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Bird community composition across a land use gradient in the eastern Democratic Republic of Congo

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Cocoa agroforestry expansion is widespread in eastern Democratic Republic of Congo, posing a significant threat to the integrity of protected areas. Despite this threat, the impact of their expansion on forest bird communities remains largely unexamined. This study investigated bird community composition in the Okapi Wildlife Reserve (OWR) and surrounding agroforestry areas using a combination of mist netting and passive acoustic monitoring. Specifically, it examined species richness, diversity, evenness, feeding guild abundance and habitat-specific indicator species across 19 sites. A total of 95 bird species were documented, with acoustic monitoring accounting for 73% and mist netting 43% of the recorded species. Significant differences in species richness, diversity and evenness were observed across habitat types. While cocoa farms exhibited higher species richness than primary forest sites or annual cultures, primary forests had the highest diversity indices, followed by cocoa farms and annual cultures. Bird communities were most even in annual cultures, compared to primary forest sites and cocoa farms. Additionally, 18 bird species showed strong associations with specific habitat types. This study highlights the importance of protected areas like the OWR for sustaining bird communities, as well as emphasising the potential value of structurally complex agroforestry landscapes for subsets of forest bird communities. Furthermore, it demonstrates the effectiveness of combining

mist netting and acoustic monitoring methods in understanding avian community composition amid land use changes.

Composition de la communauté d'oiseaux au long d'un gradient d'utilisation du sol dans l'est de la République Démocratique du Congo

L'expansion des agroforêts à cacao est très répandue dans l'est de la République Démocratique du Congo, ce qui constitue une menace importante pour l'intégrité des zones protégées. Malgré cette menace, l'impact de cette expansion sur les communautés d'oiseaux forestiers reste largement méconnu. Cette étude a examiné la composition des communautés d'oiseaux dans la Réserve de faune à Okapis (OWR) et les zones agroforestières environnantes à l'aide d'une combinaison de captures avec filets et de suivis acoustiques passifs. Elle a notamment examiné la richesse, la diversité et l'uniformité des espèces, l'abondance des guildes alimentaires et les espèces indicatrices spécifiques à l'habitat sur 19 sites. Au total, 95 espèces d'oiseaux ont été répertoriées, dont 73% documentées par le suivi acoustique et 43% par captures. Des différences significatives en termes de richesse, de diversité et d'uniformité des espèces ont été observées entre les différents types d'habitats. Si les plantations de cacao présentaient une richesse en espèces plus élevée que les sites forestiers primaires ou les cultures annuelles, les forêts primaires affichaient les indices de diversité les plus élevés, suivies par les plantations de cacao et les cultures annuelles. Les communautés d'oiseaux étaient plus uniformes dans les cultures annuelles que dans les sites de forêt primaire et les plantations de cacao. En outre, 18 espèces d'oiseaux ont montré une forte association avec des types d'habitats spécifiques. Cette étude souligne l'importance des zones protégées, telles que l'OWR, pour la préservation des communautés d'oiseaux, tout en mettant en avant la valeur potentielle des paysages agroforestiers à structure complexe pour certaines populations d'oiseaux forestiers. Elle démontre en outre l'efficacité de la combinaison des méthodes de suivis par captures (filets japonais) et enregistrements acoustiques pour comprendre la composition des communautés d'oiseaux dans un contexte de changements d'utilisation des sols.

Keywords: birds, richness, diversity, indicator species, Okapi Wildlife Reserve, biodiversity, cocoa farm, primary forest

Supplementary material: available at <https://doi.org/10.2189/xxxx>

Introduction

The Congo Basin is of critical global importance for conservation. Spanning six countries (Cameroon, the Central African Republic, Equatorial Guinea, Gabon, the Republic of the Congo and the Democratic Republic of the Congo) in Central Africa, it boasts a vast lowland forest of over 2 300 000 km², with an immense importance for biodiversity (Burgess et al. 2004) . Being the second-largest tropical rainforest in the world, the Congo Basin harbours an estimated 10% of the world's known plant and animal species (Huntley 2023). However, the biodiversity of the Congo Basin is yet to be comprehensively mapped, with numerous species unknown and undescribed, indicating the vast potential for further research in this area (Van de Perre et al. 2019).

The Democratic Republic of the Congo (hereafter referred to as DRC) possesses about 60% of the Congo Basin's forest, making it a crucial area for conservation efforts (Pyhälä et al. 2016). The biodiversity in this region is under threat from numerous factors, such as legal and illegal logging, agricultural encroachment, wildlife trade, poaching, infrastructural development, mining, climate change, and sociopolitical conflicts (Tyukavina et al. 2018; Hugé et al. 2020; Shapiro et al. 2021). The eastern region of the DRC, in particular, has experienced ongoing armed disputes for many decades, which have resulted in widespread violence, human rights abuses, and displacement of populations (Hanson et al. 2009). These conflicts have direct detrimental environmental effects, including deforestation and habitat destruction (Butsic et al. 2015; Kabuanga et al. 2021), besides hindering ecological research and conservation efforts (Draulans and Van Krunkelsven 2002; Butsic et al. 2015).

Despite the persistence of the crisis, this study and other efforts are being made to survey and document the biodiversity of the DRC and the Congo Basin as a whole. For example, recent research in the Nkuba Conservation Area revealed diverse terrestrial mammal species, including threatened species such as the Critically Endangered Grauer's gorilla *Gorilla beringei graueri* (Van Der Hoek et al. 2023). Other studies have addressed the alarming deforestation trends in the DRC, emphasising the crucial role of surveying and mapping forest extent to inform effective conservation strategies (Turubanova et al. 2018; Shapiro et al. 2021). Furthermore, an analysis of the costs of

implementing a biodiversity conservation vision for the Niger Delta-Congo Basin Forest Region estimated that an additional 76 000 km² of protected areas would be needed in the region (Blom 2004). Despite the valuable contributions of these studies towards a comprehensive understanding of biodiversity and conservation efforts in the DRC, data on many taxa, including birds, which serve as important indicators of forest disturbance, remain inconsistent and patchy (Dean 2021).

Birds are one of the most important groups for monitoring environmental change due to their wide distribution across climatic zones and habitat types, sensitivity to habitat disturbance and relative ease of study and monitoring (Macarthur and Macarthur 2013, Fraixedas et al. 2020, Jarrett et al. 2021). In addition, birds play a crucial role in providing various ecosystem services such as pollination, seed dispersal, predation, scavenging, and ecosystem engineering (Whelan et al. 2008). In agricultural systems, insectivorous birds suppress arthropods, reducing herbivore damage to plants and increasing yields (Maas et al. 2015; Ferreira et al. 2023). However, the role of cultivated systems in providing conservation benefits and serving as potential habitats for avian species is still under debate (Yashmita-Ulman et al. 2016). Cocoa agroforestry, a cash crop agricultural system that integrates forest trees with cocoa trees, has been considered a potential solution to address this challenge. While it offers hope for birds and other wildlife in tropical regions, it also threatens biodiversity as it is a leading cause of deforestation in many countries in West and Central Africa (Curtis et al. 2018).

