recuperação de áreas degradadas através de um projecto de reflorestação com espécies arbóreas nativas.

**Palavras-chave:** Angola, deflorestação, aves endémicas, floresta da escarpa, perda de floresta, preferências de habitat, perturbação humana, Kumbira, mudança no uso do solo, vegetação secundária.



## Abstract

Habitat loss due to human activities is the leading cause of species decline and extinction. This is especially true in the tropics, where most of the earth's biodiversity is concentrated and where human impacts are increasing faster. Tropical biodiversity usually declines following a gradient of decrease in vegetation complexity. However, the responses can be different and be very species-specific and landscape related. Understanding the effect of human activities on biodiversity is vital for implementing measures that will assure its conservation. Unfortunately, most information about species' responses is restricted to well-studied areas while no information is available for many tropical areas. This is the case of Angola, a high biodiverse and under-studied country. After the war of independence, Angola endured almost 30 years of armed conflicts (1974-2002), which prevented any research to take place in the country. Furthermore, current economic development and population growth are producing high pressures in natural areas. One of the most important areas for biodiversity in the country – especially birds – is the Angolan Escarpment (“Scarp”) Forest.

The main goal of this thesis was to understand the effects of deforestation and forest degradation on the bird communities of the Angolan Escarpment Forest. To do this, (i) the historical land-use changes and their effect in the composition of bird communities were described; (ii) habitat characteristics driving current species richness and presence of endemics were assessed and (iii) radio-tracking was used to obtain detailed information about home-range size and habitat preferences of the most range-restricted threatened endemic bird of Angola, the Gabela Akalat *Sheppardia gabela*. Finally, (iv) deforestation rates and carbon stocks were estimated to assess if REDD+ could be used as a conservation tool for the Angolan Escarpment Forest.

The main results of this thesis show that in the past two decades (1989 – 2010) forest cover has been maintained. However, this was achieved by the replacement of old-growth forest by secondary growth. This secondary forest is capable of maintaining a similar bird community to old-growth forest. Nevertheless, the threatened endemic species seem to be more dependent on the old-growth forest, with the Gabela Bushshrike *Laniarius amboimensis* restricted to this habitat type.

The habitat characteristics that influenced bird diversity were canopy cover and liana density. Canopy cover affected species richness and presence of Gabela Akalat while liana density had an effect in the presence of Red-crested Turaco *Tauraco erythrolophus*. No habitat characteristics were associated with the presence of the other endemics; this can be related to the low detectability of some species – Pulitzer Longbill *Macrosphenus pulitzeri* and Monteiro Bushshrike *Malaconotus monteiri* – or

the failure of the vegetation surveys to record the variables that affect these species – as was possibly the case for the Gabela Bushshrike.

The home-range size of Gabela Akalat was slightly larger than other *Sheppardia* species and it decreased with human disturbance. This species evidently avoided clearings and preferred forest habitat, but it was also capable of using agricultural areas and secondary growth. However, this capacity is likely related with a landscape matrix where natural forest patches remain.

In the last decade (2001-2014) with the return of populations to the rural areas after the end of the war, the annual deforestation rate increased to as much as 4% - representing a loss of more than 1/3 of the forest in this short period of time. Faced with this situation, the applicability of a REDD+ programme as a tool to stop and reverse this trend was evaluated. The potential exists as total carbon reserves in Kumbira were within the estimated ranges for other African forests. However, in order for REDD+ to be a successful conservation tool for the Angolan Escarpment Forest it needs to focus more in capacity building programmes aiming focusing on implementing adequate agro-forestry practices.

The results of this study offer a solid base from where to derive conservation guidelines for the Central Escarpment Forest. Conservation actions must include i) the urgent creation of a natural reserve, and ii) the mitigation of the impact of agriculture by: ii-a) using more wildlife-friendly methods, such as recovering the abandoned shade coffee plantations in the area, ii-b) the use of more efficient agricultural practices moving away from slash-and-burn, and ii-c) the recovery of degraded areas through a reforestation project with native tree species.

**Key-words:** Angola, deforestation, endemic birds, escarpment forest, forest loss, habitat preferences, human disturbance, Kumbira, land-use change, secondary growth

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# Chapter 1

## General Introduction

## **1.1. Effects of deforestation and forest degradation on biodiversity**

Natural environments around the world are being rapidly transformed in order to fulfil the requirements of a growing human population. This is particularly worrying in the tropics, where most of the earth's biodiversity is concentrated and where human impacts are advancing at a faster pace. Almost two thirds of the world's biodiversity is concentrated in the tropics, a region that represents only 7% of the planet surface (Dirzo and Raven, 2003, Bradshaw et al., 2009, Gardner et al., 2009). Furthermore, almost 65% of the biodiversity hotspots are located in the tropics (Myers et al., 2000). Unfortunately, impacts in these areas are increasing rapidly because they present a high rate of human population growth (Cincotta et al., 2000) and are home to developing nations that often have limited options regarding their use of natural resources (Bradshaw et al., 2009).

Agriculture, logging and urbanization are the main causes of deforestation, forest fragmentation and intensification of land-use in tropical areas, all having a profound effect on their biodiversity (Norris et al., 2010, Gardner et al., 2009). Agriculture is responsible for 90% of the deforestation in the tropics, of which 55% come from the clearing of natural forests (Sodhi et al., 2011). It is predicted that tropical areas in South America and Sub-Saharan Africa will suffer major agricultural expansions to fulfil the need for food of a growing human population (Laurance et al., 2014). Africa has the least cropland than other regions. Nevertheless, in the last two decades (1980-2000) the percentage of agricultural land has increased in 25% and 50% in Western and Eastern Africa respectively. Furthermore, 60% of this agricultural land came from the clearing of natural forests and 35% from disturbed forests (Gibbs et al., 2010).

Logging is also a major threat for tropical areas, as selective logging is a common practice in many tropical countries. For instance, most of the forest in Western Africa had been logged to some degree (Norris et al., 2010). The effect of logging in tropical biodiversity depends on the different management techniques and the landscape context. Selective logging events with time gaps between them allow the forest to regenerate and produce a forest structure with different tree sizes and ages, similar to a natural stand, allowing some forest species to survive on these logged forests. Logging activities also produce a change in the community composition, benefiting generalist species over forest specialists (Sodhi et al., 2008). However, intense logging negatively impacts biodiversity due to the loss of natural canopy and the increase of invasive species (Norris et al., 2010). Furthermore, the roads

constructed for logging enable access to the forests, leading to an increase in other activities such as hunting and forest clearance for agriculture, all having major impacts on biodiversity (Laurance et al., 2009, Norris et al., 2010).

Finally, despite urbanization being responsible for the lower rate of deforestation in Africa (Norris et al., 2010), it causes major disturbance to native species because infrastructures displace these species and benefit urban adapted species (Sodhi et al., 2011). Moreover, urbanization has the most lasting disturbance effects because the infrastructures remain, contrary to other human land-uses, such as agriculture and plantations, where regeneration processes take place (McKinney, 2002). Furthermore, in the case of tropical areas urbanization is expected to increase and produce a major pressure in forested areas.

The impacts of human activities in the tropics are predicted to continue and increase. Therefore, biodiversity conservation in human-modified landscapes is needed (Sodhi et al., 2011). It will be of vital importance to understand how biodiversity is affected by land-use changes in order to propose measures to assure the conservation not only of the species but also of their ecological functions and services.

The effects that human activities have on biodiversity have been studied in different groups. Biodiversity usually declines following a gradient that reflects the decrease of vegetation structure complexity (Harvey et al., 2006, Schulze et al., 2004, Bobo et al., 2006). Full-grown and late-stage forest, such as primary forests, is expected to present a higher biodiversity than simpler human modified-landscapes, such as pastures. Additionally, species that depend exclusively on the forests will be more susceptible to the transformation of these habitats than species partly-dependant on forest habitats (Gardner et al., 2009). Nevertheless, it has been shown that some of these human-modified landscapes, such as secondary forests and agroforestry systems, can conserve part of the biodiversity of the original forests and act as useful corridors linking core areas of natural forests (Gove et al., 2008, Schulze et al., 2004, Sodhi et al., 2005). However, all these responses can be very species-specific and dependent on the local context.

### **Impacts on birds**

Birds have been shown to be a particularly good indicator of ecological conditions in habitats under varying degrees of human exploitation (Sekercioglu et al., 2004, Barlow et al., 2007b, Gardner et al., 2008, Sodhi et al., 2008). As with other taxa, forest avian diversity usually declines with a decrease in the structural complexity of vegetation (Scales and Marsden, 2008, Barlow et al., 2007a). However, their response to different land-use changes can be very variable and dependent on different factors,

such as the intensity of the impact, the landscape matrix context, the species ecological traits and even the temporal scale of the study (Newbold et al., 2013, Watson et al., 2004, Newmark, 2006).

Bird diversity decreases more drastically in the higher impact human-modified habitats (Newbold et al., 2013). Therefore, intensive agricultural landscapes – such as pastures, monocultures and sun-loving crops – have considerably lower bird species and share less species with natural forests. Generalists, and especially open area species, dominate these habitats as forest specialists are unable to cope with the conditions created by intensive agriculture (Waltert et al., 2004). Specialised species such as insectivores and ant-followers are replaced by granivores and nectarivores (Norris et al., 2010).

On the other extreme, shade plantations – such as coffee and cacao – can support forest species, especially if the natural canopy is maintained (Waltert et al., 2004). This type of plantations maintains a structural complexity similar to a natural forest, with high canopy trees and understorey strata. In the specific case of shade coffee, its ability to support forest bird diversity can depend on the regional context. In Latin America, shade coffee plantations have high bird species richness and abundance. However, they present a different community composition that benefits generalists – including migrants – over forest specialists (Tejeda-Cruz and Sutherland, 2004, Harvey and Gonzales Villalobos, 2007). On the contrary, in Africa and specifically in Ethiopia, forest-specialists diversity did not differ between shade coffee plantations and natural forests. These plantations had twice as much bird species including all that were present in the natural forests. Additionally, these plantations were used as a breeding ground for the forest species. These results may be related with the fact that coffee *Coffea spp.* originated in Ethiopia. It is possible that the bird diversity evolved together with the coffee plant and therefore tolerates it better (Buechley et al., 2015). The local landscape context also affects the capacity of shade coffee to support biodiversity. Proximity to natural forest increases the capacity to support bird diversity (Tejeda-Cruz and Sutherland, 2004, Norris et al., 2010). Furthermore, in open areas, shade coffee plantations also promote bird diversity because of the maintenance of high canopy trees. However when surrounded by forests this diversity can considerably decrease (Dallimer and King, 2007, Gove et al., 2008, Dallimer et al., 2012, de Lima et al., 2013).

Shade coffee plantations can be important for bird conservation because they support more bird species than any other agricultural use (Komar, 2006). Transformation of sun loving crops or monocultures into shade coffee plantations can increase bird diversity and promote connectivity between forest remnants (Tejeda-Cruz

and Sutherland, 2004). Furthermore, the economic value of coffee can favour the maintenance of forest remnants rather than their destruction towards more open agricultural uses (Gove et al., 2008). Nevertheless, despite the apparently benefits of shade coffee over other land-uses, the conservation of natural forests continues to be of vital importance to protect the species that are more susceptible to habitat disturbance (Dallimer and King, 2007, Dallimer et al., 2009, Buechley et al., 2015).

Selective logged forests when properly managed can support forest specialists. When these areas are allowed to recover they can receive species from surrounding natural forest (Sodhi et al., 2011). Nevertheless, bird species richness in logged forests increases up to a threshold of tree removal and is always related with the increase of generalist species (Norris et al., 2010).

Similarly to both shade plantations and selective logged forests, bird species richness in secondary forests can be similar or even higher than in natural forests. However, the community composition here can be quite different, with the decrease of insectivores, understorey and floor forest specialist species (Norris et al., 2010, Barlow et al., 2007b) and also the loss of range-restricted species that usually have a high conservation value (Fjeldså, 1999, Waltert et al., 2005). Some forest species are capable of using secondary forests as long as natural forest patches are in the vicinity. The disappearance of these patches can increase these bird species vulnerability to extinction (Harris and Primm, 2004). This is also true for other human-modified habitats. Native forest cover can determine the presence of forest bird species (Sodhi et al., 2005) which may use these disturbed habitats but continue to depend on the natural forests in their surroundings (Norris et al., 2010). Despite the capacity of secondary forests to have similar bird species and act as natural corridors between primary forest remnants, primary forests continue to be irreplaceable for conserving tropical biodiversity (Barlow et al., 2007a, Barlow et al., 2010, Gibson et al., 2011).

Ecological traits also affect the response of tropical birds to habitat disturbance. Life-history traits that make species more vulnerable to habitat disturbance include: large body size, large home-ranges, slow breeding, non-migratory behaviour (Sodhi et al., 2011, Newbold et al., 2013). In relation to feeding guilds, frugivores and insectivores are more vulnerable to habitat disturbance. Usually these species decline with deforestation because of the reduction in food availability (Gray et al., 2007, Sodhi et al., 2011). Conversely, granivores increase because they benefit from the appearance of certain plants in disturbed habitats (Fjeldså, 1999).

In the particular case of endemic species, they tend to be especially sensitive to land-use changes (Scales and Marsden, 2008). Being species with small ranges, they are commonly at elevated risk of extinction because of the relatively large effects of

habitat change on their relatively small populations. For this reason they are of great conservation significance. Their response to habitat disturbance can vary: in some cases populations decrease drastically (Norris et al., 2010) and in others endemics adapt well to altered habitats (Reif et al., 2007, Dallimer et al., 2012).

Knowing the effects of human activities on biodiversity is vital to establish adequate conservation measures. Unfortunately, the areas holding the most biodiversity of the planet are also the least studied. This is the case of the tropics which holds the highest amount of data deficient species (Sodhi et al., 2011). Furthermore, most of the knowledge regarding tropical biodiversity in human-modified landscapes is restricted to very well-known study sites. Therefore, the impacts of human activities on tropical biodiversity are based in a specific ecological and human context (Gardner et al., 2010).

Africa presents the lowest deforestation rate when compared to Asia and to Central and South America (Bradshaw et al., 2009), and has the second largest continuous tropical forest in the world (Gardner et al., 2009). Despite the importance of this forest, African biodiversity – especially in the Western part – is the least studied and understood (Gardner et al., 2010, Norris et al., 2010, Gibson et al., 2011). Therefore, filling the knowledge gap about biodiversity on human-modified landscapes in tropical Africa is of vital importance for conservation, especially in extremely poor studied countries such as Angola.

## **1.2. Angola: a little known and high biodiverse country**

Angola is located on the western coast of Africa, between latitudes 4° and 18°S, and longitudes 12° and 24°E (Fig. 1a). The country borders with Namibia in the south, the Democratic Republic of Congo in the north, Zambia in the east and the Atlantic Ocean in the west. It also has an enclave, Cabinda, surrounded by the Democratic Republic of Congo and the Republic of Congo (Brazaville). The country has a land surface area of 1 246 700 km<sup>2</sup> and is divided in 18 provinces: Bengo, Benguela, Bié, Cabinda, Cuando Cubango, Cuanza Norte, Cuanza Sul, Cunene, Huambo, Huila, Luanda, Lunda Norte, Lunda Sul, Malanje, Moxico, Namibe, Uíge and Zaire (Fig. 1b).

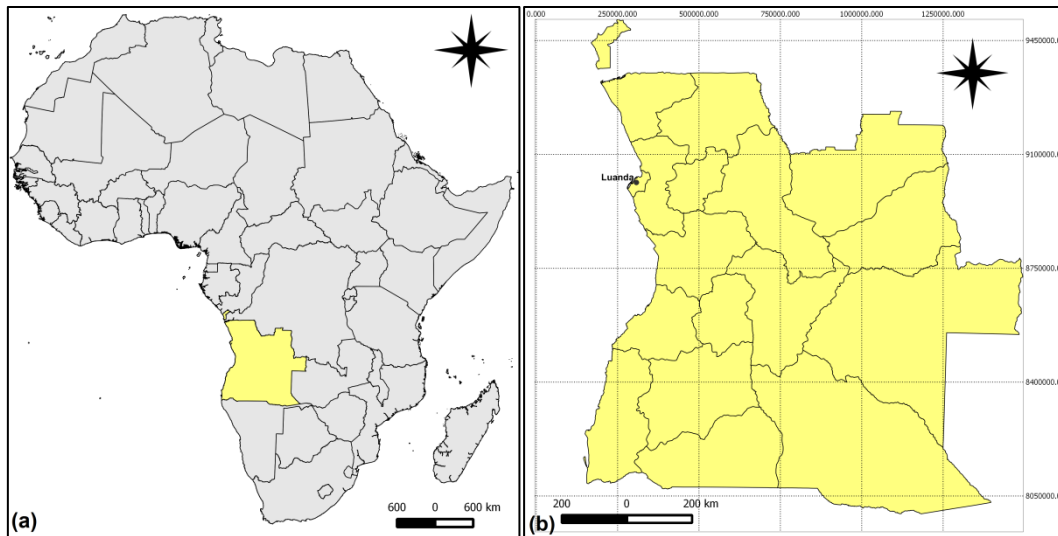


Fig. 1 (a) Location of Angola (in yellow) within Africa and (b) map of Angola with its 18 provinces

Angola is a very biodiverse country because of its location and particular geographical features. It holds six geomorphological regions: the Coast Belt, the Transition Zone, the Marginal Mountain Chain, the Old (Highland) Plateau, the Congo Basin and the Cubango-Zambezi Basin (Huntley, 1974b) (Fig. 2a). The Coast Belt is an arid and semi-arid area that extends from 12 to 200 km from the coast with a maximum elevation of 300 m. Next, is the Transition Zone where the elevation rises as you go inland. Then, the Marginal Mountain Chain with the highest point in the country: Mount Moco (2620 m). The Old Plateau includes the central highlands of Huíla, Huambo and Bié provinces. The Congo Basin has plains that range from 1000 to 1500 m. Finally, the Cubango-Zambezi Basin is a very extensive area with hills and river systems (Dean, 2001, Huntley, 1974b).

From an ecological perspective, the diversity of conditions in Angola is spectacular as they range from the extreme desert in the south, to rainforests in the north. This is caused because of the country's location in the confluence of five major biomes: Guinea-Congo Forest, Afrotropical Highlands, Zambezian Biome, Kalahari-Highveld and Namib-Karoo Biome (Dean, 2001, Huntley, 1974b) (Fig. 2b). The Guinea-Congo Forest is formed by evergreen semi-deciduous forest with canopy height of ~50 m. This biome also includes savannahs both surrounding and within these forests. The Afrotropical Highlands – Afromontane Forests – are forest patches in the slope of mountains in the provinces of Huambo, Cuanza Sul, Benguela and Huila; at altitudes between 2000 to 2500 m and with a canopy height of 10 to 15 m. The Zambezian Biome, also known as *Brachystegia* woodland, is the miombo woodland in the interior plateau of Angola and occupies up to 47% of the country's territory. Dominant species are from the genus *Brachystegia* and *Julbernardia*, with canopy height of 4-12 m

(Huntley and Matos, 1994). The Kalahari-Highveld is in the eastern edge of the Namib dessert and it is composed by sublittoral shrub lands and open woodlands, with species from the genus *Acacia*, *Commiphora*, *Colophospermum* and *Aristida*. Finally, the Namib-Karoo biome – western edge of the Namib desert – has perennial grassland, shrub lands and thickets; with *Welwitschia mirabilis* as a characteristic species and thickets rarely exceeding 4 m of height (Huntley, 1974b, Dean, 2000). The Kalahari-Highveld and the Namib-Karoo are considered part of the Southwest Arid biome in Angola.

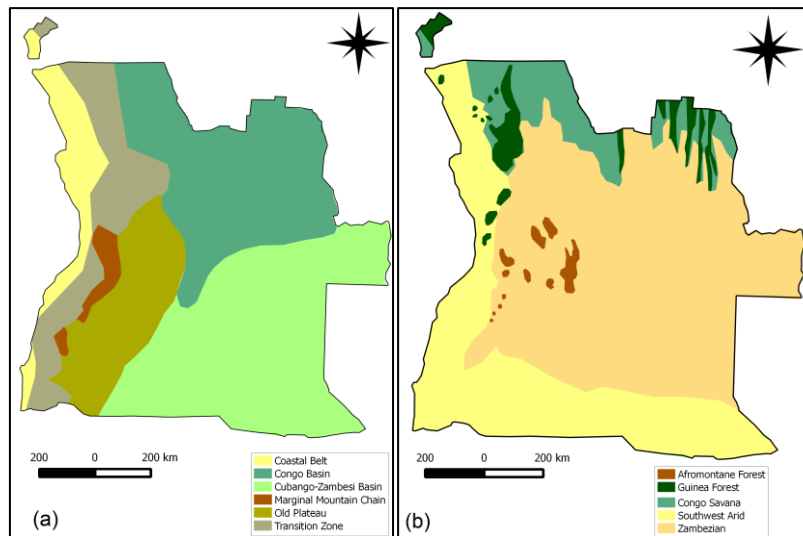


Fig. 2 (a) Geomorphological regions and (b) major biomes in Angola - adapted from Dean (2000)

The geographical characteristics and variety of biomes make Angola a country with a wide range of ecosystems (Huntley, 1974b) which translate into a high biodiversity, especially of birds (Rosa Pinto, 1983) – and probably other taxa. As a result, Angola is considered a high biodiversity country and one of the most biodiverse countries of Africa (USAID, 2008, Huntley, 1974a). Unfortunately, since its independence in 1975, Angola was submerged in a long lasting civil war that ended in 2002. The almost 30 years of armed conflict not only left the country destroyed but also full of mines, to the point “that one brigadier is quoted saying in December 1995 that *the whole of Angola should be considered a mined area*” (Dean, 2000).

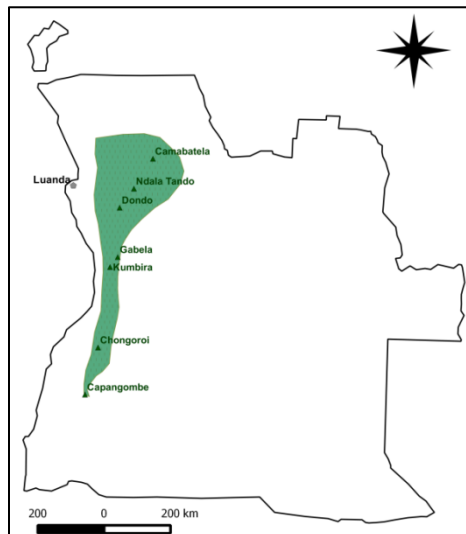
During the war no scientific research was done in Angola. Therefore, most of the biodiversity information available was collected during the colonial time and due the large extension of the country, considerable areas were not surveyed for most taxa (Crawford-Cabral and Mesquitela, 1989). Birds are the better studied group in the country, thanks to the early work of Rosa Pinto (Rosa Pinto, 1983), the skin collection in the Museum of the ISCED-Huila in Lubango and the museum in Dondo. After the war, updated information came mostly from an expedition done during the 1992 cease



fire (Hawkins, 1993), but most of the information available nowadays has been collected during recent sporadic expeditions and research projects (Ryan et al., 2004, Mills and Dean, 2007). No bird species in Angola has been studied in detail and information about their distribution and status remains inexistent or extremely limited (Dean, 2000). Therefore, Angola is a high biodiverse – little known country, where conservation initiatives lack the information needed to be implemented and where a major race is beginning to recover the lost time.

### 1.3. The Escarpment Forest and its biodiversity importance

The Angolan Escarpment Forest (or “Scarp”) is a semi-deciduous moist forest band that stretches discontinuously from the Guinea-Congo Forest in the north, going from Camabatela through Ndala Tando and Dondo, as far as 15° S in Capangombe (Huila province) in the south of the country (Hall, 1960) (Fig. 3). The width of this forest band varies between 1-15 km and its altitude goes from 350 to 1200 m. Common trees species of this forest are *Pterocarpus*, *Piptadeniastrum*, *Morus*, *Celtis* and *Albizia*. (Grandvaux-Barbosa, 1970). It is considered an impoverished outlier of the Guinea-Congo Forest, with smaller trees and lower canopy cover and understorey (Hall, 1960).



**Fig. 3** The Angolan Escarpment Forest stretches from north to south of the country - adapted from Hall (1960)

These forests are profoundly influenced by precipitation, humidity and temperature variation. Precipitation and mist are produced by clouds formed by the meeting of the cold Benguela current with the warmer tropical current of the Central Coast of Angola. These clouds travel eastward in direction to the High Plateau but are not capable of passing the mountains and condensate in mist and rain (Hawkins, 1993, Hall, 1960). The forests benefit from this “hidden condensation” especially in the night and dawn when moist coastal winds contact the cold surface of the escarpment and condensate

into the mist that fills the mountains ravines. The foliage of high canopy trees serve as condensation areas from where precipitation is released to the lower vegetation and ground. This happens especially in the dry season (known as “cacimbo” in Angola), when daily temperature variation is greater (9-12°C), so that dense fog is frequent when vegetation needs water the most (Grandvaux-Barbosa, 1970).

The average annual precipitation for the Escarpment has been calculated between to be between 1000 and 1500 mm but this value is probably vastly underestimated because it does not consider the rain produced by mist condensation (Hawkins, 1993). These forests are more dependent in this mist and therefore more affected by the topographic characteristics of exposure to the moist coastal winds rather than to rainfall. For example, even though the Highland Plateau has more annual precipitation (1600-1800 mm) and deep soils, the predominant vegetation is *Brachystegia – Jubernardia* open forest and woodland, with a canopy height of 6-15 m against a canopy height of 25-40 m for the Escarpment Forests (Grandvaux-Barbosa, 1970). Additionally, the vegetation of the Escarpment also depends in the deep ferralsols of medium and fine texture with superficial horizons rich in organic matter and humus (Castanheira Diniz, 1973). Another important geographical characteristic influencing this area is the rapid change in altitude in a small distance from the coast, especially in the area south of the Cuanza River where the scarp is steeper and well defined (Hall, 1960, Mills, 2010).

The Escarpment Forest is one of Angola’s most interesting regions in terms of biodiversity. It is located between three major biomes: the Southwest Arid of the Coastal Belt, the *Brachystegia* woodland of the Highland Plateau and the Guinea-Congo Forest. It presents affinities with all three adjacent biomes but also acts as a barrier between the drier biomes (Huntley, 1974b). This area is particularly important for the bird communities it holds because it is a centre of speciation and acts as a barrier allowing subspecies to develop on either side (Hall, 1960).

As a centre of speciation, it presents an endemic and near-endemic avifauna. This happens because the Escarpment developed in isolation during alternate wet and dry periods when the forest expanded and retracted. During the dry periods, the Escarpment was a refuge for species needing more moist conditions, species that disappeared in other areas under more extreme conditions (Hall, 1960). An example of this is the Red-crested Turaco *Tauraco erythrolophus*, an endemic species closely related to Bannerman's Turaco *Tauraco bannermani* (Njabo and Sorenson, 2009). The Escarpment also acts as a natural barrier between the Southwest Arid and the *Brachystegia* woodland biomes, allowing subspecies to evolve in each of these drier biomes.

The Escarpment can be divided into three areas according to the vegetation characteristics and avifauna: Northern, Central and Southern Escarpment Forest. This classification follows approximately the vegetation subtypes division done by Gossweiler and Mendoça (1939) and Grandvaux-Barbosa (1970).

The Northern Escarpment includes the *Cazengo Forest subtype* and goes from Canda all the way south to Dondo, north of the Cuanza river. It includes the western escarpments of Uíge, Bengo and Cuanza Norte provinces (Grandvaux-Barbosa, 1970). In this area the coastal plain is extensive and the escarpment slope is gradual. The Escarpment lacks geographical barriers and adjoins the Guinea-Congo Forest with which it shares several characteristics. The forest is formed by two or three arboreal strata, with the highest one at 30-50 m. The shrub vegetation is dense and includes many epiphytes. The most predominant tree species are from the genera *Albizia*, *Celtis*, *Ficus*, and *Sterculia*. The tree and shrub diversity decreases going southwards as the climatic conditions become drier. The bird diversity is rich in Guinea-Congo Forest species and presents a similar bird community with this biome. However, it is poor in endemic species, with Braun's Bushshrike *Laniarius brauni* being the only endemic restricted to this area (Mills, 2010).

The Central Escarpment is located from the south of the Cuanza river (9° 30'S) passing through the entire Cuanza Sul province all the way to Benguela province (11° 50' S) (Mills, 2010). It includes the *Amboim and Seles Forest subtypes* described by Grandvaux-Barbosa (1970). Forest altitude goes from 400 to 1200 m, it is foggy and most of it has been transformed into shade coffee plantations (Gossweiler and Mendoça, 1939). It presents high canopy trees that do not achieve the size and development of the Northern Escarpment Forest. The most common tree species are those that provide good shade for coffee plants, such as those from the genera *Albizia*, *Ficus*, *Maesopsis* and *Piptadeniastrum* (Castanheira Diniz, 1973). The bird community is poor in Guinea-Congo Forest species but rich in range restricted endemics (Mills, 2010). This is caused by the location of the Central Escarpment, isolated from the influence of other biomes and the Guinea-Congo Forest in particular, creating conditions favourable to speciation to take place (Hall, 1960).

The Southern Escarpment goes all the way to Capangombe. It is very narrow and fragmented, with forest patches smaller and rarer along the escarpment. This area has been described as "undifferentiated relatively moist types of woodlands and savannahs" where *Isoberlina*, *Brachystegia* and *Jubernardia* are absent or rare (Hall, 1960). The forest presents drier conditions, shorter trees and drier vegetation because of its proximity to the Southwest Arid Biome.

The Escarpment Forest is considered one of the most important areas in Angola in terms of biodiversity. Together with the Afromontane Forests of the Bailundu Highlands, it forms the Western Angola Endemic Bird Area (EBA), the only centre of bird endemism in the country. Consequently, this EBA is home to 12 of the 17 endemic species of Angola, including six Endangered and two Near-Threatened species (Dean, 2001, BirdLife International, 2015a). Despite its great biodiversity and importance it is the least known EBA in Africa (Ryan et al., 2004) and is considered a “critical” priority for bird conservation (Stattersfield et al., 1998).

Recently, major efforts have been done to overcome logistical and safety issues in order to perform bird research in the Escarpment Forest (Ryan et al., 2004, Sekercioglu and Riley, 2005, Mills, 2010, Mills et al., 2011, Mills et al., 2004, Mills and Dean, 2007, Mills et al., 2013, Cáceres et al., 2015). However, it would be expected that the Escarpment is also important for other non-studied and overlooked taxa, such as insects, reptiles and amphibians. Myers et al. (2000) proposed that the Angolan Escarpment should be considered a biodiversity hotspot, because of its exceptional endemism and threat, however he lacked the information to declare it as such.

