

# Understorey-nesting bird community responses to land use in the Korup National Park, an Afrotropical rainforest in South-Western Cameroon

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## ABSTRACT

Tropical forest biodiversity is under immense pressure due to a combination of global and local factors, including climate change and intensive land use. Birds play an important role in tropical forest ecosystems, contributing significantly to various ecosystem services. This study examined the impact of deforestation on the richness and abundance of understorey-nesting bird communities along a land-use intensification gradient in the peripheral zone of Korup National Park, Southwest Cameroon. We selected 30 sampling plots, each covering 4 ha, across five habitat types: near-primary forest, secondary forest, disturbed forest, cocoa/coffee plantations, and annual food crop fields. A total of 236 understorey bird nests were identified, representing 16 species. Our findings revealed that land use intensity significantly influenced bird species richness and abundance. Primary and secondary forests provided 75% of the nesting species and 71% of the nests. However, 19% of the species either appeared or increased in cocoa/coffee plantations and annual crop fields. Among the feeding groups, frugivores were the most sensitive group to deforestation. This study corroborates the adverse effects of forest destruction on birds communities and highlights the urgent need to address the rapid and extensive forest conversion occurring within Korup National Park. Allowing secondary forests to regenerate and preserving large patches of primary forest are essential strategies to help understorey-nesting bird communities mitigate the impacts of global changes.

## 1. Introduction

West African forests as part of biodiversity hotspots (Myers et al., 2000) support numerous species communities. In southern Cameroon, forests are common ecosystems that play important socio-economic and ecological roles. However, despite their importance Cameroonian tropical forests face numerous pressures (Brooks et al., 2002; Gardner et al., 2009), including deforestation due to human activities which results in habitat fragmentation and habitat loss for wildlife. The conversion of primary forest areas into cocoa and coffee plantations, along with other land use changes, has significantly impacted Cameroonian

tropical forests. Between 2010 and 2020, a study of FAO revealed a decrease of 560 000 ha in Cameroon's forest area (FAO, 2020), highlighting the need for conservation efforts to protect biodiversity in the region.

Birds represent one of the most diverse groups of ecosystem service providers, playing multiple ecological functions (Sekercioglu, 2006; Sekercioglu et al., 2016; Whelan et al., 2015). As primary consumers, birds in the tropical forest are involved in numerous ecosystem services including seed dispersal by frugivorous birds (Cordeiro and Howe, 2003); pest regulation by insectivorous birds (Railsback and Johnson, 2014); pollination by nectarivores species (Frick et al., 2014; Roels et al.,

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2019). Birds are also involved in soil formation including energy flow, nutrient cycling and soil structure (Cannon et al., 2019; Sekercioglu, 2006) and they constitute a substantial component in the local food trophic chain. Understorey-nesting birds are land birds that nest in forest lower stages, on the ground, or at a height of 2 m from the ground on shrubs or lianas depending on the species ecology (Waltert et al., 2005b).

Because they occupy various trophic levels and exhibit various habitat preferences, birds are particularly vulnerable to forest disturbances and are important indicators of environmental health (Lacko et al., 2018; Posa and Sodhi, 2006; Zou et al., 2014). Disturbance modifies communities, attracts some species while repelling others from their habitat (Posa and Sodhi, 2006). Although, it has been reported that native forest bird assemblages might be supported by extensive agroforestry systems (Awa et al., 2018; Gove et al., 2008; Lindell and Smith, 2003; Peh et al., 2005) and farmlands (Mulwa et al., 2012), for several species, habitat disturbances such as deforestation have a deleterious impact. Bird taxa groups or functional guilds generally respond differently to habitat modifications. Mulwa et al. (2012) found that insectivorous bird species decline in farmland systems whereas omnivores and herbivores increase when forests are turned into farmlands. Accordingly, numerous studies reported that species richness and the relative abundance of understorey species decrease with increasing forest degradation (Keller et al., 2003; Lindell and Smith, 2003; Naidoo, 2004; Posa and Sodhi, 2006; Schulze et al., 2004). This pattern can be attributed to the fact that the breeding nests are typically located at the lowest vegetation stage, which is the most affected stratum during forest disturbance (Vergara and Simonetti, 2003). Similarly, the composition of breeding bird communities is closely related to the composition of vegetation species (Fleishman et al., 2003) as nesting sites often rely on the presence of specific nest-supporting plants (Brand et al., 2010). This relationship highlights the potential consequences of vegetation

removing and cutting activities on breeding birds that depend on specific vegetation characteristics for nest construction as reported by Keller et al. (2003).

For these reasons, there is a growing concern about how bird species assemblages respond to changes in forests, especially in the tropics, where nesting biology have been relatively understudied in the context of habitat loss and degradation.

In this study, we aimed at investigating how understorey-nesting birds respond to habitat change in the Korup National Park, a typical Afrotropical forest, located in the South-West Region of Cameroon. This Afrotropical forest provided an ideal setting to investigate the patterns driving the community structure (diversity, richness and abundance) of understorey-nesting bird species along a land-use intensification gradient. The study area included two native forests (near-primary forest and old secondary forest) and three modified habitats (disturbed forest, agroforestry systems and annual food crops fields).

