

Interactive effects of elevation and newly paved road on avian community composition in a scientific reserve, Bioko Island, Equatorial Guinea

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Abstract

Understanding interactive effects between anthropogenic disturbance and abiotic factors on species turnover can help to identify and prioritize conservation of potentially vulnerable tropical bird communities. We investigated the potential factors influencing avian understory community composition along with a recently constructed road across three elevations (300, 800, and 1200 m), each with two sampling sites (road edge vs. interior forest), over a four-year period on Bioko Island, Equatorial Guinea. Insectivorous species were the most abundant guild-sampled accounting for 55% of total species diversity within the dataset followed by frequent mixed-flock followers (48%). Habitat associated with elevation was the most significant factor influencing the composition of avian communities. Additionally, we identified species with clear statistical associations for each elevation: the yellow-lored bristlebill (*Bleda notatus*), olive sunbird (*Cyanomitra obscura*), and white-tailed warbler (*Poliolias lopezi*). We found evidence for significant community differences between the disturbance edge and interior forest transects at 300 m only. Likewise, understory insectivores were found at higher numbers within the interior forest transect at this elevation. Based on the data presented here, we suggest low elevation avian understory insectivores should be considered focal species for future assessment studies in this area. Furthermore, since many traditional protected areas focus on upland habitat containing high species endemism, our findings emphasize the importance of equally conserving lowland elevations as they may house commonly overlooked, yet important and diverse segments of the bird community.

Abstract in Spanish is available with online material.

KEYWORDS

anthropogenic disturbance, conservation management, elevational gradient, ornithology, West Africa

1 | BACKGROUND

Elevational gradients are a major factor-shaping community assemblages and species distribution in the tropics, as first postulated by Janzen (1967). Although Janzen correctly predicted that abiotic influences—such as topography and climate—affect species distributions, researchers have since recognized that biotic interactions, such as territorial disputes and trophic cascades, likely restrict distributions across elevational gradients as well (Ghalambor et al., 2006; Jankowski et al., 2010). Several studies have examined how elevation and associated factors shape global species-distribution patterns among a variety of taxa (Blake & Loiselle, 2000; Jankowski et al., 2009; Lomolino, 2001; McCain, 2009). However, the effects of anthropogenic disturbance on these species-distribution patterns along elevational gradients are less well-studied. Anthropogenic disturbance (e.g., new road construction) can lead to various changes in biodiversity and ecosystem processes via alteration of soil quality, vegetation composition, tree cover, carbon sequestration, and water sheds (Becker et al., 2007). Along an elevational gradient, range restrictions and high species endemism can leave species more vulnerable when challenged by habitat disturbance associated with anthropogenic activity (Lee et al., 2005; Young et al., 1998). Thus, understanding interactive effects of elevation and disturbance on species distributions is essential for conservation management, particularly in regions experiencing high levels of anthropogenic activity.

Ninety percent of new road construction occurs in developing regions (Laurance et al., 2017), where countries often face trade-offs between economic growth and biodiversity conservation, rarely resulting in win-win scenarios (McShane et al., 2011). For instance, the recent Chinese trade route expansion project, the “Belt and Road Initiative” (also known as the “New Silk Road”), will promote infrastructure expansion, commerce and economic growth between approximately 64 nations. However, this endeavor will likely yield negative consequences for protected areas and a host of associated threatened and endangered species within the region (Ascensão et al., 2018; Li & Shvarts, 2017). Similarly, many African nations have extensive plans that will dramatically increase the number of roads in environmentally sensitive locations and protected areas (Mahmoud et al., 2017; Sloan et al., 2017). Whereas roads can benefit human populations, they almost inevitably have negative impacts on forest-dependent wildlife through habitat loss, degradation and fragmentation (Andrews et al., 2008; Balkenhol & Waits, 2009; Berthinussen & Altringham, 2012; Coffin, 2007; Laurance et al., 2007, 2014; Lunt & Spooner, 2005). Moreover, roads provide access to previously inaccessible areas, facilitating (often illegal) hunting and transport of forest resources to urban areas (Laurance et al., 2007; Young, 1994). The largely negative consequences of road construction for forest wildlife can affect a myriad species; however, some trends might be more discernible than others.

A major challenge with evaluating the effects of environmental disturbance is the ability to verify if and how habitat degradation is occurring. Tracking temporal abundance trends of species that

are associated with specific habitat types can aid in assessing overall habitat quality and ecosystem health (Carignan & Villard, 2002; Lindenmayer, 1999; McGeoch & Chown, 1998; Niemi & McDonald, 2004). Specifically, monitoring trends in species turnover within associated habitats can aid identification of community assemblage shifts. Birds are commonly used to help identify specific habitats of conservation priority within high-risk areas since they are relatively easy to survey (Gregory & van Strien, 2010), ubiquitous in nature and occupy elevated positions within the food web (Smits & Fernie, 2013).

Avian taxa can be affected by new road construction in various ways, with some species exhibiting high sensitivity and others less adversely affected (Benítez-López et al., 2017; Coffin, 2007; Develey & Stouffer, 2001; Laurance & Gomez, 2005; Laurance, Stouffer, & Laurance et al., 2004). In the Neotropics, negative consequences related to road disturbances are, especially pronounced among terrestrial insectivores (birds that walk on the forest floor), and birds associated with insectivorous mixed-species flocks (Mokross et al., 2014; Powell et al., 2015); conversely, species with diverse dietary preferences are often capable of persisting in degraded forests and forest edges (Wolfe et al., 2015). Understory birds are negatively impacted by habitat fragmentation caused by road construction, which may act as a barrier to flock movement (Avalos & Bermúdez, 2016; Develey & Stouffer, 2001). Although birds are capable of long-distance movement based on the ability of flight, experimental evidence suggests that many rainforest birds are incapable of traveling >100 m in a single flight (Moore et al., 2008), and even common rainforest species can become genetically isolated by disturbance over relatively short distances (Woltmann et al., 2012). Laurance et al. (2004) found that roads were a significant deterrent to Amazonian bird movement in the forest understory, specifically for forest-dependent insectivores and solitary species. Ecological specialization has been identified as a predictor of vulnerability to habitat fragmentation (Powell et al., 2015; Sekercioglu, 2002), exemplified by certain fragmentation-sensitive understory bird species, which are particularly susceptible to road edge effects (e.g. Laurance & Gomez, 2005; Laurance et al., 2004).

In developing regions with high rates of biodiversity such as Africa, it is important to understand how anthropogenic activity may affect local wildlife populations. For example, in South Africa, pollinating birds were less likely to visit flowers closer to the road edge irrespective of plant density or color, resulting in a two-fold decrease in pollination rates (Geerts & Pauw, 2011). Bird mortality was markedly high (1.14 birds/100 km) along a main road in southern Kalahari, South Africa, demonstrating another potential deleterious consequence of road construction on bird communities (Bullock et al., 2011). However, not all effects of road disturbance on bird communities trend negative. For example, Fairbanks (2004) found a positive relationship between bird species richness and structural habitat change (e.g., infrastructure expansion) due to high intensity human land-use in South Africa. This was potentially due to persistence of birds associated with specific vegetation types in undisturbed fragments within highly disturbed landscapes, in addition to exploitation

of disturbed areas by opportunistic bird species (Fairbanks, 2004). Thus, the magnitude and direction of effects associated with anthropogenic disturbance on bird communities can vary greatly depending on the type of disturbance and species affected.

Ecological effects related to disturbance can be exacerbated due to the interaction between anthropogenic activity and topography (Becker et al., 2007; Marini et al., 2009). There exist few data with which to understand the effects of road construction on Afrotropical birds along an elevational gradient. Despite the paucity of information, lessons can be learned from other tropical ecoregions. One such study by Shipley (2017) found an indistinct relationship between elevation and bird community composition in Santa Fe National Park, Panama; however, the data revealed a significant negative relationship between bird family diversity and disturbance levels along the elevational gradient. Specifically, family diversity was highest in high elevation sites and areas with low levels of disturbance, suggesting that bird communities may be more susceptible to anthropogenic activity at the family level (Shipley, 2017). These results indicate that the combination of elevation and disturbance can have varied effects on bird distributions, particularly at the group level. Thus, it is possible that species grouped by similar ecological traits could exhibit similar patterns of sensitivity to disturbance across an elevational gradient. However, more research is needed to better understand the effects of such interactions, particularly in developing regions where intensifying infrastructure expansions are increasingly threatening the protected areas.