#### **1.4. Central Escarpment Forest and its conservation threats**

The Central Escarpment Forest is considered the most important area for bird diversity in the Escarpment (Ryan et al., 2004). Within the Central Escarpment, the forests around Gabela are considered by BirdLife International (2015b) as an Important Bird Area (IBA). It is the most important of the 23 IBAs in the country, presenting the highest richness of endemic species, eight range restricted and six threatened species (Sekercioglu and Riley, 2005). The most important forests in this area are Kumbira and Bango because they hold all the threatened endemic species (except Gabela Helmetshrike) (Mills et al., 2010). In particular, Kumbira Forest has been identified as the most important site for the conservation of threatened Central Escarpment endemics, because it is the largest and most representative forest of the Central Escarpment (Fig. 4). Furthermore, it holds significant populations of four of the five threatened endemic birds (Gabela Bushshrike *Laniarius amboimensis*, Gabela Akalat *Sheppardia gabela*, Pulitzer’s Longbill *Macrosphenus pulitzeri*, and Monteiro’s Bushshrike *Malaconous monteir*) (Fig. 5) (Mills, 2010, Hawkins, 1993).



**Fig. 4** Kumbira Forest – photos taken by A. Cáceres and H. Costa.



**Fig. 5** Endangered Gabela Akalat *Sheppardia gabela*, Gabela Bushshrike *Laniarius amboimensis*, Pulitzer's Longbill *Macrosphenus pulitzeri*, and Near-Threatened Monteiro's Bushshrike *Malaconous monteiri* – photos taken by A.Cáceres, M.Mills, F.Olmos and T. Leventis respectively.

Most of the Escarpment Forest has ideal conditions for coffee cultivation especially in the Northern and Central Escarpment. For this reason most of the forest was transformed to shade coffee plantations during colonial times (Gossweiler and Mendonça, 1939). Understorey vegetation was cleared and only the coffee plants were maintained. High canopy trees were preserved as long as they did not produce too much shade for the coffee, otherwise they were replaced by exotic species. The Central Escarpment was identified as especially important for coffee farming during this time, producing a very appreciated variety known as “Amboim coffee” (Grandvaux-Barbosa, 1970). It is estimated that by 1970's almost 95% of the original forest was transformed to coffee plantations, or disturbed to some degree as with the planting of oil palm (*Elaeis guineensis*). Therefore, the original forest was only present in very few inaccessible areas (Castanheira Diniz, 1973, Hawkins, 1993).

During the civil war, the coffee plantations were abandoned and the understorey vegetation recovered, probably benefiting the birds (Sekercioglu and Riley, 2005, Dean, 2000, Ryan et al., 2004). During a visit to the area in the 1990s, Hawkins (1993) identified slash-and-burn agriculture for subsistence as a major threat for these forests. He estimated that around 30% of old coffee plantations had been transformed to agriculture. Abandoned coffee plantations were replaced by sun loving crops such as

sweet-potatoes, bananas, maize and cassava, eliminating completely the understorey vegetation and about 20 to 95% of the canopy cover.

Nowadays, with the end of the war, the human pressure to the forest has increased considerably. Most of the area is being slashed and burned for agriculture and the remaining high canopy trees are being logged for timber. All this deforestation is happening at a very fast pace (Mills, 2010, Cáceres et al., 2015). Despite a 50 km<sup>2</sup> protected area having been proposed for the area since the 1970's (Huntley, 1974a, Huntley and Matos, 1994), no formal protection exists for any part of the Escarpment Forest. Any conservation area should ensure the protection of the different bird communities present in the Escarpment and therefore include a network of representative sites (Mills, 2010). Furthermore, other conservation measures should be focused in the effects of human-modified landscapes on the threatened and endemic avifauna.

## 1.5. Objectives and thesis structure

The main aim of this thesis is to understand the effects of deforestation and forest degradation on the bird communities of the Central Angolan Escarpment Forest, especially the threatened endemic species. In order to achieve this, the thesis has the following specific objectives:

- (i) Assess the historical changes in land-use in Kumbira Forest and their effect in the composition of bird communities.
- (ii) Evaluate the habitat characteristics driving bird diversity, and especially the presence of endemic species.
- (iii) Investigate the habitat use of the most range-restricted threatened endemic bird in Angola: the Gabela Akalat *Sheppardia gabela*.
- (iv) Assess the potential of REDD+ as a conservation tool for the Angolan Escarpment Forest.

By achieving these objectives, solid scientific information will be generated for an area of global conservation significance and about an understudied endemism-rich avifauna, contributing to fill part of the knowledge gap present in Angola. Furthermore, this information will allow establishing strategic guidelines for the conservation of biodiversity while attending the developmental needs of the local population.

The research contained in this thesis is presented in four scientific papers already published or in the final phase for publication in international journals. These papers are organized in chapters, each chapter answers one of the specific objectives

established for this thesis. Therefore, following this introduction, the chapters of this thesis are:

Chapter 2: This chapter assesses the land-use changes of the last 20 years of the Central Escarpment Forest, by using Kumbira Forest as the study site. Remote sensing techniques were used to account the loss of forested habitats. Additionally, this chapter also compare the bird communities present in different land-uses.

Chapter 3: This chapter investigates the environmental characteristics driving bird diversity. First, the chapter analyses the best set of variables - between remote sensing and ground vegetation surveys - to model bird diversity. Then, it indicates the environmental variables affecting species richness and the presence of three endemic species Red- crested Turaco, Gabela Bushshrike and Gabela Akalat.

Chapter 4: In this chapter the home-range size and habitat preferences of Gabela Akalat are assessed using radio-tracking techniques. This chapter provides the first data on the territory size and habitat use of an Endangered and little-known endemic bird species.

Chapter 5: In this chapter, forest cover changes and deforestation rates from 1991-2001 and from 2001-2014 were assessed and aboveground carbon stocks were calculated through biomass estimation. Recommendations for the implementation of a REDD+ initiative to ensure the conservation of the forests are given.

Chapter 6: This chapter presents a general discussion of the results obtained in this thesis. Bird diversity responses to human impacts are discussed and conservation measures based in the results are proposed.

## 1.6. List of papers

The papers published or to be published in different scientific international journals that composed this thesis have very different formats. For this reason, the text, tables and figures of these papers have been formatted in a uniform way, without any modification on their content. The list of papers composing this thesis is presented below:

**Paper I** Cáceres, A., M. Melo, J. Barlow, P. Cardoso, F. Maiato, and M.S.L. Mills. 2015. Threatened birds of the Angolan Central Escarpment: distribution and response to habitat change at Kumbira Forest. *Oryx* 49: 727 - 734.

**Paper II** Cáceres, A., M. Melo, J. Barlow, R. de Lima and M. S. L. Mills. (Manuscript) Drivers of bird diversity in an understudied African centre of endemism: The Angolan Escarpment Forest. Submitted to *Bird Conservation International*.

**Paper III** Cáceres, A., M. Melo, J. Barlow, and M.S.L. Mills. 2016. Radio telemetry reveals key data for the conservation of *Sheppardia gabela* (Rand, 1957) in the Angolan Escarpment Forest. *African Journal of Ecology*. DOI: 10.1111/aje.12283.

**Paper IV** Leite, A., A. Cáceres, M. Melo, M.S.L. Mills and A. T. Monteiro. (Manuscript) The potential of REDD+ for 'small centres of endemism': A case study from the Angolan Escarpment Forest. Submitted to *Biological Conservation*.

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## **Chapter 2**

Historical land-use change and bird communities in Kumbira

**Paper I** Threatened birds of the Angolan Central Escarpment: distribution and response to habitat change at Kumbira Forest.

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## Threatened birds of the Angolan Central Escarpment: distribution and response to habitat change at Kumbira Forest

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### Abstract

Kumbira Forest is the best representative area of Angolan Central Escarpment and the only site known to hold significant populations of four of the five threatened endemic bird species of this habitat. However, the forest is disappearing as a result of human activities. Remote-sensing techniques were used to assess changes in forest cover, and bird and habitat surveys were performed to assess the effect of land-use changes on endemic species and the bird community. No relationships could be established between the presence of endemics and habitat and landscape variables. This lack of effect may be attributable to the low number of records and compounded by the mosaic structure of the landscape. Although forest cover has been maintained in Kumbira, old-growth forest has been replaced by secondary growth in many areas. Nevertheless these secondary growth forest patches can maintain a bird community similar to that found in old-growth forest.

**Keywords** Angola, endemic birds, escarpment forest, habitat loss, Kumbira, land-use change

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## Introduction

Habitat loss is a threat to biodiversity (Brooks et al., 2002) and is the leading cause of population decline and species extinction in birds (Stattersfield and Capper, 2000). This is particularly significant in the tropics, where the highest biodiversity but also the highest rates of land-use change are found (Cincotta et al., 2000).

The consequences of habitat loss have been studied for a range of taxa (Waltert et al., 2005; Norris et al., 2010), showing that biodiversity usually declines along a gradient that reflects a decrease in the complexity of the vegetation structure (Schulze et al., 2004; Harvey et al., 2006). However, most of our knowledge comes from a few tropical sites that may exhibit context-specific responses (Gibson et al., 2011). For most areas, including much of Africa and all of Angola, there is limited or no information (Gardner et al., 2009; Gibson et al., 2011).

Angola has high biodiversity as a result of its location at the confluence of six biomes (Huntley, 1974), yet it is also one of the least studied areas because of a succession of armed conflicts over almost 30 years. One of the most important areas for biodiversity is the Central Escarpment as it holds forests that are an evolutionary hotspot for birds (Hall, 1960). These forests constitute the core habitat of the Western Angola Endemic Bird Area (Stattersfield et al., 1998), are a priority for global conservation (Dean, 2001; BirdLife International, 2013a) and are some of the most important areas for bird conservation in Africa (Collar and Stuart, 1988).

Although there have been proposals for the establishment of conservation areas within this bioregion, none of the forests of the Central Escarpment fall within protected areas (Huntley, 1974). Moreover, during the 1950s and 1960s an estimated 95% of these forests were converted to large-scale coffee farming, although large-canopy trees were mostly left intact to provide shade (Hawkins, 1993). During the civil war (1974–2002) these farms were abandoned and some native vegetation recovered. However, more recently slash-and-burn agriculture has become widespread and represents a threat to most of the forest in this region (Ryan et al., 2004; Mills, 2010). The consequences of these activities for bird communities and threatened species remain unknown.

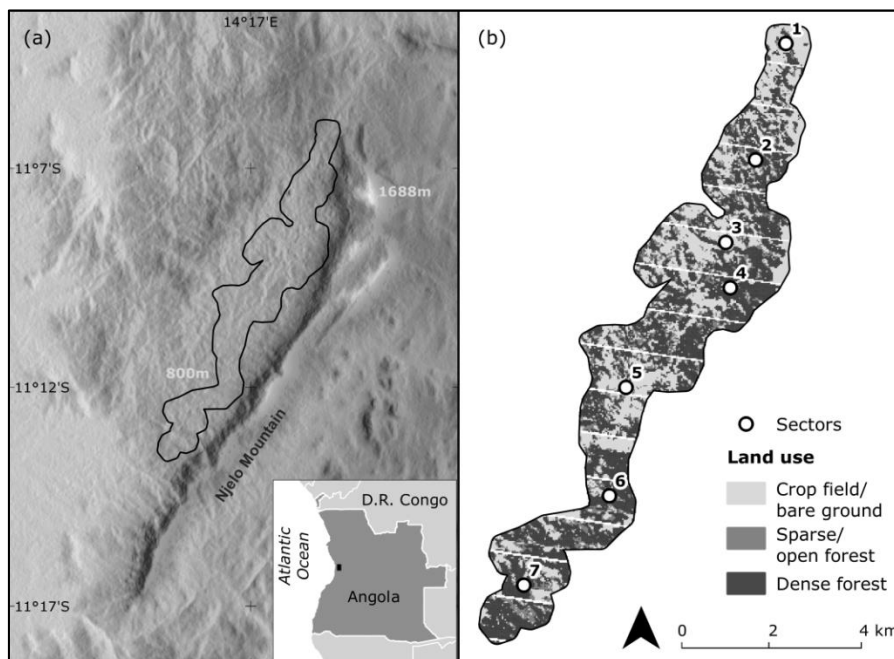
Kumbira Forest has been identified as the most important site for the conservation of threatened forest endemics of the Central Escarpment because it is the only known site to hold significant populations of four of the five threatened endemic birds (Gabela Bushshrike *Laniarius amboimensis*, Gabela Akalat *Sheppardia gabela*, Pulitzer's Longbill *Macrosphenus pulitzeri* and Monteiro's Bushshrike *Malaconotus monteiri*; Mills, 2010). The aims of this study were to determine how habitats have

changed within Kumbira Forest and the effects of these changes on the bird community and on endemic species. Specifically we assessed the changes in land-use and land cover that have occurred since the last 2 decades, identified the most important regions of Kumbira for the endemic species, and evaluated the composition of the bird community in different land-use types.

## Methods

### Study Area

Kumbira Forest is situated in the western Angolan province of Cuanza Sul, in the municipality of Conda (Fig. 1). The terrain varies from relatively flat at the bottom of the valley to steep on the slopes of Njelo Mountain. It is difficult to define exactly the limits of the forest because forest habitats gradually merge into thickets and other dense habitats associated with the escarpment. The eastern limits of the forest are most clearly delimited by the grasslands of Njelo Mountain. Here we define the northern limit of the forest as Cassungo village (11.104°S 14.311°E) and the southern limit as 11.230°S. Within this area, altitude varies from c. 680 m in the south to 1,160 m at the forest border on the slopes of Njelo Mountain.



**Fig. 1** The location of (a) Kumbira Forest in Angola and the study area (with black borders) in Kumbira Forest, (b) showing the land use for 2010 and the seven sectors where the changes of forest cover were analysed. Sector 3 and 6 were where the bird community composition was assessed.

### Changes in LULC in the past two decades

To assess changes in land-use and land cover we used Landsat 5 TM and 7 ETM+ satellite scenes (WRS-2 path 181 row 68) made available by the Earth Resources

Observation & Science Center of the U.S. Geological Survey via the USGS EarthExplorer interface (<http://earthexplorer.usgs.gov>). Such studies often benefit from using scenes from the same dates in different years (Jensen, 2005) but in this case scenes for similar dates were unavailable because of a failure on Landsat 7 and high cloud cover, and therefore we used a broader array of scenes from the dry season (May–September), when cloud cover was low (preferentially < 10%). Scenes meeting these requirements were from 1989, 1990, 1993, 1995, 1997, 2001, 2006, 2009 and 2010 (Supporting Information Table S1).

To deal with heterogeneity of images individual scenes were radiometrically normalized and an atmospheric correction was applied, using image-based methods. We applied modified dark object subtraction (DOS4) as proposed by Chavez (1996). No geometric correction was applied because the root mean square error was always a fraction of pixel dimension (< 23% for all scenes). Pre-processing analysis and calibrations were carried out in R v.3.0.0 (R Development Core Team, 2013), with Landsat (Goslee, 2011) and Raster (Hijmans and van Etten, 2013). No correction was performed on the Landsat 7 scenes and the empty lines produced by the scan line failure were treated as no data.

Unsupervised ISOCLUST classification excluding thermal bands was performed on each scene, using IDRISI Selva (Eastman, 2012). Clusters were then reclassified to pre-defined classes (or regions of interest), which were established during a visit to the study area in 2010: bare ground and crop field, sparse/open forest, and dense forest. Accuracy of land cover data for each date was assessed by comparing the resulting classification with our 2010 ground sample points, high-resolution images from QGIS Openlayers Plugin (QGIS Development Team, 2013), false colour composite images, and scatterplots from bare soil line/full canopy points from pseudoinvariant feature analysis (Maas and Rajan, 2010). We also compared the land cover spectral signatures, using the 2010 classification as a reference. Percentage cover of each class was obtained for every image to evaluate temporal changes in land-use and land cover.

We also evaluated changes in dense forest cover at seven sectors of the study area (300 m radius, 28.3 ha each sector). Sectors were selected to evaluate how changes took place in three context-specific scenarios: (1) on privately owned land, (2) where there was evidence of significant forest degradation and (3) where endemic species were present. The age of forest stands was assessed for the 2010 classification by evaluating pixel history. For each image sparse and dense forests were clumped and the reclassified images were then overlaid. To assess the areas of

old forest ( $\geq 22$  years old) we compared the fraction of unchanged forest patches in 2010 with forest area in 1989.

### **Endemic bird species distribution**

During 13 September–2 October 2010 the first visit to Kumbira Forest took place to determine the distribution of the endemic species. Bird surveys were conducted daily at 203 sample points covering the entire study area. Sample points were spaced at least 150 m apart and located within relatively uniform habitat.

At each sample point a 10-minute point count (Bibby et al., 2000) was conducted between sunrise (c. 05.45) and 10.30, always in good weather conditions (in the absence of rain, strong winds or high temperatures). Each morning 8–16 point counts were conducted, depending on accessibility and weather. Each point count was divided into two 5-minute periods. Between these periods we used a portable music player and amplifier to play a track of 30-second snippets of vocalizations of each of the endemic species: Monteiro's Bushshrike, Red-crested Turaco *Tauraco erythrolophus*, Gabela Bushshrike, Gabela Akalat and Pulitzer's Longbill. This was done to improve detectability of these species through playback.

All individuals of these species were recorded, irrespective of their distance from the sample point, to produce a more complete map of their distribution. Because playback violates one of the assumptions of point surveys, that birds do not approach the observer, only presence–absence data were used in the analysis. Where there was a possibility that individual birds had already been sampled during the sample period these were excluded to avoid double-counting.

### **Bird community in different habitats**

During a second visit to Kumbira Forest during 11–29 October 2012 sampling effort was focused in the two sectors where more endemic species had been recorded in 2010. Sample points were distributed over four previously defined land-use types: (1) slash-and-burn, (2) mixed (abandoned coffee plantations or farms), (3) secondary forest (forest patches next to roads, rivers and agricultural plots) and (4) forest (the oldest forest available in the area). To examine the differences between these types we measured habitat variables at each point. We estimated canopy height and cover within 5 m of the sample point in each cardinal direction, and understorey vegetation cover within 10 m. We calculated the mean of the four measurements of each variable for each sample point. Canopy height was measured as the maximum visible height of the canopy (Dallimer et al., 2009), using a laser rangefinder, canopy cover was measured using a convex spherical densitometer and understorey vegetation was

measured using a 2 m graduated white pole, marked every 10 cm with red tape. The 10-cm sections that were clearly visible from a 10 m distance were counted and converted to a percentage (Barlow et al., 2002). Tree density per plot was calculated by counting all the trees with diameter at breast height (DBH) > 10 cm within a 20 m radius of each sample point. The distances from the observer to the nearest tree (dist1) and the nearest neighbour to this tree (dist2) were recorded to calculate a tree density index, using the formula  $1/((\text{dist1}+\text{dist2})/2)$  (Catry et al., 2000).

Data for all bird species were collected using 10-minute point counts within a 50 m radius, with no playbacks for endemics. A total of 24 points were sampled, with three repetitions for each point at different times (early morning 5.45–07.00; mid-morning 07.00–08.15 and late morning 08.15–09.30).

### Data analysis

We used non-parametric Kruskal–Wallis and one-way permutation tests to evaluate differences in habitat variables between land-use types. Individual-based rarefaction curves were used to compare bird species richness across different land-use types (Gotelli and Colwell, 2001). Differences in bird communities were assessed using non-metric multidimensional scaling plots based on the Bray–Curtis similarity index. Overall difference of bird communities and pairwise difference in land-use types were measured and tested using ADONIS. All analyses were performed using R v.3.0.0 (R Development Core Team, 2013) and vegan (Oksanen et al., 2012).

### Results

During 1989–2010 the cover of dense forest varied in the different sectors assessed (Supporting Information Fig. S1). In 1989, 53.8% (13.4 km<sup>2</sup>) of the study area was covered by forests; by 2010 this had increased to 65.2% (15.5 km<sup>2</sup>). This represents an increase of 15.4% (2.1 km<sup>2</sup>) in total forest area. However, original forest stands (present since 1989) covered only 30.8% (7.3 km<sup>2</sup>) in 2010, which represents a 45.5% loss of original forest stands (Supporting Information Fig. S2).

A total of 100 bird species were recorded in 2010, including the five endemic species (Supporting Information Table S2). Red-crested Turaco (Fig. 2a) and Gabela Akalat (Fig. 2b) were the most widely distributed, recorded at 137 (67%) and 93 (46%) sample points, respectively. Gabela Bushshrike (Fig. 2c) was the third most recorded endemic, present at 42 points (21%); it was present in two well-defined zones but absent from most of the study area. Monteiro's Bushshrike (Fig. 2d; 16 points, 8%) and Pulitzer's Longbill (Fig. 2e; 11 points, 5%) were the least prevalent. Monteiro's

Bushshrike occurred almost exclusively in the upper third of the study area, with a few records further south, and Pulitzer's Longbill occurred almost exclusively in the upper reaches of the valley. Combining all species (excluding the non-threatened red-crested turaco; Fig. 2f), the upper third and part of the medium third of the valley were highlighted as the most important areas for the endemics and were selected for a detailed survey.



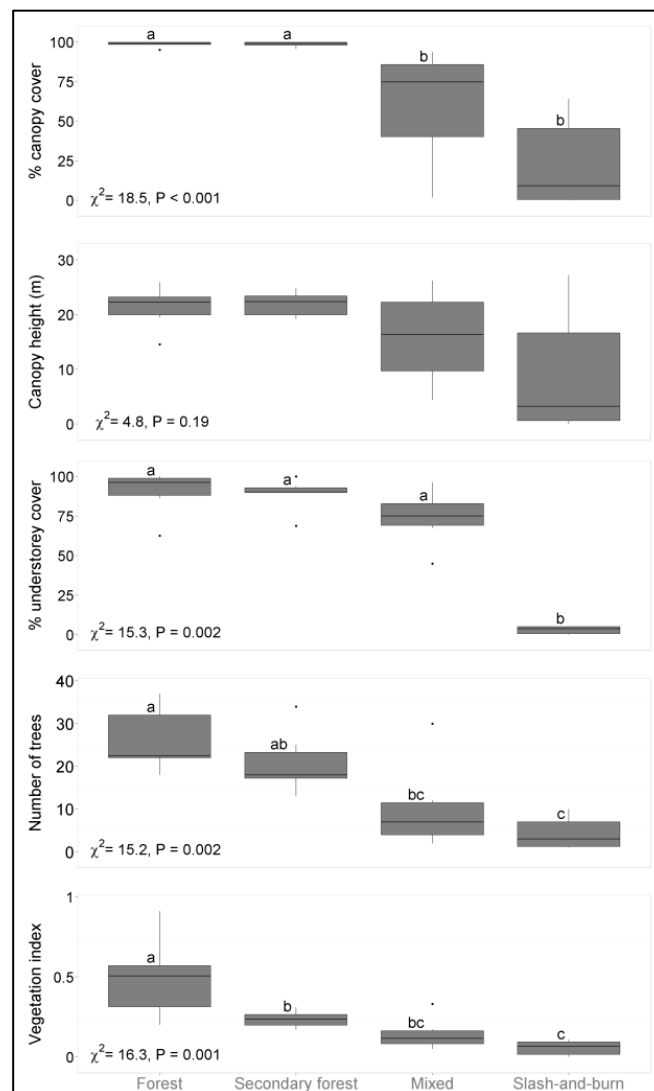
**Fig. 2** Distribution and number of individuals of (a) Red-crested Turaco; (b) Gabela Akalat; (c) Gabela Bushshrike; (d) Monteiro Bushshrike and (e) Pulitzer's Longbill registered in each sample point. The number of all threatened endemic species combined (excluded red-crested turaco) are also presented (f).

Our visual assessment of land-use types was supported by structural measurements, as there were significant differences between them (Fig. 3). We recorded 73 bird species during the survey (Supporting Information Table S3). Individual-based species accumulation curves did not reach an asymptote (Supporting Information Fig. S3) and we did not observe any difference in the species richness between forest classes. Bird community composition was significantly different between land-use types ( $p < 0.01$ , Fig. 4) although pairwise analysis did not show a significant difference between the bird community composition of forest and secondary forest, or between secondary forest

and mixed (Table 1). However, of the threatened endemics only Gabela bushshrike and Gabela Akalat were recorded, with the former apparently restricted to forest.

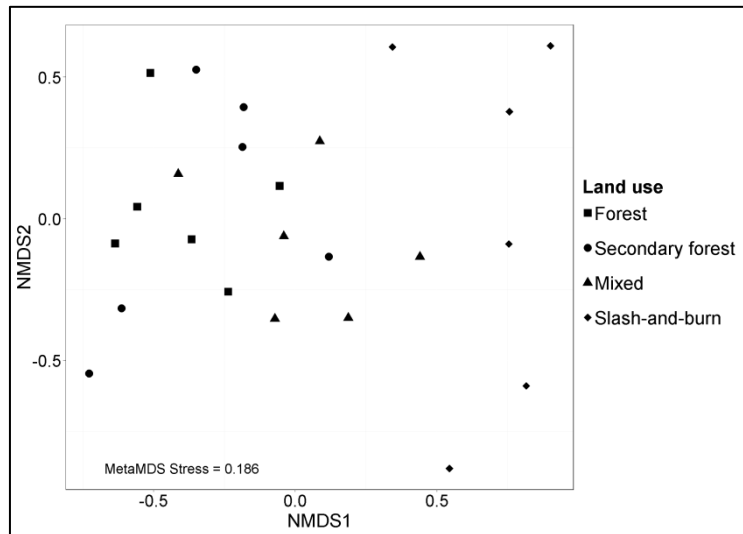
**Table 1.** Comparison of the bird community composition between different land-use types. The values were obtained by Adonis analysis using the software R. Significant levels for these comparisons are: \*  $p < 0.05$ ; \*\*  $p < 0.01$ . No significant differences were present between the forested types; and between Secondary Forest and Mix.

	Sec	Mix	Sb
Forest (For)	0.512	0.034*	0.006**
Secondary Forest (Sec)	--	0.221	0.002**
Mix (Mix)	--	--	0.032*



**Fig. 3** Values for canopy cover (in %); canopy height (in meters); understorey vegetation (in %); tree density per plot (in number of trees per plot) and tree density index (value from 0 to 1) for the different land-use types. Also the  $X^2$  and p-values are present for each habitat variable. All the habitat variables, except for canopy height, were significantly

different among land-use types. Small-case letters indicate significant groups (a, ab, b, bc, c) and the black dots are outliers.



**Fig. 4** Two axes of the non-metric multidimensional scaling (NMDS) ordination plot for bird communities in forest (squares), secondary forest (circles), mixed (triangles) and slash-and-burn (diamonds). The stress value of the NMDS was 0.186, indicating that the data was well represented in the dimensions of this analysis.

## Discussion

Remote-sensing results indicate that forest cover in Kumbira has been maintained since 1989. However, the relative stability of total forest cover masks a dynamic landscape where 34.4% of the study area was covered by forests that have regenerated since the beginning of our remote-sensing sequence in 1989. This indicates a loss of older-growth forests and their replacement with younger forests, which may have a lower conservation value (Gabela bushshrike was not present in secondary forest). Many of these younger forests are dominated by the non-native evergreen *Inga vera*.

One of the limitations to assessing changes in land-use and land cover in Kumbira is the lack of validation means for image classification, such as the lack of historical aerial photography. At present it is not possible using Landsat images to differentiate natural old-growth dense forests from secondary growth. Further ground surveys are needed to identify characteristic features of secondary forests and those dominated by *Inga vera*. These may be distinguishable if high variation in biomass corresponds to native deciduous species.

Red-crested turaco and Gabela Akalat were the most frequently recorded endemic species. Although the global population of red-crested turaco has not been quantified and is suspected to be declining, the species has a large range and is regarded as common locally. In contrast, Gabela Akalat is the most range-restricted of the escarpment's endemics (BirdLife International, 2013b). Although this species may



be common locally only c. 10% of its range has suitable habitat (Mills, 2010). Monteiro's bushshrike and Pulitzer's longbill were the least recorded endemics in the sampling points (<10%) and no analyses were performed to assess their habitat's preferences. Both species occur within a length of c. 370–400 km and width of c. 10–20 km of the escarpment and are common in drier forests (Mills, 2010). They may be relatively rare in the more humid forests of the study site.

No significant relationships were found between the presence of endemics and variables describing local condition (e.g. canopy cover, understorey vegetation) or the condition of the landscape (percentage of forest cover). These non-significant results may be explained by the sampling strategy used to maximize the recording of endemic species, as points were placed to cover as much of the study site as possible instead of in specific well-defined land-use types. As the landscape in Kumbira is fragmented and dynamic, many of the sample points were influenced by edge effects and the surrounding matrix. This will have been compounded by the use of playback, which may have attracted birds into suboptimal forest types. Furthermore, some endemic species were not recorded sufficiently to evaluate their habitat use.

Overall, our a priori disturbance classes differed considerably in characteristics and quality (Fig. 3). Although the two forest classes had a similar vertical structure (canopy cover and understorey vegetation) they differed in tree cover. Bird species richness was similar between the different land-use types, as has been found in other African forests, where bird species richness was maintained or even increased after human disturbance (Plumptre, 1997; Sekercioglu, 2002; Waltert et al., 2005). In part, these non-significant results could be attributable to a limited sample size (particularly as some trends are apparent) but further sampling is needed to consider whether spill-over effects and landscape context could have affected our observations (Barlow et al., 2010). Species richness is an unreliable index of conservation value along disturbance gradients and other African studies have shown that a decline in forest-dependant species can be offset by an increase of non-forest and generalist species (Blankespoor, 1991; Lawton et al., 1998; Fjeldså, 1999). There is some evidence for this in our study, as community composition varied between habitats (Fig. 4; Table 1) and slash-and-burn areas held a unique community, different from the other land-use types.

It is important to note that secondary forest held a similar bird community to the older-growth forest, because our remote-sensing analysis shows that old-growth forest is disappearing and being replaced by secondary forests across the Kumbira region. However, secondary forests are not always adequate replacements of primary forests for conserving tropical biodiversity (Barlow et al., 2007; Gibson et al., 2011) and their

capacity to support primary forest species is poorly understood and depends on context-specific characteristics (Chazdon et al., 2009; Dent and Wright, 2009). Although secondary forests are undoubtedly important components of the landscape for bird conservation, more work is needed to assess their role for endemic species.