We predicted that:

- (1) Native forests would support higher overall bird nesting species richness and abundance compared to modified habitats;
- (2) Species composition of nesting bird communities in forest and modified habitats would differ, with nesting species from farmlands replacing those from forests due to their higher resilience to habitat changes;
- (3) The responses of bird communities to habitat modifications would vary among taxa and guilds, with insectivorous birds being particularly susceptible to changes in insect species community.

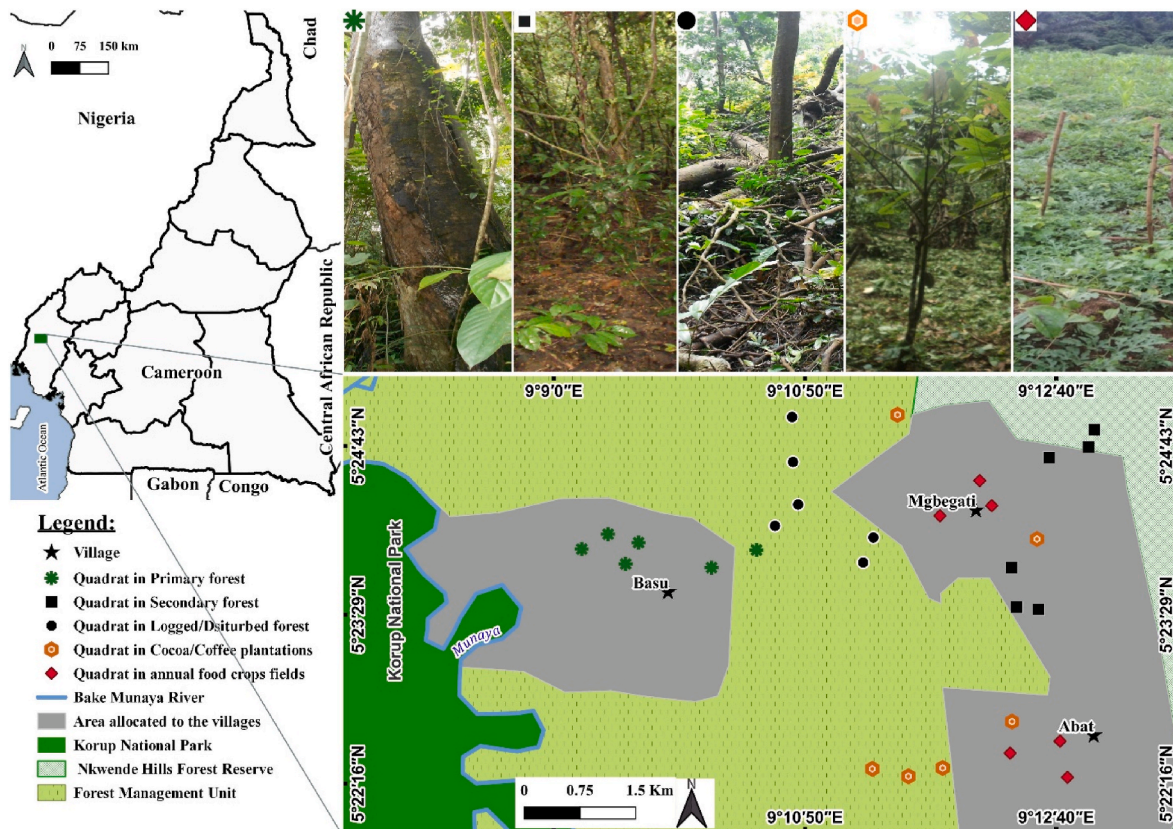


Fig. 1. Study area located in the Korup National park, an Afrotropical forest in South-Western Cameroon. Five habitats were selected along an increasing land-use intensification gradient: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

## 2. Material and methods

### 2.1. Study areas

The study was conducted in a peripheral zone bordering the Korup National Park (KNP), South-Western Cameroon (Fig. 1). The KNP is located within the Cameroon tropical forest and lies in the heart of the Guinea Congolian forest refuge. As a legal entity under the management of KNP administrators, the peripheral zone, in conjunction with the National Park, constitutes the most significant remnant of the once-vast Western Central African forest that initially spanned from the Niger Delta eastward to Cameroon and southward through Equatorial Guinea and Gabon.

The area topography is characterized by low elevations ranging from 150 to 340 m ASL. The climate is characterised by two seasons: the dry season occurring from December to February and the rainy season spanning from March to November. Four primary forest types are represented in the area, including the Atlantic Biafran Forest, the swamp forest, the Piedmont Forest and the Submontane forest (Thomas, 1995). Rubiaceae and Fabaceae tree species dominate the vegetation composition (Kenfack et al., 2007). Three permanent rivers, namely Bake-Munaya (North), Ndian (SE) and Akpasang-Korup, drain the KNP (Mbile et al., 2005). The mean annual temperature is 26.8 °C and the total annual rainfall is estimated at 3000 mm (South-West Regional Delegation for Agriculture, 2014).