We conducted the first multi-year assessment of understory avian communities along a previously undisturbed elevational gradient, now containing a newly constructed road, through the Gran Caldera Scientific Reserve (GCSR) on Bioko Island, Equatorial Guinea. Due to its previous inaccessibility, the GCSR has historically experienced minimal anthropogenic pressures (from logging, mining, conversion of forests for widespread agriculture, and human population growth) relative to protected areas on the African mainland. Thus, it is important to identify key factors governing avian distributions within the region to help mitigate effects of current and future anthropogenic disturbance. In this study, our main objectives were to: (a) compare understory avian species richness, abundance, and community composition between roadside and interior forest transects at three elevations, (b) determine if these indices were significantly impacted by an interaction between anthropogenic activity and topography, and (c) identify species that are representative of specific habitat types across elevations.

2 | METHODS

2.1 | Study area

The Gulf of Guinea is recognized as one of the most biologically diverse regions in the world and has been classified as one of the 25 global diversity hotspots of conservation concern (Jones, 1994;

Mittermeier et al., 2011; Myers et al., 2000). This area extends from the coastal forests along the Bight of Biafra from the Niger River in Nigeria eastward to the forested plateaus of the Cameroon Highlands and southward to the Sanaga River in Cameroon. Furthermore, this region is characterized by high species endemism and species richness across multiple taxa such as primates (Oates et al., 2004), amphibians (Lawson, 1993; Schiøtz, 1999), butterflies (Larson, 1997), dragonflies (Vick, 1999), fish (Reid, 1989), and birds (Lotz, 2013).

Bioko Island, Equatorial Guinea, is the largest island (2017 km²) in the Gulf of Guinea and is located approximately 37 km off the coast of Cameroon (Figure 1). Almost 50% of the island is designated as protected areas including the GCSR (510 km² of land area), which covers the southern 30% of Bioko Island. Over 200 avian species have been recorded on the island (Lepage, 2021), with four new species recently documented (Cooper et al., 2017). Currently, only two bird species are endemic to Bioko, *Zosterops brunneus* and *Batis poensis* (Borrow & Demey, 2014), but evidence suggests that up to 46 endemic subspecies may be present on the island (Eisentraut, 1973), some of which may be split into full species. Furthermore, at least six bird species with restricted ranges occur on Bioko, emphasizing the importance of this island when considering tropical bird conservation (Pérez et al., 1994).

2.2 | Data collection

We sampled along the recently constructed Luba-Ureca road (completed in 2015) within the GCSR (Figure 1). This is a paved road, approximately 6-m wide and 28-km long, ranging from the north-western coastal port town of Luba to the southern village of Ureca. The study consisted of six sampling locations: three elevations, at 300 (low), 800 (mid), and 1200 m (high), respectively, each split into two habitat types: roadside and continuous interior forest (Figure 1).

Birds were captured using mist nets and banded with numerical aluminum bands for identification following established methods (Bub, 1991; the North American Banding Council, 2001). Mist-net capture was chosen as it is a reliable method for monitoring understory passerine species (Blake & Loiselle, 2001; Gardali et al., 2000; Gram & Faaborg, 1997; Wang & Finch, 2002), especially in areas of old-growth understory (Derlindati & Caziani, 2005) as present on Bioko. A total of 14–20, 12-m mist nets (36-mm mesh) were placed perpendicular to the road for sampling at all sites regardless of elevation or location (Figure 1). For road sampling, half of the allotted nets were placed in a continuous line (only interrupted by obstacles such as trees), perpendicular to the road edge on either side of the road starting at the beginning of the tree line and extending approximately 100 m into the forest. Interior forest sampling sites were an exact replicate of road sampling sites with two net lines running parallel to one another approximately 20–30 m apart, each using half of the allotted nets. Interior net lines were placed between 500 m to 1-km west of the road to ensure spatial independence from road edge transects.

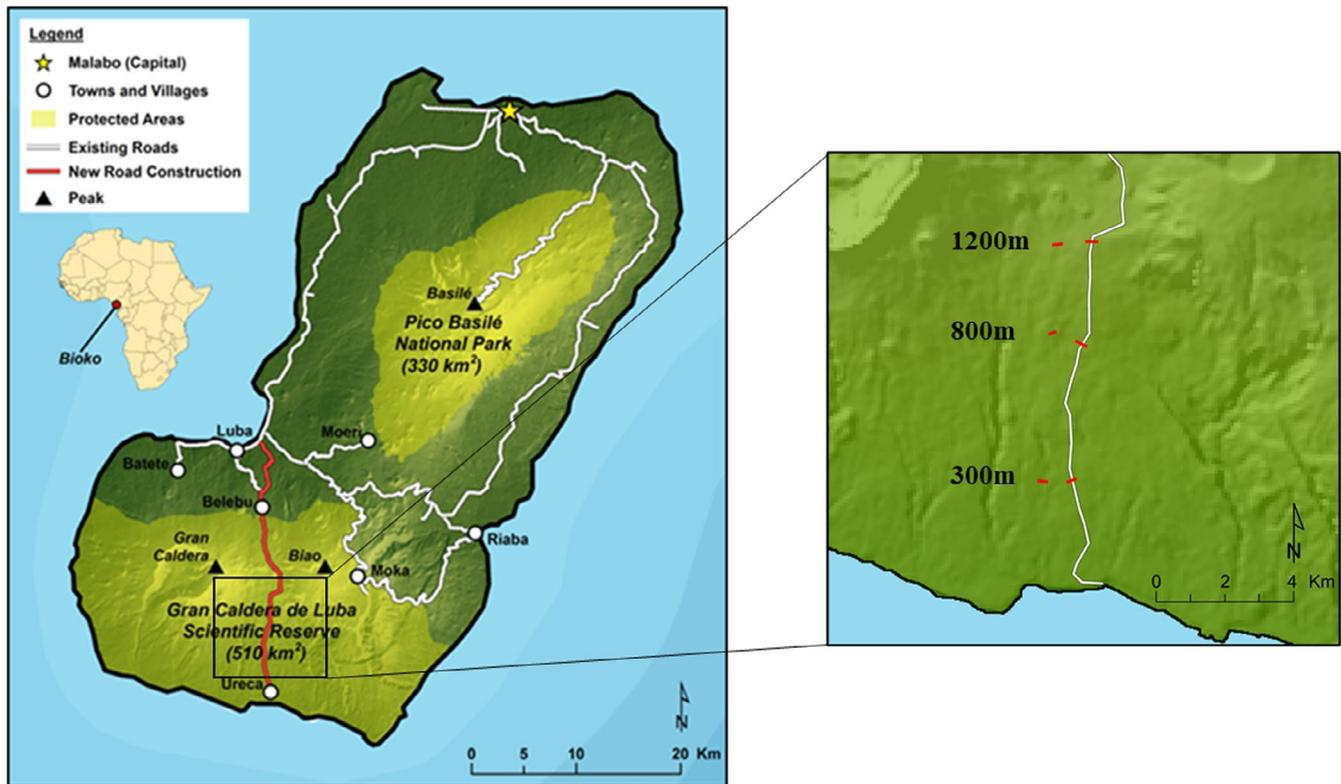


FIGURE 1 Map of Bioko Island including newly constructed Luba/Ureca road, (inset) map of survey transects along Ureca/Luba road within Gran Caldera Scientific Reserve. Red dashes indicate bird mist-net survey transects placed along road and interior transects at 300, 800 and 1200 m elevation, respectively

We sampled during the dry season from January to April along with the elevational gradient. Each elevation was sampled twice in the first year (February–March 2016), three times in the second year (February and April 2017) and twice during the third and fourth years (February 2018, January–February 2019) between 0600 and 1200 h. Two days were spent at each sampling transect (interior forest/road edge) across all three elevations for a total of 12 sampling days per sample effort. We extracted birds from mist nets and processed individuals at a temporary banding station. We recorded species, morphological measurements, age, and sex when possible, and applied an aluminum band with a unique number for individual identification. After processing, birds were released from the banding station directly, which was located in-between net lines for interior transects or walked to and released on the side of the road from that they were captured for road transects.