The avifauna of biodiversity-rich forests of Kumbira, especially the endemics, remain poorly known and it is difficult to predict how species will react to further habitat changes or whether the secondary forests are being subsidized by the remaining patches of primary forest. Further research is needed to better understand the responses of endemic birds to ongoing land-use change but there is also a need to focus research on other taxa that are less studied yet may have even more sensitive responses. Research should also examine the influence of the surrounding landscape matrix on biodiversity. Although it was not possible to demonstrate these effects in this study, landscape context may explain the patchy distribution of some of the endemic species. We hope that further conservation research can be translated into more effective policies and practices that assure the preservation of these forests.

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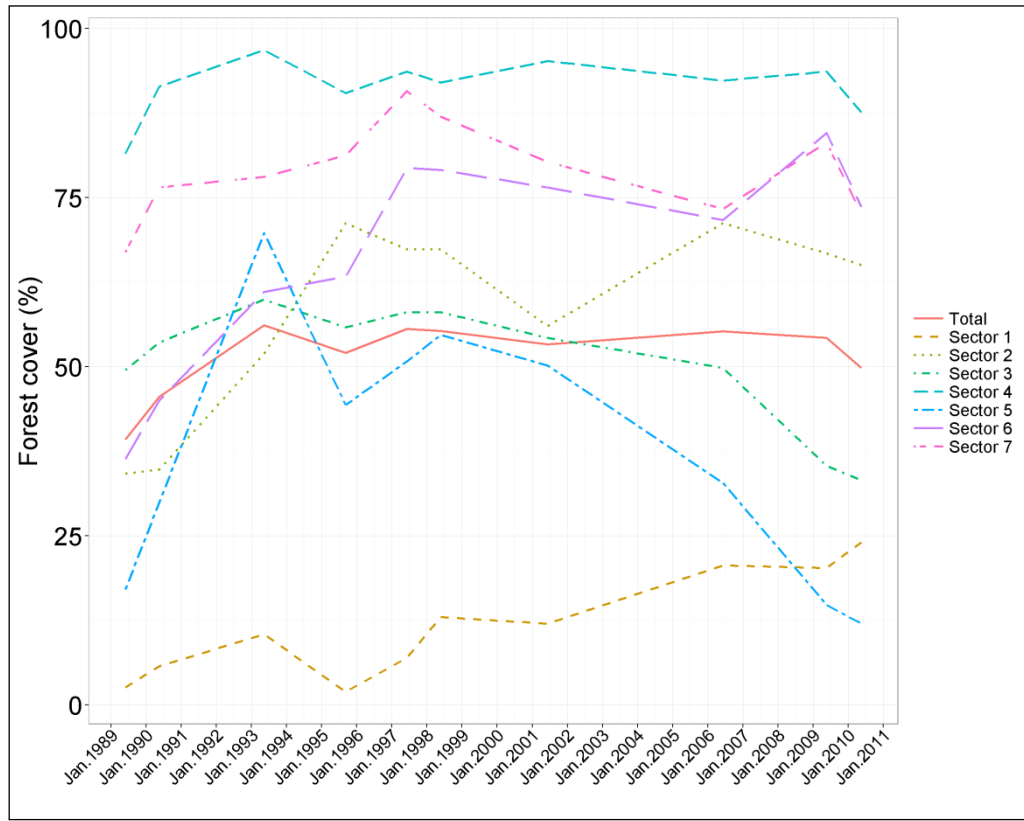
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## Supporting Information

**Table S1** Landsat scenes (1989–2010) used to assess changes in land-use and land cover in Kumbira Forest, on the Angolan Central Escarpment, with satellite, date, sun elevation, cloud cover, and root mean square error (RMSE).

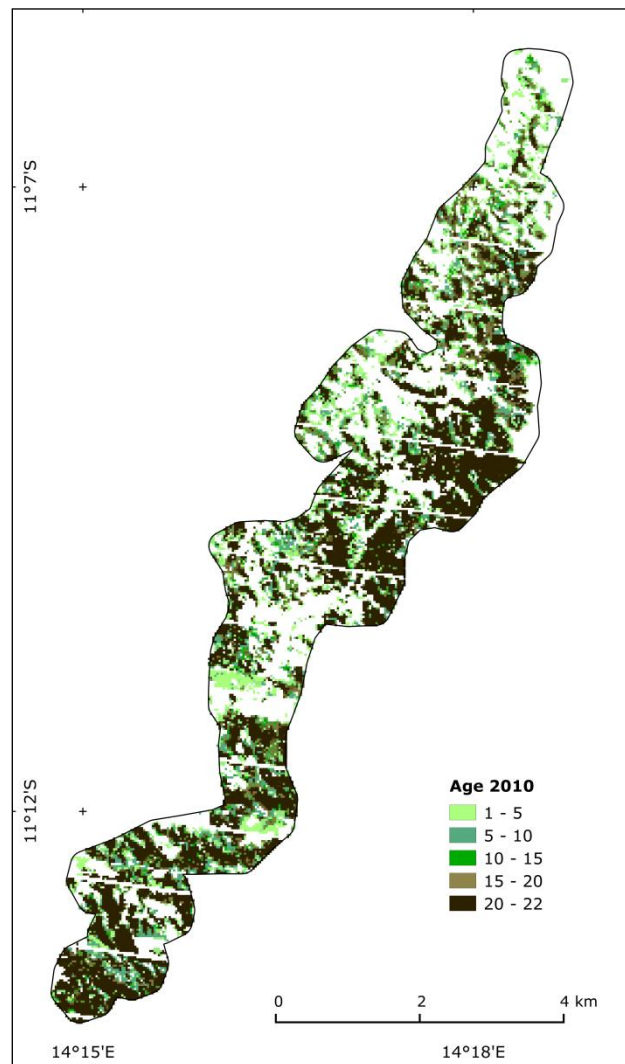
Scene ID	Satellite	Date	Sun elevation (°)	Cloud cover (%)	RMSE (m)
LT51810681989152JSA00	Landsat 5	1 June 1989	41.2	14.0	7.04
LT51810681990139JSA01	Landsat 5	19 May 1990	41.5	0.0	5.40
LT51810681993131JSA00	Landsat 5	11 May 1993	43.0	0.0	4.72
LT51810681995249JSA00	Landsat 5	6 Sep. 1995	43.9	1.0	4.56
LT51810681997158JSA00	Landsat 5	7 June 1997	40.8	1.0	6.21
LT51810681998145JSA00	Landsat 5	25 May 1998	43.8	0.0	4.67
LE71810682001161EDC00	Landsat 5	10 June 2001	43.9	4.0	4.82
LE71810682006159ASN00	Landsat 7	8 June 2006	44.1	0.0	6.74
LT51810682009143JSA01	Landsat 5	23 May 2009	45.8	7.3	5.27
LE71810682010138ASN00	Landsat 7	18 May 2010	47.3	3.5	6.20

**Fig. S1** Changes in dense forest cover (%) from 1989-2010. No major changes were observed for the entire study area (Total). However when seven circular sectors of 28.3 ha were analysed, some of them presented a decrease in forest cover.





**Fig. S2** Age of forest stands in Kumbira Forest (years), on the Angolan Central Escarpment (Fig. 1), in 2010. Forests occupied 65.2% of the study area at that time but only 30.8% of the area was covered by forest stands  $\geq 22$  years old.



**Table S2.** The 100 bird species recorded during surveys in Kumbira Forest in 2010.

Family	Scientific name	Common name
Numididae	<i>Guttera pucherani</i>	Crested guineafowl
Phasianidae	<i>Pternistis griseostriatus</i>	Grey-striped francolin
Accipitridae	<i>Accipiter melanoleucus</i>	Black sparrowhawk
	<i>Accipiter tachiro</i>	African goshawk
	<i>Kaupifalco monogrammicus</i>	Lizard buzzard
Columbidae	<i>Treron calvus</i>	African green pigeon
	<i>Turtur afer</i>	Blue-spotted wood dove
	<i>Turtur tympanistria</i>	Tambourine dove
Musophagidae	<i>Tauraco erythrolophus</i>	Red-crested turaco
Cuculidae	<i>Centropus anelli</i>	Gabon coucal
	<i>Ceuthmochares australis</i>	Green malkoha
	<i>Chrysococcyx klaas</i>	Klaas's cuckoo
Trogonidae	<i>Apaloderma narina</i>	Narina trogon
Alcedinidae	<i>Ceys pictus</i>	African pygmy kingfisher
Bucerotidae	<i>Tockus alboterminatus</i>	Crowned hornbill
Lybiidae	<i>Pogoniulus bilineatus</i>	Yellow-rumped tinkerbird
	<i>Pogoniulus subsulphureus</i>	Yellow-throated tinkerbird
	<i>Trachyphonus purpuratus</i>	Yellow-billed barbet
	<i>Tricholaema hirsuta</i>	Hairy-breasted barbet
Indicatoridae	<i>Indicator minor</i>	Lesser honeyguide
Picidae	<i>Campethera caroli</i>	Brown-eared woodpecker
	<i>Campethera nivosa</i>	Buff-spotted woodpecker
	<i>Dendropicos fuscescens</i>	Cardinal woodpecker
Eurylaimidae	<i>Smithornis capensis</i>	African broadbill
Platysteiridae	<i>Batis minulla</i>	Angolan batis
	<i>Dyaphorophyia castanea</i>	Chestnut wattle-eye
	<i>Dyaphorophyia concreta</i>	Yellow-bellied wattle-eye
	<i>Platysteira peltata</i>	Black-throated wattle-eye
Malaconotidae	<i>Chlorophoneus</i>	Orange-breasted
	<i>sulfureopectus</i>	bushshrike
	<i>Chlorophoneus viridis</i>	Gorgeous bushshrike
	<i>Dryoscopus angolensis</i>	Pink-footed puffback
	<i>Dryoscopus cubla</i>	Black-backed puffback
	<i>Laniarius amboimensis</i>	Gabela bushshrike
	<i>Malaconotus monteiri</i>	Monteiro's bushshrike
Campephagidae	<i>Campephaga petiti</i>	Petit's cuckooshrike
Oriolidae	<i>Oriolus larvatus</i>	Black-headed oriole
Monarchidae	<i>Elminia longicauda</i>	African blue flycatcher

Family	Scientific name	Common name
	<i>Terpsiphone rufocinerea</i>	Rufous-vented paradise flycatcher
	<i>Terpsiphone viridis</i>	African paradise flycatcher
	<i>Trochocercus nitens</i>	Blue-headed crested flycatcher
Paridae	<i>Parus funereus</i>	Dusky tit
Pycnonotidae	<i>Andropadus latirostris</i>	Yellow-whiskered greenbul
	<i>Bleda syndactylus</i>	Red-tailed bristlebill
	<i>Chlorocichla falkensteini</i>	Falkenstein's greenbul
	<i>Chlorocichla flaviventris</i>	Yellow-bellied greenbul
	<i>Nicator vireo</i>	Yellow-throated nicator
	<i>Phyllastrephus fulviventris</i>	Pale-olive greenbul
	<i>Pycnonotus tricolor</i>	Dark-capped bulbul
Hirundinidae	<i>Cecropis abyssinica</i>	Lesser striped swallow
	<i>Psalidoprocne pristoptera</i>	Black saw-wing
Cisticolidae	<i>Apalis binotata</i>	Lowland masked apalis
	<i>Apalis jacksoni</i>	Black-throated apalis
	<i>Apalis rufogularis</i>	Buff-throated apalis
	<i>Camaroptera harterti</i>	Hartert's camaroptera
	<i>Cisticola bulliens</i>	Bubbling cisticola
	<i>Prinia subflava</i>	Tawny-flanked prinia
Timaliidae	<i>Illadopsis fulvescens</i>	Brown illadopsis
Sylviidae	<i>Hylia prasina</i>	Green hylia
	<i>Hyliota australis</i>	Southern hyliota
	<i>Macrosphenus pulitzeri</i>	Pulitzer's longbill
	<i>Sylvietta virens</i>	Green crombec
Zosteropidae	<i>Zosterops senegalensis</i>	African yellow white-eye
Sturnidae	<i>Cinnyricinclus leucogaster</i>	Violet-backed starling
Turdidae	<i>Pseudalethe poliocephala</i>	Brown-chested alethe
	<i>Stizorhina fraseri</i>	Fraser's rufous thrush
	<i>Turdus pelios</i>	African thrush
Muscicapidae	<i>Cossypha heuglini</i>	White-browed robin-chat
	<i>Cossypha natalensis</i>	Red-capped robin-chat
	<i>Erythropygia leucosticta</i>	Forest scrub robin
	<i>Muscicapa caeruleascens</i>	Ashy flycatcher
	<i>Sheppardia gabela</i>	Gabela akalat
Nectariniidae	<i>Anthreptes seimundi</i>	Little green sunbird
	<i>Chalcomitra fuliginosa</i>	Carmelite sunbird
	<i>Cinnyris bifasciatus</i>	Purple-banded sunbird

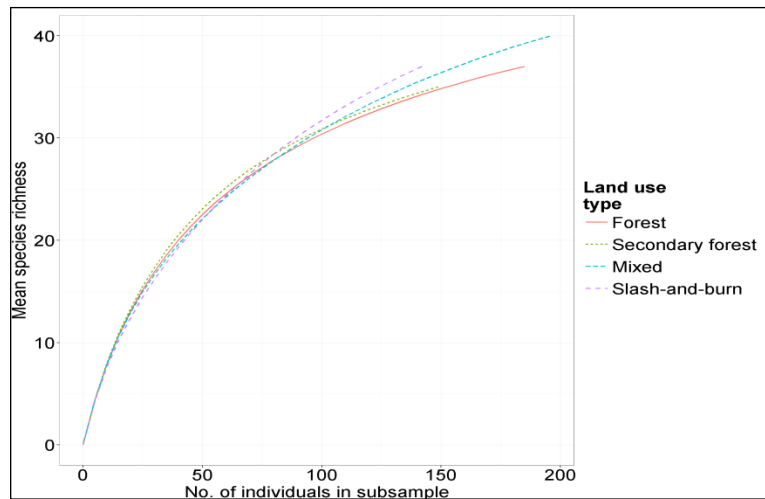
Family	Scientific name	Common name
	<i>Cinnyris chloropygius</i>	Olive-bellied sunbird
	<i>Cinnyris ludovicensis</i>	Ludwig's double-collared sunbird
	<i>Cinnyris superbus</i>	Superb sunbird
	<i>Cinnyris venustus</i>	Variable sunbird
	<i>Cyanomitra olivacea</i>	Olive sunbird
	<i>Cyanomitra verticalis</i>	Green-headed sunbird
	<i>Hedydipna collaris</i>	Collared sunbird
Passeridae	<i>Passer griseus</i>	Northern grey-headed sparrow
Ploceidae	<i>Amblyospiza albifrons</i>	Thick-billed weaver
	<i>Euplectes albonotatus</i>	White-winged widowbird
	<i>Ploceus bicolor</i>	Dark-backed weaver
	<i>Ploceus cucullatus</i>	Village weaver
	<i>Ploceus nigerrimus</i>	Vieillot's black weaver
	<i>Ploceus nigricollis</i>	Black-necked weaver
	<i>Ploceus xanthops</i>	African golden weaver
Estrildidae	<i>Cryptospiza reichenovii</i>	Red-faced crimsonwing
	<i>Estrilda astrild</i>	Common waxbill
	<i>Estrilda melpoda</i>	Orange-cheeked waxbill
	<i>Lagonosticta landanae</i>	Landana firefinch
	<i>Lonchura bicolor</i>	Black-and-white mannikin
	<i>Lonchura cucullata</i>	Bronze mannikin
	<i>Mandingoa nitidula</i>	Green twinspot
	<i>Nigrita canicapillus</i>	Grey-headed nigrita
	<i>Spermophaga ruficapilla</i>	Red-headed bluebill
	<i>Uraeginthus angolensis</i>	Blue waxbill
Fringillidae	<i>Crithagra capistrata</i>	Black-faced canary

**Table S3.** The 73 bird species recorded during surveys in Kumbira Forest in 2012.

Family	Scientific name	Common name
Phasianidae	<i>Pternistis afer</i>	Red-necked spurfowl
Accipitridae	<i>Accipiter melanoleucus</i>	Black sparrowhawk
	<i>Accipiter tachiro</i>	African goshawk
Columbidae	<i>Columba larvata</i>	Lemon dove
	<i>Treron calvus</i>	African green pigeon
	<i>Turtur afer</i>	Blue-spotted wood dove
	<i>Turtur tympanistria</i>	Tambourine dove
Musophagidae	<i>Tauraco erythrolophus</i>	Red-crested turaco
Cuculidae	<i>Centropus anselli</i>	Gabon coucal
	<i>Ceuthmochares australis</i>	Green malkoha
	<i>Chrysococcyx cupreus</i>	African emerald cuckoo
	<i>Chrysococcyx klaas</i>	Klaas's cuckoo
Trogonidae	<i>Apaloderma narina</i>	Narina trogon
Bucerotidae	<i>Bycanistes bucinator</i>	Trumpeter hornbill
	<i>Tockus alboterminatus</i>	Crowned hornbill
Lybiidae	<i>Pogoniulus bilineatus</i>	Yellow-rumped tinkerbird
	<i>Trachyphonus purpuratus</i>	Yellow-billed barbet
	<i>Tricholaema hirsuta</i>	Hairy-breasted barbet
	<i>Gymnobucco calvus</i>	Naked-faced barbet
Indicatoridae	<i>Indicator minor</i>	Lesser honeyguide
Eurylaimidae	<i>Smithornis capensis</i>	African broadbill
Platysteiridae	<i>Batis minulla</i>	Angola batis
	<i>Dyaphorophyia castanea</i>	Chestnut wattle-eye
	<i>Dyaphorophyia concreta</i>	Yellow-bellied wattle-eye
Malaconotidae	<i>Chlorophoneus viridis</i>	Gorgeous bushshrike
	<i>Dryoscopus angolensis</i>	Pink-footed puffback
	<i>Laniarius amboimensis</i>	Gabela bushshrike
Campephagidae	<i>Campephaga petiti</i>	Petit's cuckooshrike
Oriolidae	<i>Oriolus larvatus</i>	Black-headed oriole
Monarchidae	<i>Elminia longicauda</i>	African blue flycatcher
	<i>Terpsiphone</i> sp.	Paradise flycatcher
Paridae	<i>Parus funereus</i>	Dusky tit
Pycnonotidae	<i>Andropadus latirostris</i>	Yellow-whiskered greenbul
	<i>Bleda syndactylus</i>	Red-tailed bristlebill
	<i>Chlorocichla falkensteini</i>	Falkenstein greenbul
	<i>Phyllastrephus fulviventris</i>	Pale-olive greenbul
	<i>Pycnonotus tricolor</i>	Dark-capped bulbul
Nicatoridae	<i>Nicator vireo</i>	Yellow-throated nicator

Family	Scientific name	Common name
Hirundinidae	<i>Psalidoprocne pristoptera</i>	Black saw-wing
Acrocephalidae	<i>Iduna natalensis</i>	Dark-capped yellow warbler
Cisticolidae	<i>Apalis binotata</i>	Lowland masked apalis
	<i>Apalis jacksoni</i>	Black-throated apalis
	<i>Apalis rufogularis</i>	Buff-throated apalis
	<i>Camaroptera harterti</i>	Hartert's camaroptera
	<i>Cisticola bulliens</i>	Bubbling cisticola
	<i>Prinia subflava</i>	Tawny-flanked prinia
Timaliidae	<i>Illadopsis fulvescens</i>	Brown illadopsis
Sylviidae	<i>Hylia prasina</i>	Green hylia
	<i>Hyliota australis</i>	Southern hyliota
	<i>Sylvietta virens</i>	Green crombec
Zosteropidae	<i>Zosterops senegalensis</i>	African yellow white-eye
Sturnidae	<i>Cinnyricinclus leucogaster</i>	Violet-backed starling
Turdidae	<i>Pseudaethes poliocephala</i>	Brown-chested alethe
	<i>Stizorhina fraseri</i>	Fraser's rufous thrush
	<i>Turdus pelios</i>	African thrush
Muscicapidae	<i>Cossypha natalensis</i>	Red-capped robin-chat
	<i>Erythropygia leucosticta</i>	Forest scrub robin
	<i>Muscicapa caerulescens</i>	Ashy flycatcher
	<i>Sheppardia gabela</i>	Gabela akalat
Nectariniidae	<i>Chalcomitra fuliginosa</i>	Carmelite sunbird
	<i>Cinnyris bifasciatus</i>	Purple-banded sunbird
	<i>Cinnyris chloropygius</i>	Olive-bellied sunbird
	<i>Cinnyris superbus</i>	Superb sunbird
	<i>Cinnyris venustus</i>	Variable sunbird
	<i>Cyanomitra olivacea</i>	Olive sunbird
	<i>Cyanomitra verticalis</i>	Green-headed sunbird
	<i>Hedydipna collaris</i>	Collared sunbird
Ploceidae	<i>Ploceus bicolor</i>	Dark-backed weaver
	<i>Ploceus cucullatus</i>	Village weaver
	<i>Ploceus nigricollis</i>	Black-necked weaver
Estrildidae	<i>Lonchura bicolor</i>	Black-and-white mannikin
Fringillidae	<i>Crithagra capistrata</i>	Black-faced canary
	<i>Crithagra mozambica</i>	Yellow-fronted canary

**Fig. S3** Individual-based species accumulation curves. No asymptotes were reached and no differences in species richness among land-use types were observed (mixed: 40 species; slash-and-burn: 35 species; secondary forest: 35 species; forest: 37 species).



## **Chapter 3**

# Environmental drivers of bird diversity in Kumbira



**Paper II** Drivers of bird diversity in an understudied African centre of endemism: The Angolan Escarpment Forest.

Aimy Cáceres, Martim Melo, Jos Barlow, Ricardo Faustino de Lima and Michael S.L. Mills

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## Drivers of bird diversity in an understudied African centre of endemism: The Angolan Escarpment Forest

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### Abstract

Natural habitats are being rapidly lost due to human activities. It is therefore vital to understand how these activities influence biodiversity so that suitable guidelines can be established for conservation. This is particularly important in understudied, high biodiversity, areas such as the Angolan Escarpment. Here we examine which habitat characteristics drive bird diversity and endemic species presence at Kumbira Forest, a key site in the Central Escarpment Forest. Bird diversity was sampled by 10 min bird point counts, whereas habitat characteristics were measured by a combination of ground-based vegetation surveys and remotely sensed data modelling of Landsat images. GLM, multi-model inference and model averaging were used to determine the most important variables driving species richness and the presence of endemics. The remote sensing variables performed poorly in predicting presence of Red-crested Turaco and Gabela Bushshrike but they contributed significantly to explain species richness and Gabela Akalat presence, both of which were associated with greater canopy cover. Liana density and elevation were also important explanatory variables in certain cases. Conservation actions at Kumbira should focus on increasing canopy cover and maintaining forest integrity (as measured by liana density), as these actions are likely to have the most positive outcomes for the avifauna.

**Keywords** Angola, bird diversity, endemics, generalized linear model, Kumbira, model averaging

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## Introduction

Habitat loss due to human activities is the most important threat to biodiversity (Brooks et al., 2002) and the main cause of population declines and species extinctions in birds (Stattersfield and Capper, 2000). This is especially significant in the tropics, where almost 70 percent of global biodiversity is concentrated (Bradshaw et al., 2009) and human impacts are increasing at an accelerating pace (Cincotta et al., 2000). Despite primary forests being irreplaceable for maintaining tropical biodiversity (Gibson et al., 2011), modified landscapes such as secondary growth and agroforestry systems can also hold important biodiversity and connect core areas for conservation (Schulze et al., 2004, Gove et al., 2008, Cáceres et al., 2015). Therefore, to implement successful conservation strategies it is important to assess biodiversity in human-modified landscapes (Chazdon et al., 2009, Gardner et al., 2009), and to identify the key factors influencing biodiversity in these landscapes. This is especially the case for extinction-prone species, such as those that are range-restricted or especially sensitive to human activities.

African biodiversity is globally important but extremely understudied (Norris et al., 2010, Gardner et al., 2010, Gibson et al., 2011). This is particularly true for Angola: while it is considered one of the most biodiverse countries of Africa due its location at the confluence of five different biomes, it is very poorly known as a result of almost 30 years of armed conflict (Huntley, 1974, USAID, 2008). The Escarpment Forest constitutes one of the most important areas for biodiversity in the country, although it could not be designated as a 'biodiversity hotspot' due to the lack of information available at the time of the 'hotspot' analyses (Myers et al., 2000). In the case of birds, arguably the best-studied taxonomic group in Angola, these forests are of key conservation importance. The Escarpment Forest is an important evolutionary hotspot (Hall, 1960) where most of the endemic bird species of Angola are found, and it is the most important habitat of the Western Angola Endemic Bird Area, the only centre of bird endemism in the country. Because no protected area is located within this habitat, it has been identified as a critical conservation priority for birds, not only for Angola (Dean, 2001, BirdLife International, 2015a) but for Africa as a whole (Collar and Stuart, 1988).

By the 1960s it was estimated that 95 percent of the original forests had been converted to shade-coffee plantations, which left the high canopy trees intact (Hawkins, 1993). During the civil war (1975-2002) these plantations were abandoned, allowing forest habitats to recover (Ryan et al., 2004, Sekercioglu and Riley, 2005). The end of the war led to the migration of human populations back to rural areas like the Central

Escarpment Forest, and since then slash-and-burn agriculture and logging have become major threats to these forests (Mills, 2010, Cáceres et al., 2015). It is therefore important to understand the impacts that these human activities are having on the forests, such as how they are affecting habitat characteristics, which in turn influence bird diversity and the distribution and abundance of threatened endemics.

The main aim of this study was to understand the environmental drivers influencing bird diversity at Kumbira Forest, a key site for threatened endemic birds in Angola (Mills, 2010). Because conservation planning will be most effective if it is based on regional-scale species distribution models, we first assess if variables obtained through remote sensing techniques contribute to explain bird diversity in Kumbira. Then, we use locally collected ground variables obtained through vegetation surveys to model species richness and presence of endemic birds. Finally, we propose conservation guidelines based on the results.

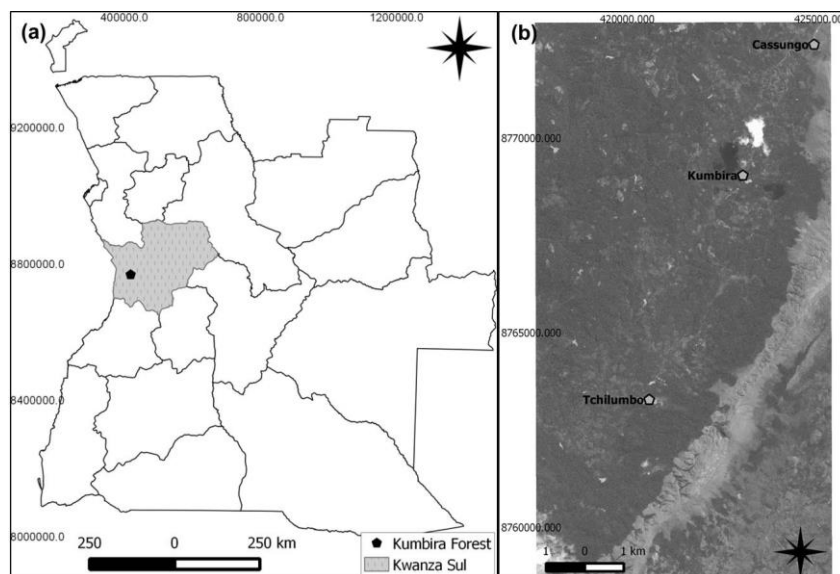
## Methods

### Study Area

Kumbira Forest is the most representative and important site for the conservation of threatened endemic birds of the Central Angolan Escarpment. It holds significant populations of four of the five threatened endemics of this region, namely of the Endangered Gabela Bushshrike *Laniarius amboimensis*, Gabela Akalat *Sheppardia gabela* and Pulitzer's Longbill *Macrosphenus pulitzeri*, and Near Threatened Monteiro's Bushshrike *Malaconous monteiri* (Data Deficient at the time that field work was done). Gabela Akalat is the most range-restricted of the Angolan endemics with an estimated range of only c. 650 km<sup>2</sup>, although it can be locally common, as it is at Kumbira. Gabela Bushshrike has a wider distribution (c.1800 km<sup>2</sup>), occurring both further north and south (at Gungo) of Kumbira Forest, while Pulitzer Longbill and Monteiro Bushshrike have ranges of c. 3700 km<sup>2</sup> and 8000 km<sup>2</sup> respectively (Mills, 2010). Additionally, Kumbira is also home to the endemic, although more widespread (c. 190000 km<sup>2</sup>), Red-crested Turaco *Tauraco erythrolophus* (BirdLife International, 2015b).

Kumbira Forest is located in the municipality of Conda, in the western Angolan province of Kwanza Sul (11.107°S, 14.336°E). The exact limits of Kumbira forest are difficult to define in the west, because the forest gradually merges with dense habitats associated with the escarpment. The eastern limit is nevertheless clearly delimited by the grasslands of the Njelo Mountain, which rises to 1,688 m and runs north-east/south-west. Here we define the southern limit of the forest as 11.230°S and the

northern limit as Cassungo village (11.104°S 14.311°E) (Fig. S1). The terrain within this area varies from relatively flat in the valley bottoms, to steep on the slopes of Njelo Mountain, with altitudes varying from c. 680 to 1,160 m asl.



**Fig.1** (a) Location of Kumbira Forest, Kwanza Sul province, Angola. (b) Study site with the most important villages: Cassungo, Kumbira and Tchilumbo.

### Bird Data

MSLM sampled bird communities by means of 10 min point counts (Bibby et al., 2000) from 13 September 2010 to 2 October 2010, between sunrise (c. 0545h) and 1030h, except when weather was poor (rain or strong wind). All birds seen and heard were recorded within a 50 m radius of each sample point, and points were spaced >150 m apart to avoid double-sampling individuals. Each 10 min point count was divided into two 5 min periods. In order to map the presence of the five key species, a pre-composed track consisting of 30 s snippets of the vocalisations of Monteiro's Bushshrike, Red-crested Turaco, Gabela Bushshrike, Gabela Akalat and Pulitzer's Longbill was played between these two periods, to increase their detectability. Playback was done using an Ipod (Apple, Cupertino) and RadioShack Mini Amplifier speaker (RadioShack Corporation, Fort Worth), always at the same volume. Because playback violates the point count assumption that birds do not approach the observer, we only use playback data for the analysis of species presence. To avoid double-counting, we excluded all observations that could refer to birds that had already been registered.