A unique characteristic of the KNP is the presence of approximately 4800 indigenous residents who inhabit 28 villages within the peripheral area. These communities engage in a range of subsistence activities to sustain their livelihoods, including fishing, hunting, and cultivating food crops such as cassava, plantain, banana and cocoyam. Additionally, cash crops like cocoa, coffee, and oil palm, and various forest products are harvested (Mbile et al., 2005; Siewe et al., 2017). The diverse livelihood activities of the indigenous communities within the KNP peripheral zone reflect their deep-rooted connection to the land and its resources. These practices not only contribute to their subsistence but also play a role in local economies, cultural traditions, and social structures. In addition, the peripheral zone of the KNP has experienced active forest exploitation for timber production in the Forest Management Unit area (see Fig. 1), with minimal management by the park authorities in this region.

The avifauna of the study area is typical of lowland rainforests, as reported by Fishpool et al. (2001). Rodewald et al. (1994) documented around 420 bird species in the region, a finding later corroborated by Bobo et al. (2005). Fishpool et al. (2001) identified 184 species that are exclusively restricted to this biome. Dominant taxa groups within the avifauna include flycatchers (Muscicapidae), Old World warblers (Sylviidae), bulbuls (Pycnotidae), sunbirds (Nectariniidae), and weavers (Ploceidae) (Bobo et al., 2005; Rodewald et al., 1994). Although the avifauna may be affected by the activities of the indigenous communities living within the KNP, the present study focuses specifically on the impacts of land cover changes.

### 2.2. Experimental design

Samplings of understorey-nesting bird nests were conducted in area surrounding Mgbegati, Abat and Basu villages (between 5°21'18"-5°25'38" N and 9°06'29"-9°15'07" E) (Fig. 1). These sites were strategically chosen along a deforestation gradient.

First, we selected five habitats representing the deforestation gradient as follow: (1) Primary Forest (PFO) consisting of pristine primary forests with about 570 trees/ha (Waltert et al., 2005b) free of any anthropogenic activities; (2) Old secondary forest (SFO) consisting of an old secondary forest with about 530 trees/ha (Waltert et al., 2005b) and experiencing only minimal anthropogenic activity; (3) Primary logged/disturbed forest (DFO) where selective logging was undertaken within the five years prior to the study; (4) Cocoa/coffee plantations (CCP) with about 377.8 trees/ha (cocoa/coffee trees excluded) (Waltert

et al., 2005b), characterized by intensive cocoa, coffee, and plantain production, and subject to regular clear-cutting activities and chemical treatments taking place three times per year; (5) Annual food crops fields (ACF) with about 107.8 trees/ha (Waltert et al., 2005b) where the land is used for cultivating subsistence food crops.

Secondly, we considered each habitat type (PFO, SFO, DFO, CCP and ACF) as a distinct stratum. Due to the irregular distribution of habitats in the study area, we established six 200 m × 200 m plots within each stratum, totalling 30 plots. This approach was based on a trial methodology (Scherrer et al., 2009), with a minimum distance of 500 m between plots to minimize spatial dependencies (Bobo, 2007) (Fig. 1).

### 2.3. Data collection

From April to August 2013, we conducted systematic nest searches and observed adult bird behaviour five days per week within the sampling plots. Nests were recorded in vegetation at least 2 m high to document the presence and distribution of adult birds. To facilitate the relocation of nest during subsequent monitoring, flags were placed at least 5 m from the nest following method suggested by Dion et al. (2000). The nests were monitored every three days until either nest failure or successful fledging of the nestlings, as recommended by Buler and Hamilton (2000).

Bird species were identified and classified using a combination of field guides and reference books (Borrow and Demey, 2001; Fry et al., 1988, 2000; Fry and Keith, 2004; Keith et al., 1992; Serle and Morel, 1977). Each species was assigned to a dietary functional group as previously described (Del Hoyo et al., 2019), resulting in four primary dietary groups: Omnivores, insectivores, frugivores, and nectarivores. Nest were not assigned to species based solely on nest records, as the guides did not provide sufficient or clear nest templates for understorey-nesting birds. Instead, nests were categorized as "Open" (cup or plate-shaped) or "Enclosed" (pouch or dome-shaped). Only understorey-nesting bird species breeding during the sampling period were included in the study. Additional information on bird sampling can be found in a companion study (Tonleu et al., 2018).

### 2.4. Data analysis

Because no single index can adequately describe all aspects of community structure, we used a combination of those that reflect richness, diversity, dominance and evenness (Magurran and McGill, 2011; Tsafack et al., 2019).

We used three indices (Fisher, Shannon and Simpson indices) to express the diversity of the understorey-nesting bird nests, following the standard formulas (Gotelli and Chao, 2013; Magurran and McGill, 2011). Richness of nests was assessed using the abundance-based coverage estimator (ACE) and Chao-1 (Gotelli and Chao, 2013) indices.

We calculated dissimilarity in understorey-nesting bird nests community composition between habitats and between sites of the same habitat using Sørensen index (SI) (Magurran and McGill, 2011). Indices and estimators were computed using R packages "vegan" version 2.6-2 (Legendre and Legendre, 1998; Oksanen et al., 2013), "BiodiversityR" (Kindt and Kindt, 2019) and "MASS" (Ripley et al., 2013).