Cocoa cultivation is rapidly expanding in the DRC, including zones such as North-Kivu Province near Virunga National Park, and areas around Mambasa near the Okapi Wildlife Reserve in Ituri Province, despite the ongoing conflict in this area. De Beule et al. (2014) predicted that the rate of cocoa expansion in the Mambasa territory could result in the loss of 67-178 km² of forest in the decade 2014 to 2024. Using measures of Global Forest Loss and associated road improvement in the Eastern DRC, preliminary analysis conducted during this study to assess potential forest loss due to cocoa production estimated approximately 18% of forest loss within a five year period (2015 - 2019). Further simulations estimated additionally, a potential loss of approximately 260 km² of forest cover in the eastern part of the OWR within the next five years as a result of a road improvement and construction project in the area (Harrigan et al. 2022). This is a critical

issue for conservation efforts and biodiversity as it contributes to deforestation and habitat loss for many bird species. However, cocoa agroforestry systems are recognised to be more biodiversity-friendly compared to other agricultural systems in highly fragmented landscapes (De Beenhouwer et al. 2013; Niether et al. 2020).

For birds, these ecological benefits have been shown to depend on various factors. For instance, our recent study in Cameroon showed that shady cocoa farms with more forest cover provide better habitat for sensitive bird species, suggesting shade management is crucial for wildlife-friendly cocoa production (Jarrett et al. 2021). Also, Cabral et al. (2021) examined the effects of local and landscape features on the richness and abundance of bird communities in cocoa farms in Brazil. They found that these bird-friendly systems work best when surrounded by more forest and less cattle pasture. While these agroforestry systems cannot fully replace natural forests, they can help bird populations survive in altered habitats. Despite 174 documented bird species at the Okapi Wildlife Reserve's Epulu research station (<https://ebird.org/hotspot/L1083083>), the full picture of this region's avian diversity remains incomplete. While ongoing efforts through various projects are commendable in keeping knowledge of the biodiversity alive, little is known about bird communities in a gradient of land use change in this area. There is a critical need for more comprehensive and up-to-date information on avian populations in this ecologically diverse environment (Sekercioglu et al. 2002, Jarrett et al. 2021).

Several methods have been used to assess bird biodiversity. Capture data and wildlife acoustics are crucial tools for determining species composition, abundance and diversity in bird populations (Dawson and Efford 2009; Doser et al. 2021; Jarrett et al. 2022). Hence, we use a dual approach of mist netting and acoustic monitoring to estimate variation in bird species richness, diversity and evenness in a gradient of primary forest, cocoa farms and mixed annual cultures in the eastern region of the DRC. Bioacoustics complemented with capture data are effective tools for determining species composition, abundance, and diversity in bird populations (Dawson and Efford 2009, Doser et al. 2021, Jarrett et al. 2021). For the purpose of this study, we define the following terms: species richness is the number or count of different species in a given area; species abundance is the relative abundance of species; and species diversity is the function of species richness and the abundance or evenness of individuals distributed among species

(Hurlbert 1971). Specifically, we aim to (1) determine bird diversity (expressed as species richness, Shannon-Wiener and Simpson indices, and evenness measures) and how it varies between primary forests, cocoa farms and annual cultures using mist netting and passive acoustic monitoring; (2) examine the differences in bird feeding guild abundance between habitat types using mist net captures and (3) determine indicator species of the surveyed habitat types using mist netting and acoustic recording units.

There has been very little research on avian communities in the DRC, particularly in the crisis zones due to insecurity concerns. We contribute to bridge this knowledge gap by providing new baseline data on avian biodiversity across diverse habitats. These data are essential to guide conservation efforts, including protected areas management and governance, enabling the development of effective strategies to protect bird populations in these changing landscapes. In addition, we assess the effectiveness of acoustic wildlife recording units for monitoring the very high diversity of birds from this biodiversity hotspot.

Methods

Study area

Field collections occurred in the forest and agricultural sites within and around the Okapi Wildlife Reserve (OWR, headquartered in Epulu village) and Mambasa territory, located in Ituri Province of northeast Democratic Republic of Congo (Figure 1). This region, surrounding the ~13 000 km² OWR, is one of Central Africa's most intact forest landscapes (Stephenson and Newby 1997; Wilkie et al. 1998). The reserve lies roughly 100 km northwest of Virunga National Park and 300 km east-northeast of the bustling city of Kisangani with geographical coordinates ranging from 1°00' to 2°42'N and 28°02' to 29°08'E (Plumptre 1997). Elevation varies from 500 m in the western reaches to 1000 m in the easternmost regions, with an average annual rainfall of 1680 mm. The rainy seasons extend from March through May and August through November while a relatively dry period occurs from mid-December to February. The OWR is known to host the largest population of endangered okapis *Okapia johnstoni*, along with nationally significant populations of other IUCN Red-listed species including African forest elephants *Loxodonta cyclotis* and eastern chimpanzees *Pan troglodytes schweinfurthii* (Yanggen et

al. 2010). Additionally, it is home to at least 14 other primates, 14 ungulates, nearly 400 bird species, a range of valuable timber species, and some of Africa's densest above-ground carbon stocks, especially *Gilbertiodendron dewevrei* and *Cynometra alexandri* monodominant stands (Lewis et al. 2013; L'Roe et al. 2023). Cocoa cultivation and other perennial crops are not permitted within the OWR. However, to ensure effective management, a land use zoning plan is being implemented to balance biodiversity conservation with sustainable livelihood opportunities for the local communities. This zoning plan designates specific areas for hunting, agriculture (mainly annual food crops), settlement, and conservation (Yanggen et al. 2010).

Field surveys

In June and July of the year 2022, bird surveys were conducted in twelve cocoa farms using automated recording units. In the same months of the year 2023, bird surveys were conducted in four primary forest sites and three annual cultivated farms using automated recording units and mist nets. Habitat characterization was performed according to descriptions from Waltert et al. (2005) and Tchoumbou et al. (2020), taking into account canopy cover, proximity and/or intensity of human activity, and the type of crop cultivated. Primary or undisturbed forests were characterized by their dense canopy cover of over 90%, dominated by tall and mature trees, with minimal human interference. Cocoa farms represented agroforestry systems where land was primarily used for cocoa production, while annual cultures featured a mix of food crops such as beans, maize and cassava including small patches of old palm trees.

Mist netting

Birds were captured following established protocols (Tchoumbou et al. 2020, Jarrett et al. 2021). Between 10 and 20 mist nets, each measuring 12 meters in length and 3 meters in height, were placed along established transects at each site. Site accessibility, especially in marshy or high-risk areas, accounted for the variation in the number of mist nets installed per site. Each site was sampled for two consecutive days, with nets opened between dawn and midday (6:30–12:30). Net checks were made every 15–20 minutes, and nets were promptly closed if it started to rain. Captured birds were placed in

breathable cloth bags for subsequent processing, after which birds were fitted with uniquely numbered metal rings and measured for wing and tail length and body mass. Species identification was primarily achieved using two comprehensive bird field guides, namely Sinclair and Ryan (2010) and Borrow and Demey (2014). Three individual birds with complex plumage distinctions were later identified by bird experts using photographs of individuals captured during sampling.