### Environmental variables – ground variables recorded *in situ*

Habitat characteristics were measured by AC in a circular sample plot of 10 m radius around each bird sampling point. The following variables were sampled: (i) elevation

(elev) by GPS; (ii) canopy height (ch) as the maximum visible height of the canopy (Dallimer et al., 2009), using a Nikon 550 Laser rangefinder (Nikon Corporation, Tokyo); (iii) canopy cover (cc) with a convex spherical densiometer (Forestry Suppliers Inc., Jackson); (iv) shrub cover (shrub) as the percentage of vegetation cover at the shrub level (0.15-1.5m) along a 10 m transect; and (v) liana density (ld) as the number of lianas along a 10 m transect. Canopy height and canopy cover were the average of four measurements taken at 5 m in each cardinal direction from the sample point,

To estimate above-ground biomass (AGB) at each sample plot, we measured height and diameter at breast height (DBH) of all trees with a DBH > 10 cm. Tree height was measured with a clinometer and DBH with a measuring tape. AGB was calculated using a pantropical allometric equation (Chave et al., 2014) that relates AGB of a tree to DBH, total height and wood density. Since it was not possible to identify the species of trees to obtain specific wood densities, we applied a constant wood density of  $0.59 \text{ g/cm}^3$ , the average reported for trees in Africa (Henry et al., 2010). Finally, biomass estimates were converted to carbon values using the fraction of 0.47 MgC, as recommended for tropical and subtropical regions (Paustian et al., 2006), and standardized per area (MgC/ha).

### **Environmental variables derived from remote sensing**

Spectral indices and forest cover (xfor) were calculated from Landsat 7 ETM+ satellite image (WRS-2 path 181 row 68) with low cloud cover (<10%) from 18 May 2010, obtained from the U.S. Geological Survey (USGS) and Earth Resources Observation & Science Center (EROS) via the EarthExplorer interface (<http://earthexplorer.usgs.gov>). It was radiometric normalized and atmospheric corrected using Modified Dark Object Subtraction (DOS), as proposed by Chavez (1996). The empty lines of the Landsat 7 scene produced by the scan failure were treated as “no data”, and excluded from analyses.

The following spectral indices were calculated for a 50 m radius circular plot around each bird sampling point: (i) Land Surface Water Index (LSWI), calculated as the normalized proportion between Near Infrared (NIR) and Short Wave Infrared (SWIR), represents the amount of moisture present in the leaves and soil (Xiao et al., 2002); (ii) Blue-Red ratio Index (BR) that is the normalized difference between the Blue and Red bands and represents the shadow produced by the canopy; and (iii) Enhanced Vegetation Index (EVI) that optimizes vegetation signal in regions with high biomass and reduces atmosphere influences (Huete et al., 2002).

Using supervised classification with Maximum Likelihood Algorithm (MLA) (Jensen, 2005) the scene was classified in “Forest” and “Non-Forest”. Regions of

Interest were chosen based on field knowledge of the study area. Accuracy of the forest class was assessed by comparing the resulting classification with the 2010 sample points and Google Earth high resolution images. Based on this information we estimated the forest cover percent in a 50 m circular plot around each bird sampling point. All sample points located in the gaps produced by the Landsat 7 scan failure were excluded from this analysis.

**Table 1.** Environmental variables obtained through vegetation surveys (ground variables) and remote sensing.

Variables	Description	Unit	Group
Elevation (elev)	Elevation at each sample point	Meters	Ground
Canopy Cover (cc)	Percent of canopy cover	%	Ground
Canopy Height (ch)	Maximum visible height of the canopy	meters	Ground
Shrub cover (shrub)	Percent of vegetation cover at shrub level (0.15 – 1.5)	%	Ground
Liana density (ld)	Number of lianas in a 10 m transect	#lianas/ meter	Ground
Above-ground carbon (c)	Carbon per area estimated from above-ground biomass (AGB)	Mg/ha	Ground
Land Surface Water Index (LSWI)	Proportion between Near Infrared (NIR) and Short Wave Infrared (SWIR) bands and represents the amount of moisture present in the leaves and soil	---	Remote sensing
Blue- Red Ratio Index (BR)	Normalized difference between Blue and Red bands and represents the shadow produced by the canopy	---	Remote sensing
Enhanced Vegetation Index (EVI)	Optimizes vegetation signal in high biomass areas and reduces atmosphere influences	---	Remote sensing
Forest Cover (xfor)	Percent of the forest mask in a 50 m circular plot around each sample point	%	Remote sensing

### Data Analysis

Generalized Linear Models (GLM) (Nelder and Wedderburn, 1972) were used to evaluate bird responses to environmental variables (Zuur et al., 2007). The environmental variables used in this study are present in Table 1. Bird responses were represented by species richness and by the presence of endemic species that were

recorded in over 20 percent of the point counts, namely Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. All variables were standardized and collinearity was assessed by Spearman rank correlation coefficients, which does not assume linear relations between variables. Variables with coefficients of over 0.7 were removed from the analyses (Zuur et al., 2009). The variables maintained in the analyses were chosen based in their biological importance and management relevance.

To assess whether remote sensing variables (spectral indices and forest cover) provided additional information for modelling bird diversity in Kumbira, we modelled species richness and the endemic species presence using a dataset with remote sensing and ground variables. Then, we identified the best models for each group of variables: (i) the “null model” (with no explanatory variables); (ii) only ground (hereafter “Ground Models”); (iii) only remote sensing (hereafter “RS Models”); and (iv) ground and remote sensing (hereafter “Combined Models”).

Only sample points that had both spectral indices and forest cover estimates were used in the analyses – those affected by Landsat 7 scan failure were excluded. Model performance was evaluated using Akaike’s Information Criterion with small sample size correction (AICc), Akaike weights ( $\omega$ ) and evidence ratio (Hurvich and Tsai, 1989, Anderson and Burnham, 2002, Burnham and Anderson, 2002, Burnham and Anderson, 2004).

To assess the environmental variables driving bird diversity at Kumbira Forest, GLMs were constructed with the larger dataset that included only the ground variables of all the sample points (N=201). An adjusted coefficient of determination was used ( $R^2$ ) to assess the predictive power of the models. Model averaging was performed to obtain coefficients estimates for all models with a AICc difference ( $\Delta AICc$ ) smaller than 10 (Burnham and Anderson, 2002, Burnham et al., 2011). Plotting of coefficients estimates and standard errors were used to identify key variables, and their relative variable importance (RVI) was also calculated. All analyses were performed using R 3.2.0 software (R Core Team, 2015) and the packages *Vegan 2.0-9* (Oksanen et al., 2012) and *MuMIn 1.9.13* (Barton, 2013).

## Results

A total of 201 bird point counts were performed and 100 bird species registered. The mean species richness per point count was  $10.4 \pm 3.4$  species (range = 1- 23). Red-crested Turaco was the most-registered endemic, recorded at 68 percent of the point counts (n=136), followed by Gabela Akalat (46%, n= 92) and Gabela Bushshrike (21%,



n=42). Monteiro Bushshrike and Pulitzer Longbill were present only in 7 percent (n=15) and 5 percent (n=11) of the point counts respectively. Vegetation characteristics were measured for all the sample points but spectral indices (LSWI, EVI and BR) and forest cover were only estimated for 132 out of 201 points due to the Landsat 7 scan failure.

### **Effects of remote sensing variables**

Canopy height was strongly correlated with canopy cover (cor = 0.70, p-value < 0.001) and thus excluded from the analysis, as was blue-red ratio with forest cover (cor = 0.73, p-value < 0.001) (Supporting Information, Fig. S1). Both canopy cover and forest cover were retained for analyses because of their importance for species richness and Gabela Akalat presence, and their relevance to forest management.

Combined Models had the lowest AICc for species richness and presence of Gabela Akalat, whereas Ground Models had the lowest AICc for presence of Red-crested Turaco and Gabela Bushshrike (Table 2). Combined Models for species richness greatly outperformed both RS Models and Ground Models, as shown by the high evidence ratios (29.2 and 118.4 respectively). Second ranked models (Combined Models for Red-crested Turaco and Gabela Bushshrike, and RS Models for Gabela Akalat) also performed well in predicting presence of key species (evidence ratios of 1.2-1.6). However RS Models performed poorly in predicting presence of Red-crested Turaco and Gabela Bushshrike, and ranked below the null models.

**Table 2.** Best models generated for each group of variables (N null, G ground, RS remote sensing, and G+RS ground+remote sensing) for species richness and the presence of Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. The rank of each model is included (from 256 possible models), followed by the variables included in each model, the model log-likelihood (logLik), the Akaike's Information Criterion with small sample size correction (AICc), AIC differences ( $\Delta AICc$ ), Akaike weights ( $\omega$ ) and evidence ratio. The variables used were EVI – enhanced vegetation index, LSWI – land-surface water index, xfor – forest cover, c – carbon, cc – canopy cover, elev – elevation, ld – liana density and shrub – shrub cover.

Response Variable	Variable groups	Model rank #	Variables in model	logLik	K	AICc	$\Delta AICc$	$\omega$	Evidence ratio
Species Richness	G+RS	1	ld, xfor	-174.53	3	357.38	0.00	0.1113	
	RS	56	xfor	-178.97	2	364.13	6.75	0.0038	29.2
	G	97	cc, ld	-179.31	3	366.93	9.55	0.0009	118.4
	N	246		-186.80	1	377.69	20.31	0.0000	25714.8
Red-crested Turaco	G	1	elev, ld	-82.66	3	171.50	0.00	0.0319	
	G+RS	3	c, elev, ld, xfor	-80.78	5	172.03	0.53	0.0245	1.3
	N	26		-85.95	1	173.93	2.42	0.0095	3.4
	RS	41	xfor	-85.35	2	174.79	3.28	0.0062	5.2
Gabela Akalat	G+RS	1	c, EVI, xfor	-84.15	4	176.61	0.00	0.0490	
	RS	3	xfor	-86.71	2	177.51	0.90	0.0312	1.6
	G	38	c, cc	-87.14	3	180.46	3.85	0.0071	6.9
	N	87		-89.97	1	181.98	5.37	0.0033	14.7
Gabela Bushshrike	G	1	elev, ld	-65.88	3	137.95	0.00	0.0528	
	G+RS	2	elev, ld, xfor	-64.97	4	138.25	0.30	0.0455	1.2
	N	70		-70.75	1	143.52	5.57	0.0033	16.2
	RS	111	xfor	-70.42	2	144.93	6.98	0.0016	32.7

### Role of habitat characteristics in determining bird diversity in Kumbira

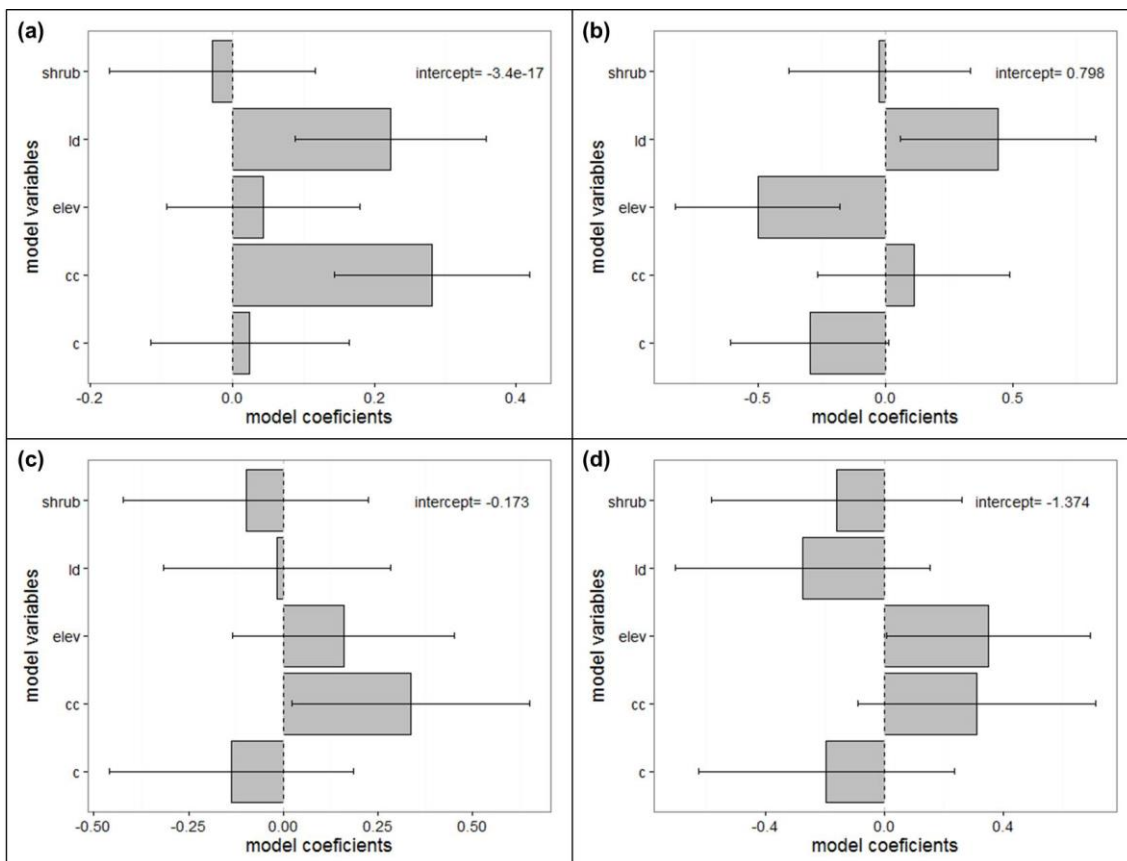
To assess the drivers of bird diversity at Kumbira Forest, GLM models were performed with all the sample points (N=201) and ground variables (Table 1). All models with AICc < 10 were averaged to obtain coefficient estimates and the relative importance for each variable (Table 3, Fig. 1).

Species richness was positively affected by canopy cover and liana density ( $R^2_{\text{averaged}} = 0.15$ , range = 0.11 – 0.16). In the case of the endemic species, Red-crested Turaco was positively affected by liana density but negatively by elevation ( $R^2_{\text{averaged}} = 0.08$ , range = 0.03 – 0.12). Gabela Akalat was positively affected by canopy cover ( $R^2_{\text{averaged}} = 0.02$ , range = 0 – 0.05) and Gabela Bushshrike was positively affected by elevation ( $R^2_{\text{averaged}}=0.031$ , range = 0 – 0.0734, Supporting Information Table S1 - S4). Despite the influence of these variables on the models, they still presented high levels of unexplained variation.

**Table 3.** Relative variables importance (RVI) and averaged coefficients estimates obtained from generalised linear models with ground variables (c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover) for species richness and the presence of Red-crested Turaco, Gabela Akalat and Gabela Bushshrike. Only models with  $\Delta AICc < 10$  were included in the analysis. The grey shading highlights variables with the highest relative importance values and the asterisks indicate variables significance.

	Species Richness		Red-crested Turaco		Gabela Akalat		Gabela Bushshrike	
	RVI	Coef.	RVI	Coef.	RVI	Coef.	RVI	Coef.
c	0.268	0.025	0.679	-0.298	0.349	-0.138	0.362	-0.1951
cc	1.000	<b>0.282***</b>	0.307	0.110	0.798	<b>0.338*</b>	0.554	0.3127
elev	0.299	0.044	0.992	<b>-0.503**</b>	0.388	0.159	0.729	<b>0.3512*</b>
ld	0.992	<b>0.223**</b>	0.883	<b>0.443*</b>	0.267	-0.016	0.474	-0.276
shrub	0.271	-0.029	0.268	-0.024	0.308	-0.098	0.334	-0.1591

Significance levels for *p-value* are (\*)<0.05, (\*\*)<0.01, and (\*\*\*)<0.001



**Fig. 2** Model averaging coefficients estimates for ground variables (N = 201) and models with  $\Delta < 10$  for (a) species richness, (b) Red-crested Turaco, (c) Gabela Akalat and (d) Gabela Bushshrike presence. All averaged coefficients are presented in grey bars and the standard errors in lines. A variable is significant when its averaged coefficients ( $\pm$  standard errors) do not overlap 0.

## Discussion

The use of remotely sensed data is becoming more widespread in conservation planning. For example, spectral indexes and classification maps are often used to infer habitat suitability and examine environmental drivers of biodiversity (Huete et al., 2002, Pettorelli et al., 2005). We demonstrate here that the utility of this approach is rather limited and species specific for the Angolan Central Escarpment. For example, RS models performed very poorly in explaining the presence of Red-crested Turaco and Gabela Bushshrike, being even outperformed by null models. However, in predicting species richness and the presence of the Endangered Gabela Akalat, remote sensing contributed important information, although it performed best when combined with ground variables.

The limited predictive performance of models based on Landsat imagery is not entirely surprising. While Landsat imagery can be used well over long temporal and large spatial scales (Kerr and Ostrovsky, 2003, Wang et al., 2010), it is less useful for biodiversity studies conducted at smaller scales and in more complex environments

(Aplin, 2005, Nagendra and Rocchini, 2008) where spectral indexes do not directly relate to wildlife presence or abundance (Nagendra, 2001). Furthermore, the approach is also limited by the lack of adequate Landsat images for the study region, where cloud cover is very high for most of the year. In recent years new technologies have been developed to deal with these problems, such as hyperspatial images, hyperspectral sensors, Lidar and synthetic aperture radar SAR, among others. These technologies have been used successfully elsewhere (Gillespie et al., 2008, Naidoo et al., 2012, Pettorelli et al., 2014). Nevertheless, they are still underused in tropical areas, due to security issues, data coverage and high costs (Nagendra and Rocchini, 2008). This represents a major limitation to our knowledge, as most of the planet's biodiversity is concentrated in these areas in developing countries that have limited resources and funding (Turner et al., 2013). Hopefully, this situation will change with the continuing development of these technologies at lower prices.

Remote sensing variables did provide a good approximation for some ground variables, like canopy cover. Forest cover (remote sensing) was correlated with canopy cover (vegetation survey) ( $cor=0.6$ ,  $p\text{-value}<0.001$ ) and influenced bird species richness and Gabela Akalat presence. This is encouraging, as obtaining variables derived from remote sensing is easier, faster and cheaper than spending time in the field collecting ground data, and it can be extrapolated across large regions.

The difference in the ability of remote sensing to predict the presence of different species likely relates to their life history and behaviour. The poor performance of remote sensing variables for Red-crested Turaco and Gabela Bushshrike can be related with satellite imagery resolution and scale issues. Despite the 30 m resolution of Landsat imagery, the variables obtained from them do not seem to detect the characteristics affecting these birds. These species have larger home-range sizes than Gabela Akalat and therefore their territories might include more of the mosaic-like landscape of Kumbira, where small spatial changes might not to be detected by the Landsat images.

Environmental variables collected in situ – elevation, canopy cover, shrub cover, liana density and carbon – seem to be good predictors of bird diversity in Kumbira but even the best models had high levels of unexplained variation. In particular, species richness was positively influenced by liana density and canopy cover. Canopy cover is indirectly related to habitat disturbance and affects the presence of birds, especially forest specialists (Mammides et al., 2015). Regarding liana density, lianas usually increase in gap areas and as part of the successional process of secondary growth (Schnitzer and Bongers, 2002). However, most of the original forest in Kumbira was cleared by the 1970s and replaced by shade coffee

plantations (Hawkins, 1993). The abandonment of these plantations caused by the war allowed understorey vegetation to regenerate – with lianas included – while maintaining the original canopy. After the war, with the return of people to the area, human disturbance has been dominated by slash-and-burn, which destroys all forest. It is therefore likely that in Kumbira, liana presence is indicative of the more natural forest – as lianas can only grow if there are trees in the first place – rather than open areas disturbed mainly by slash-and-burn agriculture. Moreover, liana density is related with canopy height ( $cor=0.37$ ,  $p\text{-value}<0.001$ ) and this link also seems to indicate that lianas in Kumbira are associated with the most natural forest.

Canopy cover also predicted Gabela Akalat presence. Higher canopy cover sample points were located in forest areas – old-growth and secondary forest – which confirms the description of Gabela Akalat as a forest-dependant bird (Collar, 2005) and agrees with a previous study on this species based on radio-tracking (Cáceres et al., 2016). In other areas of Africa, the presence of threatened endemic forest birds is also related to canopy cover and structure (Dallimer and King, 2007, Dallimer et al., 2012, de Lima et al., 2013, Mammides et al., 2015). Canopy cover was highly correlated with canopy height, therefore Gabela Akalat might also be affected by canopy height and other aspects of mature forests including canopy structure and understorey humidity. The presence of Red-crested Turaco was positively affected by liana density, likely reflecting its association with the most natural forests in Kumbira. This species was also negatively affected by elevation, being more frequent at lower elevations. Sample points at different elevations, with and without Red-crested Turaco, were not obviously different, but it may be possible that as the forest goes into the scarp, its canopy height decreases and becomes denser, affecting the presence of Red-crested Turaco.

Elevation affected positively Gabela Bushshrike presence. This agrees with the records for this species, always above  $> 730$  m (Mills, 2010). However, as the elevation gets higher the forest gives way to mountain grasslands, no longer suitable for this endemic, only registered in this study between 812 – 988 m. Unlike the other endemics, no habitat characteristic was identified as driving the presence of this species. This can be related with the lack of statistical power due to the low detectability of this endemic (present just in 20% of the sample points) or the failure of the vegetation surveys to record the habitat characteristics that are driving this species presence. It may also be related to the ecology of this very mobile predatory species, belonging to a taxonomic group that usually needs large territories for foraging (Fry and Bonan, 2013), and hence is not affected by habitat differences at the small scale used here.

## Conservation Implications

Our study provides some important insights into the conservation of one of Africa's critical priority areas for bird conservation. Many of the results indicate that conservation efforts should focus on the maintenance of canopy cover by protecting the remaining forest. For example, canopy cover affects both overall species richness and the Gabela Akalat presence. The endangered Gabela Akalat is the key priority for conservation at Kumbira because it is the most range-restricted of the Angolan endemics with an estimated suitable range of only c. 650 km<sup>2</sup> (Mills, 2010). As a result, this species is particularly sensitive to forest loss and depends on the maintenance of canopy cover at Kumbira for its survival.

Protecting high quality mature forest in the region is challenging as the extent and condition of forests are threatened by slash-and-burn agriculture and logging of high canopy trees for timber (Mills, 2010, Cáceres et al., 2015). Protected areas are widely used in conservation, but at present no area of the Angolan Central Escarpment Forest has formal protection status. A proposal for the establishment of a c. 50 km<sup>2</sup> strict nature reserve was put forward in the past (Huntley and Matos, 1994) but has yet to be implemented. Alternative approaches to protected areas could involve local populations. These include increasing forest cover through reforestation initiatives, with native tree species. Such action has recently been initiated in Kumbira with the establishment of an experimental nursery as part of a project funded by the Conservation Leadership Programme. Wildlife friendly agriculture may also be beneficial (Gove et al., 2008, Buechley et al., 2015). In this context, we recommend as a priority research into the economic viability of recovering the abandoned shade coffee plantations and on the impacts such action could have on biodiversity, together with the evaluation of other more biodiversity-friendly agricultural practices.

Any conservation actions require good baseline data on the occurrence of the most important species. For most species, our study demonstrates the importance of basing this on good quality data from ground surveys, complemented by remote sensing variables. However, it is encouraging that the presence of the most endangered species, the Gabela Akalat, can be predicted by remote sensing variables, as this provides hope that large-scale mapping can be used to identify priority areas. However, the models we present here had very low explanatory power, indicating the role of unmeasured factors such as landscape context and resource availability. Some of these may be resolved by using newer and more refined remotely sensed measures, which would also provide a basis to examine other areas of the Central Angolan Escarpment Forest, such as the forest of Bango-Seles 25 km to the South. In addition, future research should aim at including other taxa such as plants, amphibians and

insects that may be more sensitive to human disturbance and may not reflect the patterns of bird diversity (Kremen et al., 2008). This information is critically important for effective conservation and sustainable planning required to protect the unique biological richness of this region.

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**Table S1.** Set of models generated for species richness. Here are listed all possible variables in the models, followed by degrees of freedom (df), model log-likelihood (logLik), Akaike's Information Criterion with small sample size correction (AICc), AIC differences ( $\Delta$ AICc), Akaike weights ( $\omega$ ) and adjusted coefficient of determination (adjR<sup>2</sup>). c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover.

	(Intercept)	c	cc	elev	ld	shrub	df	logLik	AICc	$\Delta$ AICc	$\omega$	adjR <sup>2</sup>
11	-6.05E-17	NA	0.278872	NA	0.223486	NA	4	-268.41	545.02	0	3.65E-01	0.159
15	1.82E-17	NA	0.288224	4.41E-02	0.213701	NA	5	-268.20	546.70	1.68	1.57E-01	0.161
27	-3.26E-17	NA	0.288467	NA	0.23137	-0.0310208	5	-268.32	546.94	1.92	1.40E-01	0.160
12	-5.96E-17	0.0243281	0.269525	NA	0.22443	NA	5	-268.35	547.01	1.98	1.35E-01	0.160
16	-1.17E-17	0.0251605	0.278651	4.45E-02	0.214581	NA	6	-268.13	548.70	3.68	5.80E-02	0.162
31	1.09E-17	NA	0.293887	3.95E-02	0.22017	-0.0214498	6	-268.16	548.74	3.72	5.68E-02	0.161
28	-3.17E-17	0.0253971	0.278987	NA	0.232584	-0.0319177	6	-268.25	548.94	3.91	5.16E-02	0.160
32	-1.92E-17	0.0258184	0.284286	3.97E-02	0.221328	-0.0222967	7	-268.09	550.76	5.73	2.08E-02	0.162
3	-3.06E-17	NA	0.318272	NA	NA	NA	3	-273.97	554.07	9.04	3.97E-03	0.108
7	6.79E-17	NA	0.334109	9.15E-02	NA	NA	4	-273.06	554.32	9.30	3.48E-03	0.116
19	-2.68E-17	NA	0.306187	NA	NA	0.03412842	4	-273.86	555.92	10.90	1.57E-03	0.109
23	8.14E-17	NA	0.317608	9.88E-02	NA	0.05019416	5	-272.82	555.94	10.92	1.55E-03	0.119
4	-3.00E-17	0.0144865	0.312806	NA	NA	NA	4	-273.95	556.11	11.09	1.43E-03	0.108
8	6.91E-17	0.017098	0.327731	9.19E-02	NA	NA	5	-273.03	556.37	11.35	1.25E-03	0.117
20	-5.77E-17	0.0137324	0.301111	NA	NA	0.03382825	5	-273.84	557.99	12.97	5.58E-04	0.109
24	8.24E-17	0.0161929	0.311665	9.92E-02	NA	0.04989933	6	-272.79	558.02	12.99	5.50E-04	0.119
10	-1.35E-17	0.1247417	NA	NA	0.269043	NA	4	-275.24	558.68	13.66	3.94E-04	0.096
9	-1.62E-17	NA	NA	NA	0.272651	NA	3	-276.94	560.01	14.98	2.03E-04	0.079
26	-4.06E-17	0.118156	NA	NA	0.255109	0.04575508	5	-275.04	560.38	15.36	1.69E-04	0.097
14	-5.04E-17	0.1242563	NA	-5.10E-03	0.27	NA	5	-275.24	560.78	15.76	1.38E-04	0.096
25	-1.01E-17	NA	NA	NA	0.252728	0.06453756	4	-276.53	561.27	16.25	1.08E-04	0.083
13	-3.50E-17	NA	NA	-1.73E-02	0.275851	NA	4	-276.91	562.03	17.00	7.41E-05	0.079
30	-1.28E-18	0.1185526	NA	7.22E-03	0.253142	0.04777122	6	-275.03	562.49	17.47	5.86E-05	0.098
29	-4.13E-17	NA	NA	8.31E-05	0.252705	0.06456148	5	-276.53	563.37	18.35	3.78E-05	0.083
18	-1.45E-18	0.1133933	NA	NA	NA	0.12523491	4	-281.35	570.89	25.87	8.79E-07	0.035
17	-2.27E-18	NA	NA	NA	NA	0.14255481	3	-282.64	571.41	26.38	6.81E-07	0.022
22	4.74E-17	0.117747	NA	7.25E-02	NA	0.13933008	5	-280.82	571.95	26.93	5.18E-07	0.040

	<b>(Intercept)</b>	<b>c</b>	<b>cc</b>	<b>elev</b>	<b>ld</b>	<b>shrub</b>	<b>df</b>	<b>logLik</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>ω</b>	<b>adjR<sup>2</sup></b>
2	-1.28E-17	0.1325219	NA	NA	NA	NA	3	-282.92	571.97	26.95	5.13E-07	0.019
21	6.99E-17	NA	NA	6.53E-02	NA	0.15584955	4	-282.22	572.65	27.63	3.66E-07	0.026
1	-1.57E-17	NA	NA	NA	NA	NA	2	-284.71	573.47	28.45	2.42E-07	0.000
6	3.71E-17	0.136637	NA	4.59E-02	NA	NA	4	-282.71	573.63	28.60	2.24E-07	0.021
5	2.08E-17	NA	NA	3.36E-02	NA	NA	3	-284.59	575.31	30.28	9.68E-08	0.001



**Table S2.** Set of models generated for Red-crested Turaco presence. Here are listed all possible variables in the models, followed by degrees of freedom (df), model log-likelihood (logLik), Akaike’s Information Criterion with small sample size correction (AICc), AIC differences ( $\Delta$ AICc), Akaike weights ( $w$ ) and adjusted coefficient of determination (adjR<sup>2</sup>). c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover.