We used a generalized linear models (GLM) to examine the relationships between different habitat types and nest species diversity, richness, evenness, and abundance (Dobson and Barnett, 2018). Our model formula,  $NestSpeciesIndex \sim habitat-1$ , allowed us to assess the individual effects of all five habitats in the model summary. When the distribution of the species index or its log transformation did not follow normal distribution, we specified Poisson family. And where necessary, we used a Negative binomial model to correct overdispersion of residuals in the Poisson model. Therefore, we conducted GLMs using the default Gaussian family for response variables with normal distributions (Diversity Shannon and Diversity Simpson indices) and we applied log-transformation to Richness ACE and Richness Chao1 indices

distributions to achieve normality. The distributions of number of nests within feeding groups did not conform to normality even after transformation, we used the Poisson family. In the case of distributions of the total number of nests, Diversity Fisher's  $\alpha$ , and Pielou evenness indices, we used negative binomial models to correct overdispersion in Poisson GLM.

Two-Dimensional correspondence analysis was used to visualize similarities among nesting bird communities in different habitat types using the *ordihull* (convex hulls) and *ordiellipse* (ellipsoid hulls) functions in the R package "vegan" version 2.6–2 (Legendre and Legendre, 1998; Oksanen et al., 2013). A one-way multiple analysis of variance (MANOVA) was performed to compute differences between bird groups (e.g. those preferring natural forests vs those preferring disturbed habitats) across different habitats (Krzanowski, 1988). All analyses were conducted with the statistical software R (R Core Team, 2021).

### 3. Results

Our study identified a total of 236 nests of understory nesting birds representing 16 species belonging to two families, Nectariniidae (19 nests) and Pycnonotidae (137 nests) (Table 1). The remaining 80 nests were attributed to four unidentified species. GLM showed a significant effect of the type of habitat on the distribution of the total number of nests, all habitats were significantly important ( $P < 0.0001$ ) to explain the variability of the number of nests except the cocoa/coffee plantations habitat (Table 2). Secondary forest (SFO) exhibited the highest number of nests, with 8 and 61 nests belonging to Nectariniidae and Pycnonotidae respectively. In contrast, Cocoa/Coffee plantations (CCP)

**Table 1**

Total number of nests and bird species sampled in the five habitats. In parentheses N and P represent families respectively Nectariniidae and Pycnonotidae; f, i, n and o represent trophic group respectively frugivores, insectivores, nectarivores and omnivores. Habitat types: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields. For each habitat, the total number of nests (N) and the number of species observed (S) are specified.

Family	Species	PFO (N = 70; S = 12)	SFO (N = 97; S = 12)	DFO (N = 47; S = 9)	CCP (N = 7; S = 4)	ACF (N = 15; S = 5)
Nectariniidae	<i>Cinnyris chloropygius</i> (N, n)	3	4	0	0	5
Nectariniidae	<i>Cyanomitra olivacea</i> (N,n)	1	4	2	0	0
Pycnonotidae	<i>Arizelocichla montana</i> (P,o)	0	0	0	1	2
Pycnonotidae	<i>Bleda eximius</i> (P,i)	1	8	1	0	0
Pycnonotidae	<i>Bleda notatus</i> (P,i)	2	9	4	0	0
Pycnonotidae	<i>Chlorocichla flavicollis</i> (P,f)	5	4	1	0	0
Pycnonotidae	<i>Crimiger chloronotus</i> (P, i)	1	0	0	0	0
Pycnonotidae	<i>Eurillas ansorgei</i> (P,o)	0	1	0	0	0
Pycnonotidae	<i>Eurillas latirostris</i> (P,o)	13	8	9	3	0
Pycnonotidae	<i>Eurillas virens</i> (P,o)	12	26	8	0	1
Pycnonotidae	<i>Nicator chloris</i> (P,i)	2	4	3	1	6
Pycnonotidae	<i>Phyllastrephus icterinus</i> (P,i)	0	1	0	0	0
-	Unknown sp1	3	1	3	0	0
-	Unknown sp2	26	27	16	0	1
-	Unknown sp3	0	0	0	2	0
-	Unknown sp4	1	0	0	0	0

**Table 2**

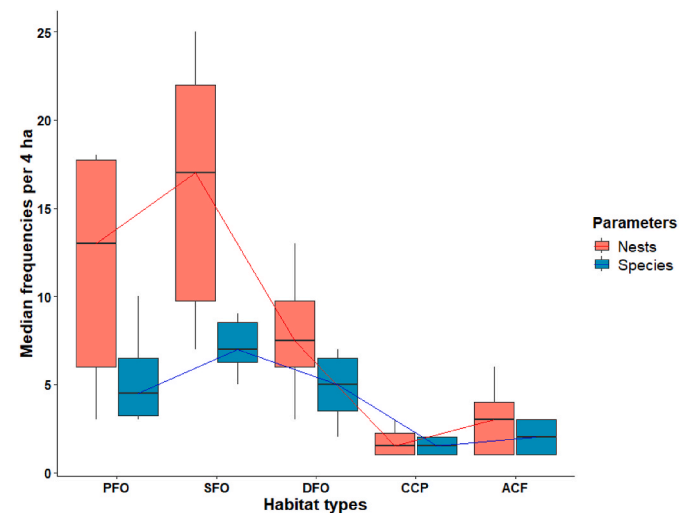
Results of generalized linear models (GLMs) for total number of nests, number of nests grouped by feeding guilds and diversity and richness indices in the different habitats. Estimates  $\pm$  Standard error of each habitat are presented. Model AIC and the variance explained by the different habitats ( $R^2$ ) are also presented. Significant effects are marked with the following the significance codes: 0 '\*\*\*\*' 0.001 '\*\*\*' 0.01 '\*\*' 0.05 '.' 0.1 '.' 1