2.3 | Habitat characteristics

The low elevation site was primarily composed of primary and secondary forest lowland vegetation. The mid elevation site was a mix of primary and secondary transitional forest while the high elevation site consisted of montane fern forest. To visualize site characteristics in context of the wider habitat, we derived habitat indices from satellite imagery using the Google Earth Engine (GEE) cloud computing platform (Gorelick et al., 2017). Due to the potential effect of

canopy height on mist-netting capture rates (Mallory et al., 2004), we included a layer of canopy height, derived from the “Global Forest Canopy Height, 2019” dataset (Potapov et al., 2021). As an index of general vegetational composition, we calculated the modified soil-adjusted vegetation index (MSAVI) in GEE. This vegetation index has increased dynamic range over the normalized difference vegetation index (NDVI) and reduced soil background bias (Qi et al., 1994), making it particularly useful for detecting successional stages of forests (Hecht & Saatchi, 2007). The calculation was based on cloud-filtered Landsat 8 images covering the sampling period (2016–2019), with the final index being a 4-year median. For a closer comparison of these habitat indices, we extracted index values for a 250-m diameter circle covering each treatment-elevation combination, using the “raster” package in R (Hijmans & Etten, 2020).

2.4 | Statistical analysis

Data analysis was completed in R version 3.5.3 (2019-03-11; R Core Team, 2019). Statistical analyses were grouped into two types: ordination to identify community turnover between road and forest sites, as well as elevation, and regression to understand what specific groups might be causing community changes. Both analyses were based on mist-net capture rates. Statistical tests were conducted with the significance level $\alpha = 0.05$ for rejecting null hypotheses. Recaptured birds were removed from the analyses.

Communities were compared between treatments and elevations using ordination (Non-metric Multidimensional Scaling = NMDS) with the package “vegan” (Oksanen et al., 2019), using Bray-Curtis dissimilarity indices. The NMDS was based on species-specific capture rates for each field season (excluding recaptures), standardized by 100 mist-net hours (number of hours nets open \times total number of 12 m mist nets), a common standardization method used for mist-net data (Ralph, 1976). To visually compare community groups between elevations and transects, we highlighted clusters of communities using the “ordiellipse” function from “vegan.” The different field seasons were highlighted to distinguish elevation effects from year effects. We used PERMANOVA tests with the function “adonis” in “vegan” with 10,000 permutations to test for differences between the permuted datasets compared to the observed differences between clusters. The PERMANOVA tests were done twofold to compare between treatments, at each elevation separately, and to compare between elevations (for each treatment separately, as well as treatments pooled). We constrained permutations by year using the “strata” argument, to account for non-independence between the field season samples. Reported F -values and R^2 -values correspond to the PERMANOVA test output. We compared species richness between sites using capture-based rarefaction curves created with the “specaccum” function in the package “vegan.” Species were classified into guilds (insectivore, frugivore, nectarivore, granivore, mixed-flock follower, ant-follower) based on descriptions in the literature (Bannerman, 1953; Borrow & Demey, 2001), as well as expert knowledge. While these guilds are not mutually exclusive, they were analyzed independently to avoid any issues of overlap in the analysis.

We used Generalized Linear-Mixed Models (GLMM) in the package “lme4” (Bates et al., 2014) for all analyses of capture rates. The fit of all constructed models was investigated visually and statistically using a simulation-based approach in the package “DHARMA” (Hartig, 2019). Models with good fit showed no significant deviation in the QQ plot of simulated residuals and passed a non-parametric dispersion test (function “testDispersion()”). We included the collection date, nested in year, as a random intercept term in all models to account for the temporal replication in the study design. All models contained treatment (road vs. interior transect) and elevation, as well as an interaction between the two, as fixed main effects. To analyze overall captures at the different sites, we modeled total capture rates using a negative binomial distribution, since this resulted in an improved fit over the Poisson distribution. Total capture rates were modeled using the total net hours of the day as an offset term to normalize sampling effort in the study.

To analyze the functional composition of bird communities, we modeled proportional capture rates of feeding guilds by specifying the dependent variable as the capture rate of the respective guild divided by the total capture rates, with total capture rate specified as a weighted term in the model. Proportional capture rates were chosen since they reflect the relative composition of guilds in the environment better than absolute capture rates. Significance of terms was retrieved using the function “Anova” from the package “car”

(Fox & Weisberg, 2011), using the default Type-II test. Reported χ^2 values correspond to the ANOVA test result. We did not conduct stepwise selection from the initial model, due to the issues associated with model simplification (Burnham et al., 2011; Mundry, 2011). We estimated the marginal means for covariates based on the model using the “emmeans” function in the “emmeans” package (Length, 2019), and conducted Tukey's post hoc tests for pairwise comparisons using the “pairs” function.

We conducted an analysis using the package “indicpecies” in R (Cáceres & Legendre, 2009) to identify those species significantly associated with habitat type, which could be used as proxies to evaluate community integrity within the study area. Indicator values and permutation tests were calculated in the function “multipatt” using the indicator index value (IndVal) with 10,000 permutations. This function identifies groups of sampling sites that are most strongly associated with observed species distribution patterns (Cáceres et al., 2010). These data were pooled by site to ensure that the separate sampling days within a site were not interpreted as independent sampling units by the functions in the package.

3 | RESULTS

We captured and banded 931 individuals of 52 bird species (Table 1) over 6179 mist-net hours across six sampling locations and four years (Table S1). Canopy species, carnivores, as well as rare species (caught fewer than three times over the whole study period) were excluded from analyses since they were unreliably sampled by mist nets, leaving a total of 869 individuals representing 33 species (Table 1). Most captures were insectivores (55%) followed by nectarivores (18%), granivores (2%), and frugivores (<1%). Due to the small sample sizes, granivores and frugivores were excluded from capture rate analyses. When classified by forest strata, understory specialists comprised most captures (73%) followed by all-level (20%) and mid-level specialists (5%). Ant-following species accounted for 23% of total species, which increased to 40% if occasional ant-followers were included (Table 2).

3.1 | Habitat characteristics

Based on indices derived from satellite data, canopy height was very similar between 300 and 1200 m and was largely consistent throughout both study sites; however, more heterogeneity was observed in canopy height at 800 m (Figure 2a,c). This difference did not appear to affect overall capture rates as there was no clear statistical difference between transects at 800 m ($p = 0.09$). According to MSAVI, vegetational composition was strikingly similar between elevations and largely consistent within each study site (Figure 2b,d). Together, these findings suggest that transect locations were generally representative of the surrounding habitat within the study sites, and that bird community data were representative of each elevation.

TABLE 1 Number of captures for all species sampled separated by elevation (m) and transect type (road edge vs. interior forest)

Species	300 m		800 m		1200 m		Total captures
	Road	Interior	Road	Interior	Road	Interior	
<i>Accipiter toussenelii</i> ^a	0	0	0	1	0	1	2
<i>Alethe diademata</i>	15	28	6	7	1	1	58
<i>Anthodiaeta collaris</i> ^a	0	0	0	0	1	0	1
<i>Anthreptes seimundi</i>	3	2	1	0	0	0	6
<i>Apalis rufogularis</i> ^a	0	0	0	0	0	2	2
<i>Apaloderma vittatum</i> ^a	0	0	0	1	0	1	2
<i>Arizelocichla tephrolaema</i> ^a	0	0	1	0	2	1	4
<i>Bleda notatus</i>	14	16	0	1	0	0	31
<i>Camaroptera chloronota</i> ^a	0	0	0	0	2	0	2
<i>Campethera nivosa</i>	0	0	2	1	0	1	4
<i>Chamaetylas poliocephala</i>	1	0	14	23	33	24	95
<i>Chrysococcyx cupreus</i> ^a	0	0	0	0	1	0	1
<i>Cinnyris batesi</i> ^a	0	0	0	0	0	2	2
<i>Cinnyris minullus</i> ^a	0	0	0	0	1	0	1
<i>Cinnyris reichenowi</i>	0	0	0	0	1	3	4
<i>Cinnyris ursulae</i> ^a	0	0	0	0	1	1	2
<i>Corythornis leucogaster</i> ^a	11	4	1	0	0	0	16
<i>Cossyphicula roberti</i>	0	0	1	1	5	3	10
<i>Criniger calurus</i>	3	0	3	0	0	0	6
<i>Cryptospiza reichenovii</i>	0	0	3	3	4	4	14
<i>Cyanomitra cyanolaema</i> ^a	3	1	0	0	0	0	4
<i>Cyanomitra obscura</i>	25	24	44	19	3	1	116
<i>Cyanomitra oritis</i>	0	0	2	0	15	10	27
<i>Deleornis fraseri</i> ^a	3	1	1	0	0	0	5
<i>Dyaphorophya castanea</i> ^a	0	2	0	0	0	0	2
<i>Dyaphorophya chalybea</i>	0	0	0	0	3	1	4
<i>Eurillas curvirostris</i> ^a	0	0	0	0	1	0	1
<i>Eurillas gracilirostris</i> ^a	0	0	3	0	0	0	3
<i>Eurillas latirostris</i>	21	9	22	19	51	34	156
<i>Eurillas virens</i>	15	5	6	3	2	2	33
<i>Halcyon badia</i> ^a	0	2	0	0	0	0	2
<i>Hedydipna collaris</i>	1	0	0	0	0	2	3
<i>Hylia prasina</i>	5	2	3	4	0	0	14
<i>Illadopsis cleaver</i>	0	0	4	2	0	3	9
<i>Illadopsis rufipennis</i>	0	0	1	2	0	0	3
<i>Mandingoa nitidula</i>	0	1	0	0	4	0	5
<i>Neocossyphus poensis</i>	5	15	3	3	0	0	26
<i>Nigrita canicapillus</i> ^a	0	0	0	1	0	0	1
<i>Phyllastrephus icterinus</i>	6	5	0	0	0	0	11
<i>Phyllastrephus poensis</i> ^a	0	0	1	0	0	1	2
<i>Phylloscopus herberti</i>	0	0	0	0	4	3	7
<i>Ploceus bicolor</i> ^a	0	0	0	0	0	1	1