	(Intercept)	c	cc	elev	ld	shrub	df	logLik	AICc	$\Delta$ AICc	$w$	adjR <sup>2</sup>
14	0.8060029	-0.28415	NA	-0.5277	0.45433	NA	4	-117.87	243.94	0.00	0.2989	0.115
13	0.7896822	NA	NA	-0.4884	0.426913	NA	3	-119.61	245.34	1.41	0.1479	0.093
16	0.8091374	-0.33095	0.130981	-0.50834	0.425815	NA	5	-117.60	245.51	1.58	0.1358	0.118
30	0.8059233	-0.28182	NA	-0.53181	0.460689	-0.01731	5	-117.86	246.03	2.09	0.1049	0.115
29	0.7903613	NA	NA	-0.50531	0.452329	-0.06451	4	-119.54	247.28	3.35	0.0561	0.094
15	0.7897053	NA	-0.00798	-0.49004	0.429013	NA	4	-119.61	247.42	3.49	0.0523	0.093
32	0.8096766	-0.3302	0.150118	-0.52022	0.444314	-0.06041	6	-117.55	247.53	3.59	0.0496	0.119
6	0.775076	-0.25686	NA	-0.44407	NA	NA	3	-121.22	248.55	4.62	0.0297	0.072
8	0.7831896	-0.3373	0.222742	-0.42048	NA	NA	4	-120.42	249.03	5.10	0.0234	0.082
31	0.7903913	NA	0.012466	-0.5038	0.450655	-0.06844	5	-119.54	249.38	5.44	0.0197	0.094
5	0.7628697	NA	NA	-0.4139	NA	NA	2	-122.67	249.40	5.46	0.0195	0.052
22	0.7786386	-0.27643	NA	-0.42253	NA	0.133605	4	-120.88	249.97	6.04	0.0146	0.076
24	0.7837762	-0.33769	0.196869	-0.41133	NA	0.070745	5	-120.33	250.97	7.03	0.0089	0.083
21	0.7644519	NA	NA	-0.39786	NA	0.087576	3	-122.52	251.16	7.22	0.0081	0.054
7	0.7643647	NA	0.083932	-0.40104	NA	NA	3	-122.53	251.19	7.25	0.0080	0.054
23	0.7650971	NA	0.060941	-0.39232	NA	0.066439	4	-122.45	253.11	9.18	0.0030	0.055
10	0.7657008	-0.21697	NA	NA	0.333743	NA	3	-123.58	253.29	9.35	0.0028	0.040
9	0.7583267	NA	NA	NA	0.320847	NA	2	-124.67	253.39	9.46	0.0026	0.025
12	0.7712924	-0.3006	0.222852	NA	0.291848	NA	4	-122.74	253.67	9.74	0.0023	0.051
4	0.7552993	-0.30865	0.276285	NA	NA	NA	3	-124.18	254.49	10.55	0.0015	0.032
26	0.7681303	-0.23736	NA	NA	0.29385	0.126452	4	-123.28	254.77	10.83	0.0013	0.044
1	0.7382676	NA	NA	NA	NA	NA	1	-126.51	255.04	11.10	0.0012	0.000
11	0.7591609	NA	0.096838	NA	0.299787	NA	3	-124.47	255.07	11.13	0.0011	0.028
2	0.7445415	-0.20491	NA	NA	NA	NA	2	-125.53	255.12	11.18	0.0011	0.014
25	0.7588277	NA	NA	NA	0.293473	0.081135	3	-124.54	255.19	11.26	0.0011	0.027
18	0.7523067	-0.23906	NA	NA	NA	0.208455	3	-124.64	255.41	11.47	0.0010	0.026
28	0.7715715	-0.30253	0.201082	NA	0.274664	0.065443	5	-122.66	255.63	11.69	0.0009	0.052
20	0.7576382	-0.31121	0.226602	NA	NA	0.134417	4	-123.85	255.90	11.97	0.0008	0.036
17	0.743033	NA	NA	NA	NA	0.1645	2	-125.92	255.91	11.97	0.0008	0.008
3	0.7422525	NA	0.149045	NA	NA	NA	2	-126.03	256.13	12.19	0.0007	0.007
27	0.7592288	NA	0.079075	NA	0.285306	0.053459	4	-124.42	257.05	13.11	0.0004	0.029
19	0.7445153	NA	0.103022	NA	NA	0.126524	3	-125.73	257.58	13.64	0.0003	0.011

**Table S3.** Set of models generated for Gabela Akalat presence. Here are listed all possible variables in the models, followed by degrees of freedom (df), model log-likelihood (logLik), Akaike’s Information Criterion with small sample size correction (AICc), AIC differences ( $\Delta$ AICc), Akaike weights ( $\omega$ ) and adjusted coefficient of determination (adjR<sup>2</sup>). c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover.

	(Intercept)	c	cc	elev	ld	shrub	df	logLik	AICc	$\Delta$ AICc	$\omega$	adjR <sup>2</sup>
3	-0.172006	NA	0.287602	NA	NA	NA	2	-136.58	277.22	0.0000	0.1459	0.0266
7	-0.173917	NA	0.318783	0.1703981	NA	NA	3	-135.89	277.91	0.6899	0.1033	0.0356
4	-0.172524	-0.1601	0.349397	NA	NA	NA	3	-136.05	278.23	1.0118	0.0880	0.0335
19	-0.172913	NA	0.334877	NA	NA	-0.12944199	3	-136.23	278.59	1.3711	0.0735	0.0311
8	-0.17463	-0.157	0.37895	0.1676578	NA	NA	4	-135.39	278.99	1.7734	0.0601	0.0420
1	-0.169559	NA	NA	NA	NA	NA	1	-138.60	279.23	2.0077	0.0535	0.0000
11	-0.171935	NA	0.290764	NA	-0.0178112	NA	3	-136.57	279.26	2.0462	0.0524	0.0267
23	-0.174597	NA	0.354432	0.1558818	NA	-0.10488782	4	-135.67	279.55	2.3341	0.0454	0.0384
20	-0.173091	-0.1579	0.395052	NA	NA	-0.12647107	4	-135.73	279.65	2.4365	0.0431	0.0377
15	-0.173803	NA	0.331443	0.1834227	-0.0584975	NA	4	-135.82	279.84	2.6191	0.0394	0.0365
12	-0.172442	-0.1612	0.354188	NA	-0.0243464	NA	4	-136.04	280.28	3.0662	0.0315	0.0337
5	-0.169964	NA	NA	0.1125428	NA	NA	2	-138.29	280.64	3.4192	0.0264	0.0042
27	-0.172974	NA	0.333724	NA	0.01537885	-0.13380611	4	-136.23	280.66	3.4431	0.0261	0.0312
24	-0.175024	-0.155	0.412801	0.153154	NA	-0.10173349	5	-135.19	280.68	3.4659	0.0258	0.0446
16	-0.174551	-0.1597	0.393959	0.1818903	-0.0644161	NA	5	-135.30	280.91	3.6926	0.0230	0.0432
9	-0.1696	NA	NA	NA	0.03298837	NA	2	-138.58	281.21	3.9941	0.0198	0.0004
2	-0.16959	-0.0256	NA	NA	NA	NA	2	-138.59	281.23	4.0159	0.0196	0.0002
17	-0.169562	NA	NA	NA	NA	-0.00715844	2	-138.60	281.26	4.0457	0.0193	0.0000
31	-0.174518	NA	0.357713	0.1641465	-0.0309308	-0.09477234	5	-135.65	281.62	4.3993	0.0162	0.0386
28	-0.173116	-0.1575	0.394313	NA	0.00772156	-0.12866272	5	-135.72	281.76	4.5376	0.0151	0.0377
21	-0.169973	NA	NA	0.1158896	NA	0.01647524	3	-138.28	282.69	5.4676	0.0095	0.0043
6	-0.169976	-0.0156	NA	0.1111498	NA	NA	3	-138.28	282.69	5.4685	0.0095	0.0043
13	-0.169978	NA	NA	0.110199	0.01272871	NA	3	-138.28	282.69	5.4726	0.0095	0.0042
32	-0.174969	-0.1568	0.417573	0.1633874	-0.0383237	-0.08916282	6	-135.16	282.75	5.5327	0.0092	0.0450
10	-0.169632	-0.0266	NA	NA	0.03375971	NA	3	-138.56	283.24	6.0204	0.0072	0.0006
25	-0.169614	NA	NA	NA	0.03891877	-0.01921298	3	-138.57	283.26	6.0387	0.0071	0.0005
18	-0.16959	-0.0251	NA	NA	NA	-0.00333739	3	-138.59	283.29	6.0766	0.0070	0.0002
22	-0.169988	-0.0182	NA	0.1147863	NA	0.01902689	4	-138.27	284.75	7.5339	0.0034	0.0044
14	-0.169992	-0.0163	NA	0.1086087	0.01350137	NA	4	-138.28	284.76	7.5420	0.0034	0.0043
29	-0.16998	NA	NA	0.1138647	0.00785067	0.01362709	4	-138.28	284.77	7.5472	0.0034	0.0043
26	-0.169642	-0.0244	NA	NA	0.03843925	-0.01535624	4	-138.55	285.31	8.0923	0.0026	0.0007
30	-0.169995	-0.0182	NA	0.1127779	0.00779286	0.01619608	5	-138.27	286.85	9.6350	0.0012	0.0044

**Table S4.** Set of models generated for Gabela Bushshrike presence. Here are listed all possible variables in the models, followed by degrees of freedom (df), model log-likelihood (logLik), Akaike's Information Criterion with small sample size correction (AICc), AIC differences ( $\Delta$ AICc), Akaike weights ( $\omega$ ) and adjusted coefficient of determination (adjR<sup>2</sup>). c – carbon, cc – canopy cover, elev – elevation, ld – liana density, shrub – shrub cover.

	(Intercept)	c	cc	elev	ld	shrub	df	logLik	AICc	$\Delta$ AICc	$\omega$	adjR <sup>2</sup>
15	-1.398236	NA	0.301902	0.4113347	-0.3309844	NA	4	-99.10	206.40	0.0000	0.0964	0.0598
5	-1.357536	NA	NA	0.3049394	NA	NA	2	-101.34	206.74	0.3374	0.0815	0.0259
13	-1.373097	NA	NA	0.3415879	-0.2557456	NA	3	-100.44	207.01	0.6071	0.0712	0.0396
16	-1.413335	-0.2544	0.39607	0.4108218	-0.3404305	NA	5	-98.35	207.01	0.6086	0.0711	0.0709
7	-1.373926	NA	0.23694	0.351059	NA	NA	3	-100.48	207.09	0.6864	0.0684	0.0390
8	-1.387632	-0.2412	0.321901	0.3491518	NA	NA	4	-99.81	207.82	1.4187	0.0474	0.0491
23	-1.388341	NA	0.320165	0.3256553	NA	-0.2321732	4	-99.85	207.90	1.5008	0.0455	0.0485
31	-1.40452	NA	0.347771	0.387927	-0.2921182	-0.142274	5	-98.88	208.07	1.6623	0.0420	0.0630
1	-1.331235	NA	NA	NA	NA	NA	1	-103.03	208.07	1.6691	0.0419	0.0000
6	-1.361132	-0.1116	NA	0.2960127	NA	NA	3	-101.17	208.46	2.0542	0.0345	0.0286
21	-1.360766	NA	NA	0.2856214	NA	-0.1043661	3	-101.18	208.47	2.0710	0.0342	0.0284
24	-1.400485	-0.2334	0.396045	0.324697	NA	-0.2224435	5	-99.22	208.75	2.3470	0.0298	0.0579
32	-1.417767	-0.2467	0.431857	0.3896167	-0.3043064	-0.1259983	6	-98.18	208.79	2.3871	0.0292	0.0734
14	-1.375457	-0.0952	NA	0.3325843	-0.2489949	NA	4	-100.32	208.84	2.4364	0.0285	0.0415
29	-1.373174	NA	NA	0.3375884	-0.2495146	-0.016142	4	-100.44	209.09	2.6824	0.0252	0.0396
9	-1.341427	NA	NA	NA	-0.1891151	NA	2	-102.52	209.10	2.6965	0.0250	0.0078
3	-1.338524	NA	0.158829	NA	NA	NA	2	-102.60	209.26	2.8539	0.0231	0.0066
17	-1.338804	NA	NA	NA	NA	-0.1619511	2	-102.60	209.26	2.8551	0.0231	0.0066
19	-1.357747	NA	0.263556	NA	NA	-0.2753955	3	-101.63	209.39	2.9823	0.0217	0.0215
2	-1.336622	-0.1371	NA	NA	NA	NA	2	-102.75	209.56	3.1563	0.0199	0.0043
11	-1.352373	NA	0.193833	NA	-0.2295315	NA	3	-101.89	209.91	3.5025	0.0167	0.0175
4	-1.351528	-0.2368	0.24193	NA	NA	NA	3	-101.90	209.92	3.5192	0.0166	0.0174
20	-1.368577	-0.2277	0.336807	NA	NA	-0.2656065	4	-100.99	210.19	3.7891	0.0145	0.0312
22	-1.363501	-0.0984	NA	0.2802926	NA	-0.0906465	4	-101.05	210.30	3.8916	0.0138	0.0304
12	-1.366488	-0.2464	0.283608	NA	-0.2398944	NA	4	-101.13	210.47	4.0672	0.0126	0.0291
10	-1.346017	-0.1292	NA	NA	-0.1834383	NA	3	-102.27	210.66	4.2600	0.0115	0.0117
27	-1.365408	NA	0.275379	NA	-0.1751394	-0.2288855	4	-101.26	210.72	4.3152	0.0111	0.0272
25	-1.344612	NA	NA	NA	-0.1497134	-0.1165171	3	-102.32	210.75	4.3498	0.0110	0.0110
30	-1.375458	-0.0949	NA	0.3320384	-0.2481048	-0.0023212	5	-100.32	210.94	4.5399	0.0100	0.0415
18	-1.342391	-0.1138	NA	NA	NA	-0.144346	3	-102.42	210.95	4.5483	0.0099	0.0095
28	-1.376881	-0.2351	0.353297	NA	-0.1863945	-0.214554	5	-100.57	211.46	5.0525	0.0077	0.0376
26	-1.348002	-0.1137	NA	NA	-0.1500997	-0.0979178	4	-102.13	212.46	6.0604	0.0047	0.0138

## **Chapter 4**

Home-range size and habitat preferences of the  
Endangered and range-restricted Gabela Akalat

**Paper III** Radio telemetry reveals key data for the conservation of  
*Sheppardia gabela* (Rand, 1957) in the Angolan Escarpment Forest

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## Radio telemetry reveals key data for the conservation of *Sheppardia gabela* (Rand, 1957) in the Angolan Escarpment Forest

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### Abstract

Biodiversity information in Angola is limited or non-existent, hindering the design and implementation of conservation strategies. The Escarpment Forest is one of the most important areas for bird diversity in the country. However, there is almost no information about the territorial needs and habitat preferences of its threatened endemic birds. This study evaluated these needs and preferences in Gabela Akalat *Sheppardia gabela*, a range-restricted endemic to the Central Escarpment. Eighteen individuals of this species were captured and radio-tracked with the objectives of establishing their territory size (through home-range size estimates) and habitat preferences using compositional analysis. Home-range sizes were slightly larger than other *Sheppardia* species and Gabela Akalat evidently avoided clearings and preferred forest habitat, although it was also able to use farmland areas and secondary growth to a lesser extent. Conservation measures should focus on the preservation of remaining old-growth forest through the establishment of a nature reserve in Kumbira. To assure the success of such an initiative, the local population should participate in planning, administration and enforcement. We outline some measures that could help address the economic needs of the local community while maintaining forest cover.

**Keywords** Compositional analysis, Gabela Akalat, habitat use, home-range size, minimum convex polygons, radio-tracking

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## Introduction

Many globally important biodiversity areas lack the baseline data required to guide and implement appropriate conservation strategies. Even basic natural history information about threatened and especially endemic species in these areas is limited or non-existent. This is the case in Angola, an African country with high biodiversity because of its location at the confluence of five different biomes (Huntley, 1974). However, with the rapid economic development of the country, human activities are putting pressure on natural areas. Conservation measures are therefore urgently needed, especially in the most important biodiversity areas. Unfortunately, owing to over 30 years of armed conflict, knowledge about this biodiversity is seriously limited and outdated, rendering the formulation and implementation of such measures extremely challenging.

One of the most important areas for biodiversity in Angola is the Escarpment Forest. This forest presents affinities with all three adjacent biomes: the South-West Arid, the *Brachystegia* woodlands and the Congo-Guinean Forest, but it also acts as a barrier between them (Dean, 2001). The Escarpment Forest is also a major evolutionary hotspot for birds (Hall, 1960) and constitutes the main habitat of the only centre of avian endemism in the country, the Western Angola Endemic Bird Area (Stattersfield et al., 1998). It is considered a critical priority for global conservation (Dean, 2001) and is one of the most important forests in Africa for bird conservation (Collar and Stuart, 1988). It only failed to qualify as a biodiversity hotspot because the appropriate information was unavailable at the time (Myers et al., 2000).

Kumbira Forest is the best known and single most representative area of the Central Escarpment, holding significant populations of three Endangered endemic birds: Gabela Bushshrike *Laniarius amboimensis*, Pulitzer's Longbill *Macrosphenus pulitzeri* and Gabela Akalat (Mills, 2010). Unfortunately, these forests are rapidly being cleared by human populations for agriculture and timber. Furthermore, the virtual absence of detailed information about the habitat requirements of these species represents a major obstacle to the development of efficient, effective and realistic conservation strategies for the forest and the key elements of biodiversity it contains.

The main objective of this study was to fill some of the key ecological knowledge gaps by understanding the territorial needs and habitat preferences of the Endangered Gabela Akalat, the most range-restricted endemic bird of Angola (Mills, 2010). This species was selected for this study for two reasons: first, its apparently strong dependence on forest habitats makes it particularly sensitive to ongoing land-use changes (Collar, 2005a, Cáceres et al., 2015); second, its abundance within the study site was sufficient to provide quantitative data on its ecological requirements.

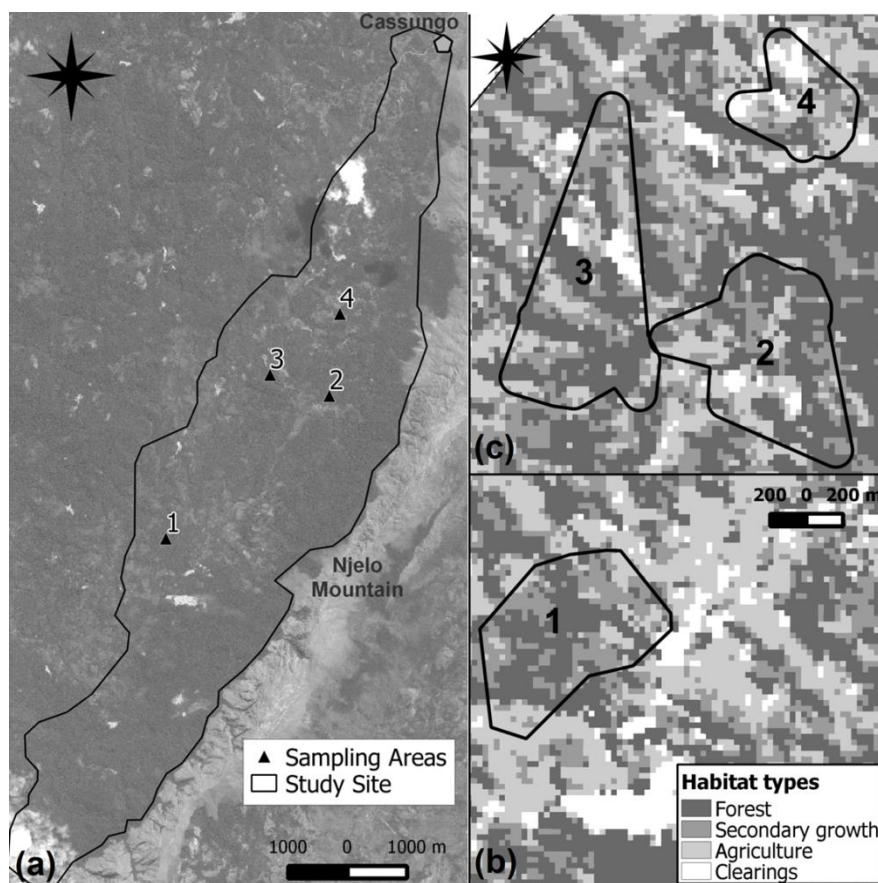
Specifically, we sought to: (i) identify the territorial needs of Gabela Akalat by estimating its home-range size using different methods; (ii) assess variation in home-range sizes depending on different forest types; and (iii) determine the species' habitat preferences. Finally, we used these results to discuss conservation strategies for this endemic endangered species.

## Methods

### Study Area

We performed fieldwork at Kumbira Forest from 14 June to 17 July 2013, 31 May to 29 June 2014 and 2 August to 31 August 2014. Fieldwork was always conducted in the dry season – non-breeding season for the Gabela Akalat – because in the rainy season the roads are flooded and the study site is inaccessible. Kumbira is located in the municipality of Conda within the western Angolan province of Kwanza Sul. The eastern limits of the forests are clearly delimited by the grasslands of Njelo Mountain. However it is difficult to define the other exact limits of the forest because the habitat gradually merges into other dense vegetation types associated with the escarpment. As in a previous study, we defined the northern limit as Cassungo village (11.104°S 14.311°E) and the southern limit as 11.230°S 14.250°E (Cáceres et al., 2015) (Fig. 1a). We selected four sectors of the study site (from hereafter “sampling areas”) to radio-track birds from areas with different forest characteristics. Despite different habitat types (forest, secondary growth, agriculture and clearings) were present in these sampling areas, we classified them according to the characteristics of their forest, so they were classified as: (i) Invasive – forest understorey and canopy is dominated by the invasive *Inga vera* – (ii) Natural –best old-growth forest in the study site – (iii) Mixed – forest with presence of a non-dominant *Inga vera* and other species – (iv) Coffee – abandoned shade coffee plantations that are being transformed to agricultural plots (Fig. 1b and Fig 1c).





**Fig. 1** (a) Study site in Kumbira Forest with the four sampling areas (1-4); (b) Sampling areas were defined according to the forest type: 1 Invasive; (c) 2 Natural; 3 Mixed and 4 Coffee. Sampling areas size and shapes were defined following Aebischer et al. (1993) for compositional analysis to assess habitat preferences. Land-cover/habitat types map is also presented.

## Radio-tracking

We captured birds using mist-nets and playback of vocalisations to increase capture probability. Birds were ringed and weighed, and DNA sexing was done from tail feathers (Griffiths et al., 1998). We attached VHF radio transmitters (Pico Pip Ag 379 from Biotrack, Dorset, UK) to the birds' mantle feathers using eyelash glue. Transmitters did not exceed 5% of the bird's body weight (transmitter = 0.55g) as recommended by Kenward (2001).

We tracked the birds using TR-100 telemetry receivers (Communication Specialist, California) and 3-element Yagi antennas (Biotrack, Dorset). In 2013, we followed two birds for 10 days, recording their locations every two hours between 07h00 and 17:00h. In 2014, we followed 16 birds for five days and we recorded their locations every hour between 07h00 and 17h00, except at 13h00. In both years, we made a total of 50–60 location attempts and each attempt included 2–7 bearings. One observer followed the birds using the existing trail system in the study site. Established points –located in gaps and higher areas– were used to record the bearings. For each

location attempt, the observer collected the bearings of one bird at the time, and then moved to the next bird. Within each sampling hour, the same order to radio-track the birds was used so that the time lapse between location attempts would be similar.

We estimated the locations of each individual by triangulation, using the software Locate III (Pacer Computing, 2011). Although three bearings should ideally be used to calculate a location, in some cases ( $n=154$ , 23.8%) we were compelled to use only two bearings. This happened when the bird was suspected to have moved between bearing readings, as indicated by the last bearing determining a completely different direction and a larger time lapse ( $> 5$  minutes).

### **Estimating home-range sizes**

We estimated home-range sizes only for birds that had more than 30 successful locations (Kenward, 2001) using minimum convex polygons (MCP) with 95% and 100% locations, and also kernel contours using all locations with a reference and least square cross-validation (LSCV) smoothing parameters (Kernohan et al., 2001). Then, we compared the different estimates using Wilcoxon-rank sum test (Bauer, 1972) and Bonferroni correction to address for multiple comparisons (Dunn, 1961).

Different methodological considerations led us to favour the use of MCP over kernel contours for further analyses. Kernel contours can be poor for samples sizes below 50 locations and perform badly in highly fragmented landscapes, as they exclude potentially important areas between the areas of highest occurrence probability (Blundell et al., 2001, Riley et al., 2003, Sekercioglu et al., 2007). Furthermore, although MCP estimates of home-range size tend to increase with the number of locations (White and Garrot, 1990), this approach successfully addresses the patchy landscape in Kumbira, reduces overlap between territories, and allows comparisons with other studies (Kenward, 2001). Finally, home-range sizes obtained with MCP 95 for birds in the different sampling areas were compared using non-parametric Kruskal Wallis and one-way permutation tests.

### **Habitat preferences**

We used land-cover classes to define the major habitat types and created a land-cover/habitat types map using Landsat 8 satellite imagery from 6 June 2014 made available by the Earth Resources Observation & Science Center of the U.S. Geological Survey via the EarthExplorer interface (<http://earthexplorer.usgs.gov>). Principal component analysis (PCA) was performed on atmospherically (DOS1) and topographically (Minnaert) corrected bands 1–7. An unsupervised Simple K-means classification was performed on the first three PCA components using WEKA, a

software library with a collection of machine-learning algorithms for data-mining software (Hall et al., 2009). We reclassified the eight initial clusters, using field data and high-resolution imagery provided by Google Earth from the QGIS OpenLayers plugin (QGIS Development Team, 2013), to four classes: forest, secondary growth (natural regenerated vegetation including secondary forest and scrubs), agriculture (well-established farmland) and clearings (recently slashed-and-burned fields and urban areas).

We assessed habitat preferences by comparing habitat use and availability through compositional analysis (Aebischer et al., 1993). This was based on the nature of habitat selection performed by animals at two levels: (i) the second-order selection determines the individual home-range in a landscape and (ii) the third-order selection refers to the individual's habitat preferences within its home-range (Johnson, 1980). To assess second-order selection we defined as used habitat the MCP with 95% locations and the available habitat was the four sampling areas where birds were captured (Fig. 1b and Fig. 1c). These sampling areas were defined following a similar approach used by Aebischer et al. (1993). However, due the higher mobility of the Gabela Akalat when compared to the pheasant species used by Aebischer (*Phasianus colchicus*), we decided to enlarge the sampling area by creating a 90 m buffer (equivalent to three 30 m Landsat pixels) around the birds' MCP with 100% locations. For the third-order selection, we defined as used habitat the locations obtained with more than three bearings, whereas the available habitat was given by the MCP with 100% locations (Kauhala and Auttila, 2010). Percentages of habitat type were estimated for the used and available habitats in both selection orders. For this analysis, we only used birds from 2014 because the high cloud cover (>10%) did not allow us to obtain a Landsat image from 2013 to create a land-cover/habitat types map. All analyses were done with *R v. 3.1.1* (R Core Team, 2015) and the extension packages *Raster* (Hijmans and van Etten, 2013), *Adehabitat HR* for home-range estimations and *Adehabitat HS* for habitat preferences (Calenge, 2006).

## Results

### Estimating home-range size

The location attempts that successfully gave a location were in the 70–96% range (Table 1). One individual (M12) was excluded from the analysis because the transmitter stopped emitting a signal after two days of radio-tracking (16 successful locations).

**Table 1** Radio-tracked birds in Kumbira Forest. Information included is: bird identification (ID), year bird was captured (year), bird's sex (sex), bird's weight in g (w), sampling area where bird was radio-tracked (sampling area), number of days the bird was radio-tracked (days), number of location attempts (location attempts), number of successful locations (successful locations) and the percent of location attempts that gave a successful location (success percent).

ID	year	sex	w	sampling area	days	location attempts	successful locations	success percent
F1	2014	F	16.6	Invasive	5	44	42	95.5
F2	2014	F	13.0	Natural	5	50	46	92.0
F3	2014	F	12.0	Mixed	5	49	33	67.3
F4	2014	F	11.6	Coffee	5	50	47	94.0
F5	2014	F	11.2	Coffee	5	50	47	94.0
F6	2014	F	11.4	Coffee	5	50	46	92.0
M1	2013	M	14.0	Coffee	10	46	37	80.4
M2	2013	M	13.3	Coffee	10	57	47	82.5
M3	2014	M	14.5	Invasive	5	50	42	84.0
M4	2014	M	12.5	Invasive	5	50	46	92.0
M5	2014	M	12.9	Invasive	5	48	48	100.0
M6	2014	M	12.5	Invasive	5	46	33	71.7
M7	2014	M	15.0	Natural	5	50	41	82.0
M8	2014	M	14.0	Natural	5	47	45	95.7
M9	2014	M	13.0	Mixed	5	50	45	90.0
M10	2014	M	13.0	Mixed	5	50	48	96.0
M11	2014	M	14.0	Mixed	5	48	39	81.3
M12	2014	M	12.1	Coffee	2	18	16	88.9

Home-range size estimates varied depending on the methods used. Using MCP with 100% locations, home-range size for Gabela Akalat was  $10.0 \pm 12.8$  ha ( $n=17$  birds). This value decreased considerably when outliers were excluded by using MCP with 95% locations, where home-range size was  $4.3 \pm 4.2$  ha. When using Kernel contours, the home-range estimate was  $7.2 \pm 7.5$  ha with the least square cross-validation smoothing parameter and  $13.0 \pm 14.2$  ha with reference smoothing parameter (Table 2). However, only estimates obtained using MCP with 95% locations and Kernel contour with reference smoothing parameter were significantly different from the estimates obtained with other methods ( $p < 0.05$ ; Wilcoxon-rank sum test; Supporting Information Fig S1). Home-range size estimates did not differ between the sexes (11 males, 6 females; Wilcoxon test,  $p > 0.05$ ).

Two males, with no juvenile plumage as described by Sekercioglu and Riley (2005), had the largest home-range sizes (MCP 95 = 12.9 and 12.4, Table 2). A female had the smallest home-range size (MCP 95 = 0.3 ha, Table 2) and she was captured with a male in the same net and time. This female may have been paired as its home-range overlapped with that of the male (Fig. 2a, female F1 and male M3).

In three of the sampling areas, the home-ranges of three to four birds overlapped. This overlapping occurred between males and females (Fig. 2b and Fig. 2c) or only females (Fig. 2d).

Home-range sizes in the four sampling areas were different ( $X^2=8.84$ ,  $p=0.03$ ; Kruskal Wallis test). Specifically, home-range sizes in the Natural sampling area were larger (MCP 95 =  $10.1 \pm 3.1$ ), while the estimates for Coffee and Invasive sampling areas did not differ between them (Fig. 3).