Habitat types: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

Models	PFO	SFO	DFO	CCP	ACF	AIC ( $R^2$ )	
Total number of nests	2.46 $\pm$ 0.20***	2.78 $\pm$ 0.18***	2.06 $\pm$ 0.21***	0.56 $\pm$ 0.42	1.10 $\pm$ 0.31***	155.32 (0.95)	
<b>Diversity and Richness indices</b>							
Diversity	1.35 $\pm$ 0.29***	1.66 $\pm$ 0.27***	1.90 $\pm$ 0.26***	-0.83 $\pm$ 0.65	0.56 $\pm$ 0.37	136.37 (0.76)	
Fisher's $\alpha$	1.38 $\pm$ 0.17***	1.66 $\pm$ 0.17***	1.38 $\pm$ 0.17***	0.22 $\pm$ 0.17	0.45 $\pm$ 0.17*	39.16 (0.90)	
Diversity	0.69 $\pm$ 0.08***	0.76 $\pm$ 0.08***	0.70 $\pm$ 0.08***	0.16 $\pm$ 0.08	0.28 $\pm$ 0.08**	-5.24 (0.91)	
Diversity	1.98 $\pm$ 0.31***	2.52 $\pm$ 0.31***	2.17 $\pm$ 0.31***	0.23 $\pm$ 0.31	0.81 $\pm$ 0.31*	75.65 (0.87)	
Estimator ACE	2.04 $\pm$ 0.20***	2.26 $\pm$ 0.20***	1.87 $\pm$ 0.20***	0.65 $\pm$ 0.20**	0.88 $\pm$ 0.20***	49.09 (0.93)	
Richness	Chao1	-0.12 $\pm$ 0.43	-0.12 $\pm$ 0.43	-0.07 $\pm$ 0.43	-1.14 $\pm$ 0.72	-0.77 $\pm$ 0.60	64.23 (0.34)
Pielou evenness	<b>Feeding groups</b>						
Frugivores	-0.18 $\pm$ 0.45	-0.41 $\pm$ 0.50	-1.79 $\pm$ 1	-19.30 $\pm$ 3.8e3	-19.30 $\pm$ 3.8e3	43.62 (0.64)	
Insectivores	0.00 $\pm$ 0.41	1.30 $\pm$ 0.21***	0.29 $\pm$ 0.35	-1.79 $\pm$ 10	0.00 $\pm$ 0.41	92.90 (0.45)	
Nectarivores	-0.41 $\pm$ 0.50	0.29 $\pm$ 0.35	-1.10 $\pm$ 0.71	-19.30 $\pm$ 3.8e03	-0.18 $\pm$ 0.45	60.60 (0.46)	
Omnivores	1.43 $\pm$ 0.20***	1.76 $\pm$ 0.17***	1.04 $\pm$ 0.24***	-0.41 $\pm$ 0.50	-0.69 $\pm$ 0.58	121.31 (0.71)	

had the lowest number of nests, with only 5 from Pycnonotidae family and none from Nectariniidae family (Table 1, Fig. 2). Overall, 8% of the nests were classified as "Enclosed", while 92% were classified as "Open" nests.

All nests were positioned at least 1 cm above ground level. *Eurillas virens* was the most prevalent species, occupying 47 nests across all habitats except in CCP. In contrast, *Chlorocichla flavicollis*, *Crimiger*



**Fig. 2.** Differences in the median frequencies of nests and species among the five habitats. Habitat types: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

*chloronotus* and *Phyllastrephus icterinus* were the least abundant species, with each observed in only one nest within the PFO habitat for *C. flavicollis*, and in the SFO habitat for *C. chloronotus* and *P. icterinus* (Table 1).

3.1. Variation of community structure between forest habitats

We observed significant impact of the type of habitat on bird species diversity among the different habitats (Table 2). Across all three diversity indices (Fisher, Shannon and Simpson), cacao/coffee plantations (CCP) exhibited the lowest diversity (Table 3) and non-significant effect (Table 2), followed by annual culture farms habitat (ACF) habitat (Table 3) which was however significant for Shannon and Simpson indices but not for Fisher diversity index (Table 2).

The forest habitats (Primary – PFO; Secondary – SFO and Disturbed – DFO) showed high diversity levels and strong significance for all three diversity indices, although the order varied depending on index used.

For the Fisher diversity index, the order of diversity levels was PFO < SFO < DFO, while for the Shannon diversity index, the order was DFO = PFO < SFO ( $p < 0.0001$ ). For the Simpson diversity index, the order was PFO < DFO < SFO ( $p < 0.0001$ ).