(Continues)

TABLE 1 (Continued)

Species	300 m		800 m		1200 m		Total captures
	Road	Interior	Road	Interior	Road	Interior	
<i>Pogoniulus scolopaceus</i> ^a	1	0	0	0	0	0	1
<i>Poliolais lopezi</i>	0	0	2	2	20	29	53
<i>Sheppardia bocagei</i>	0	0	2	4	25	23	54
<i>Stiphornis erythrothorax</i>	29	39	20	7	1	5	101
<i>Stizorhina fraseri</i> ^a	0	1	0	0	0	0	1
<i>Terpsiphone rufiventer</i>	3	1	0	0	3	5	12
<i>Zosterops senegalensis</i>	0	1	0	5	3	1	10

^aNote: Indicates species excluded from analysis after filtering.

TABLE 2 Total captures based on forest strata, guild and primary food source separated by elevation (m) and transect type (road vs. interior forest)

Strata	300 m		800 m		1200 m		Total captures (%)
	Road	Interior	Road	Interior	Road	Interior	
All levels	25	12	23	19	60	42	181 (20)
Canopy	3	1	3	0	0	0	7 (<1)
Mid-level	17	8	5	4	4	6	44 (5)
Mid-level/canopy	0	1	0	5	3	1	10 (1)
Understory	118	127	112	78	111	106	652 (73)
Guild							
Frequent mixed-species flock	89	93	84	67	52	46	431 (48)
No mixed-species flock	3	2	8	6	44	42	105 (12)
Obligate mixed-species flock	6	5	0	0	0	0	11 (1)
Occasional mixed-species flock	29	35	24	11	30	31	160 (18)
Rare mixed-species flock	36	14	28	22	53	36	189 (21)
Primary food source							
Carnivore	11	4	1	0	0	0	16 (2)
Frugivore	0	0	4	0	1	1	6 (<1)
Frugivore-insectivore	36	15	28	27	56	37	199 (22)
Granivore	0	1	3	3	8	4	19 (2)
Insectivore	84	102	61	57	94	97	495 (55)
Nectarivore	32	27	47	19	19	16	160 (18)
Ant-following							
Frequent ant-follower	35	59	23	34	34	25	210 (23)
Non ant-follower	99	55	99	61	119	102	535 (60)
Occasional ant-follower	29	35	21	11	26	28	150 (17)

3.2 | Species richness

Overall, rarefaction curves indicated that species richness was highest along interior forest transects at 300 and 1200 m and along the road transect at 800 m (Figure 3). Species richness was lowest along interior transects at 800 m elevation and the greatest disparity in species richness between road and interior transects occurred at this elevation. Lastly, species richness was almost identical between road vs interior transects at 300 m elevation. (Figure 3).

3.3 | Capture rates

We found a clear difference in the number of individuals captured between years ($\chi^2_3 = 33.18$, $p < 0.001$; Figure S1), based on the model using total capture rates per 100 mist-net hours (fitted total capture rates) as a response variable. However, a linear decline in total capture rates was not significant when “year” was used as a numeric variable in the model ($\chi^2_3 = 1.02$, $p = 0.31$). No significant difference was observed in total capture rates across study years ($\chi^2_3 = 2.1$, $p = 0.56$).

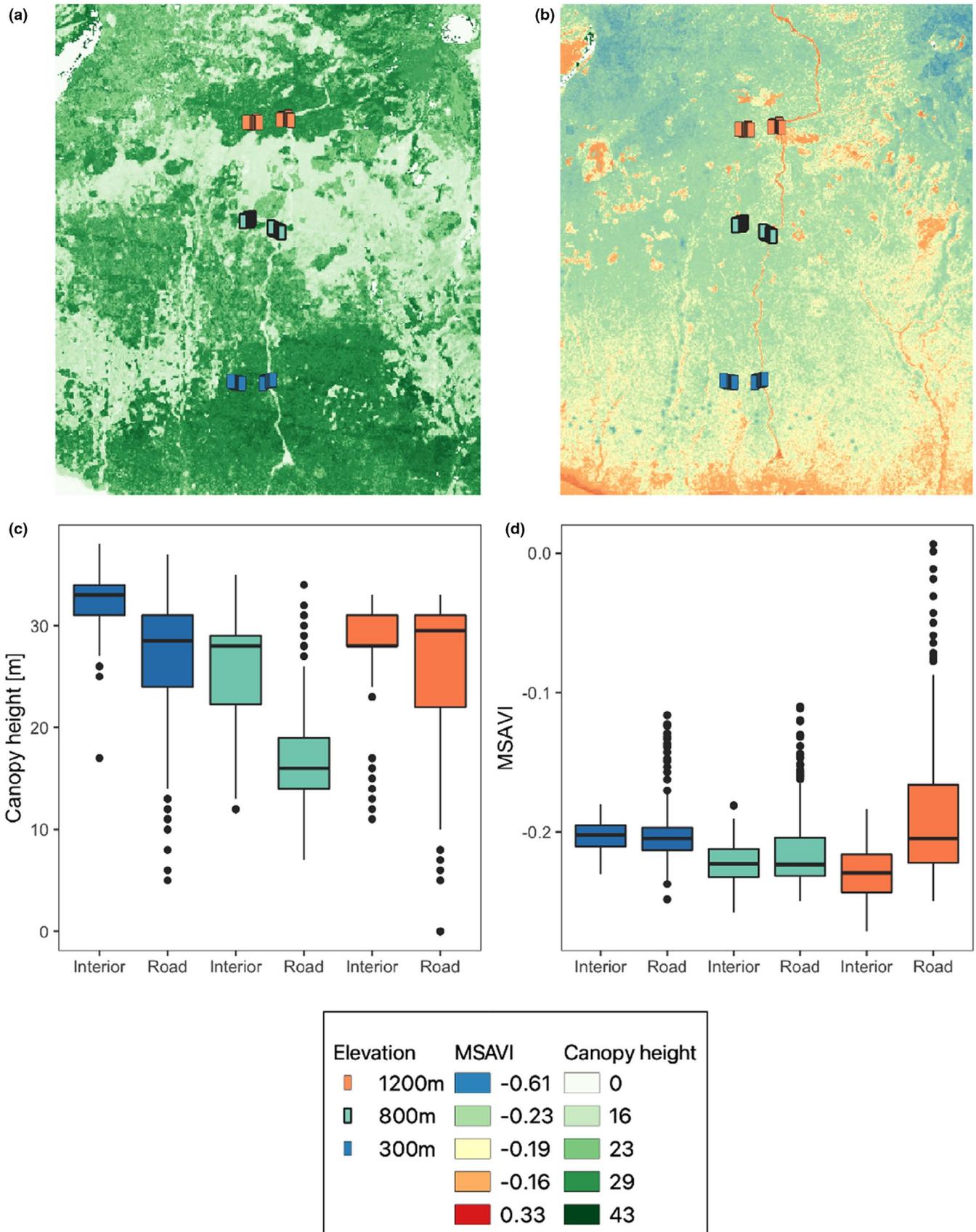


FIGURE 2 Habitat index maps at 30 m resolution for area surrounding transects based on satellite imagery for a) canopy height and b) MSAVI; followed by boxplots showing corresponding numerical values for c) canopy height in meters and d) MSAVI, extracted for a 250 m radius around each elevation-treatment combination