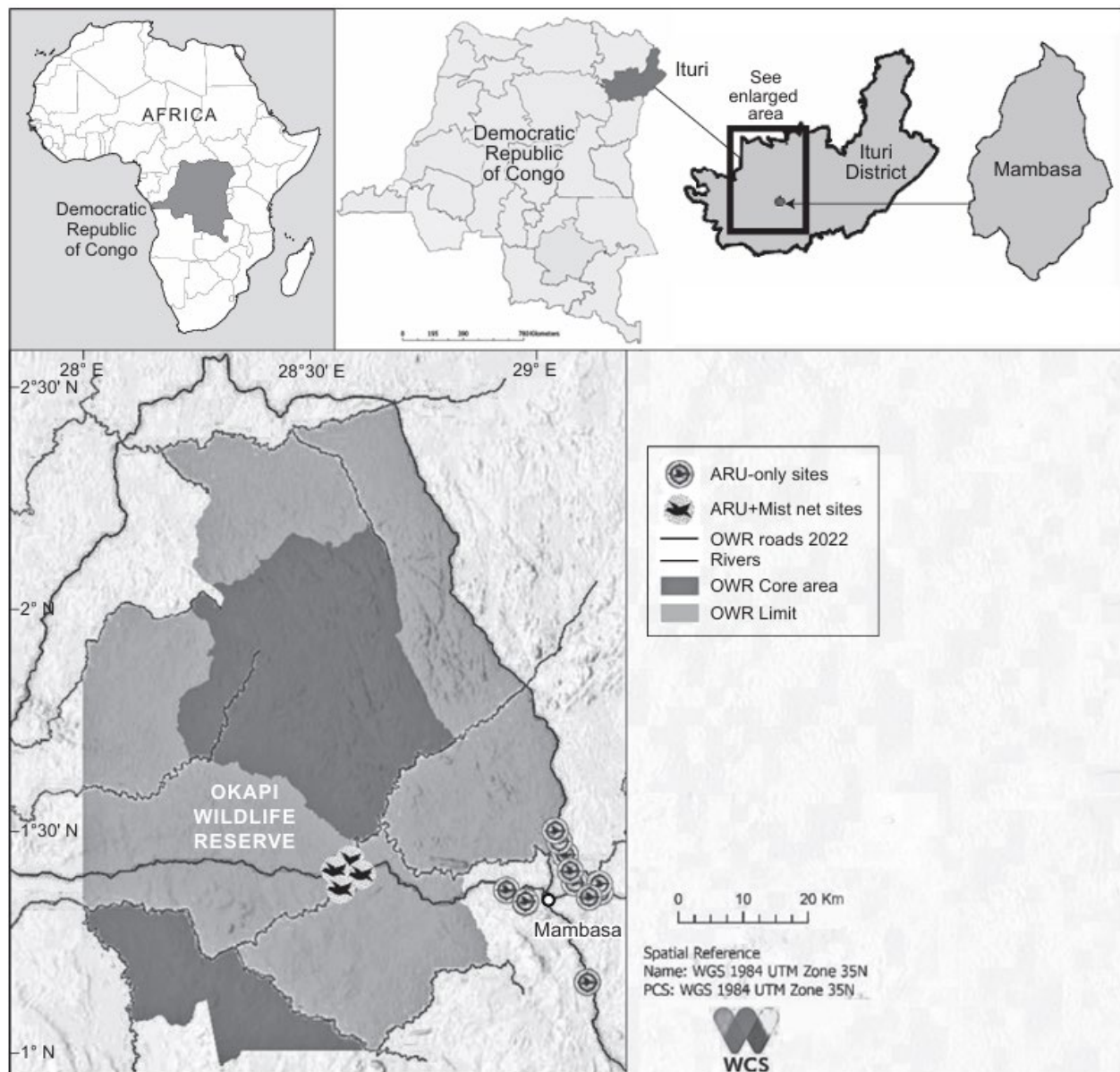


Figure 1: Map of field sites in the Okapi Wildlife Reserve and Mambasa territory, Democratic Republic of Congo. (Prepared by Alex Badhera of WCS, Epulu).

Passive acoustics

At each study site, passive acoustic units (Song Meter Micro; Wildlife Acoustics, Inc.) were strategically positioned to capture ambient bird vocalizations. Each recording unit per site was placed at approximately 2 m above ground level and programmed to record at intervals of 30 min from dawn to midday (i.e. 6.30–7.00, 7.30–8.00, etc). These recorders were operated for two days per site and captured sound at a sample rate of 24 000 Hz (Toenies and Rich 2021). This resulted in about 3 hours per day of recording per site; the total number of recording periods was 44 for primary forest sites, 33 for annual culture sites, and 144 from cocoa farm sites. Collectively, these recordings totalled 6 630 minutes of unique bird vocalizations. However, for this study, we focused on the first 15 minutes of each bird recording, ensuring a focused analysis of bird detection, richness and diversity. Recordings were subsequently assessed manually by expert knowledge of Afrotropical bird songs (SEIJ), assigning species to their first occurrence of singing in each 15 minute cut. Any bird song that was not identified to species level was omitted from our analyses.

Data analysis

To ensure comparability across methods and sites, we standardized bird detections as the frequency of songs heard per 15-minute interval within each hour of sampling per day per site. Similarly, bird capture data was standardized to reflect capture abundance per mist net hour per day at each sampling site. Thus, for acoustic data the sampling unit was a 15 minute period, and for mist-netting a mist-net hour. All data analyses were performed in RStudio version 4.3.3 (R Core Team 2024). We estimated bird species richness (S) and plotted species accumulation curves using the “iNEXT” package, which measures and predicts richness in communities or assemblages based on sample size (Hsieh et al. 2016). For each sampling unit, we calculated Shannon-Weiner (H') and Simpson (D') indices of biodiversity using the “vegan” package (Oksanen et al. 2025). In addition, evenness (J') was calculated using Simpson's diversity index divided by the natural

logarithm of species richness (S) to assess the abundance distribution among species within the bird community. Ranging from 0 to 1, a higher J' indicates a more balanced community, while a lower value suggests dominance by a few species. Shannon-Wiener index ranges from 0 to 5 (although typically between 1.5 and 3.5) and Simpson's index ranges from 0 to 1. A high Shannon-Wiener diversity (H') coupled with low Simpson's diversity (D') depicts high species diversity, as outlined by Ntongani and Andrew (2013).