Both ACE richness estimator and Chao richness indices revealed significant variations in bird species richness between habitats (Table 2). The observed order of species richness was SFO < PFO < DFO < ACF < CCP. Almost all recorded species (12 over 16) were present in primary and secondary forests, whereas only four species were observed in cacao/coffee plantations (Table 1).

Although there were no significant differences in evenness values between habitats, CCP showed the lowest value and DFO had the highest evenness value (Tables 2 and 3).

3.2. Variation of feeding groups between habitats

The nests found belonged to nesting birds from four feeding groups. Frugivores, insectivores, nectarivores and omnivores. The omnivorous group was most represented with 84 nests, while the frugivores group was the poorest with only 10 nests (Table 4). The distribution of feeding groups was not uniform across habitats. The secondary forest (SFO) habitat had the highest number of nests for insectivores, nectarivores and omnivores. However, due to the low number of frugivores nests, no significant differences were observed between habitats (Table 2).

3.3. Species similarities between sampling stations (beta diversity)

Pairwise dissimilarity analysis of bird species composition between sites of the same habitats showed higher values for disturbed forest (DFO) sites ( $0.40 \pm 0.19$ ) and primary forest (PFO) sites ( $0.39 \pm 0.12$ ), slightly lower value for secondary forest (SFO) sites ( $0.36 \pm 0.11$ ) and annual food crops field (ACF) sites ( $0.37 \pm 0.34$ ); and the lowest for cacao/coffee plantations (CCP) sites ( $0.27 \pm 0.40$ ).

Comparing bird species composition between habitats, high dissimilarity values were observed between DFO and ACF ( $0.69 \pm 0.08$ ), PFO and ACF ( $0.68 \pm 0.12$ ), SFO and ACF ( $0.61 \pm 0.11$ ) and SFO and CCP

Table 3

Mean diversity (Fisher's  $\alpha$ , Shannon and Simpson indices), richness (ACE and Chao1 indices) and evenness (Pielou index) values in the five habitats. Habitat types: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

	PFO	SFO	DFO	CCP	ACF
Diversity Fisher's $\alpha$	3.851	5.259	6.717	0.437	1.744
Diversity $H_s$ (Shannon)	1.384	1.661	1.383	0.222	0.448
Diversity Simpson	0.687	0.762	0.699	0.157	0.28
Richness Estimator ACE	10.454	12.114	8.904	0.5	2.1
Richness Chao1	7.583	9.111	6.167	1.661	1.667
Pielou evenness $H_s/\ln S$	0.883	0.883	0.93	0.32	0.464

Table 4

Number of understorey bird nests per family and feeding group in the different habitats. Habitat types: PFO - Primary forest, SFO - secondary forests, DFO - disturbed forests, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

	PFO	SFO	DFO	CCP	ACF	Total
Family						
Nectariniidae	4	8	2	0	5	19
Pycnonotidae	36	61	26	5	9	137
Feeding group						
Frugivores	5	4	1	0	0	10
Insectivores	6	22	8	1	6	43
Nectarivores	4	8	2	0	5	19
Omnivores	25	35	17	4	3	84

Unidentified species were excluded.

( $0.59 \pm 0.08$ ). Intermediate dissimilarity was observed between PFO and CCP ( $0.52 \pm 0.08$ ) and between DFO and CCP ( $0.51 \pm 0.09$ ). The lowest Sørensen incidence values were detected between CCP and ACF ( $0.48 \pm 0.42$ ), PFO and SFO ( $0.46 \pm 0.14$ ), DFO and SFO ( $0.46 \pm 0.13$ ), and PFO and DFO ( $0.37 \pm 0.12$ ).

A Two-dimensional ordination derived from correspondence analysis indicated overlapping communities between PFO, SFO and DFO, forming a group while CCP and ACF communities exhibited slight overlap but remain distinct from the first group (Fig. 3). A one-way MANOVA performed on sample scores extracted from the two-dimensional ordination showed significant difference between the five habitats ( $F = 7.5526, p < 0.001$ ).