FIGURE 3 Rarefaction curves displaying total species richness for each treatment (road: dashed line vs. interior sites: solid, green line) and the corresponding elevation

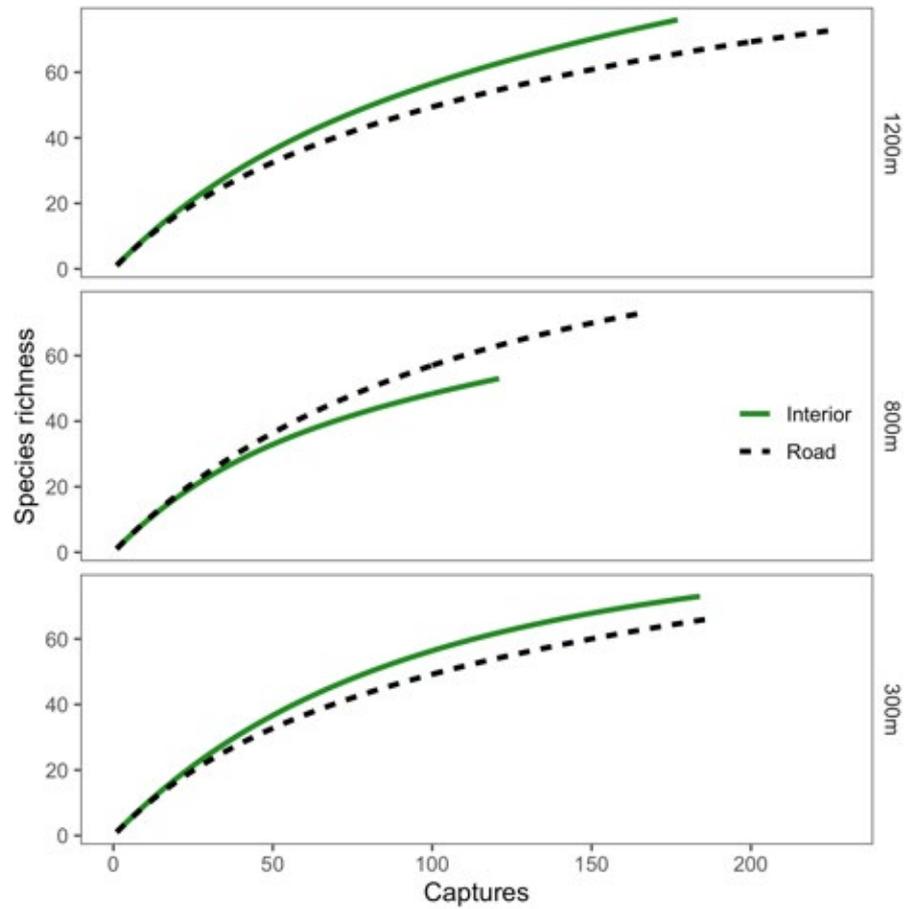
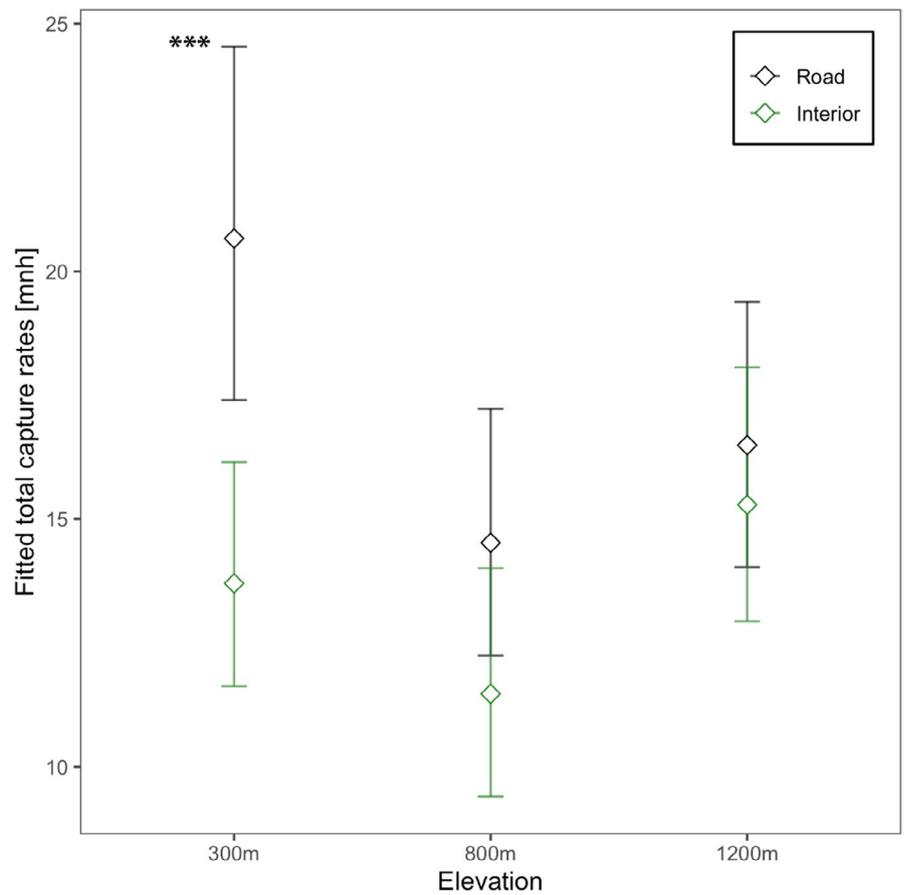


FIGURE 4 Overall abundance (per 100 mist-net hours) for each elevation (300, 800 and 1200 m) across treatments for all study years. Asterisks represent the degree of statistical difference between treatments, based on post hoc test



We found strong statistical differences in total capture rates in the post hoc test between road and interior transects at 300 m elevation only ($p = 0.001$). No clear statistical differences were detected between road and interior transects at 800 and 1200 m elevation ($p = 0.09$, $p = 0.46$, respectively; Figure 4).

Capture rates of guilds varied with elevation (Figure 5). Elevation interacted with transect type as a statistically clear predictor of proportional capture rates in ant-followers ($\chi^2_2 = 6.6$, $p = 0.038$), but not in the other guilds (insectivores: $\chi^2_2 = 1.1$, $p = 0.58$, mixed-flock followers: $\chi^2_2 = 3.5$, $p = 0.18$, nectarivores: $\chi^2_2 = 1.1$, $p = 0.57$). Proportions of ant-followers were statistically clearly different at 300 meters ($p = 0.002$), with an average of 23% higher proportions in the interior compared to the road transects. There was further evidence for different proportional capture rates at 300 m for insectivores and mixed-flock followers ($p = 0.048$, $p < 0.001$, respectively; Figure 5).

3.4 | Community analysis

Based on the NMDS plot, we observed visually and statistically clear community differences among the three elevations (treatments pooled: $F = 6.93$, $R^2 = 0.61$, $p < 0.01$; Figure 6). These differences were also observed when comparing only road sites or only interior sites across elevations (Road: $F = 8.77$, $R^2 = 0.38$, $p < 0.01$, Interior: $F = 8.23$, $R^2 = 0.34$, $p < 0.01$). We also found visual indications of community differences between road and forest interior transects at 300 m based on NMDS analysis, although this was not clear based on the PERMANOVA test (300 m: $F = 0.75$, $R^2 = 0.11$, $p = 0.63$; 800 m: $F = 1.38$, $R^2 = 0.19$, $p = 0.1$; 1200 m: $F = 0.46$, $R^2 = 0.07$, $p = 0.75$; Figure 7). With higher elevation, the community samples increasingly overlapped between these transects (Figure 7).