Species variations among habitats were assessed by fitting Generalized Linear Models (GLMs) with Shannon-Weiner, Simpson or evenness indices as response variables with a Gaussian distribution while a Poisson distribution was used for models with species richness as a response variable. Habitat was included as an explanatory variable in all models and each model was then compared to a null model using the Akaike Information Criterion (AIC) value to identify the best-fitting model for each data type. Non-parametric Kruskal-Wallis tests were used to assess statistical significance for models violating normality assumptions. Furthermore, indicator species analyses were performed using the "indicspecies" package to determine bird occurrence and their sensitivity to particular habitat types (De Cáceres et al. 2012). This analysis reflects how well a species or a combination of species is associated with a specific habitat based on its abundance and how often it is found there. The indicator index value (IndVal) is estimated as a product of two components, A and B according to Dufrêne and Legendre (1997). A is a measure of the relative abundance of a species within a target site group, whereas B measures the relative frequency of the species within a target site group. To calculate species indicator indices using acoustic recordings, we used a simpler version, where both components were solely based on presence-absence data (De Cáceres et al. 2012). In addition, we visualized differences in species composition between habitat types using a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis dissimilarity matrix (Oksanen et al. 2025).

For bird capture data, we estimated relative abundance as the number of individuals per species in a given habitat. For determining differences in functional feeding groups between habitats, birds were classified into six feeding guilds based on their predominant diet as described by Gray et al. (2007). These consisted of frugivores (fruit consumers), nectarivores (nectar feeders), insectivores (arthropod eaters), granivores (nut and seed

eaters), carnivores (large arthropods and vertebrate prey), and omnivores (two or more food types).

Results

Bird species composition and richness

We had 1 949 bird detections using acoustic monitoring and 287 individuals captured using mist nets. In total, 95 bird species belonging to 29 families and 10 bird orders were identified (Supplementary Table S1). Of these 95 species, 43% ($n = 41$) were documented during mist-netting, and 73% ($n = 71$) during acoustic monitoring. Passeriformes dominated the species list, with 18 families and 56 species. This was followed by the order Piciformes with 3 families and 11 species. The least represented bird orders were Psittaciformes (2%), Musophagiformes (2%), Accipitriformes (2%) and Trogoniformes (1%). We detected one endangered species, the African Grey Parrot *Psittacus erithacus* (family Psittacidae) through acoustic monitoring only. All other recorded species were categorized as Least Concern (LC) according to the IUCN Red List (IUCN 2021).

Rarefaction curves revealed substantial differences in bird richness between habitat types for both automatic song records and mist net captures (Figure 2). Of the two habitats surveyed using mist nets, primary forest emerged as the most species-rich with 37 species compared to annual cultures with 13 species. The acoustic survey showed that cocoa farms harboured the highest bird richness, with a total of 56 recorded species, followed by primary forests (49 species), and with annual cultures having the lowest species richness (32 species; Figure 2). Similarly, habitat was a significant predictor of bird richness using both surveyed methods (Figure 3). Both methods identified a set of 17 shared species whereas 54 species were exclusively detected by acoustic monitoring and 24 species by mist netting.

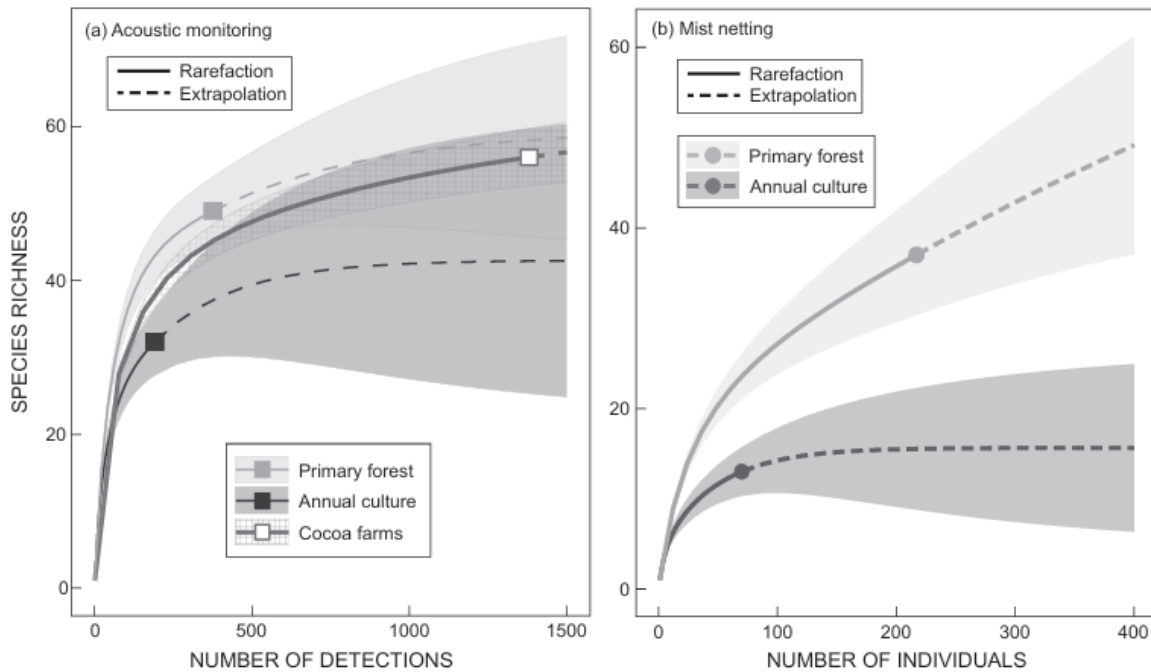


Figure 2: Rarefaction and extrapolation (R/E) sample-sized-based curves showing the observed (straight lines) and estimated (dotted lines) number of bird species related to the number of captures using mist nets (right) and the number of detections in acoustic monitoring (left), across various habitat types in the Okapi Wildlife Reserve and Mambasa territory, Democratic Republic of Congo. Shaded areas specify the level of confidence at 95%

Bird diversity across habitats using mist net captures and acoustic surveys

With both survey methods, bird diversity varied across primary forest and agricultural habitats (Figure 4, Supplementary Figure S1). We found significant differences in diversity measures and species evenness between primary forest and annual cultures for mist netting data (cocoa farms were not sampled using mist nets; Supplementary Figure S1 and Table S2). Shannon-Wiener and Simpson's diversity estimates for birds were significantly higher in primary forest habitats than in annual cultures by an average of 0.55 ($t = 2.27$, $df = 12$, $p < 0.05$) and 0.09 ($t = 2.22$, $df = 12$, $p < 0.05$) respectively. However, evenness was higher in annual cultures as opposed to primary forest sites ($t = -2.41$, $df = 12$, $p < 0.05$). Likewise, bird diversity estimates were significantly higher in primary forest sites compared to the two agricultural sites surveyed with acoustic recorders (Figure 4,

Supplementary Table S3). Shannon-Wiener and Simpson's indices for forests significantly increased by an average of 0.94 ($t = 11.01$, $df = 142$, $p < 0.001$) and 0.36 ($t = 12.22$, $df = 142$, $p < 0.001$), relatively to annual cultures, and by 0.33 ($t = 4.37$, $df = 142$, $p < 0.001$) and 0.10 ($t = 3.85$, $df = 142$, $p < 0.001$), relatively to cocoa farms. Annual cultures had the lowest bird species diversity. As with the mist net captures, annual cultures showed the greatest evenness of birds, followed by primary forests and cocoa farms (Figure 4).