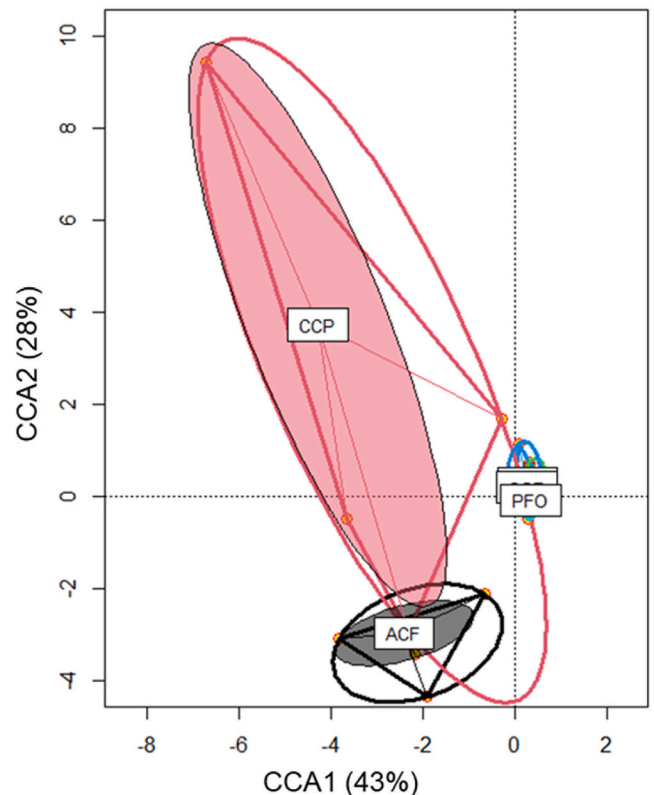


Fig. 3. Correspondence analysis biplot presenting community similarity among understorey-nesting birds sampled in the five habitats. Analysis is based on abundance data. Habitat types: Forested habitats PFO - Primary forest, SFO - secondary forests and DFO - disturbed forests overlapped, CCP - cocoa/coffee plantations and ACF - annual food crop fields.

#### 4. Discussion

We investigated how understorey-nesting birds community structure and composition change along a deforestation gradient. We found that forested habitats support richer and more abundance bird community compared to cultivated habitats. We also found that understorey-nesting birds pertained to four feeding groups which were frugivores, insectivores, nectarivores and omnivores. Our analyses of Beta diversity showed similarities between the three less disturbed habitats (forested habitats) while the two heavily modified habitats, cocoa/coffee plantations and annual crop fields were separated.

##### 4.1. Variation of community structure between forest habitats

As predicted, undisturbed forested sites host a greater abundance and species richness of nesting birds compared to than heavily modified habitats. Disturbed forests, cocoa/coffee plantations and annual food crop fields exhibit high turnover, which disrupt bird nesting and result in reduced numbers of bird individuals and species in these habitats. In contrast, the presence of nest-supporting plant species in natural forests (primary forest and old secondary forest) provide essential habitat for nesting birds (Brand et al., 2010; Pasinelli et al., 2016), promoting higher levels of birds diversity and abundance. This trend is consistent with previous studies conducted in tropical forests of South China (Zou et al., 2014), North Indonesia (Sodhi et al., 2005), the Ituri Forest in former Zaire (Plumptre, 1997), and new Guinea (Marsden et al., 2006). These studies reported a decreasing trend in forest birds species richness, species density and population density along a gradient of increasing perturbation. Similarly, Zou et al. (2014) found higher bird richness and capture rate in natural forests compared to modified habitats. However, some studies reported higher bird diversity in modified habitats than in natural forests (Mulwa et al., 2012; Neuschulz et al., 2011). This discrepancy may be attributed to the increased vegetation structural heterogeneity in disturbed habitats, providing a greater variety of micro-habitats and ecological niches for bird species (Gomes et al., 2008; Gove et al., 2008; Mulwa et al., 2012).

Contrary to expectations, our study revealed that bird communities in annual food crop fields are more diverse than those in cocoa/coffee plantations among heavily modified habitats. This surprising finding can be attributed to the heterogeneity of landcover that we observed in annual crop fields, which supports a wider range of bird species. While annual crop fields exhibit high turnover, they provide more diverse habitats compared to cocoa/coffee sites, which are predominantly monocultures despite their evergreen nature. However, this result may be unique to our study site as cocoa/coffee plantations are generally considered to harbour a higher diversity of species, just below that of the forest systems (Estrada et al., 1997).

Many studies investigating bird diversity along a gradient of increasing forest destruction have shown that some species groups such as the bulbuls (particularly *Eurillas* spp.) and some flowerpeckers are well adapted to habitat modification (Johns, 1996). This suggests that the extent of disturbance can play a crucial role in determining bird species richness and abundance as birds have different ecological requirements and different levels of sensitivity to environmental changes (Gomes et al., 2008; Lawton et al., 1998). In this study, 75% of species monitored decreased substantially or disappeared along the disturbance gradient from natural forests to modified habitats (PFO > SFO > DFO > CCP > ACF), while 19% of species appeared or increased, and 6% of species showed no clear pattern in response to disturbance. In Indonesia, numerous bird species recorded in the tropical forest have also been severely affected by forest conversion into agroforests, with only a limited number of species benefiting from this modification (Thiollay, 1995). In contrast, a study in Cameroon's tropical forests by Lawton et al. (1998) found that about 66–80% of the bird species observed in the most disturbed sites were not present in natural forests, whereas, Gomes et al. (2008) realised that 83% of native birds species inhabited in all

disturbed habitats. The persistence of the forest species in such areas can be influenced by their species-specific ecological traits or behaviours (Naidoo, 2004; Sodhi et al., 2005). Notably, Waltert et al. (2005a) found that *Eurillas latirostris*, an omnivorous species belonging to the Pycnonotidae family, showed a preference for secondary forests and agroforestry systems. Interesting, our study revealed a preference for nesting in primary forest, which could be attributed to availability or abundance of suitable nest sites, a key factor in passerine habitat selection (Steele, 1993). Interestingly, while diversity indices generally followed the disturbance gradient, with higher values in primary forests (PFO > SFO > DFO > CCP > ACF), secondary forests exhibited higher richness (for both Chao and ACE richness indices). This indicates that secondary forests provide even more favourable habitats for species occurrence, though slightly less so for species population establishment, as abundances were higher in primary forest sites.