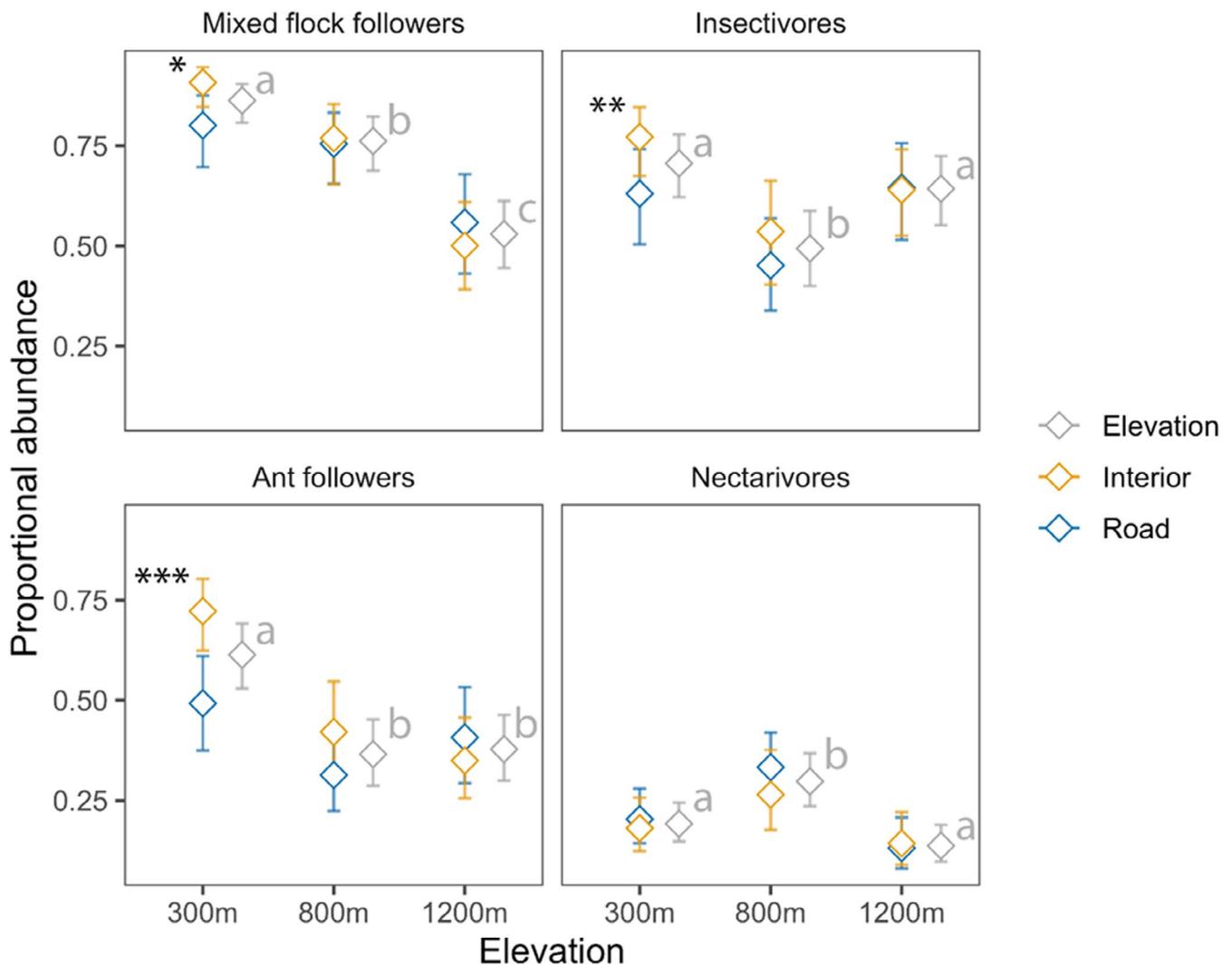


FIGURE 5 Estimated marginal means of proportional abundance for the four most common foraging guilds in the study. Error bars represent the asymptotic confidence intervals. Stars represent the degree of statistical difference between treatments, based on post hoc test. Different letters represent statistically different pairwise contrasts for elevations from the post hoc test

FIGURE 6 NMDS plot of bird communities, based on Bray-Curtis dissimilarity indices using abundances standardized by 100 mist-netting hours. Points represent sampled communities at a given date. Point types represent the field seasons. Ellipses represent 95% confidence intervals of clusters by elevation (blue = 300 m, green = 800 m, red = 1200 m)

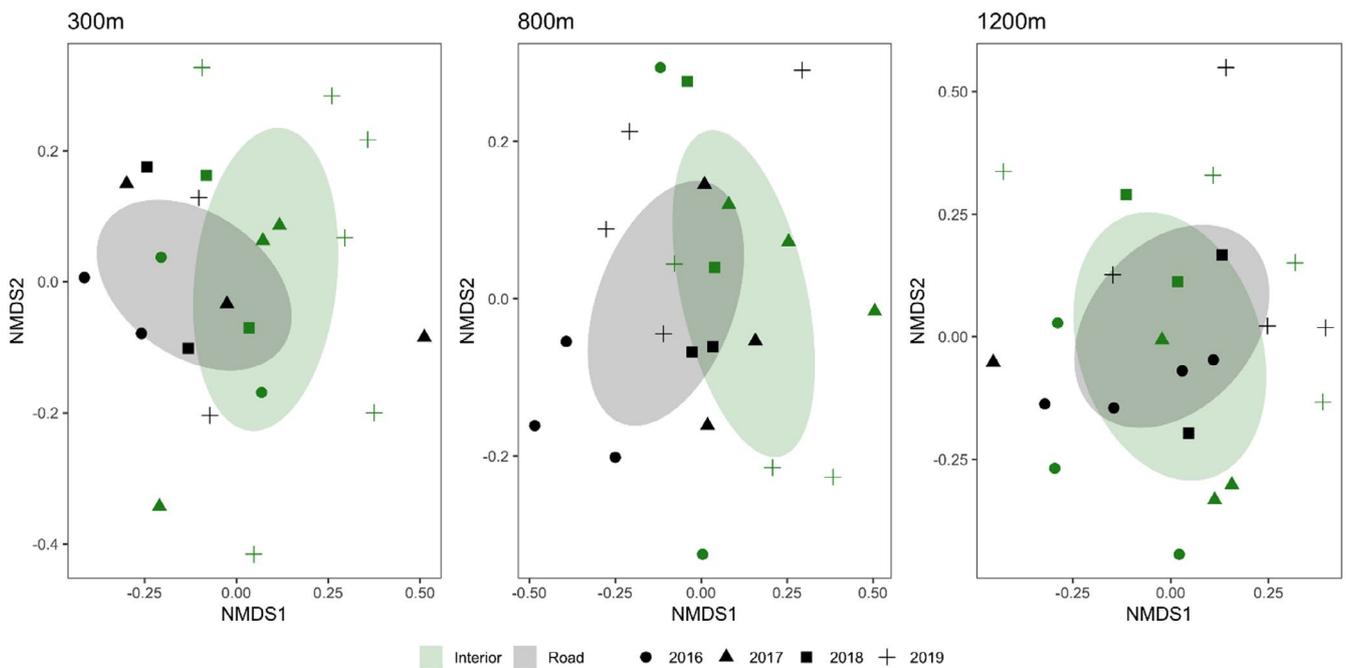
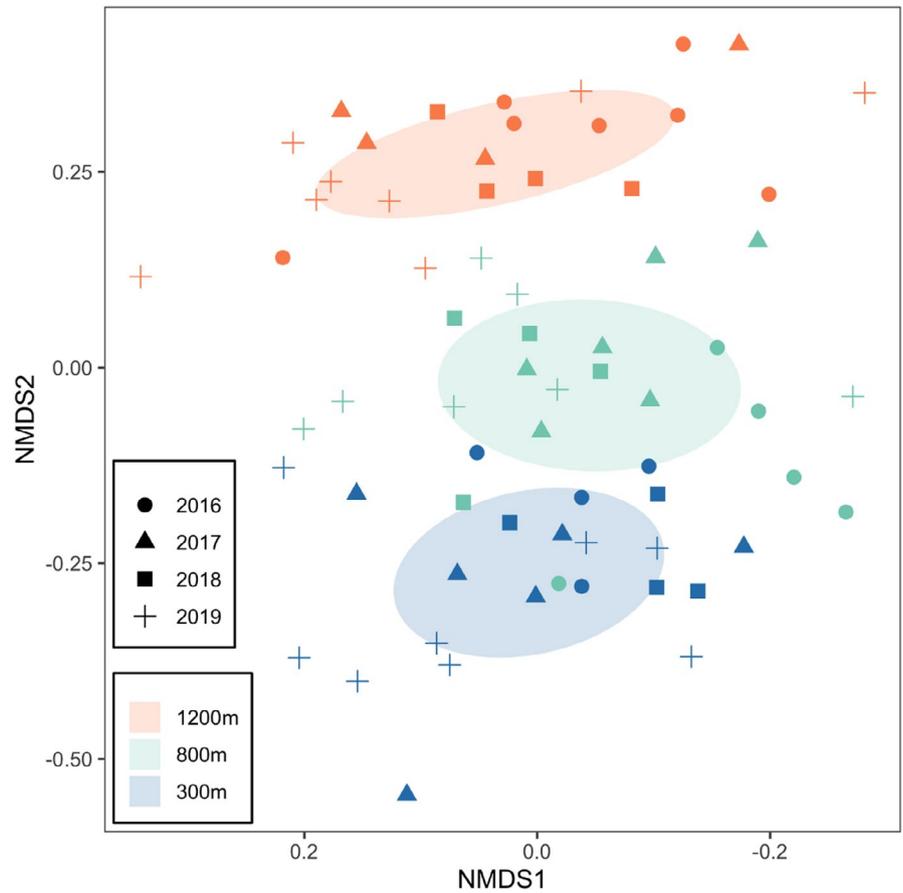