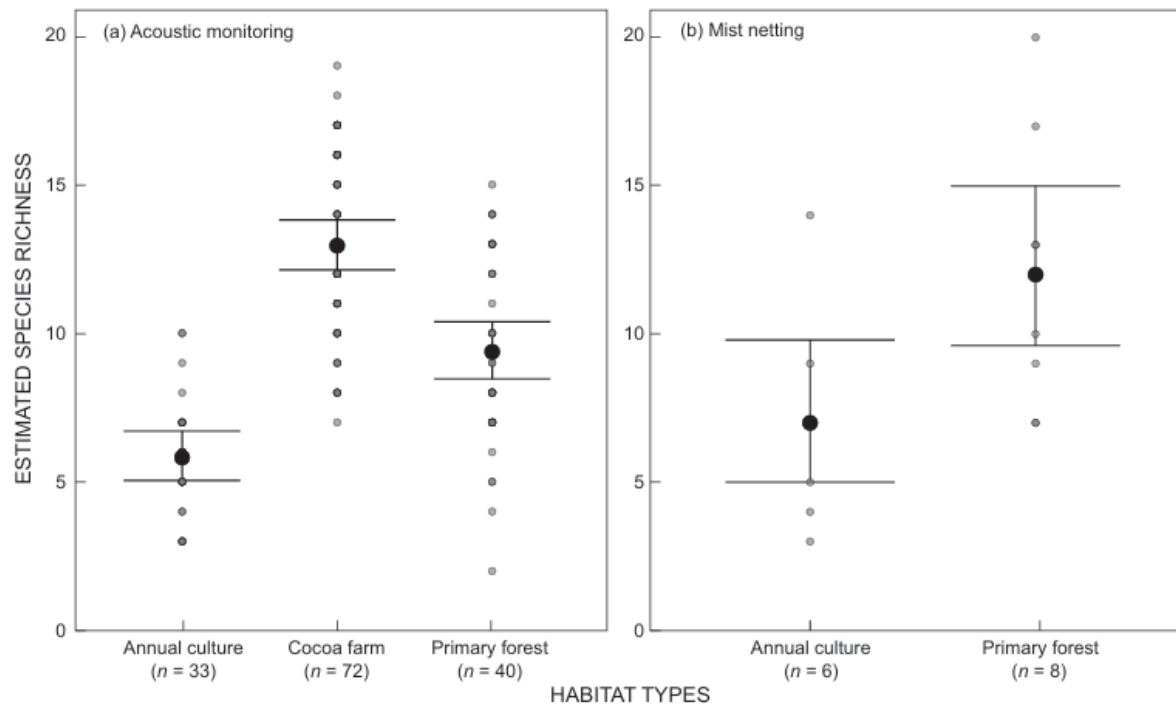


Figure 3: Bird species richness in forest and agricultural sites using acoustic monitoring (left) and mist net captures (right) in the Okapi Wildlife Reserve and Mambasa area in the Democratic Republic of Congo

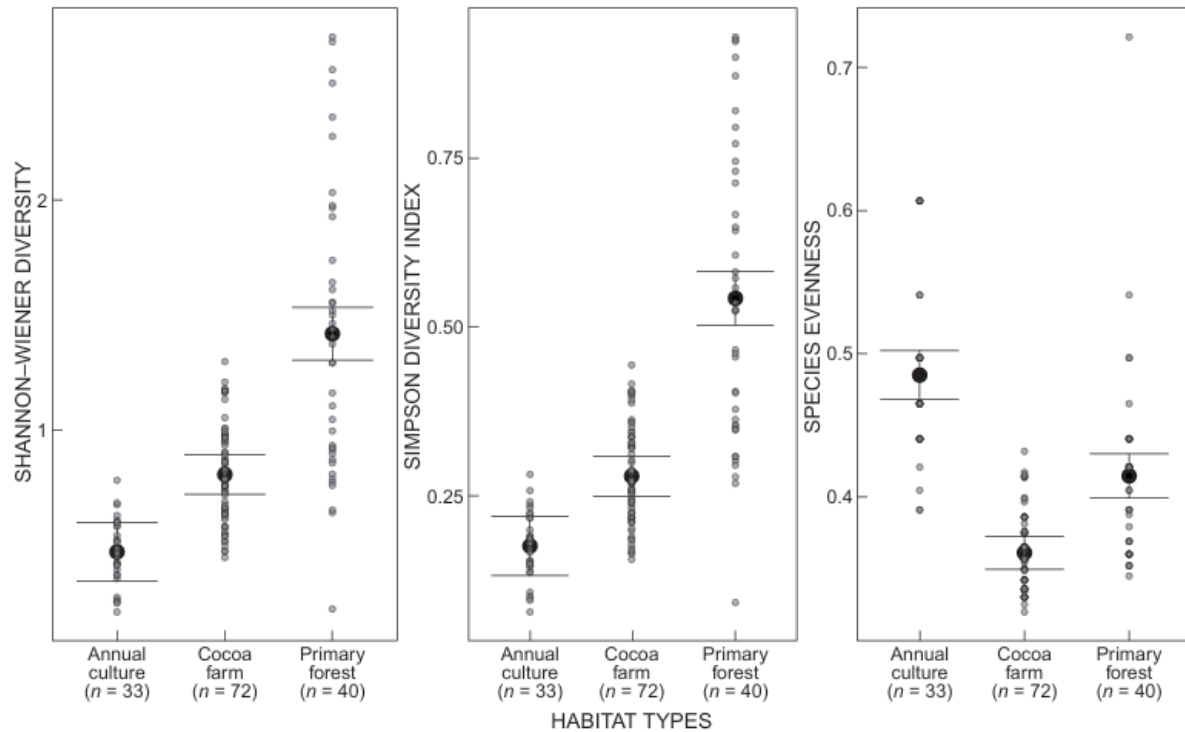


Figure 4: Variation in bird species diversity (Shannon-Wiener and Simpson indices) and evenness in primary and agricultural habitats using acoustic monitoring in the Okapi Wildlife Reserve and Mambasa territory, Democratic Republic of Congo