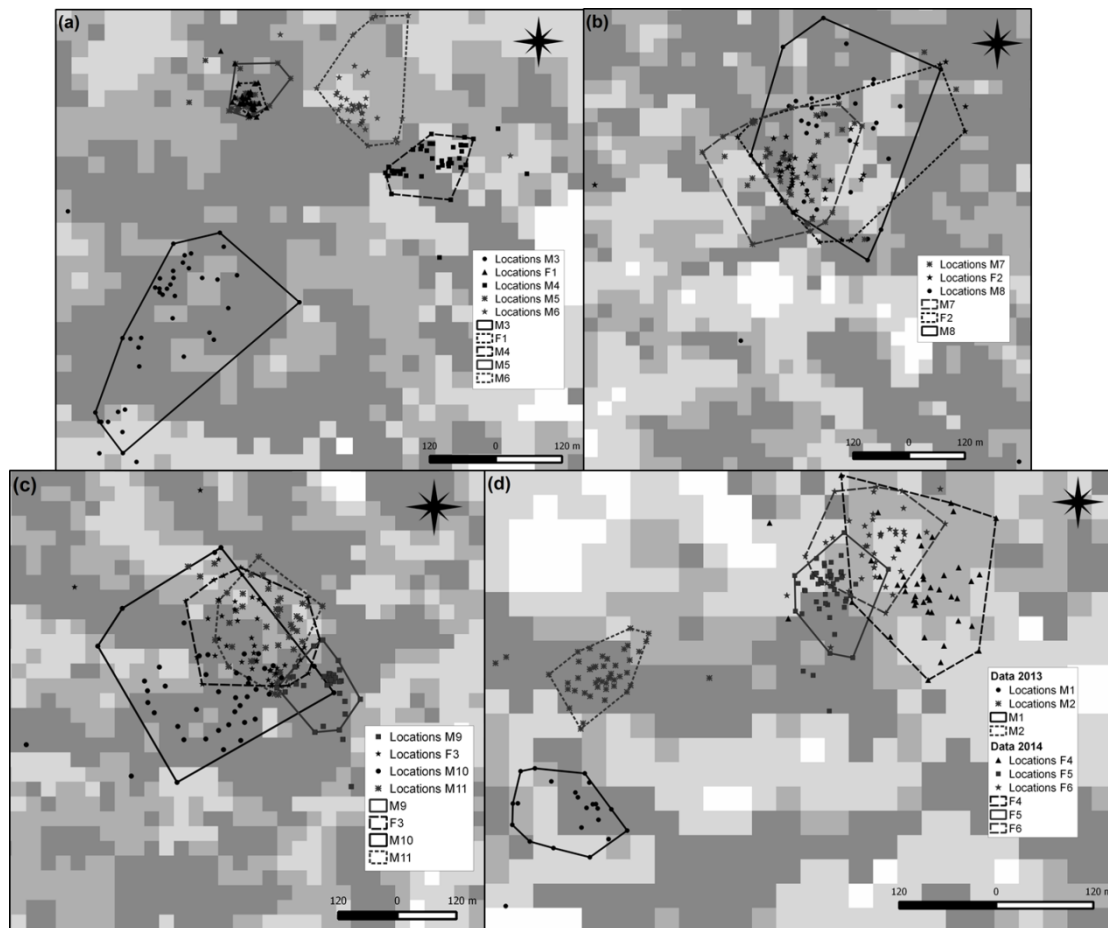
### **Habitat preferences**

The habitat type with the highest percentage use was always forest (second-order selection =  $51.9 \pm 29.4\%$ ; third order selection =  $52.1 \pm 31.6$ ). This was followed by secondary growth (second-order selection =  $33.8 \pm 21.1\%$ ; third order selection =  $30.2 \pm 19.1\%$ ) and agriculture (second-order =  $14.3 \pm 12.0\%$ ; third order selection =  $17.7 \pm 17.4\%$ ) In the case of clearings, even though this habitat was available, it was never used by the birds (Table 3).

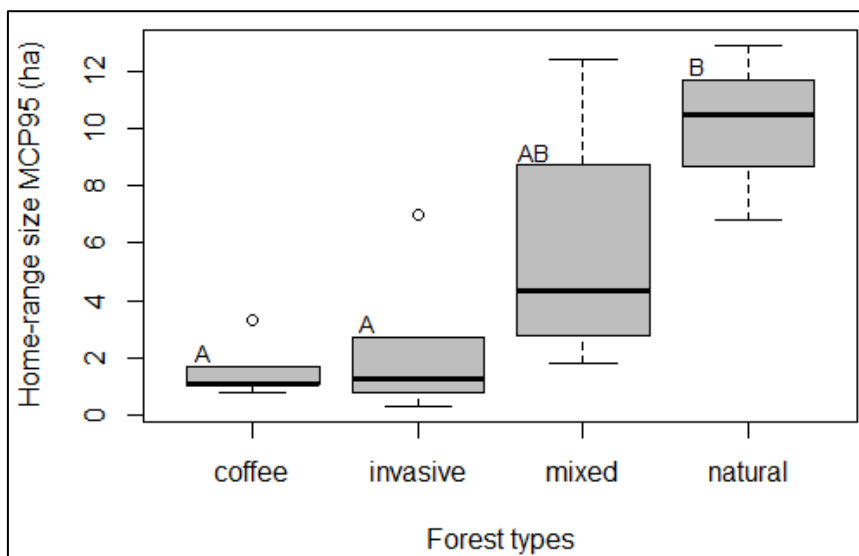
Habitat preferences were significant ( $p < 0.05$ ,  $n=15$ ). Therefore, habitat use was non-random when selecting a home-range within the landscape (second-order selection,  $p=0.001$ ) and when using this home-range (third-order selection,  $p=0.03$ ). In both cases, habitat preferences had the following order: forest, secondary growth, agriculture and clearings. Birds preferred forest habitats over other habitats and consistently avoided clearings. Even though forest was more used than secondary growth and agriculture less used than secondary growth and forest, these preferences were not significant.

**Table 2.** Home-range size estimates (in hectares) for Gabela Akalats with > 30 locations (M12 was excluded from analysis, successful locations =16). Mean, standard deviation and ranges – mean  $\pm$  SD (range) – are presented for females (n=6), males (n=11) and total birds (n=17). Total were calculated across all individuals. Estimation methods were minimum convex polygons with 95% (MCP 95) and 100% locations (MCP 100) and kernel contours with 100% locations with least square cross-validation ( $\text{Kernel}_{\text{ISCV}}$ ) and reference smoothing parameter ( $\text{Kernel}_{\text{ref}}$ ).

ID	Home-range size (ha)			
	MCP 95	MCP 100	$\text{Kernel}_{\text{ISCV}}$	$\text{Kernel}_{\text{ref}}$
F1	0.3	0.5	0.5	0.9
F2	10.5	15.4	9.3	21.7
F3	5.0	11.4	11.2	14.8
F4	3.3	8.3	5.4	9.7
F5	1.1	1.5	2.1	2.3
F6	1.7	2.4	4.1	3.9
M1	1.1	2.0	3.8	5.3
M2	0.8	1.8	2.2	2.5
M3	7.0	11.4	8.2	20.0
M4	1.3	3.5	1.6	4.5
M5	0.8	1.4	0.5	1.8
M6	2.7	7.0	2.9	8.8
M7	6.8	13.0	12.7	19.4
M8	12.9	36.4	23.9	47.9
M9	1.8	2.5	1.4	4.4
M10	12.4	46.3	25.1	44.9
M11	3.7	4.6	7.6	9.0
<b>Females (n=6)</b>	<b>3.7 <math>\pm</math> 3.4 (0.3 – 10.5)</b>	<b>6.6 <math>\pm</math> 5.6 (0.5 – 15.4)</b>	<b>5.4 <math>\pm</math> 3.8 (0.5 – 11.2)</b>	<b>8.9 <math>\pm</math> 7.4 (0.9 – 21.7)</b>
<b>Males (n=11)</b>	<b>4.7 <math>\pm</math> 4.3 (0.8 – 12.9)</b>	<b>11.8 <math>\pm</math> 14.6 (1.4 – 46.3)</b>	<b>8.2 <math>\pm</math> 8.4 (0.5 – 25.1)</b>	<b>15.3 <math>\pm</math> 15.8 (1.8 – 47.9)</b>
<b>Total (n=17)</b>	<b>4.3 <math>\pm</math> 4.2 (0.3 – 12.9)</b>	<b>10 <math>\pm</math> 12.8 (0.5 – 46.3)</b>	<b>7.2 <math>\pm</math> 7.5 (0.5 – 25.1)</b>	<b>13 <math>\pm</math> 14.2 (0.9 – 47.9)</b>



**Fig. 2** Land-cover/habitat types map, locations of radio-tracked Gabela Akalats and minimum convex polygons with 95% locations (MCP 95) in the different sampling areas. **(a)** Invasive: birds F1, M3, M4, M5 and M6; **(b)** Natural: F2, M7 and M8; **(c)** Mixed: F3, M9, M10 and M11; and **(d)** Coffee: F4, F5, F6, M1 and M2. Habitat types colours are the same as in Figure 1.



**Fig. 3** Boxplot of home-range estimates of Gabela Akalats obtained using minimum convex polygons with 95% locations (MCP 95) for the different sampling areas: Coffee ( $1.6 \pm 1.0$ ;  $n=5$ ), Invasive ( $2.4 \pm 2.7$ ;  $n=5$ ), Mixed ( $5.7 \pm 4.6$ ;  $n=4$ ) and Natural ( $10.1 \pm 3.1$ ,  $n=3$ ). Home-range sizes among sampling areas were significantly different ( $X^2=8.84$ ,  $p=0.03$ ; Kruskal Wallis test). The cap letter in the upper part of each boxplot (A, AB and B) corresponds to significance groups according to the one-way permutation tests ( $p < 0.05$ ). Home-range sizes in the "Natural" sampling area were larger than in other areas.



**Table 3.** Habitat types percentages for all sampled Gabela Akalats (n=15) for (a) second-order selection between minimum convex polygons (MCP) using 95% locations and sampling areas; and (b) third-order selection between locations and MCP using 100% locations.

<b>a) second-order Selection: MCP 95 (used habitat)</b>					<b>Sampling areas (available habitat)</b>			
	Forest	Secondary growth	Agriculture	Clearings	Forest	Secondary growth	Agriculture	Clearings
F1	100.0	0.0	0.0	0.0	48.9	38.3	12.7	0.2
F2	43.6	32.5	23.9	0.0	54.9	28.9	12.9	3.3
F3	50.9	41.8	7.3	0.0	48.7	32.5	14.1	4.7
F4	0.0	64.9	35.1	0.0	32.3	36.2	9.2	22.3
F5	50.0	41.7	8.3	0.0	32.3	36.2	9.2	22.3
F6	5.6	55.6	38.9	0.0	32.3	36.2	9.2	22.3
M3	73.1	20.5	6.4	0.0	48.9	38.3	12.7	0.2
M4	69.2	7.7	23.1	0.0	48.9	38.3	12.7	0.2
M5	88.9	11.1	0.0	0.0	48.9	38.3	12.7	0.2
M6	10.3	75.9	13.8	0.0	48.9	38.3	12.7	0.2
M7	38.2	42.1	19.7	0.0	54.9	28.9	12.9	3.3
M8	43.7	33.8	22.5	0.0	54.9	28.9	12.9	3.3
M9	90.5	9.5	0.0	0.0	48.7	32.5	14.1	4.7
M10	64.0	25.7	10.3	0.0	48.7	32.5	14.1	4.7
M11	51.2	43.9	4.9	0.0	48.7	32.5	14.1	4.7
<b>second-order (mean±SD)</b>	<b>51.9 ± 29.4</b>	<b>33.8 ± 21.1</b>	<b>14.3 ± 12.0</b>	<b>0.0 ± 0.0</b>	<b>46.7 ± 7.6</b>	<b>34.5 ± 3.6</b>	<b>12.4 ± 1.7</b>	<b>6.4 ± 8.1</b>

<b>b) third-order selection: Locations (used habitat)</b>					<b>MCP 100 (available habitat)</b>			
	Forest	Secondary growth	Agriculture	Clearings	Forest	Secondary growth	Agriculture	Clearings
F1	100.0	0.0	0.0	0.0	80.0	20.0	0.0	0.0
F2	75.0	25.0	0.0	0.0	40.5	29.2	30.4	0.0
F3	65.0	30.0	5.0	0.0	50.8	34.9	14.3	0.0
F4	2.2	57.8	40.0	0.0	11.8	36.6	36.6	15.1
F5	36.2	31.9	31.9	0.0	53.3	40.0	6.7	0.0
F6	4.4	40.0	55.6	0.0	20.0	48.0	32.0	0.0
M3	45.5	27.3	27.3	0.0	67.5	24.6	7.9	0.0
M4	45.2	21.4	33.3	0.0	38.5	20.5	41.0	0.0
M5	100.0	0.0	0.0	0.0	68.8	25.0	6.3	0.0
M6	15.2	48.5	36.4	0.0	24.1	57.0	19.0	0.0
M7	50.0	42.3	7.7	0.0	39.9	31.8	28.4	0.0
M8	25.0	64.3	10.7	0.0	50.5	21.8	22.0	5.7
M9	93.9	6.1	0.0	0.0	85.7	14.3	0.0	0.0
M10	79.1	14.0	7.0	0.0	50.0	29.4	15.4	5.3
M11	44.7	44.7	10.5	0.0	45.1	47.1	7.8	0.0
<b>Third-order (mean±SD)</b>	<b>52.1 ± 31.6</b>	<b>30.2 ± 19.1</b>	<b>17.7 ± 17.4</b>	<b>0.0 ± 0.0</b>	<b>48.4 ± 20.3</b>	<b>32.0 ± 11.6</b>	<b>17.9 ± 12.9</b>	<b>1.7 ± 4.0</b>
<b>TOTAL (mean±SD)</b>	<b>52.0 ± 30.5</b>	<b>32.0 ± 20.2</b>	<b>16.0 ± 15.1</b>	<b>0.0 ± 0.0</b>	<b>47.6 ± 15.4</b>	<b>33.2 ± 8.7</b>	<b>15.1 ± 9.6</b>	<b>4.1 ± 6.8</b>

## Discussion

We showed that radio-tracking can provide novel insights into the territory size and habitat requirements of an endangered and little-known endemic bird species. Home-range size for Gabela Akalat varied depending on the estimation methods used. Considering the lowest estimate obtained with a method that excludes outliers and addresses the patchy landscape of Kumbira, home-range size for this species was slightly larger (MCP 95 =  $4.3 \pm 4.2$  ha) than territory sizes estimated for other *Sheppardia* species (0.5 – 3 ha/pair:(Keith et al., 1992)). The estimates of this study were obtained in the dry season when other tropical passerines have also shown larger home-ranges than during the rainy season (Lindsell, 2001, Sekercioglu et al., 2007). It coincides with the non-breeding season for this species, when territories are probably not yet established as shown by the overlap in the home-ranges of several birds. This overlapping could be produced by birds being more tolerant to congeners, floaters birds exploring and attempting to establish a breeding territory (as in two occasions birds were observed fighting a conspecific), or the presence of family groups with offspring from the previous season. Furthermore, it is possible that Gabela Akalat occupies territories in pairs with the male establishing the territory and then patrolling and defending it, as described for the Thrush family (Collar, 2005b). However this observation was limited to one putative pair of birds that were captured at the same time and net and their territories overlapped (Fig 2a, female F1 and male M3). Unfortunately with the data collected in this study we were not able to distinguish between these alternatives.

Home-range size estimates from natural forest – old-growth forest in the study site – were significantly larger than estimates from disturbed forests types (invasive, mixed and coffee) (Fig 3). Individuals in disturbed areas may have larger territories in an attempt to maintain the same amount of suitable habitat as if they were in natural areas. In one study in Costa Rica, bird species had considerably larger home-range sizes in less forested areas (Sekercioglu et al., 2007). However, this is not the case in this study where the most disturbed areas seem to have the smallest home-ranges. It is possible than in these disturbed areas – especially in the coffee area (MCP 95 =  $1.6 \pm 1.0$ ) where abandoned shade coffee plantations were being slashed-and-burned – birds might retract their territories and concentrate in the forest remnants still present in the area. Further research should focus in estimating home-range sizes during the breeding season when birds are more territorial; address the high variability of these estimates (as described by the high values of standard deviation) by increasing sample size; and compare breeding success between different forest types.

Although being a species strongly associated with forest (Collar, 2005a), we demonstrate that the Gabela Akalat does manage to use or at least move through other human-modified habitats, mainly secondary growth and agricultural lands. However, forest does remain the preferred habitat of Gabela Akalat – it constituted the main habitat of its home-range and was the habitat where this species spent most time. Slash-and-burn techniques, commonly used to generate farm plots in Kumbira, create clearings that are evidently avoided by Gabela Akalat. These clearings do not have any type of vegetation (complete lack of canopy and understorey) that could be used by this species. However, the species was able to use secondary growth and agriculture habitats, typical of the mosaic landscape of Kumbira, but always to a lesser extent than forests. Both secondary growth and agriculture seem to have vegetation that can be used by the species. However, the use of these modified habitats is likely to be dependent on the presence of forest patches nearby (BirdLife International, 2013). Further research should be done to know if these preferences are maintained over the breeding season and assess the influence of the surrounding matrix. Breeding success in forest versus secondary growth should also be estimated, to determine if secondary growth is able to sustain viable populations of Gabela Akalat (Liu et al., 2011).

It is vital to maintain the remaining forests in Kumbira and adopt policies that promote the recovery of the degraded areas. Of primary importance is the establishment of a natural reserve to protect some of the remaining forest. Despite formal proposals to protect part of the Central Escarpment Forest (Huntley, 1974, Mills, 2010), no protected area has been created yet. This reserve should include the areas closer to Njelo Mountain where old-growth forest is still present. Moreover, to assure the success of such a reserve in Kumbira, the economic needs of the local population have to be attended to.

Actions could focus on promoting the recovery of degraded areas through a programme of natural regeneration and reforestation with native species. Such a programme would provide local employment and increase the forest area, benefiting the Gabela Akalat and probably other endemic birds. Other actions could centre on the rehabilitation of former shade coffee plantations, as they maintain a canopy mimicking the structure of the original forest and are capable of conserving forest bird diversity (Buechley et al., 2015). During the 1970s, Angola was one of the biggest producers of coffee and it is estimated that up to 95% of the Escarpment Forest was already under shade coffee production at that time (Hawkins, 1993). However, nowadays these plantations are abandoned and being destroyed to plant sun-loving crops. Research regarding coffee production and viability of plantations at Kumbira could help to determine their profitability. Furthermore, agricultural areas should be more effectively

managed, with slash-and-burn of old forest replaced by more efficient use of existing farmland and of the numerous degraded or abandoned plots that are widespread in the area.

This study is a part of a larger ongoing effort to supply solid data for practical conservation in Angola and to fill the biodiversity knowledge gap in the country. Despite its limitations and constraints, it was able to provide important insights into the ecology of Gabela Akalat, although further research – including models to map the species distribution, seasonality and the needs of the other endangered species – would provide a stronger basis on which conservation management can be more effectively implemented.

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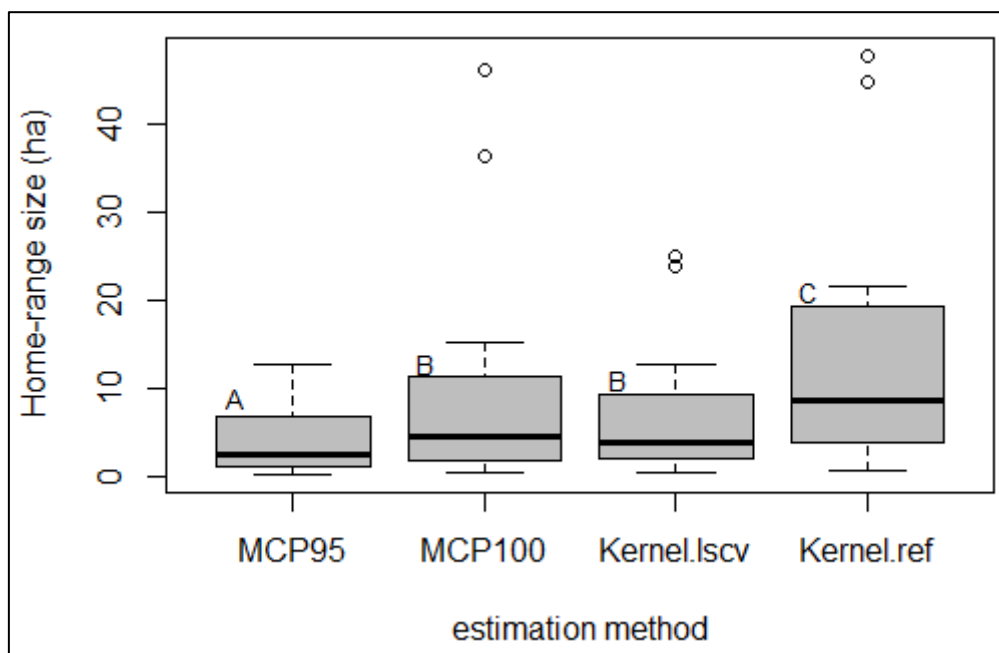
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## Supporting Information

**Fig. S1.** Boxplot of home-range estimates for the Gabela Akalat obtained with different methods: minimum convex polygons with 95% (MCP95) and 100% locations (MCP100), kernel contours with least square cross-validation (Kernel.lscv) and reference smoothing parameter (Kernel.ref). The cap letter in the upper part of each boxplot (A, B and C) corresponds to significance groups according to the Wilcoxon-rank sum test with Bonferroni correction. Estimates obtained with MCP 95 and Kernel.ref were significant different from other methods. MCP95 was preferred for further analyses because it addresses the patchy landscape in the study site, excludes outliers and reduces overlap between home-ranges.





## **Chapter 5**

The potential of REDD+ as a conservation tool  
for the Angolan Escarpment Forest

**Paper IV** The potential of REDD+ for ‘small centres of endemism’:

A case study from the Angolan Escarpment Forest

Ana Leite, Aimy Cáceres, Martim Melo, Michael S. L. Mills and António T. Monteiro

Submitted to *Biological Conservation*

## The potential of REDD+ for 'small centres of endemism': A case study from the Angolan Escarpment Forest

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### Abstract

Tropical deforestation contributes to the increase of human-induced CO<sub>2</sub> and is the major cause of biodiversity loss. With the objective of tackling climate change, the Reduce Emissions from Deforestation and Forest Degradation (REDD+) program has the goal to economically compensate countries that reduce deforestation. However, REDD+ potential for producing non-carbon benefits –such as biodiversity conservation – has not been deeply assessed. The main goal of this study was to evaluate the potential of REDD+ as a tool for the conservation of small forest centres with an endemic-rich biodiversity like Kumbira, part of the Angolan Escarpment Forest. Specifically, we assessed forest cover change and deforestation rates from 1991, 2001 and 2014; estimated aboveground carbon stocks through biomass calculation; and provided recommendations to maximize emissions reduction and conservation potential. During the first ten years (1991-2001) no forest loss was detected in the area. This changed rapidly with the post-war return of people, which led to an annual deforestation rate of 4% for 2001-2014. The average above ground carbon was 89.4 Mg/ha. When considering a forest of ~8000 ha, the total carbon pool present in Kumbira was ~714200 MgC. The use of REDD+ for the conservation of small centres of endemism requires moving away from purely market-based mechanisms towards local capacity building programmes. This could be achieved in the Angolan Escarpment Forest by targeting the funds towards the creation of a protected area and in promoting conservation-friendly agriculture, such as shade coffee that was already produced in this area during the colonial time.

**Keywords** Above ground carbon, carbon stocks, deforestation, endemic, Kumbira, REDD

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## Introduction

Tropical deforestation is responsible for the loss of 32% of the world total forest area (Hansen et al., 2013), contributing significantly to the increase of human-induced CO<sub>2</sub> emissions to the atmosphere (van der Werf et al., 2009) and global biodiversity loss (Baillie et al., 2004). With the world's attention focused in tackling climate change, the important role of forests falls under the umbrella of the Reduce Emissions from Deforestation and Forest Degradation (REDD+) program, a post-Kyoto protocol created by the United Nations Framework Convention on Climate Change (UNFCCC). The REDD+ goal is to mitigate emissions by financially rewarding countries that reduce deforestation and forest degradation and, at the same time, to promote sustainable forest management, protect biodiversity and enhance rural livelihoods (UNFCCC, 2010). However, this apparent win-win solution faces multiple environmental and economic challenges (Phelps et al., 2012) with several pilot projects stagnating or being abandoned (Sunderlin et al., 2015). Recently, REDD+ was even considered one of the latest “*conservation fads*”, defined as “approaches that are embraced enthusiastically and then abandoned” (Redford et al., 2013). The main challenges in the implementation of REDD+ are the leakage effect and the non-permanence problem. The former occurs when a reduction of deforestation in a target area increases the process of deforestation in other regions or countries. The latter highlights the risk that any reductions in emissions gained from current efforts to halt deforestation may be lost in the future due to the unpredictability of voluntary contributions in the long-term (Phelps et al., 2011). The voluntary market is currently the only global market for trading REDD+ credits, where the carbon price is significantly lower than on the compliance market (Conte and Kotchen, 2010). An oversupply of cheap REDD+ credits can prevent real reductions from occurring and increase investor preference for low-cost emissions mitigation rather than co-benefits (Phelps et al., 2011).

There is little agreement over the potential of REDD+ in yielding non-carbon benefits because REDD+ is first and foremost interested on its global ability to reduce CO<sub>2</sub> emissions and deforestation rates. Therefore, countries with large remaining forest areas and high deforestation rates offer the possibility of high-return REDD+ actions. On the other hand, projects that assess non-carbon dimensions such as quality of forest governance, conservation priorities, local rights and tenure frameworks are able to create more attractive and lower-risk investments (Phelps et al., 2010a). In such projects, the application of the co-benefit principle is expected to identify many biodiverse important regions that are easily overlooked by the dominant REDD+

selection criteria. This is particularly true for areas of endemism. These areas of global conservation significance are small but offer high returns from a conservation perspective (Kier et al., 2009, de Lima et al., 2013). At the same time, although these regions hold a small proportion of the world's terrestrial carbon stocks they can give an important contribution to emission reductions as they are often carbon-rich forests (Magnago et al., 2015). Moreover, high biodiversity value is often associated with high carbon stocks, even if the opposite does not necessarily happens (Talbot, 2010, de Lima et al., 2013). Sub-national projects are also more likely to guarantee local rights. National-level REDD+ initiatives recentralize forest governance and consequently reduce the role of local community-based management, making forests more vulnerable to external pressures (Phelps et al., 2010b). Large-scale national projects may also represent a major challenge for countries with limited governance capabilities, which is the case for many tropical forest-rich countries (Phelps et al., 2010a).

The Angolan Escarpment ("Scarp") Forest constitutes one of the most biologically interesting regions in Angola (Ryan et al., 2004; Mills, 2010; Cáceres et al., 2015) as a result of being located at the confluence of three different biomes (Guinea-Congo forest in the north, miombo woodlands in the east and the arid deserts of Namib in the south). It has affinities with these adjoining biomes, but also acts as a barrier between them, which has resulted in a high diversity of vegetation types and significant levels of endemism (Hall, 1960, Huntley, 1974, Dean, 2001). This forest represents the main habitat of the Western Angola Endemic Bird Area (Stattersfield et al., 1998) and has been considered one of the most important areas for bird conservation in Africa (Collar and Stuart, 1988) and a priority for global conservation (Dean, 2001, BirdLife International, 2015). Unfortunately, because of the decades of armed conflicts, there is a huge lack of knowledge regarding the Scarp Forest - as most of the biodiversity of Angola. This even prevented the classification of the Scarp Forest as a biodiversity hotspot by Myers et al. (2000).

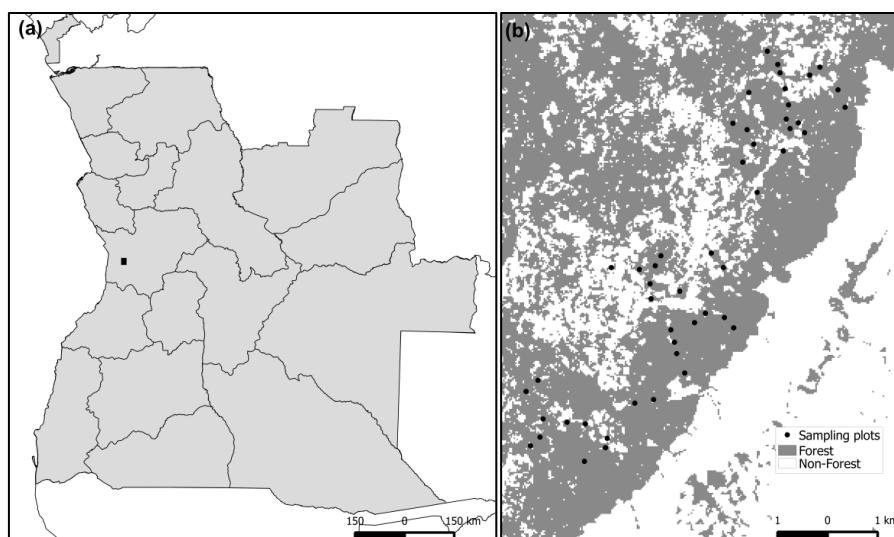
The end of the war produced a renewed interest in the biodiversity of the country (Pitra et al., 2006, Mills and Dean, 2007, Chase and Griffin, 2011), but also a growth of human population in rural areas, drastically increasing the pressure in natural ecosystems. The Scarp Forest was not an exception. Despite almost 95% of the natural forest having been converted to shade coffee plantation during the colonial time (Hawkins, 1993), it is believed that their abandonment due to the war allowed the forest to recover (Sekercioglu and Riley, 2005). Since the end of the war the forest has been rapidly disappearing due slash-and-burn agriculture done by an increasing number of small farmers (Ryan et al., 2004, Mills, 2010, Cáceres et al., 2015)

The main goal of this study was to assess the potential of REDD+ as a tool for the conservation of small forest centres with an endemic-rich biodiversity and to evaluate the practical aspects required for the implementation of such strategy. In order to achieve this, we chose a real study system combining different aspects of this problematic: poorly documented but endemic-rich small forests. The chosen study system was Kumbira Forest that is considered the largest known forest remnant and most representative area of the Central Angolan Scarp and holds significant populations of the threatened endemic bird species (Sekercioglu and Riley, 2005, Mills, 2010, Cáceres et al., 2015). In order to achieve the main goal, we: (i) assessed forest cover change and deforestation rates from 1999, 2001 and 2014 in Kumbira forest; (ii) we estimated aboveground carbon stocks through biomass calculation and used these results to (iii) provide recommendations to maximize emissions reduction and conservation potential of the Angolan Escarpment Forest and; (iv) propose the best avenues for using REDD+ in similar situations.