FIGURE 7 NMDS plot of bird communities, based on Bray-Curtis dissimilarity indices using abundances standardized by 100 mist-netting hours. Points represent sampled communities at a given date. Point types represent the field seasons. Ellipses represent 95% confidence intervals of clusters by treatments (green = interior, black = road)

3.5 | Species significantly associated with elevation

Based on the “indicspecies” analysis, we did not identify any species significantly associated with either road or interior forest transects between elevations; however, we did identify species significantly associated with elevation alone (Table 3). *Bleda notatus* exhibited the strongest association with low elevation transects, whereas *Poliolais lopezi* exhibited the strongest association with high elevation transects. Several species were significantly associated with a combination of two elevations, with *Cyanomitra obscura* most strongly associated with low and middle elevations (300 + 800 m), and *Chamaetylas poliocephala* being the only species significantly associated with middle and high elevations (800 + 1200 m; Table 3).

4 | DISCUSSION

Overall, elevation was the strongest predictor of community composition, with clear visual clustering of communities sampled during the different field seasons at 300, 800, and 1200 m, respectively. This result likely reflects the preference of bird species for habitats associated with specific elevations within the study area. Changes in overall fitted capture rates across study years did not show a significant linear decline, thus, these results may be indicative of natural oscillations in abundance patterns between the study species. However, we did observe higher total capture rates at 300 m as compared to other elevations including significantly higher proportional capture rates of ant-following, insectivorous and mixed-flock following species along interior forest versus road edge transects at this elevation. These results suggest certain guilds may be more sensitive to disturbance at low elevations within the region, perhaps due to similarities in ecological and life-history traits. Although the present study lacked spatial replication, we argue that biogeographic factors

have likely shaped species distributions within the region, and our dataset is a nested subset of the avian communities found on Bioko Island and mainland West Africa as they exhibit corresponding patterns of biodiversity based on their recent geographic connectivity (Cronin et al., 2014; Jones, 1994). Additionally, we identified species with statistically evident associations with each elevation, irrespective of transect type. To our knowledge, this study is the first to investigate the effects of road construction on bird species distributions across a steep Afrotropical elevational gradient.

4.1 | Patterns of species richness

Species accumulation curves exhibited similar trends between road and interior forest transects at 300 and 1200 m elevations; however, slightly higher richness values were observed for each transect type at 1200 m. Overall, differences in species richness between road and interior transects were minimal for each elevation. These findings are consistent with a recent study showing little variation in species accumulation curves regardless of road proximity among bird populations in Costa Rica (Avalos & Bermúdez, 2016). Lastly, higher species richness was observed along the road edge at the mid elevation site (800 m). Previous studies have found increased nest density along road edges among passerine species in the tropics (Battin, 2004). In this case, it was suggested the road was operating as an ecological trap of sorts where individuals selected suboptimal sites without obvious fitness or reproductive benefits (Battin, 2004). More research is needed to determine if this phenomenon is occurring within the present study area. Future work on Bioko should consider the use of nesting density and indices of fitness (e.g., survival) in order to help characterize bird behavior in response to anthropogenic disturbance. Although little difference in species richness was observed between road and interior transects, this metric may fail to capture differences in community composition based on factors such as foraging ecology and habitat preference between sites.

4.2 | Species sensitive to disturbance at low elevations

Understory insectivores (mixed-flock followers, ant-followers, and insectivores) exhibited higher proportional capture rates among interior transects as compared to road edge transects at 300 m. Specialist bird species are particularly susceptible to habitat alteration (Habel et al., 2019) and more specifically, insectivorous birds can be highly sensitive to anthropogenic disturbance exemplified by severe declines among this guild within logged versus unlogged forest in Ghana (Arcilla et al., 2015). Similar results were found among understory insectivores in Costa Rica and Thailand, where negative correlations were observed between overall abundance and road proximity (Avalos & Bermúdez, 2016; Khamcha et al., 2018). This observation may be attributed to a lack of road-crossing behavior seen among these guilds. For example, Laurance et al. (2004) found

TABLE 3 Results from the “indicspecies” analyses

Species	Elevation (m)	Indicator value	p-Value
<i>Bleda notatus</i>	300	0.98	<0.001
<i>Phyllastrephus icterinus</i>	300	0.87	<0.001
<i>Cyanomitra obscura</i>	300 + 800	0.98	<0.001
<i>Alethe diademata</i>	300 + 800	0.95	<0.001
<i>Stiphornis erythrothorax</i>	300 + 800	0.93	0.002
<i>Neocossyphus poensis</i>	300 + 800	0.83	0.007
<i>Chamaetylas poliocephala</i>	800 + 1200	0.99	<0.001
<i>Poliolais lopezi</i>	1200	0.9	<0.001
<i>Sheppardia bocagei</i>	1200	0.89	<0.001
<i>Cyanomitra oritis</i>	1200	0.83	0.001
<i>Phylloscopus herberti</i>	1200	0.79	0.004

Note: Indicator value of (1.0) suggests strong association with a given site. p-values represent the significance of indicator value.

that forest-dependent insectivores exhibited clearly repressed road-crossing movements compared to edge and gap species. Likewise, ant-following species and other insectivores in the present study area may be further range restricted along an elevational gradient due to decreased arthropod abundance at higher elevations. Indeed, Supriya et al. (2019) found a negative relationship between arthropod abundance and elevation was more likely with decreasing latitude on a global scale. This finding is applicable to the present study area as Bioko is situated on the equator. Additionally, fragmentation likely affects movement and space usage of this guild when considering that ant-following birds have large home ranges (to include multiple nomadic ant colonies) and are reluctant to cross open areas between fragmented habitats, leaving these species particularly sensitive to road disturbance (Lees & Peres, 2008; Stratford & Stouffer, 1999). Thus, the decrease in understory insectivores along road transects at 300 m suggests these species could be sensitive to habitat edge formation in the present study.

4.3 | Role of elevation in shaping avian community composition

Elevation was the most significant factor governing community composition based on NMDS plots in the present study area, as indicated by clustering of communities at 300, 800, and 1200 m irrespective of transect type or sampling season. Similar associations have previously been found between bird species distributions and elevation (Blake & Loiselle, 2000; Young et al., 1998), however, one must exercise caution when interpreting these results as a multitude of variables are likely responsible for species distributions across elevations (Avalos & Bermúdez, 2016; Lomolino, 2001; Rahbek & Graves, 2001). Indeed, elevation is often closely linked with other explanatory variables (e.g., temperature, precipitation, vegetation) influencing species range limits, particularly in tropical montane regions where niche partitioning is common (Lundberg & Moberg, 2003; McCain, 2009; Young et al., 1998). For example, Hořák et al. (2019) found that spatial distributions of birds along an Afrotropical elevational gradient were significantly influenced by factors beyond just elevation, such as forest structural traits (e.g., tree community composition, leaf area index). However, elevation was a significant determining factor when assessing avian functional diversity, thus emphasizing the role of habitat suitability in shaping species distributions between elevational bands (Hořák et al., 2019).

The significance of elevation influencing community composition may be readily explained by the concept of niche conservatism, where species movements are constrained by both abiotic and biotic factors influencing survival and reproductive success. Furthermore, local water availability and temperature variables are strong predictors of avian distributions across elevations (McCain, 2009). This suggests that niche conservatism may be driving elevational diversity in birds as these abiotic factors are significant determinants of climate and vegetation. While previous studies have proposed that dietary niche, range, and behavior are important drivers of bird movement

and habitat preference (Lundberg & Moberg, 2003), evidence also suggests that variation in fine-scale habitat suitability, even within elevational bands, can significantly shape bird species distributions along a tropical elevational gradient (Hořák et al., 2019). The strong association between elevation and community composition in our study suggests some of these species may be significantly range limited and thus more sensitive to disturbance, as evidenced by potential road edge avoidance among understory insectivores at 300 m. Similar results have been found among neotropical submontane species who exhibit limited elevational ranges due to ecological specialization leaving them more vulnerable to habitat disturbance (Lee et al., 2005). However, no such effects were observed among birds at 800 and 1200 m in the present study, highlighting a discrepancy in sensitivity patterns. As Bioko is a land bridge island (LBI), the avian community composition has likely been shaped in accordance with the principles of island biogeography (MacArthur & Wilson, 1963; Valente et al., 2020; Wilson & MacArthur, 1967), since the island was last connected to the mainland approximately 11,000 years ago. Thus, due to the filtering out of more sensitive species over time, the present avian community on Bioko is likely well-adapted to elevational bands of habitat leaving some species less sensitive to anthropogenic disturbance. This could potentially account for the discrepancy in sensitivity found between species at different elevations in the present study.