Indicator species determination and relative bird abundance

Our indicator species analyses identified several bird species that were significantly associated with specific habitat types. Of the 41 species identified by mist netting, the Slender-billed Greenbul *Stelgidillas gracilirostris* was the only species significantly associated with primary forest sites ($R = 0.57$, $p < 0.05$), with no species linked to annual cultures or to a combination of both annual cultures and primary forest sites. Acoustic monitoring, however, identified 17 out of 71 recorded species with strong associations to primary forests, cocoa farms and annual cultures (Supplementary Table S2). Among these habitats, 12 bird species were significantly associated with at least one habitat type and 5 species were linked to two different habitat types. The African Grey Parrot had a strong association with annual cultures ($R = 0.887$, $p < 0.001$), while Little Greenbul *Eurillas virens* ($R = 0.718$, $p < 0.015$), Blue-spotted Wood Dove *Turtur afer* ($R = 0.771$, $p < 0.004$) and Green Crombec *Sylvietta virens* ($R = 0.616$, $p < 0.047$) were significantly

linked to both annual cultures and cocoa farms. The Yellow-throated Tinkerbird *Pogoniulus subsulphureus* ($R = 0.71$, $p < 0.011$) was a significant indicator of cocoa farms and primary forest habitats, and the Red-tailed Greenbul *Criniger calurus* ($R = 0.717$, $p < 0.014$) was significantly associated with annual cultures and primary forest sites. In addition, nine bird species were significantly associated with primary forest habitats: Blue-headed Wood Dove *Turtur brehmeri*, Fraser's Rufous Thrush *Stizorhina fraseri*, Forest Robin *Stiphrornis erythrothorax*, Icterine Greenbul *Phyllastrephus icterinus*, Xavier's Greengul *Phyllastrephus xavieri*, Fire-crested Alethe *Alethe castanea*, Red-chested Cuckoo *Cuculus solitarius*, Chocolate-backed Kingfisher *Halcyon badia* and Hairy-breasted Barbet *Tricholaema hirsuta*. Cocoa farms had two species significantly associated with this habitat: Green-backed Camaroptera *Camaroptera brachyura* and White-breasted Nigrita *Nigrita fusconotus* (see details in Supplementary Table S4). Although, few species were shared between agricultural and primary forest sites, our NMDS ordination analyses revealed a distinct community composition in primary forest sites compared to annual cultures and cocoa farms using both mist netting and acoustic recordings (Figure 5).

Mist net capture data showed that insectivores ($t = 4.24$, $df = 12$, $p < 0.001$) were significantly more abundant in primary forests compared to annual cultures, whereas omnivore ($t = 2.18$, $df = 12$, $p = 0.89$) and nectarivore abundance showed no significant difference between the two habitats ($t = 0.36$, $df = 12$, $p = 0.67$) (Supplementary Table S5).

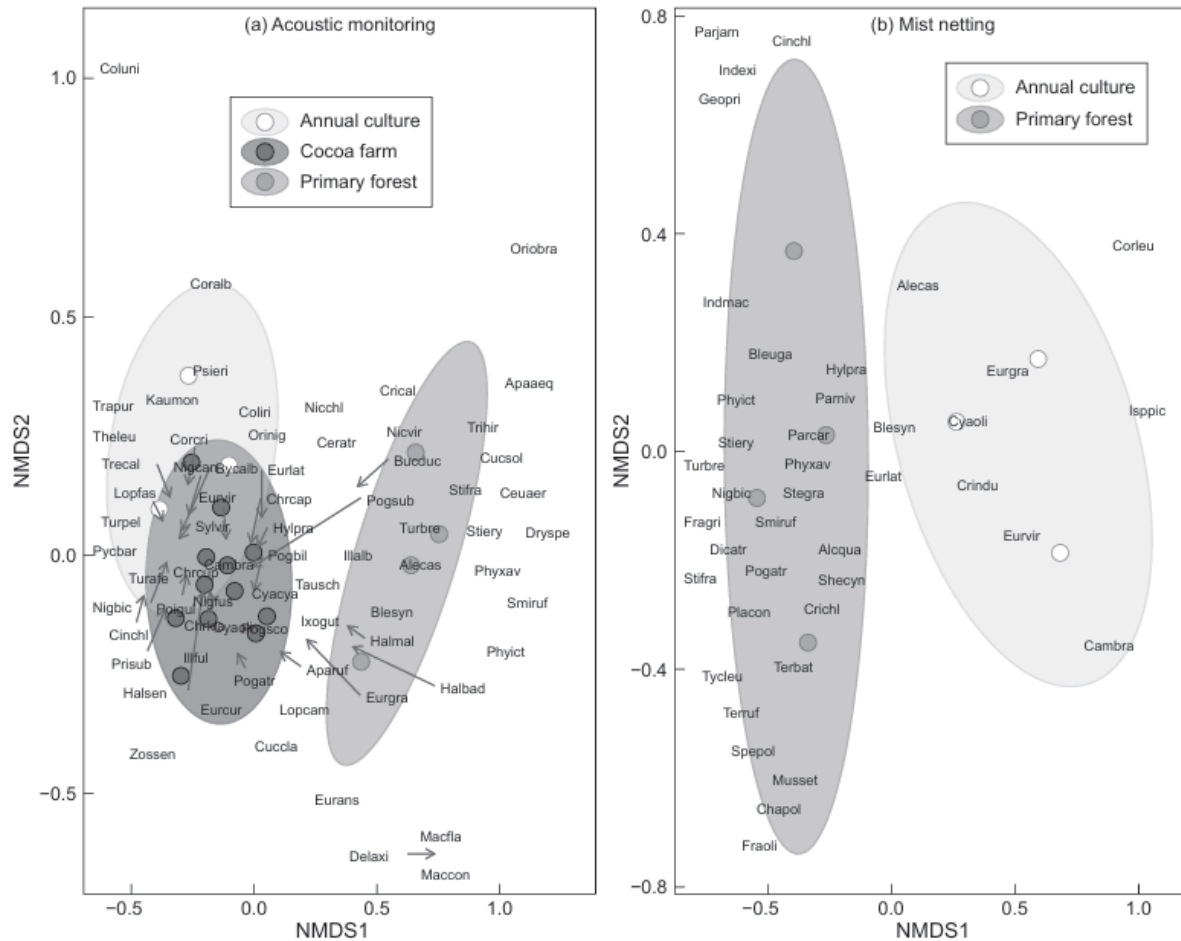


Figure 5: NMDS ordination plot showing bird communities across habitat types in the Okapi Wildlife Reserve and Mambasa territory, Democratic Republic of Congo, using mist net abundance data and acoustic presence-absence data. Points indicate sampled communities at a particular site per habitat, and ellipses represent 95% confidence interval. Bird species names are indicated in six letter codes (first three letters of the genus and of the species), listed in Supplementary Table S1

Discussion

Here we investigated the richness, diversity, and abundance of bird species inhabiting disturbed and undisturbed habitats within and around the Okapi Wildlife Reserve (OWR) in the northeast region of the Democratic Republic of Congo. We employed a combination of mist netting and acoustic monitoring to assess avian community differences between habitat types, with acoustic monitoring accounting for a 73% of total bird records and mist

netting accounting for 43%. Habitat was a significant predictor of bird richness, diversity, and evenness, and also determined the abundance in bird feeding groups.