##### 4.2. Understorey-nesting bird guilds and families responses to habitat destruction

Our results indicate that nesting-frugivores are the most adversely impacted by forest modification because they rarely construct their nests in disturbed habitats. The primary food source for frugivores, fruits, is largely found on trees however, habitat modifications in our study area often involve a shift from highly diverse tree systems to open monoculture crop fields or Cocoa/Coffee plantations, resulting in diminished food availability for these species. Frugivorous birds contribute significantly to seed dispersal, facilitating forest regeneration and maintaining plant diversity. Our result suggests that the absence of essential resources such as fruit-bearing trees and appropriate nesting sites in heavily modified habitats may limit the survival of nesting frugivores, highlighting the critical need to preserve intact forests for their conservation.

In addition, we found a consistent decrease in the abundance of nectarivores/Nectariniidae, insectivores, omnivores and pycnonotids from natural forests to modified habitats. This result supports previous research in both tropical (Plumptre, 1997; Waltert et al., 2005b) and subtropical ecosystems, where insectivores have been identified as one of the most sensitive guilds to forest conversion (Mulwa et al., 2012; Tschamtké et al., 2008). Particularly, our results suggest that secondary forests tend to provide superior nesting habitats than primary forests for all groups except frugivores. This is probably due to the higher diversity of habitats found in secondary forest compared to primary forest. Agroforests have been found to support high abundance of nectarivores (Tschamtké et al., 2008; Waltert et al., 2005a), frugivores (Tschamtké et al., 2008) and omnivores (Greenberg et al., 2000; Thiollay, 1999). Consistent with our results, Waltert et al. (2005a) also observed a significant decline in pycnonotids populations in response to increasing habitat destruction within the same study area.

##### 4.3. Understorey-nesting bird communities turnover along the forest destruction gradient

The pairwise dissimilarity of understorey-nesting bird communities highlights an overlap in species composition among forest habitats, as well as between the heavily modified habitats communities (CCP and ACF). This suggests that certain native understorey-nesting bird species, such as frugivores *Chlorocichla flavicollis* may be intolerant of habitat modification and are replaced by other bird communities like some pycnonotids (*Arizelocichla montana*, *Nicator chloris* and *Cinnyris chloropygius*) in heavily modified habitats. This difference in species composition can be attributed primarily to the high turnover of habitat guilds along the gradient of increasing forest destruction (Mulwa et al., 2012). Our observations contrast with those of Fleishman et al. (2003), where similarities in breeding birds species composition were observed between sites.

Studies in other tropical forests environments have showed that

certain understorey species such as *Culicicapa ceylonensis*, *Rhipidura perlata*, *Philentoma velatum* and *Rhinomyias umbratilis*, appear to be intolerant of forest destruction (Johns, 1996; Mulwa et al., 2012; Posa and Sodhi, 2006; Thiollay, 1995). Species composition has also been shown to change significantly in response to modified environmental conditions (Gove et al., 2008; Marsden et al., 2006; Neuschulz et al., 2011). These alterations in species abundance, composition and functional diversity serve as important indicators of human disturbance on ecosystems (Neuschulz et al., 2011). In the current study area, the continuous changes in forests species from site to site along the gradient of forest destruction can be attributed to the gradual replacement of lost forest-dependent species by species typical of open habitats (Waltert et al., 2005a).

This study reveals that the nests found in various habitats within the peripheral zone of Korup National Park belong to different bird species with distinct nesting sites requirements. Our findings indicate an important decline in species richness and abundance of understorey-nesting birds and nesting sites along the gradient of increasing forest destruction. However, some nesting bird species display resilience to habitat disturbance, resulting in the emergence of two separate communities: forest-nesting bird communities (including near primary forest, secondary forest, and disturbed forest) and heavily modified habitat-nesting bird communities (comprising cocoa/coffee plantations and annual culture farms). Although the study indirectly suggests evidence that selective logging in secondary and disturbed forests has a relatively minor negative impact on native understory-nesting bird species, implementing reduced-impact logging techniques in the region remains crucial for preserving nesting sites.

Despite past disturbances, it is essential to acknowledge that resources and diverse microhabitats persist in open canopy forest. Moreover, our study suggests that regenerating secondary forests and near primary forests can improve understorey-nesting bird species richness and abundance. A potential limitation to this study is its focus on nesting birds, as other bird species may utilize habitats for various functions. To gain a comprehensive understanding of bird community dynamics in response to habitat changes, future research should consider examining a broader range of bird species in the Korup National Park.

#### CRediT authorship contribution statement

**Jean Tonleu:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Noelline Tsafack:** Writing – review & editing, Writing – original draft. **Kadiri S. Bobo:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Sebastien Lhoumeau:** Writing – review & editing. **Wilfried G.T. Lontchi:** Methodology, Data curation. **Cyrille L.T. Tanebang:** Methodology, Investigation, Data curation. **Mpoame Mbida:** Writing – original draft, Validation, Supervision, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Data availability

Data will be made available on request.

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