4.4 | Species significantly associated with elevation

Species exhibiting strong statistical associations with elevations could be valuable for tracking species turnover and identifying temporal changes in bird communities along an elevational gradient (Blake & Loiselle, 2000; Jankowski et al., 2009; Young et al., 1998). Using the current dataset, we were able to identify species with statistically evident associations for all three elevations. The ant-following greenbul *Bleda notatus* was most strongly associated with 300 m elevation and is a lowland species commonly found among evergreen, swamp and secondary forest and exhibits high site fidelity (Fishpool et al., 2019). The abundant sunbird *Cyanomitra obscura* was the species most strongly associated with both 300 and 800 m elevation and utilizes a diversity of forest habitats and food sources, while exhibiting altitudinal migration based on food and water availability (Cheke & Mann, 2019), potentially explaining its association with multiple elevations. Lastly, the warbler *Poliolais lopezi* was the strongest indicator species found at 1200 m elevation. This species is commonly found within transitional and montane forest and employs a largely insectivorous diet while foraging among moist, dense understory vegetation (Pearson, 2019). Montane regions on Bioko experience frequent and voluminous rainfall, likely making this region particularly suitable for *P. lopezi*. These findings are significant as tracking turnover among species exhibiting high elevational fidelity could aid in identifying important shifts in bird community composition (Beaudrot et al., 2016; Lindenmayer, 1999). Additionally, these results support our overall findings, which suggest that factors

associated with elevation are the most significant drivers of bird species distributions in the present study area.

4.5 | Implications for conservation management

Our results suggest a need for long-term monitoring of effects associated with habitat disturbance across elevations to identify accurate trends regarding species compositions. Correspondingly it has been proposed that bird population parameters are best suited for monitoring long-term responses to environmental change as opposed to short-term responses (Temple & Wiens, 1989). Understory insectivorous species appear to be sensitive to road presence at low elevations as notably lower proportional abundance numbers were observed along road edge sampling transects at 300 m. It is possible these guilds are exhibiting road edge avoidance at low elevations. Specifically, ant-following species may be most affected since nomadic ant colonies tend to avoid large clearings associated with road construction. These findings, along with previous data, suggest that understory insectivores may be particularly sensitive to edge habitat formation. As such, these species should be considered a high conservation priority when planning future infrastructure expansion in the region. Actions can be taken to reduce the effects of disturbance such as limiting the size and width of new road construction, minimizing the impact of new road construction (e.g., limiting traffic and secondary/tertiary road construction), engaging in restoration and rehabilitation of disturbed sites and supporting conservation of biodiversity at similar but geographically different sites (IUCN, 2020).

4.6 | Caveats and future work

Mist-net capture is an often-used method for surveying understory passerine species (Blake & Loiselle, 2001; Gardali et al., 2000; Gram & Faaborg, 1997; Wang & Finch, 2002), especially in areas of old-growth understory (Derlindati & Caziani, 2005), hence why this method was selected for use on Bioko Island. Several advantages are associated with using this technique: Counts are not as prone to identification bias, detection of cryptic and quiet species (e.g., *Picathartes oreas*) often missed by point counts, useful, when expertise in visual and auditory identification of local avifauna is lacking, and observers can examine each captured individual in hand (Dunn & Ralph, 2004). One disadvantage of mist netting is the fact that capture probability differs between species (e.g., Blake & Loiselle, 2001). We attempted to address this issue by refraining from comparing species capture rates directly. Instead, we compared guilds as functional groups in the habitat, a method often preferred, where a full study of the species in the habitat is difficult to achieve (Simberloff & Dayan, 1991). At present, there is a lack of Equatoguinean ornithologists with expertise in song identification, which further restricts the use of additional sampling methods, but offers opportunities for capacity building and future collaboration.

Limitations with the use of mist nets can be a lack of capture of sedentary and canopy species, missing certain portions of the bird community at large and spatial constraints based on limits of net coverage (Blake & Loiselle, 2000; Rappole et al., 1998; Wang & Finch, 2002). Comparative studies between mist netting and point counts have shown similar results regarding species richness, diversity and distributions between the two methods, but large bodied species tended to be underrepresented by mist-net capture alone (Derlindati & Caziani, 2005; Wang & Finch, 2002). In the present study, we missed larger understory species that may have relocated due to hunting pressure, but this requires further study. Likewise, we missed some canopy species (e.g., hornbills, cuckoos) that are common to the study area. Thus, we limited our analysis to small understory species to account for these limitations associated with mist netting.

Logistical and financial limitations prohibited spatial replication across sampling sites in our study, and statistical methods were chosen to account for this study limitation. If taken in isolation, we cannot be certain that our results are generalizable to broader avian communities. However, the chosen transects represented a cross-section of typical habitat at each elevation based on indices of canopy height and MSAVI, suggesting the avian community sampled on the southern slope of Bioko during the present study represents a typical subset of the avian community within the GCSR. Evidence also suggests that our present dataset could represent a nested subset of the avian community on mainland West Africa within the Gulf of Guinea. Due to their recent geographic connectivity, Bioko and the area around Mount Cameroon are more similar in patterns of biodiversity and endemism as compared to other islands within the Cameroon volcanic island chain (Cronin et al., 2014; Jones, 1994). Of the 52 total species we identified (before data filtering) in the present study, 36 (67%) were found in studies conducted on the mainland spanning across a comparable elevational range (30–2200 m asl) on and around Mount Cameroon (Nana, 2015; Nana et al., 2014; Petruř, 2019; Sedláček et al., 2015). Thus, we argue that avian communities on Bioko are indeed representative of corresponding communities on mainland Africa.

For the present study, we lacked pre-road construction data on avian diversity and abundance in the area. As such, we focused on interacting factors affecting overall avian community composition (e.g., road presence, elevation) as opposed to conducting a true impact-assessment study. Future studies should focus on several key areas: (1) discerning between road, elevation, and other influential factors to identify specific effects associated with each, (2) including additional metrics such as species movement, population stability (e.g., survival/reproductive rates), and body condition to help prioritize the identification of species/guilds most sensitive to anthropogenic disturbance, (3) monitoring specific species to track temporal changes in community composition and lastly, (4) the incorporation of data from multiple faunas as standard practice to quantify effects associated with disturbance.

5 | CONCLUSIONS

Elevation was a key factor influencing avian community composition within the present study area, and we were able to identify species that were statistically associated with each elevation across all study transects. However, additional factors associated with elevation, such as vegetation structure and composition, were likely major contributors to community patterns observed in the present study. Understorey insectivores appear to be sensitive to habitat edge formation at low elevations as these species seemed to exhibit road edge avoidance at 300 m. Furthermore, the fact that these effects were significant at low elevations among species found on both Bioko Island and parts of mainland Africa suggests our conclusions may be more broadly applicable across lowland Afrotropical environments. These findings emphasize the need for conserving lowland elevations as they may house important and diverse segments of the bird community. Traditional protected areas tend to focus on upland habitat with high species endemism, which may overlook key lowland species who are sensitive to disturbance (Shiple, 2017). Together these data highlight the importance of maintaining large blocks of continuous habitat along elevational gradients where bird species distributions may be largely governed via biotic and abiotic factors associated with altitude.

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

AUTHORS CONTRIBUTIONS

SCM and JHW contributed equally to the present manuscript including study design, methodology, field sample collection, data analysis, and drafting of the manuscript. AME participated in field season planning, sample collection and data curation. EL participated in sample collection and data curation. MF participated in project administration and supervision. JW participated in study design, methodology, writing and funding acquisition. MKG participated in study design, project administration, writing, supervision, and funding acquisition. LP participated in study design, methodology, sample collection, writing, supervision, and funding acquisition.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rjdfn2zbp> (Miller et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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