In terms of species richness, this study identified 95 bird species representing 27 families and 10 orders. Of this number, we recorded 61 of the 174 bird species listed on eBird.org for our study area while 34 bird species are yet to be reported on the ebird database, making it a total of 198 bird species identified so far in the Epulu Research Station of the Okapi Wildlife Reserve and Mambasa territory. The difference in species richness observed in our study compared to eBird is likely due to the eBird data consisting of a larger group sampled over a wider area, that is resident, non-resident, vagrant, aquatic species etc, while our sampling likely missed a significant portion of the rarer, cryptic, nocturnal or canopy species that contribute to the overall bird community in the area. In this study, fieldwork was conducted in June and July of both sampling years, hence, we did not account for seasonal variations that could potentially influence species composition at a given time. Also, due to insecurity and logistic constraints, we had limited access to other key areas which constitutes the mosaic of habitats in the OWR. Rather, we sampled birds mainly in the southern part of the reserve which is dominated by tall *Gilbertiodendron dewevrei* monodominant trees characterized by a sparse sub-canopy layer and an open understorey. Identifying 34 species not listed in eBird indicates the spatiotemporal variability in this region. Thus, this highlights the need for a wider and extensive sampling effort to fully assess the true biodiversity of the region. Cooleman et al. (2015) recorded 51 species in old-growth and regrowth forest sites in the Yagambi reserve in the DRC, while Barrie et al. (2025) recently identified 78 bird species in primary and disturbed secondary rainforest habitats in the lowland rainforest of Equatorial Guinea. Higher species richness has been reported in other tropical regions, particularly when extensive assessments are performed or employing a combination of multiple survey methods (Hopping and Klinck 2024; Vargas-Daza et al. 2023). For instance, Vargas-Daza et al. (2023) recorded 99 bird species in a Neotropical rainforest using camera traps and mist nets. Hopping et al. (2024) identified 127 bird species using automatic recording units in Southwestern Amazon. Meanwhile, Kupsch et al. (2019) recorded 198 bird species along a deforestation gradient in Southwest Cameroon using bird point counts. As expected, in our study, Passeriformes dominated with 57 recorded species, reflecting

a highly diverse group and Piciformes (which consist of woodpeckers, honeyguides, and tinkerbirds) ranked second on the list with 11 species and 3 families, demonstrating their remarkable ability to thrive in diverse habitats.

Our results revealed a contrasting pattern between species richness, diversity, and evenness across habitats. Cocoa farms supported the highest bird species richness, followed by primary forests and annual cultures, whereas primary forests consistently exhibited the highest species diversity (Shannon-Wiener and Simpson indices), with cocoa farms and annual cultures showing lower values. In contrast, annual cultures exhibited the highest evenness. These patterns indicate that although more species were detected in cocoa farms, bird communities in primary forests were more even in their abundances, with fewer dominant species and a richer representation of forest specialists. Annual cultures, despite being the poorest in both richness and diversity, showed a more uniform distribution of species abundances, suggesting a simplified community dominated by a few species. The high species richness in cocoa farms aligns with our previous observations in Cameroon, where cocoa farms supported a greater richness of bird species than undisturbed forests (Jarrett et al. 2021). One possible explanation for this pattern lies in the structural heterogeneity provided by cocoa farms, which range from open, sun-drenched plantations to shaded farms that closely resemble natural forests in structure (Sonwa et al. 2007, Jarrett et al. 2021). This heterogeneity likely supports a broader set of generalists, canopy and edge-associated species. For example, Van Bael et al. (2007) reported the same patterns of species richness between cacao farms and nearby forest fragments in Panama, with cocoa farms being rich in flycatchers, tanagers, and migratory warblers, while lacking understory insectivores. Other studies have reported opposite trends. Waltert et al. (2005) found no difference in species richness from forest to farmland in an Afrotropical landscape, but emphasized the importance of tree cover in tropical land use systems for maintaining resident forest bird populations. Similarly, previous work in Cameroon observed no significant difference in average richness, abundance, or diversity in bird communities in response to habitat fragmentation, although individual feeding groups responded differently to habitat disturbance (Tchoumbou et al. 2020).

In contrast, species diversity was highest in primary forests demonstrating the importance of the OWR as a biodiversity hotspot. The OWR is known for its distinct mixed forest types with high structural diversity and complexity supporting a wide range of wildlife, including birds (Plumptre 1997; Yanggen et al. 2010). Many studies from various tropical regions, including the Neotropics and Asia, support the findings of high species diversity in primary forests compared to agricultural sites (Round et al. 2006, Dawson and Efford 2009, Rocha et al. 2015, Bhat et al. 2023). However, the transition from mature forests to agricultural landscapes usually leads to a decline in understorey insectivores, ant-followers and forest specialists while nectarivores and frugivores generally increase in abundance (Faria et al. 2006, Maas et al. 2016, Jarrett et al. 2021). In our data, typical forest-dependent species such as *Phyllastrephus icterinus/xavieri*, *Smithornis rufolateralis*, *Sheppardia cyornithops* etc were detected or captured only within the primary forest, while other species such as *Alethe castanea*, *Stiphornis erythrothorax*, etc which were additionally detected or captured in cocoa farms occurred in relatively low numbers compared to primary forest. These observed variations in relative abundance and distribution patterns in these sensitive forest species indicates their sensitivity to habitat degradation. Furthermore, our NMDS ordination with both surveyed methods revealed a distinct community composition between primary forest and agricultural habitats despite a broad overlap. This distinction is largely driven by the occurrence of forest specialists, Ant followers (e.g *Criniger chloronotus*, *Alethe castanea*, *Bleda syndactylus*), terrestrial insectivores (e.g *Stiphornis erythrothorax*) and even mixed-flocked species (e.g *Phyllastrephus icterinus*, *Phyllastrephus xavieri*) in primary forest compared to agricultural habitats. These findings contributes to the growing knowledge that fragmented habitats such as African agroforestry systems may have rich avifauna but lack sensitive specialized forest understorey insectivores (Cordeiro et al. 2015, Jarrett et al. 2021, Barrie et al. 2025). Additional findings using mist net data reveals insectivore abundance was significantly higher in primary forest compared to annual cultures, while nectarivore and omnivore abundances did not change between both habitat types. Insectivores, known for their high habitat specificity and preference for forest interiors, are particularly sensitive to deforestation and land use changes (Sekercioglu et al. 2002, Luther et al. 2024, Barrie et al. 2025). Omnivores and nectarivores, with their more generalist diets, appear to be more

adaptable to various habitats, including agricultural areas with less structural complexity (Sekercioglu et al. 2002, Luther et al. 2024). Captures of both feeding guilds were dominated by *Cyanomitra olivacea* and *Eurillas latirostris*. These two species are ubiquitous, non-migratory, and known to inhabit a wide variety of Afrotropical habitats (Nguembock et al. 2019). Therefore, while other more specialized guilds decreased with disturbance, the abundance of these species likely remains stable across habitats.