## Methods

### Study Area

Fieldwork was done from June 4<sup>th</sup> to 22<sup>nd</sup>, 2014, in Kumbira Forest. This forest is located in the western Angolan province of Cuanza Sul, municipality of Conda (Fig.1a). The eastern limit of the forest is defined by the grasslands of Njelo Mountain, while the western limits are difficult to define because the forest blends with other dense habitats present in the Scarp. For the purpose of this study, the study site was defined to comprise all forest between the Njelo Mountain range in the east, with the northern limit set at Cassungo village (11.104°S 14.311°E) and the southern limit at 11.230°S 14.250°E (Fig. 1b), as in Cáceres et al. (2015). Within this area, the elevation varies from 250 m in the western margins to 1,160 m at the forest limit closest to the Njelo Mountain.



**Fig. 1 (a)** Location of Kumbira Forest (black square) in Kwanza Sul province of Angola and **(b)** Sampling plots (black circles) in the study site.

### Forest cover change and deforestation rates

Landsat scenes from 1991, 2001 and 2014 were used to assess trends in forest cover across the study area. These scenes were obtained from the Earth Resources Observation & Science Center of the U.S. Geological Survey (USGS) via the EarthExplorer interface (<http://earthexplorer.usgs.gov>, accessed 14 May 2014) and from the data server of the Global Land Cover Facility (<http://glcf.umd.edu/>, accessed 8 October 2014) of the University of Maryland (Supporting Information Table S1). The scenes were atmospherically corrected using dark-object subtraction (Chavez, 1996) and radiometric normalized using the Pseudo Invariant Features method (PIFs) (Schott et al., 1988, El Hajj et al., 2008).

A supervised classification was performed using the Maximum Likelihood Algorithm (MLA). Training and validation data were visually selected across the satellite scene using high-resolution imagery from Google Earth and field data. The scenes were classified into “Forest” and “Non-forest” classes. “Forest” was defined as areas where tree crowns covered more than 10% of the ground and where trees had a minimum height of 5 m, as described by FAO (2001). This can include forests with human intervention such as shade coffee plantations. The classification accuracy was verified through overall accuracy (OA), confusion matrix (Pontius et al., 2004) and Kappa coefficient (K) (Congalton, 1991). All training and validation samples were tested with Jeffries–Matusita distance (Trigg and Flasse, 2001). All analyses were done in ENVI 4.7 (Exelis Visual Information Solutions, Boulder, Colorado).

Forest change for each period (1991-2001 and 2001-2014) was obtained by post-classification change detection distinguishing between later forest cover and

earlier forest cover. This technique is the most accurate in forest change detection with Landsat data (Huang et al., 2009). The annual rate of deforestation was calculated with Puyravaud (2003) equation.

### **Estimation of aboveground carbon stocks**

Aboveground carbon stocks represent the main carbon pool in tropical forests and are the most susceptible to deforestation and degradation (Nascimento and Laurance, 2002, Gibbs et al., 2007, Houghton, 2007). Moreover, unlike other carbon components, they can be estimated using cost-effective protocols (Berenguer et al., 2015).

Sampling plots were selected a priori considering the supervised classification map of 2014 and sampling was done only within “Forest” areas, because “Non-Forest” areas present low amounts or no amounts of biomass. In order to minimize the influence of edge effects, all sites were established considering a 50 m buffer distance to previously established trails.

In each sampling plot, a 10x10 m square plot was established and within it the diameter at breast height (DBH) and tree height was collected for all trees with a DBH > 5 cm. DBH was measured using a measuring tape or a calliper (trees < 10 cm). The tree height was measured with a clinometer (when the tree < 10 m) or a Nikon 550 Laser (Nikon Corporation, Tokyo) rangefinder (when the tree > 10 m).

Aboveground biomass (AGB) was calculated using the pantropical allometric equation proposed by Chave et al. (2014). This equation relates the AGB of a tree to its DBH, total height, and wood density. It was not possible to identify the species of trees and therefore obtain specific wood densities. Therefore, we applied an average wood density of 0.59 g/cm<sup>3</sup> corresponding to the values reported for trees in Africa (Henry et al., 2010). Biomass estimates were converted to carbon values using the fraction of 0.47, as recommended for tropical and subtropical regions (Paustian et al., 2006) and standardized per area (MgC/ha).

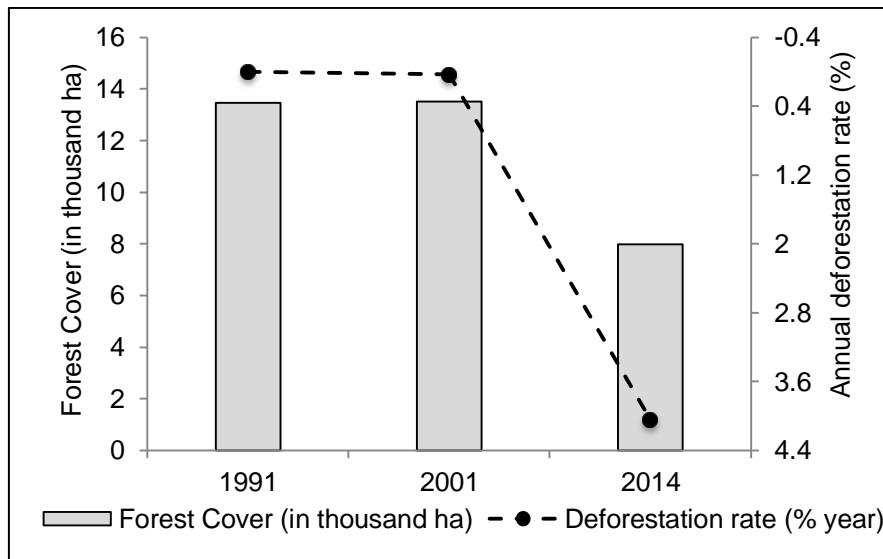
## **Results**

### **Forest cover change and deforestation rates**

The accuracy assessment of the MLA classification indicated that accurate Forest/Non-forest maps were obtained for the years 1991, 2001 and 2014 (Supporting Information Table S2). During the first 10 years (1991-2001) of the analysis, forest cover remained constant with a deforestation rate of -0.03%. In contrast, almost 41% of the forest was



lost in the following 13 years (2001-2014) giving a mean deforestation rate of 4.04% per year (Fig. 2 and Table 1).



**Fig. 2** Forest cover and deforestation rates (%) for the years 1991, 2001 and 2014 in Kumbira. The very slight increase of forest area between 1991 and 2001 was followed by a considerable decrease for the period 2001-2014.

**Table 1.** Forest cover changes in Kumbira for the 1991-2001 and 2001-2014 periods.

Year	Class	Area (ha)	Area (%)	Deforestation rate (% per year)
1991	Forest	13466.52	39.2	
	Non-forest	20893.68	60.8	
2001	Forest	13501.53	39.3	
	Non-forest	20858.67	60.7	
2014	Forest	7988.85	23.3	
	Non-forest	26371.35	76.7	
Change 1991-2001	Forest	35.01	0.26	-0.03
Change 2001-2014	Forest	-5512.68	-40,8	4.04

### Estimation of aboveground carbon stocks

A total of 496 trees were recorded across 49 sampling plots. The average AGC per plot was 89.4 Mg/ha (SD = 126.4) with a minimum value of 0.7 Mg/ha and a maximum of 737.1 Mg/ha (Supporting Information Table S3). Considering a forest area of ~80 km<sup>2</sup> (corresponding to the 7988.85 ha of forest present in 2014, Table 1), the total aboveground carbon pool present in Kumbira forest was on ~714200 MgC.

## Discussion

This study documents levels of unprecedented forest loss that, if not reversed immediately, can lead to the disappearance of most of the Angolan Escarpment Forest in the upcoming decades. Our aim of investigating the potential and modes of using the REDD+ program for the conservation of small endemic centres gained therefore a particular pertinence.

Changes in forest cover in Kumbira are in close agreement with the human demographic changes associated with the war, a large depopulation of Angola rural regions during the war followed by a major return when peace was signed to the rural areas by the mid-00's (USAID, 2008). During the last decade of the war (1991-2001) no significant changes in forest cover were detected, corroborating a lack of any major anthropogenic impact at that time. This changed in peace time when the estimated annual deforestation rate for Kumbira was of 4.04%.

In order to get a better understanding of what a 4% annual deforestation rate may represent in terms of the scale of anthropogenic impact, it is worthwhile comparing it with other estimates for Angola. Such comparisons should not be taken at face value since different studies use different scales. Still, it is noticeable that from 2000 to 2005, a period covering the first three post-war years, the estimated mean rate of forest loss for the Angolan Scarp ecoregion was of 0.42% (Buchanan et al., 2011). This study did cover a much larger area and used a larger grid, but the 10 times difference remains striking. The current deforestation rate for Kumbira is also much higher than the latest national deforestation rate estimate of 0.21% (FAO, 2010). This highlights how national and regional estimates are of little use to inform site-specific strategies, since they can mask realities on the ground (Phelps et al., 2010a). A country with such a diverse array of landscapes (from deserts to rainforests) will necessarily have a large variation in habitat conversion rates in general, and deforestation rates in particular. Deforestation in Kumbira shows no signs of slowing down and, if anything, it is actually increasing as illegal logging has recently joined slash-and-burn agriculture in the clearing of the forests (Cáceres et al., 2015).

Despite the recognized small size of our plots that may have underestimated stem density and biomass, we found an average aboveground carbon for Kumbira close to the range values (118 – 202 Mg/ha) found in the most recent studies conducted on REDD+ target countries in Central Africa (Lewis et al., 2009, Nasi et al., 2009, Saatchi et al., 2011, Baccini et al., 2012). Nevertheless, we have to consider that the aboveground carbon stocks in the Scarp forests located in the north of Kwanza River are probably higher due their stronger affinities with the vegetation-types from the

Guinea-Congo forest. Furthermore, this study did not include specific values of wood density because the identification of tree species was not possible. Ignoring the variation of wood density among species can introduce bias in the overall estimates of aboveground biomass (Baker et al., 2004, Muller-Landau, 2004, Henry et al., 2010, Fayolle et al., 2013, Chave et al., 2014). On the other hand, some researchers argue that there is little evidence of species-specific allometric relationships (Malhi et al., 2006, Gibbs et al., 2007) and that there might not be a general relationship between forest biomass and wood density (Stegen et al., 2009).

The Angolan Scarp illustrates clearly how threatened biologically-rich small forests are easily overlooked by the large-scale REDD+ models even if they present valuable carbon stocks. Sites should be prioritised based on their known or assumed biological value and/or on evidence suggesting large human impacts – like the conversion of miombo woodland to charcoal (Cabral et al., 2011). In the event of future REDD+ projects being implemented in the region, the allocation of REDD+ funds should prioritize the delimitation and management of a protected area to conserve the remaining old-growth forest located at the higher slopes of the Scarp, less accessible and less suitable for agriculture activities. The maintenance of a reserve offers the possibility to increase the production of live tree biomass, while still offering habitat that is suitable for a significant number of endemic species (Gilroy et al., 2014, Magnago et al., 2015).

Conservation planning is often focused on protected areas, but REDD+ should also pay attention and provide incentives for the sustainable use of the landscapes surrounding conservation areas. Shaded agroforestry systems provide refuge for several animal groups (Bhagwat et al., 2008) and also have high potential to sequester carbon (Nair et al., 2009). In addition, shaded systems can reduce land-use pressure on conservation areas while enhancing rural livelihoods. It has been estimated that by 1970s up to 95% of the Angolan Scarp Forest was converted into shade coffee plantations by the Portuguese settlers (Hawkins, 1993). After the independence and during the war, most of the plantations were abandoned (Hawkins, 1993). REDD+ is a potential finance mechanism that could provide incentives for the rehabilitation of these shaded plantations, turning the current land use scheme of slash-and-burn agriculture into an agro-forestry system based on the recovery of the shade coffee plantations. Retaining canopy cover and tree diversity on coffee farming contributes for increasing carbon storage and has repeatedly been shown to be beneficial for biodiversity (Bhagwat et al., 2008, Clough et al., 2011, Caudill et al., 2014). For example, shade coffee plantations provide suitable habitat for Andean primate populations (Guzmán et al., 2016), for forest specialist birds in Ethiopia, as well as insectivores (Buechley et al.,

2015) nectarivores and frugivores (Sekercioglu, 2012), which can in turn benefit crop production.

Coffee production may provide a viable economic alternative for the local communities of the Scarp if a traditional coffee agroforestry model is implemented. Such system is based on small scale, community-based, farmers that come together in cooperatives or associations with links to international certification systems (e.g. organic, fair trade, biodiversity and/or livelihood-friendly) (De Beenhouwer et al., 2013, Jha et al., 2014). This allows smallholders to retain land titles, to access more easily credit and technical support and to sell their coffee at higher prices, which is essential to create resilience to the fluctuations of the coffee market worldwide, and to social and environmental changes (Bacon, 2010, Jha et al., 2014). Still, a key problem is that during the first years of recovering the coffee plantations, the returns from coffee exportation may not be sufficient to cover the costs. Additionally, market fluctuations and an increasing demand for coffee may lead farmers to intensify traditional agroforestry systems and expand the cultivated area, which will then decrease the benefits for biodiversity (DeFries et al., 2010). It is here that the REDD+ framework could step-in and meet its mission of climate change mitigation through the reduction of deforestation and forest degradation while enhancing both rural livelihoods and biodiversity. This would be done by directing REDD+ funds to support programmes aiming at training farmers in both shade coffee production and in the implementation and running of cooperatives able to ensure the economic viability of such projects.

REDD+ is a program with the clear aim of reducing emissions at a minimum cost, while also contributing to sustainable development. Nevertheless, its implementation has been hindered by its current contradictions of being a market-based mechanism. Paying for “ecosystem services” presupposes that the payment value will cover not only the opportunity costs of the extraction but also the revenue gained through externalization of the extractive markets. This has been deemed “untenable” for an offset market as REED+ that depends on voluntary contributions (Fletcher et al., 2016). In order to make REDD+ relevant, the priority should be to move it away from market-based mechanisms through the relocation of the forests resources under local control (Phelps et al., 2010b, Fletcher et al., 2016). Also, from a financial point of view it must be understood that an approach that was good in one situation is not necessarily replicable in other (Redford et al., 2013). Each project needs to be adapted to specific issues including the region scale, past and current features of forest dynamics and the governance context of the country.

This study demonstrates that it may be possible to co-opt REDD+, devised for very large forest extensions, for the conservation of small but extremely important

forests from a biodiversity perspective. This will require a paradigm shift within the REDD+ program, moving away from purely market-based mechanisms towards local capacity building programmes. In the case of the unique but highly threatened Angolan Scarp Forest, REDD+ funds could be used both to fund the creation of a protected area in the best forest remnants and in promoting the development of agro-forestry strategies that are able to address human development while creating the conditions for the maintenance of the Scarp biota and its evolutionary potential. Shade coffee plantations appear as the best candidate for a conservation-friendly agriculture. Interestingly, in the case of the Angolan Scarp, such system had already been implemented successfully in the past for purely economic reasons – making it much easier to test the potential for its recovery.

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## Supporting Information

**Table S1.** Satellite data used to analyse trends in forest cover across Kumbira Forest, Angola.

Sensor	Acquisition date	Source
LANDSAT 5TM	07-06-1991	GLCF
LANDSAT 7ETM+	30-09-2001	USGS
LANDSAT 8 OLI-TIRS	02-03-2014	USGS

**Table S2.** Results of the habitat classification accuracy assessment for 1991, 2001 and 2014 in Kumbira, Angola. OA=Overall Accuracy and K= Kappa coefficient.

Year	Class	Omission error (%)	Commission error (%)	
1991	Forest	1.9	1.9	OA= 98.2% K = 0.9673
	Non-forest	1.69	0	
2001	Forest	0	3.6	OA = 97.9% K = 0.9573
	Non-forest	4.73	1.69	
2014	Forest	3.92	0	OA= 97.5% K = 0.9483
	Non-forest	0	6.15	

**Table S3.** Number of trees (N° trees), mean diameter-at-breast height (DBH), mean tree height, aboveground biomass (AGB) and aboveground carbon (AGC) for each sampling plot.

ID plot	N° trees	DBH (cm)	tree height (m)	AGB (Mg/ha)	AGC (Mg/ha)
L23	35	7.6	8.1	62.30	29.28
L24	15	12.6	8.3	323.75	152.62
L26	8	9.1	7.1	18.91	8.89
L28	10	12.4	5.9	36.96	17.37
L29	19	10.3	8.3	83.29	39.15
L30	6	35.4	16.1	568.34	267.12
L37	11	19.5	16.5	318.10	149.51
L38	19	6.4	5.4	15.68	7.37
L39	8	15.9	8.8	189.56	89.09
L42	7	10.3	6.0	494.01	232.19
L41	1	6.9	6.7	2.25	1.06
L51	6	17.1	12.9	84.69	39.80
M11	3	45.3	13.8	594.77	279.54
M12	7	13.8	10.9	101.98	47.93
M13	8	12.6	9.8	144.65	67.98
M14	8	15.2	7.3	264.38	124.26
M15	16	7.6	7.5	23.31	10.95
M16	17	14.3	12.1	594.86	279.58
M17	7	17.1	6.5	160.63	75.50
M18	11	10.3	5.0	35.68	16.77
M19	2	28.3	20.1	122.67	57.65
M20	12	11.7	6.4	136.92	64.35
M21	6	8.5	5.1	10.95	5.15
M43	7	11.8	12.1	69.34	32.59
M44	20	7.8	5.5	28.38	13.34
M45	4	51.5	15.8	1568.18	737.04
M46	3	5.6	4.2	1.44	0.68
M47	12	10.2	8.5	61.43	28.87
M48	10	12.9	9.5	118.33	55.61
M49	2	52.1	14.3	626.96	294.67
M50	9	7.6	5.3	10.07	4.73
M52	25	7.9	7.8	45.72	21.49
M54	7	6.9	6.5	8.90	4.18
H01	18	11.5	9.4	137.29	64.53
H02	7	19.6	12.4	336.69	158.24
H03	12	14.2	10.3	255.17	119.93
H04	4	11.8	6.8	16.15	7.59
H05	5	10.0	6.3	15.17	7.13
H06	7	20.6	10.7	200.52	94.24
H07	13	10.5	11.0	77.38	36.37
H08	11	15.0	8.9	297.31	139.74
H09	9	13.2	8.9	92.84	43.63
H31	4	19.8	11.3	177.32	83.34
H32	6	15.1	10.8	88.86	41.76
H33	2	39.4	17.8	525.41	246.94
H34	6	9.4	6.6	22.41	10.53
H35	32	7.8	8.1	69.88	32.84
H36	9	9.8	7.6	45.43	21.35
H53	10	9.8	5.5	31.76	14.93

## **Chapter 6**

### **General Discussion**

## 6.1. Land-use changes and bird diversity in Kumbira forest

Kumbira Forest is a very fragmented and dynamic landscape. In the 1970s up to 95% of the Escarpment Forest was already transformed to shade coffee plantations (Hawkins, 1993), with Kumbira included, as shown by all the abandoned infrastructures – hospital, school, houses, factory, stores, etc. – of the CADA Amboim (“Companhia Angolana de Agricultura” – Angolan Company of Agriculture) present in the area (Fig.1). In these plantations, the understorey vegetation was cleared and replaced by coffee plants, especially robusta coffee (*Coffea canephora*) while the original forest canopy was maintained in order to provide shade for the coffee plants (Grandvaux-Barbosa, 1970). Some exotic trees species were also introduced to produce shade for the coffee, such as *Grevillea robusta* and *Inga vera* (Fig. 2).



**Fig. 1** (a) Abandoned hospital and (b) workers' houses near Tchilumbo village. All these infrastructures belonged to the Angolan Company of Agriculture in Amboim (CADA Amboim) – photos taken by A. Estrelinha and M. Mills respectively



**Fig. 2** Coffee plantation shaded with *Grevillea robusta* trees – photo taken by A. Estrelinha

During the war (1974 – 2002) these plantations were abandoned and the understorey vegetation regenerated, which probably benefited the birds. However, with the end of the war, slash-and-burn agriculture became the major economic activity. The canopy trees are logged and the understorey vegetation is completely cleared and burned to give way to sun loving crops such as sweet potato, tomato, cassava and maize. This

farming is disorganized, with farm plots scattered all over the area – next to secondary growth, scrubs or even in the middle of the forest – which creates a mosaic-like landscape. This is in part related with the land tenure. The land is given in concessions of 5 – 30 years to private owners. Most of the land is divided in large properties belonging to owners who usually live in the cities (Luanda, Sumbe, Gabela, etc.). The remaining land belongs to the local community, but is not enough for everyone. Therefore, local people have to make an agreement with the large states' landlords to cultivate in their lands in exchange for a percentage of the production; alternatively they resort to maintaining unauthorised farm plots “hidden” in the middle of the forest.

The forest seems to have been maintained in the past two decades in Kumbira, when, in fact, what happened was a replacement of old-growth forest by secondary forest. While in areas close to human settlements forest cover has clearly decreased, the overall forest cover from 1989 to 2010 has increased in 15.4% (Chapter 2; Fig, S1). However, old-growth forest stands (present since 1989) covered only 30.8% of the area in 2010, which represents a drastic decrease of 45.5% of old-growth forest since 1989 (Chapter 2). Using the equation of Puyravaud (2003), returned an annual deforestation rate of 2.89%, which is quite high when compared with annual rates for West Africa of 1.09% (1990 – 2000) and 0.35% (2000 – 2010) (Mayaux et al., 2013). This value increases with the forest change and deforestation rate analysis done in Chapter 5, where the estimated annual deforestation rate from 2001 to 2014 for Kumbira was of 4.04%. This represented a forest loss of 41% in 13 years. This 4% rate is 10 times higher than deforestation rates estimations for the Angolan Scarp ecoregion (Buchanan et al., 2011) and 20 times higher relatively to the national estimates (FAO, 2010). The different estimates of deforestation rates obtained here likely reflect the different study scales used: 2500 ha on chapter 2 and 35000 ha on chapter 5. When the analysis of Chapter 5 is restricted to a smaller area (10000 ha), the estimate of the annual deforestation rate falls to 1.58%. The methods used to classify the Landsat scenes (unsupervised ISOCLUST classification in Chapter 2 and supervised classification with Maximum Likelihood Algorithm in Chapter 5) may have also contributed to the discrepancy between estimates. This clearly illustrates the difficulties of obtaining precise deforestation rates. Independently of the exact deforestation values, the reality is that the forests in Kumbira are disappearing at rates that are very high when compared with other regional or national values, and may even be deemed ‘catastrophic’ if they are close to the 4% deforestation rate .

These comparisons highlight how national and regional deforestation estimates will often miss small, but biologically rich and unique, areas at risk of disappearing due to excessive forest loss, as is the case of Kumbira. The scale of forest loss was directly



observed during the four years of this study, when many forest areas were completely cleared between visits. The remaining old-growth forest stands ( $\geq 22$  years old) are now mainly restricted to the areas closer to Njelo Mountain, and possibly were not transformed during the colonial times as a way to protect water catchments. Nowadays, these forest areas might be spared from slash-and-burn agriculture due their difficult access together with steep slopes inappropriate for agriculture.

Secondary and old-growth forests often hold similar bird diversity when compared with more disturbed land-uses, such as agricultural lands and clearings. Nevertheless, the bird community composition can differ greatly between secondary and natural forest, with a decrease of insectivores and forest specialists in the latter (Barlow et al., 2007b, Norris et al., 2010). This was not the case in this study, where bird species richness and community composition were similar in both forested habitats. This could be explained by their similar canopy and understorey structure (Chapter 2; Fig. 3). The capacity of secondary forest to maintain a similar bird community may depend on the surrounding matrix. Secondary forest can maintain forest specialists if natural forest patches occur nearby. These species will use secondary forest but continue to depend on the natural forest patches (Harris and Primm, 2004, Sodhi et al., 2005, Norris et al., 2010). This is likely to be happening in the mosaic-like landscape of Kumbira. For example, Gabela Bushshrike was registered in 2013 in an area of secondary forest (abandoned shade coffee plantation) surrounded by agricultural plots but connected to old-growth forest closer to the Njelo Mountain. In 2014, the species was registered calling from the old-growth forest but not present in the secondary forest that was being cleared. By 2015, Gabela Bushshrike was no longer registered in the old-growth forest that was being heavily slashed-and-burned.

The threatened endangered endemic bird species – Gabela Akalat and Gabela Bushshrike (Fig. 3) – were only registered in forested habitats, with Gabela Bushshrike mainly present in old-growth forest. These endemics are critically important because they are restricted to the Escarpment Forest. The Gabela Akalat in particular is the most range-restricted endemic bird of Angola (Mills, 2010), whereas the Gabela Bushshrike has a wider range and has been registered in other areas south and north of the Central Escarpment Forest.

A more detailed study of the Gabela Akalat (through radio-tracking) showed that this species can use forest, secondary growth and agricultural lands while consistently avoids open areas. This species seems capable to use these disturbed habitats and to persist in the fragmented landscape of Kumbira, similar to other Endangered endemic birds in Africa (Reif et al., 2007). However, these preferences might be influenced by

the matrix context, mainly old-growth forest patches in the surroundings. Furthermore, it would be interesting to know up to what degree of fragmentation can be tolerated by this species and if it is capable of successfully breeding in these disturbed habitats.

Gabela Akalat has a home-range size slightly larger ( $MCP\ 95 = 4.3 \pm 4.2\ ha$ ) than territory sizes for other *Sheppardia* species which had been described in 0.5 – 3 ha/pair (Keith et al., 1992). Previous population estimations done for Gabela Akalat considered the territory sizes for other *Sheppardia* species and different amounts of suitable habitat, obtaining a population size of 21 800 – 26 000 individuals (Sekercioglu and Riley, 2005, Mills, 2010). Considering a territory of 4.3 ha/pair (in order to account for the overlapping of home-ranges of several birds in this study) and the same amounts of suitable habitat used in previous studies we obtain a population size of 3023 – 15209 individuals, which is considerably lower.

However, home-range sizes were obtained during the non-breeding season, when birds have not yet established their breeding territories and are more tolerant to congeners (as shown by the overlapping of home-ranges). Breeding birds are expected to become more concentrated around the nest and consequently will have smaller territories which can translate in higher population estimates.



**Fig. 3** (a) Gabela Akalat *Sheppardia gabela* and (b) Gabela Bushshrike *Laniarius amboimensis*– photos taken by F. Olmos

It was reassuring to see that secondary forest was able to maintain a similar bird community to that of old-growth forest; especially because the remote sensing analysis showed that this forest is being cleared and eventually replaced by secondary forest. Nevertheless, it remains uncertain if this bird community could be sustained in secondary forest in the absence of old-growth forest nearby. This forest, where all Endangered endemics occur, should therefore continue to be treated as the key habitat for the conservation of the forest-restricted species. It is widely acknowledged that these forests are irreplaceable for conserving tropical biodiversity (Barlow et al., 2007a, Barlow et al., 2010, Gibson et al., 2011), especially for range-restricted species with

high conservation value such as threatened endemics (Fjeldså, 1999, Waltert et al., 2005).

Evaluating the real capacity of secondary forests to hold the original forest biodiversity will always be limited due to the shifting baselines of many tropical areas that present a history of human disturbance. In these areas, due to the historic disturbance, the original biodiversity have already changed, presenting a new baseline for biodiversity and therefore for any comparison produced with the biodiversity present in the area due contemporary human disturbance. This is the case of Kumbira, where most of the forest was transformed to shade coffee plantations since 1930 (Gossweiler and Mendonça, 1939). It is possible that this perturbation changed the original forest biodiversity, producing a new baseline, meaning that the most sensitive species may already have been lost from the best forests and creating an adapted community dependant in forest cover as shown by this study. Data from really undisturbed areas are extremely important to guide conservation planning and management (Gardner et al., 2009). However, it is a major challenge to obtain such data, especially in areas, like Kumbira, that present a history of human disturbance, and in a country like Angola where no research was done for several years.

## 6.2. Conservation Implications

Here I use my data, the wider literature and my personal experiences of the region to outline four methods that could be used to meet both conservation and development aims in the region.

1. *Development of a protected area network.* Despite its high biodiversity importance and major threats, no area of the Angolan Escarpment Forest enjoys any type of protection. Proposals to establish a c. 50 km<sup>2</sup> nature reserve within the Escarpment Forest have been done since the 1970s (Huntley, 1974, Sekercioglu and Riley, 2005, Mills, 2010). Unfortunately, none of them have been implemented yet. A nature reserve in Kumbira should focus in protecting the last remnants of natural forest, especially the areas of more intact forest near the Njelo Mountain. Other areas should be assessed and considered for protection too, such as the forest of Bango-Seles 25 km south from Kumbira. The nature reserves should not only be created in the legislation but active law enforcement should be implemented to protect the forest from human activities, especially slash-and-burn agriculture and logging. Furthermore, for the nature reserves to successfully protect the forest, the economic needs of the local population have to be fulfilled. In this case, the reserves could be developed to attract ecotourists and to

capture funding for forest conservation, such as REDD+. It has been presented that a REDD+ initiatives could be used to fund the creation and maintenance of a natural reserve, if focused in the development of local capacities.

2. *More effective land-sharing.* Land-sharing is a strategy to minimize the impact of agriculture on biodiversity that involves joining biodiversity conservation and agriculture production by using wildlife-friendly methods (Green et al., 2005, Phalan et al., 2011). The recovery of the shade coffee plantations would maintain forest cover while producing an income from agriculture for the local population. Shade coffee plantations are capable of supporting a similar bird diversity to natural forest (Buechley et al., 2015), especially if the natural canopy is maintained (Waltert et al., 2004). Between 1945 and 1960 Angola was the first coffee producer of Africa and the third of the world (Wheeler and Pélissier, 2009). The Escarpment Forest has ideal conditions for cultivating Robusta coffee (*Coffea canephora*), and the particular environmental conditions of the Central Escarpment Forest allow the production of a very appreciated variety of coffee, known as the “Amboim coffee” (Gossweiler and Mendonça, 1939).

The main reason for the abandonment of these plantations was the war. Nowadays, the low coffee prices and the high production costs do not make this crop economically attractive for farmers and most of the berries are left to rot in the abandoned plantations. However, with the recent decrease of oil prices and the devaluation of the national currency, coffee farming seems to be becoming profitable. A strategy of producing high quality certified organic and biodiversity-friendly coffee would contribute towards making this a profitable activity. The economic viability of coffee production in Kumbira should therefore be assessed, as this activity promotes the maintenance of the remaining natural forest canopy, reversing the current trend towards more open land-uses such brought about by slash-and-burn agriculture (Gove et al., 2008).