Although cocoa farms and annual cultures are modified habitats, cocoa farms showed high diversity measures due to its diverse structure, including remnant forest trees kept for shade, and providing a more suitable environment for birds compared to monoculture or mixed food crop farms, which lack tall trees or patches of forest fragments (Waltert et al. 2005; Yahya et al. 2022). The absence of mist net captures in cocoa farms limits our ability to directly compare species richness across all surveyed habitats. However, the acoustic monitoring findings suggest that cocoa farms with diverse tree cover provide crucial habitats for birds, particularly in fragmented landscapes. Thus, highlighting the importance of adequate agroforestry systems and their role in biodiversity conservation.

Mist net data identified *Stelgidillas gracilirostris* as an indicator species of primary forest in the region. Although typically associated with a wide range of habitats, including secondary forests, farmlands and gardens, this species was unexpectedly the second most abundant captured in primary forest after *Eurillas latirostris*. The relative abundance of *Stelgidillas gracilirostris* in these monodominant stands may simply reflect the availability of food resources such as better foraging ground and structural complexity compared to agricultural habitats (Mariano-Neto and Santos 2023). However, we require standardised mist-netting in cocoa farms to reliably evaluate the species' response between cocoa agroforestry and primary forest habitats. In addition, this species was undetected by acoustic monitoring in all habitats suggesting a discrepancy between mist net captures and acoustic detectability. The species' preference for upper canopy likely hindered its detectability by acoustic monitors or perhaps its vocalization period occurred outside the operational window of the recording units. Among the species whose vocalizations were captured by passive acoustic monitoring, several were identified as forest indicator species. This includes: *Cuculus solitarius*, *Stizorhina fraseri*, *Stiphornis erythrothorax*, *Halcyon badia*, *Tricholaema hirsuta*, *Turtur brehmeri*, *Phyllastrephus*

icterinus, *Phyllastrephus xavieri*, and *Alethe castanea*. This makes them valuable indicators for monitoring the impacts of anthropogenic activities and guiding conservation strategies (Simamora et al. 2021). This dataset identified *Eurillas virens*, *Turtur afer*, and *Sylvietta virens* as indicators of annual cultures and cocoa farms, in accordance with their ability to thrive in agricultural landscapes, whereas *Psittacus erithacus* was associated to annual cultures only. Tamungang et al. (2016) examined the habitat preference of *Psittacus erithacus* in Cameroon, observing the seasonal use of the oil palm tree *Elaeis guineensis* by this species, as opposed to diverse tree species and mixed vegetation plots. This behaviour was attributed to the oil palms providing readily available food sources (palm nuts), suitable roosting sites, and open areas within the crown for social interaction (Tamungang et al. 2016). This may suggest that for certain species, a balance between diverse food options and specific structural elements within a habitat might be more important than simply high tree density.

Overall, we observed similar patterns in species richness, diversity and evenness of birds in agricultural and primary forest habitats using both mist netting and acoustic monitoring. Sample coverage estimates from mist netting indicated the need for further sampling to fully determine the species richness in the surveyed habitats, whereas rarefaction curves from acoustic monitoring showed an almost complete sampling across various habitat types. Mist nets have been traditionally used for capturing birds, especially in studies focusing on migration patterns and population monitoring (Roark and Gaul 2021). They are effective in capturing a wide range of bird species, including those that may not be easily detected through other methods (Chmel et al. 2016). Although mist nets have proved useful for assessing bird diversity in different habitats (Vargas-Daza et al. 2023) or for studying seed-dispersal interactions (Rumeu et al. 2023), they have limitations, as some species avoid mist nets after initial captures (affecting recapture rates and biasing results: Roche et al. 2013), and sampling of the bird community will always be incomplete. Mist nets are particularly effective for monitoring understorey passerines, but their efficacy is limited for non-passerine birds (like raptors) and mid-story to canopy species.

On the other hand, passive acoustic monitoring has become popular in bird research as it is generally cheap, easy to implement, and provides a non-intrusive way to monitor

bird populations (Roark and Gaul 2021). In addition, they are particularly useful in remote or seasonally inaccessible habitats (Freitas et al. 2023). However, manual identification of species, as it was the case in this study, can be resource-intensive and time-consuming and although feasible, abundance estimates from acoustic data can be prone to errors resulting from overestimation via double-counting or underestimation through signal saturation (Dawson and Efford 2009, Jarrett et al. 2022).

Recent developments in the use of machine learning and sophisticated automated models are enhancing the efficiency and accuracy of automatic song identification and analysis (Dawson and Efford 2009, Marsland et al. 2019). However, these acoustic approaches are still poorly developed in many parts of Africa. While both methods used in this study were equally effective for common passerines and two non-passerine species: *Turtur brehmeri* and *Pogoniulus atroflavus*, acoustic monitoring extended species detectability to a more wider taxonomic spectrum including hornbills, trogons, cuckoos, turacos and raptors, but failed to detect a substantial number of the understorey forest-dependent species (such as *Chamaetylas poliocephala*, *Muscicapa sethsmithi*, *Sheppardia cyornithopsis*, *Parmoptila jamesoni*, *Spermophaga poliogenys*, *Geokichla princei*, *Tychaemon leucosticte*, *Bleda ugandae*, *Platysteira concreta* etc) and a few canopy-dwelling species (*Fraseria olivascens*, *Stelgidillas gracilirostris*) captured solely through mist netting. The observed detection patterns are likely driven by a wide range of factors, such as functional traits and diel activity patterns (Anderson et al. 2015) and temporal heterogeneity (Hopping and Klinck 2021) of afrotropical avian communities. External variables, including adverse weather conditions and observer identification skills may also influence species detection variability (Dorazio 2014). Therefore, future studies must take into consideration the limitations and advantages between mist netting and acoustic monitoring to ensure a more robust, unbiased and accurate characterization of avian assemblages. Our study highlights the use and importance of combining two or more approaches in assessing bird communities in tropical landscapes.

Conclusion

Based on mist net captures and passive acoustic surveys, we demonstrate how bird communities respond to land use change in a highly diverse Afrotropical landscape. Species diversity measures decreased with the level of habitat disturbance, with annual cultures supporting the least diverse bird communities. Cocoa farms showed greater species richness than primary forest and annual cultures, yet their avian community lacked sensitive forest specialists found in primary habitats. Thus, demonstrating the distinct bird communities between habitat types. The growing demand for cocoa and agricultural expansion around the OWR pose threats to biodiversity and the protected area. This study underscores the critical need for continued bird diversity and abundance assessments to guide conservation strategies in a landscape with increasing human needs. We provide a list of indicator species associated with various habitats, enabling targeted efforts during environmental change monitoring. Our study serves as a valuable baseline for future research on bird communities in an understudied region, and on how these are affected by different anthropogenic land uses.

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Conflict of interest — The authors declare no conflict of interest.

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