Other agroforestry systems could be implemented to replace slash-and-burn agriculture, such as alley cropping that has been used successfully in Latin America to stop farmers from clearing new areas of forest (Hands et al., 2012). It will always be crucial to assess the capacity of alternative agroforestry systems and shaded plantations to maintain bird diversity, and especially the threatened endemic species, before defining an agro-forestry strategy for the area.

3. *Agricultural development to allow land-sparing.* Land-sparing consists in separating land for agriculture from land for biodiversity conservation. Crop production is intensified and maximized in the agricultural lands while conservation lands are

protected from any further agricultural expansion (Balmford et al., 2005, Phalan et al., 2011). In this particular case, more effective agricultural practices should be adopted for the production of subsistence crops. Research and agricultural assistance is needed to assess whether slash-and-burn of natural forest could be replaced by the more efficient and intensive use of existing farm plots, therefore avoiding further deforestation. However, land-sparing presents a major pitfall related with land tenure and government decisions, especially in developing countries, where agricultural expansion might overcome the need for conserving biodiversity.

4. *Enhancing the value of forests for local people.* Agricultural change needs to be accompanied by programmes aiming to recover forest cover in degraded areas. This action could be implemented together with the local community by establishing a native tree species nursery for a future reforestation project. Such an action would address two important issues in the conservation strategy: (i) the increase of forest cover with native tree species (especially those which have important uses for local communities) and (ii) generate employment for the local community. At the moment, an experimental nursery has been established in Kumbira, as part of a project funded by the Conservation Leadership Programme. In this nursery, we are assessing if native tree species can successfully grow in a controlled environment and we are also training people of the local community as nursery keepers. All this is done with the objective of starting a reforestation project in the near future.

### **6.3. Future Work**

The major contribution of this thesis was to generate data on bird diversity and ecology for Angola, a high biodiverse and understudied country. In particular, this thesis has studied the forest cover dynamics in the last 20 years of a representative area of the Escarpment Forest, one of the most important regions for biodiversity in the country. It has also produced information about the home-range size and habitat preferences of the endangered and understudied Gabela Akalat, the most range-restricted endemic of Angola. Finally, it has assessed the potential of REDD+ to be used as a conservation strategy for this forest. The integration of this information provides a solid base for designing conservation actions. However, the real work is going to start now, by making sure that conservation measures required to achieve the protection of the Escarpment Forest are implemented, together with further research needed to continue filling the knowledge gap in Angola.

The effect of the mosaic-like landscape of Kumbira should be included in future biodiversity research. It will be important to assess if the trends are maintained when the effect of fragmentation, connectivity and the size of natural forest patches are included. Despite suspecting that matrix effects are present, the data failed to prove this effect, probably because the experimental design was not done to deal with such a fragmented landscape.

Further ecological information should be collected for other forest-restricted species, and especially the other threatened endemics. In the case of Gabela Bushshrike, a pilot radio-tracking study was done with two individuals of this species. However, they were very difficult to capture and follow. Maybe this kind of study could be implemented using more advanced technology (GPS tracking) or in other areas where the species is more abundant. A similar approach should be considered for the Pulitzer Longbill and the Monteiro Bushshrike that had a very low detectability in the study site (<7% sample points). Moreover, other potential areas should be more extensively assessed for the presence of endemics, such as the forests in Bango-Seles. For instance, species distribution models could be used to predict other areas where Gabela Akalat and other endemics might be present. In addition, other areas of the Escarpment Forest should be evaluated, like the Northern and Southern Escarpment that hold different bird communities.

From a REDD+ perspective, the Northern Escarpment should also be considered to calculate carbon reserves. The estimations obtained in this thesis are from the small forest of Kumbira in the Central Angolan Escarpment. The tall gallery forests of Uíge, in the Northern Escarpment, which present affinities with the Guineo-Congo Forest are likely to hold higher carbon reserves and, hence, help make a stronger case for a REDD+ programme for the Angolan Escarpment Forest.

Research should also be extended to other taxa – such as plants, insects, amphibians – that might be more sensitive to human disturbance and may have different responses relatively to the birds (Kremen et al., 2008).

## **6.4. Improving research and the ecological knowledge base in Angola**

There is still a lot of research to be done in Angola, and not only related with birds of the Escarpment Forest as very little is known about other areas and taxa. Yet there are many difficulties of working in Angola – I outline these below and highlight some potential solutions as a guide to future research initiatives.

Angola is a very expensive country. Its capital, Luanda, is the city with the highest cost of living for expatriates (Mercer, 2015). Furthermore, the lack of infrastructures and services produces high prices for low quality services. For example, the budget for my first one month fieldtrip to Angola in 2012 was equivalent to the same amount of money I used for a one year project in the Peruvian Amazon, which included three fieldtrips of one month for three researchers. It is expected that with the developing of infrastructures and the diversification of the economy this situation will improve in the following years. However, at the moment, Angola is in a major economic crisis. The decrease of oil prices had led to a drastic devaluation of the national currency (kwanza) and restraint of the importation of products because of the lack of foreign currency. The prices for basic products (fuel, food, medicines, water, etc.) have doubled or tripled in the last year. Even if such situation may be deemed advantageous for organisations holding foreign currency, it seriously curtails the prospects of in-country conservation projects or initiatives, dependent on national currency. This is particularly problematic, as such in-country project, led by Angolans, are the ones expected to be sustainable and produced long-term benefits.

Another major challenge is the limited local capacity for ecological research. There are few Angolan specialists in different taxa. All of them are working to improve the biodiversity knowledge of their country, but their efforts are not sufficient to cover a very large and diverse country where no research has been done for c. 30 years. Furthermore, there are few students interested in biodiversity conservation and also a lack of post-graduate courses that could allow students to develop their capacities in this area. This can be addressed with partnerships between Angolan and international organizations to implement national capacity building through joint research projects and post-graduate education with clear career lines. Some partnerships already exist, such as the scientific protocol between the Angolan Instituto Superior de Ciências da Educação de Huíla (ISCED-Huíla) and the Portuguese Research Center in Biodiversity and Genetic Resources (CIBIO-InBIO); or ISCED-Huíla and the University of Hamburg in Germany. However, further partnerships should be developed, especially including government institutions, such as the Environment Ministry and the Superior Education and Science Ministry.

Due to the limited local capacity, foreign researchers have to travel to the country to build capacity and to assist Angolan colleagues with research projects. However obtaining a visa to Angola can be a very time-consuming bureaucratic process and the visa is usually limited to a 30 days stay. This issue has been successfully addressed with the existing scientific protocols of collaboration with Angolan Institutions who kindly assist foreign researchers with invitation letters so they

can obtain a visa, but it would be useful if this was further advanced by the introduction of longer “visiting researcher” visas and greater support for visiting academics and students.

Another problem that needs to be considered is the land mines. Angola is considered one of the most heavily land mined countries in the world (MAG, 2015). The land mines were laid around villages, water sources and roads, causing that most of their victims would be civilians. The absence of adequate records of the location of land mines has hindered demining efforts, and land mines continue to cause casualties, even 13 years after the war. Consequently, Angola has one of the highest rates of land mine injuries per capita in the world (Human Rights Watch, 1993, Halo Trust, 2015). Land mines were not a problem in the region of this study. However, their existence has to be considered when doing research in other areas, especially in heavily affected provinces, where their presence seriously undermines the viability of most ecological survey techniques. One way to address this problem is to contact demining organizations (e.g., HALO Trust) for information and support when visiting a potential dangerous area.

There are still many obstacles to overcome on the road to improve research and fill the ecological knowledge gap in Angola. The country is recovering from a long-lasting war, and busy reconstructing its infrastructures and improving the basic services. Personally, it has been a great challenge to conduct a PhD project in Angola but at the same time it has been extremely self-rewarding. I have produced information about the highly biodiverse and threatened Angolan Scarp Forest and also ecological knowledge of understudied endemic species. Above all, this information can assist initiatives aiming at conservation these forests and its unique biodiversity, contributing to the race to recover the lost time that the more than 30 years of war stole from this country.

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## Appendix

**Table 1.** Bird point counts done in 2010. Waypoint coordinates (latitude and longitude) and elevations are presented. The date and hour when the bird point count was performed is also included.

Waypoint	Latitude	Longitude	Elevation (m)	Date	Hour
24	-11.1549	14.2969	867	14/09/2010	6:54
25	-11.1558	14.2981	897	14/09/2010	7:16
26	-11.1560	14.2997	912	14/09/2010	7:42
27	-11.1543	14.3005	946	14/09/2010	8:07
28	-11.1536	14.3017	956	14/09/2010	8:30
29	-11.1524	14.3023	942	14/09/2010	8:50
30	-11.1510	14.3024	951	14/09/2010	9:12
31	-11.1498	14.3019	922	14/09/2010	9:32
32	-11.1484	14.3017	908	14/09/2010	9:53
33	-11.1474	14.3009	878	14/09/2010	10:14
34	-11.1460	14.3013	886	14/09/2010	10:36
42	-11.1536	14.2960	856	15/09/2010	6:53
43	-11.1535	14.2942	883	15/09/2010	7:16
44	-11.1544	14.2932	880	15/09/2010	7:39
45	-11.1545	14.2918	881	15/09/2010	8:01
46	-11.1556	14.2905	879	15/09/2010	8:20
47	-11.1551	14.2887	882	15/09/2010	8:43
48	-11.1561	14.2877	888	15/09/2010	9:03
49	-11.1572	14.2869	898	15/09/2010	9:24
50	-11.1581	14.2859	902	15/09/2010	9:42
51	-11.1593	14.2853	916	15/09/2010	10:00
52	-11.1606	14.2847	890	15/09/2010	10:17
53	-11.1614	14.2836	885	15/09/2010	10:35
54	-11.1632	14.2833	885	15/09/2010	10:56
59	-11.1559	14.2960	877	16/09/2010	7:00
60	-11.1573	14.2961	889	16/09/2010	7:19
61	-11.1582	14.2967	898	16/09/2010	7:38
62	-11.1596	14.2965	900	16/09/2010	7:57
63	-11.1590	14.2954	850	16/09/2010	8:23
64	-11.1580	14.2944	848	16/09/2010	8:46
65	-11.1586	14.2932	848	16/09/2010	9:10
66	-11.1588	14.2918	857	16/09/2010	9:30
67	-11.1597	14.2908	837	16/09/2010	9:49
68	-11.1609	14.2898	830	16/09/2010	10:07
69	-11.1620	14.2891	827	16/09/2010	10:27
84	-11.1534	14.2923	853	17/09/2010	7:01
85	-11.1520	14.2924	857	17/09/2010	7:20
86	-11.1507	14.2926	853	17/09/2010	7:40
87	-11.1493	14.2924	828	17/09/2010	8:01
88	-11.1480	14.2919	822	17/09/2010	8:21
89	-11.1467	14.2916	825	17/09/2010	8:41
90	-11.1462	14.2929	824	17/09/2010	9:03
91	-11.1464	14.2946	860	17/09/2010	9:24
92	-11.1456	14.2958	861	17/09/2010	9:43
93	-11.1464	14.2972	868	17/09/2010	10:02
94	-11.1480	14.2954	859	17/09/2010	10:23
111	-11.1568	14.2897	870	18/09/2010	7:03
112	-11.1573	14.2885	853	18/09/2010	7:22
114	-11.1586	14.2880	819	18/09/2010	7:42
115	-11.1595	14.2871	817	18/09/2010	8:02
121	-11.1558	14.2926	870	18/09/2010	8:54
122	-11.1572	14.2929	847	18/09/2010	9:15
126	-11.1525	14.2970	881	18/09/2010	10:16
127	-11.1522	14.2983	886	18/09/2010	10:38
160	-11.1452	14.2980	845	19/09/2010	6:58

**Table 1 (cont.).** Bird point counts done in 2010. Waypoint coordinates (latitude and longitude) and elevations are presented. The date and hour when the bird point count was performed is also included.

Waypoint	Latitude	Longitude	Elevation (m)	Date	Hour
161	-11.1439	14.2984	835	19/09/2010	7:16
162	-11.1425	14.2983	843	19/09/2010	7:36
163	-11.1415	14.2992	836	19/09/2010	7:57
164	-11.1403	14.2999	868	19/09/2010	8:17
166	-11.1412	14.3011	869	19/09/2010	8:38
167	-11.1420	14.3020	880	19/09/2010	8:57
170	-11.1392	14.2992	861	19/09/2010	9:25
171	-11.1378	14.2990	884	19/09/2010	9:46
172	-11.1367	14.2983	862	19/09/2010	10:05
173	-11.1355	14.2971	869	19/09/2010	10:25
192	-11.1468	14.2987	854	20/09/2010	7:05
193	-11.1454	14.2990	852	20/09/2010	7:28
194	-11.1446	14.3017	861	20/09/2010	8:02
195	-11.1433	14.3013	861	20/09/2010	8:23
199	-11.1444	14.3032	876	20/09/2010	8:50
201	-11.1453	14.3043	914	20/09/2010	9:12
203	-11.1444	14.3051	924	20/09/2010	10:10
204	-11.1458	14.3028	882	20/09/2010	10:42
205	-11.1472	14.3028	907	20/09/2010	11:06
210	-11.1630	14.2880	807	21/09/2010	7:29
211	-11.1642	14.2875	810	21/09/2010	7:47
212	-11.1655	14.2868	810	21/09/2010	8:06
213	-11.1668	14.2867	847	21/09/2010	8:28
214	-11.1680	14.2860	853	21/09/2010	8:47
215	-11.1693	14.2866	834	21/09/2010	9:05
216	-11.1705	14.2860	844	21/09/2010	9:28
217	-11.1714	14.2849	839	21/09/2010	9:47
218	-11.1720	14.2837	822	21/09/2010	10:05
219	-11.1715	14.2824	831	21/09/2010	10:24
220	-11.1719	14.2810	851	21/09/2010	10:44
221	-11.1717	14.2796	838	21/09/2010	11:03
231	-11.1345	14.2981	840	22/09/2010	7:05
234	-11.1349	14.2994	872	22/09/2010	8:08
235	-11.1336	14.2998	867	22/09/2010	8:14
236	-11.1319	14.3001	897	22/09/2010	8:37
237	-11.1309	14.3013	916	22/09/2010	8:50
238	-11.1301	14.3025	940	22/09/2010	9:07
239	-11.1300	14.3040	968	22/09/2010	9:38
240	-11.1282	14.3042	988	22/09/2010	9:51
241	-11.1268	14.3050	999	22/09/2010	10:07
242	-11.1260	14.3064	988	22/09/2010	10:14
243	-11.1245	14.3069	989	22/09/2010	10:34
244	-11.1227	14.3072	999	22/09/2010	10:53
271	-11.1643	14.2824	855	23/09/2010	7:19
272	-11.1649	14.2811	836	23/09/2010	7:37
273	-11.1654	14.2798	845	23/09/2010	7:56
274	-11.1663	14.2788	842	23/09/2010	8:14
275	-11.1677	14.2775	842	23/09/2010	8:35
276	-11.1693	14.2781	832	23/09/2010	8:58
277	-11.1706	14.2777	822	23/09/2010	9:17
278	-11.1724	14.2770	827	23/09/2010	9:39
279	-11.1737	14.2766	819	23/09/2010	9:58
280	-11.1749	14.2760	822	23/09/2010	10:17
290	-11.1330	14.2948	890	25/09/2010	6:55
291	-11.1318	14.2954	870	25/09/2010	7:13

**Table 1 (cont.).** Bird point counts done in 2010. Waypoint coordinates (latitude and longitude) and elevations are presented. The date and hour when the bird point count was performed is also included.

Waypoint	Latitude	Longitude	Elevation (m)	Date	Hour
292	-11.1307	14.2964	851	25/09/2010	7:31
293	-11.1293	14.2971	854	25/09/2010	7:49
294	-11.1278	14.2977	888	25/09/2010	8:09
295	-11.1264	14.2978	894	25/09/2010	8:29
296	-11.1248	14.2984	886	25/09/2010	8:51
297	-11.1241	14.2999	878	25/09/2010	9:13
298	-11.1227	14.3002	894	25/09/2010	9:33
299	-11.1219	14.3016	896	25/09/2010	9:52
300	-11.1210	14.3027	905	25/09/2010	10:10
301	-11.1198	14.3035	911	25/09/2010	10:28
302	-11.1184	14.3044	914	25/09/2010	10:46
308	-11.1171	14.3049	904	26/09/2010	7:00
309	-11.1157	14.3047	914	26/09/2010	7:20
310	-11.1145	14.3054	925	26/09/2010	7:38
311	-11.1132	14.3060	920	26/09/2010	7:58
312	-11.1122	14.3070	945	26/09/2010	8:25
313	-11.1109	14.3072	955	26/09/2010	8:47
314	-11.1097	14.3079	958	26/09/2010	9:06
315	-11.1083	14.3080	984	26/09/2010	9:27
316	-11.1069	14.3084	996	26/09/2010	9:46
317	-11.1057	14.3087	1001	26/09/2010	10:07
318	-11.1058	14.3074	1024	26/09/2010	10:26
325	-11.1444	14.2906	827	27/09/2010	7:02
326	-11.1430	14.2905	827	27/09/2010	7:24
327	-11.1418	14.2897	861	27/09/2010	7:43
328	-11.1420	14.2883	836	27/09/2010	8:02
329	-11.1430	14.2873	830	27/09/2010	8:21
330	-11.1444	14.2863	842	27/09/2010	8:41
331	-11.1448	14.2848	827	27/09/2010	9:02
332	-11.1467	14.2841	820	27/09/2010	9:25
333	-11.1481	14.2839	827	27/09/2010	10:00
334	-11.1485	14.2826	823	27/09/2010	10:17
335	-11.1499	14.2825	826	27/09/2010	10:56
336	-11.1506	14.2811	837	27/09/2010	11:00
345	-11.2110	14.2595	799	28/09/2010	6:50
346	-11.2131	14.2600	812	28/09/2010	7:10
347	-11.2133	14.2585	802	28/09/2010	7:29
348	-11.2136	14.2570	817	28/09/2010	7:46
349	-11.2144	14.2558	852	28/09/2010	8:05
350	-11.2154	14.2549	813	28/09/2010	8:22
351	-11.2167	14.2554	820	28/09/2010	8:39
352	-11.2176	14.2564	821	28/09/2010	8:56
353	-11.2188	14.2568	808	28/09/2010	9:13
354	-11.2201	14.2567	829	28/09/2010	9:31
355	-11.2205	14.2554	828	28/09/2010	9:48
356	-11.2198	14.2543	824	28/09/2010	10:06
357	-11.2193	14.2529	823	28/09/2010	10:25
358	-11.2194	14.2515	803	28/09/2010	10:44
359	-11.2202	14.2504	790	28/09/2010	11:00
360	-11.2220	14.2506	755	28/09/2010	11:19
361	-11.2106	14.2581	800	29/09/2010	6:49
362	-11.2095	14.2570	812	29/09/2010	7:09
363	-11.2089	14.2556	797	29/09/2010	7:27
364	-11.2094	14.2542	823	29/09/2010	7:47
365	-11.2084	14.2533	829	29/09/2010	8:07

**Table 1 (cont.).** Bird point counts done in 2010. Waypoint coordinates (latitude and longitude) and elevations are presented. The date and hour when the bird point count was performed is also included.

Waypoint	Latitude	Longitude	Elevation (m)	Date	Hour
366	-11.2082	14.2519	817	29/09/2010	8:25
367	-11.2076	14.2544	835	29/09/2010	8:44
368	-11.2076	14.2566	823	29/09/2010	9:02
369	-11.2066	14.2576	813	29/09/2010	9:19
370	-11.2056	14.2586	828	29/09/2010	9:36
371	-11.2050	14.2599	833	29/09/2010	9:53
372	-11.2046	14.2633	847	29/09/2010	10:14
373	-11.2046	14.2648	851	29/09/2010	10:30
374	-11.2042	14.2663	867	29/09/2010	10:46
375	-11.2041	14.2677	860	29/09/2010	11:02
376	-11.2040	14.2692	861	29/09/2010	11:34
384	-11.1809	14.2737	812	30/09/2010	6:41
385	-11.1835	14.2719	796	30/09/2010	7:06
386	-11.1848	14.2724	805	30/09/2010	7:23
387	-11.1851	14.2709	820	30/09/2010	7:39
388	-11.1847	14.2696	826	30/09/2010	7:56
389	-11.1883	14.2723	850	30/09/2010	8:18
390	-11.1894	14.2715	850	30/09/2010	8:37
391	-11.1910	14.2710	850	30/09/2010	8:54
392	-11.1923	14.2715	848	30/09/2010	9:11
393	-11.1942	14.2717	856	30/09/2010	9:31
394	-11.1956	14.2718	872	30/09/2010	9:48
395	-11.1969	14.2721	870	30/09/2010	10:07
396	-11.1981	14.2733	887	30/09/2010	10:25
397	-11.1995	14.2736	890	30/09/2010	10:41
398	-11.2003	14.2725	901	30/09/2010	11:01
407	-11.1796	14.2745	798	01/10/2010	6:41
408	-11.1787	14.2733	817	01/10/2010	7:05
409	-11.1796	14.2722	812	01/10/2010	7:24
410	-11.1805	14.2713	829	01/10/2010	7:41
411	-11.1794	14.2705	837	01/10/2010	7:57
412	-11.1784	14.2713	829	01/10/2010	8:15
413	-11.1771	14.2719	827	01/10/2010	8:32
414	-11.1752	14.2725	826	01/10/2010	8:53
415	-11.1729	14.2726	828	01/10/2010	9:13
416	-11.1708	14.2722	819	01/10/2010	9:34
417	-11.1691	14.2720	827	01/10/2010	9:52
418	-11.1670	14.2710	836	01/10/2010	10:11



**Table 2.** Bird point counts done in 2012. Waypoint coordinates (latitude and longitude), elevations and land-use types are presented. The dates and hours when the bird point count (with repetitions) was performed are also included.

Waypoint	Latitude	Longitude	Elevation (m)	Type	Dates	Hours
22M	-11.1573	14.2894	871	Mix	19, 20 and 21 Oct 2012	6:03, 7:15 and 8:20
24F	-11.1568	14.2873	876	Secondary forest	19, 20 and 21 Oct 2012	6:25, 7:40 and 8:48
25SB	-11.1552	14.2884	883	Slash-and-burn	19, 20 and 21 Oct 2012	6:43, 8:00 and 9:06
29F	-11.1536	14.2949	878	Secondary forest	19, 20 and 22 Oct 2012	6:20, 7:30 and 8:35
30SB	-11.1549	14.2946	859	Slash-and-burn	19, 20 and 22 Oct 2012	6:40, 7:13 and 8:17
35F	-11.1488	14.2947	868	Secondary forest	19, 21 and 22 Oct 2012	5:58, 7:45 and 8:30
36M	-11.1461	14.2972	874	Mix	19, 21 and 22 Oct 2012	6:34, 7:06 and 9:07
37SB	-11.1474	14.2961	876	Slash-and-burn	19, 21 and 22 Oct 2012	6:14, 7:25 and 8:47
55F	-11.1475	14.3010	884	Forest	20, 21 and 22 Oct 2012	6:43, 6:59 and 9:28
56F	-11.1486	14.3018	909	Forest	20, 21 and 22 Oct 2012	6:24, 7:16 and 9:07
57F	-11.1500	14.3020	924	Forest	20, 21 and 22 Oct 2012	6:05, 7:32 and 8:34
61M	-11.1802	14.2665	798	Mix	24, 25 and 27 Oct 2012	6:04, 7:53 and 9:12
63M	-11.1829	14.2607	768	Mix	24, 25 and 27 Oct 2012	6:00, 7:18 and 9:06
65F	-11.1818	14.2622	760	Secondary forest	24, 25 and 27 Oct 2012	6:43, 8:02 and 8:41
67SB	-11.1809	14.2603	781	Slash-and-burn	24, 25 and 27 Oct 2012	6:22, 8:02 and 8:41
69SB	-11.1820	14.2703	800	Slash-and-burn	24, 25 and 27 Oct 2012	6:44, 7:19 and 8:36
70F	-11.1814	14.2685	785	Secondary forest	24, 25 and 27 Oct 2012	6:29, 7:34 and 8:52
72SB	-11.1742	14.2728	818	Slash-and-burn	24, 25 and 27 Oct 2012	6:04, 7:56 and 8:50
73M	-11.1759	14.2715	832	Mix	24, 25 and 27 Oct 2012	6:25, 7:37 and 8:34
75F	-11.1773	14.2701	813	Secondary forest	24, 25 and 27 Oct 2012	6:43, 7:19 and 8:17
76F	-11.1910	14.2818	960	Forest	26 Oct 2012	6:00, 7:27 and 8:21
77F	-11.1902	14.2806	950	Forest	26 Oct 2012	6:38, 7:43 and 8:35
78F	-11.1893	14.2817	954	Forest	26 Oct 2012	7:03, 8:02 and 8:52
AbacaxiCoffee	-11.1539	14.2968	865	Mix	19, 20 and 22 Oct 2012	6:00, 7:48 and 8:53











**Table 3 (cont.).** Bird abundance in point counts of 2010. Only data before the 5 minutes endemics playback and the most registered species (total abundance >7) are presented. Endemics are in bold and marked with \*.

Wpoint	Falkenstein's Greenbul	Dark-capped Bulbul	Olive Sunbird	<b>Red-crested Turaco*</b>	Olive-bellied Sunbird	Hartert's Camaroptera	Collared Sunbird	Purple-banded Sunbird	Yellow-throated Nicator	Buff-throated Apalis	Yellow-whiskered Greenbul	<b>Gabela Bushshrike*</b>	Green Crombec	Brown Illadopsis	<b>Gabela Akalat*</b>	African Thrush	Green-headed Sunbird	Blue-headed Crested Flycatcher	Superb Sunbird	Yellow-bellied Wattle-eye	Pink-footed Puffback	Forest Scrub Robin	Southern Hylota	Yellow-rumped Tinkerbird	Carmelite Sunbird	African Broadbill	Pale-olive Greenbul	African Blue Flycatcher	Black-necked Weaver	Black-faced Canary	Green Hylia	Grey-headed Nigrita	African Green Pigeon	African Yellow White-eye	Fraser's Rufous Thrush	<b>Pulitzer's Longbill*</b>	Angola Batis	Dark-backed Weaver	Bubbling Cisticola	<b>Monteiro's Bushshrike*</b>		
292	0	1	0	<b>0</b>	0	0	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	<b>0</b>	0	0	0	0	<b>0</b>			
293	1	0	0	<b>0</b>	1	0	0	1	0	0	0	<b>1</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>		
294	1	1	1	<b>0</b>	0	0	1	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>		
295	1	1	1	<b>0</b>	0	0	0	1	0	0	0	<b>1</b>	0	0	<b>0</b>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>	
296	1	1	1	<b>0</b>	1	0	1	1	0	0	1	<b>1</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	<b>0</b>	0	0	0	0	<b>0</b>
297	0	1	1	<b>0</b>	1	1	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>	
298	1	1	0	<b>0</b>	1	0	0	1	0	0	0	<b>0</b>	1	0	<b>0</b>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>	
299	1	1	1	<b>0</b>	0	1	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	<b>0</b>	0	0	0	0	<b>0</b>
300	1	0	0	<b>0</b>	1	1	0	1	1	1	1	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
301	1	1	0	<b>0</b>	0	0	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
302	0	1	0	<b>0</b>	1	0	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>1</b>	
308	1	1	0	<b>1</b>	1	0	0	0	0	1	0	<b>0</b>	0	1	<b>0</b>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>	
309	1	1	0	<b>0</b>	0	0	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	1	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
310	1	1	1	<b>0</b>	1	1	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
311	0	1	1	<b>0</b>	1	1	0	1	0	0	0	<b>0</b>	0	0	<b>1</b>	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
312	1	1	0	<b>0</b>	0	1	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
313	1	1	1	<b>1</b>	1	1	0	1	0	0	1	<b>0</b>	0	0	<b>0</b>	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	<b>1</b>	0	0	0	0	<b>0</b>
314	1	1	0	<b>0</b>	1	1	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
315	1	0	0	<b>0</b>	0	0	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
316	1	1	0	<b>0</b>	1	1	0	0	1	0	0	<b>0</b>	1	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
317	0	1	0	<b>0</b>	1	1	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	<b>1</b>	0	0	0	0	<b>0</b>
318	1	1	0	<b>1</b>	1	0	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>









**Table 3 (cont.).** Bird abundance in point counts of 2010. Only data before the 5 minutes endemics playback and the most registered species (total abundance >7) are presented. Endemics are in bold and marked with \*.

Wpoint	Falkenstein's Greenbul	Dark-capped Bulbul	Olive Sunbird	<b>Red-crested Turaco*</b>	Olive-bellied Sunbird	Hartert's Camaroptera	Collared Sunbird	Purple-banded Sunbird	Yellow-throated Nicator	Buff-throated Apalis	Yellow-whiskered Greenbul	<b>Gabela Bushshrike*</b>	Green Crombec	Brown Illadopsis	<b>Gabela Akalat*</b>	African Thrush	Green-headed Sunbird	Blue-headed Crested Flycatcher	Superb Sunbird	Yellow-bellied Wattle-eye	Pink-footed Puffback	Forest Scrub Robin	Southern Hylota	Yellow-rumped Tinkerbird	Carmelite Sunbird	African Broadbill	Pale-olive Greenbul	African Blue Flycatcher	Black-necked Weaver	Black-faced Canary	Green Hylia	Grey-headed Nigrita	African Green Pigeon	African Yellow White-eye	Fraser's Rufous Thrush	<b>Pulitzer's Longbill*</b>	Angola Batis	Dark-backed Weaver	Bubbling Cisticola	<b>Monteiro's Bushshrike*</b>			
414	1	0	0	<b>0</b>	1	1	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>		
415	1	0	1	<b>1</b>	1	0	1	1	1	0	0	<b>0</b>	0	0	<b>1</b>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
416	0	1	0	<b>1</b>	1	0	0	0	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
417	1	1	0	<b>1</b>	0	0	0	1	0	0	0	<b>0</b>	0	0	<b>0</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
418	0	0	1	<b>2</b>	1	1	1	1	0	0	0	<b>0</b>	1	0	<b>0</b>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	<b>0</b>	0	0	0	0	<b>0</b>
Total	147	146	113	<b>107</b>	95	71	64	63	52	47	37	<b>33</b>	28	24	<b>24</b>	23	19	18	18	18	17	16	15	15	14	13	12	11	11	10	10	10	9	9	9	<b>9</b>	8	8	7	7	<b>7</b>		

