



Spatiotemporal patterns in an Afrotropical montane forest bird community

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ABSTRACT

Understanding how species richness and diversity patterns vary across time and space is essential for predicting how biodiversity will respond to anthropogenic threats and for effective conservation planning. Tropical montane forests are among the most biodiverse places in the world, yet high rates of endemism and narrow physiological tolerances place tropical montane species among the most vulnerable to anthropogenic impacts. Therefore, it is of the utmost importance to understand how ecological communities are structured along elevational and spatial gradients, particularly in the Afrotropics, which are historically understudied despite their unique climate and rich biodiversity. Here we examine how the Afrotropical montane bird community of Nyungwe National Park in Rwanda is spatially and temporally structured with respect to elevation and geography. We show that despite the absence of geographic barriers, avian communities are spatially structured across the elevational gradient with significant regional differences in both species composition and richness, and that high elevation assemblages are comprised of fewer species compared to lower and middle elevations. We find evidence for overall stability in species richness during this study period (2001–2011) yet differing season-specific trends across the elevational range of the study. Specifically, the high elevation assemblage exhibited a wet season-specific increase in richness, congruent with predicted upslope elevational shifts for low and middle elevation species. Our findings suggest that anthropogenic factors may have different effects on richness patterns depending on elevation and region, and that protected areas large enough to encompass the full range of geographic and elevation gradients are required to effectively conserve Afromontane bird communities.

1. Introduction

Identifying spatial and temporal variation in community structure and species richness is essential for assessing the conservation importance of landscapes and predicting how biodiversity will respond to anthropogenic threats such as habitat loss and climate change. High levels of beta diversity make montane tropical forests the most biodiverse regions on the planet (Montaño-Centellas et al.,

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2021; Myers et al., 2000; Rahbek and Graves, 2001), yet they are among the most vulnerable to the effects climate change and habitat loss, threats that exacerbate the adverse effects of one another (Harris et al., 2011; Sodhi and Smith, 2007; Williams et al., 2022). An estimated 87 % of terrestrial bird species found above 1000 m in elevation occur in the tropics (La Sorte and Jetz, 2010). Tropical avifauna are characterized by narrower physiological tolerances that correspond to reduced elevational and geographic ranges (Jankowski et al., 2010; Janzen, 1967; Jetz et al., 2007; Sekercioğlu et al., 2008; Şekercioğlu et al., 2012), higher rates of endemism, and increased specialization (Jankowski et al., 2009), all of which are predicted to elevate the extinction risk for these species (Birand et al., 2012; Gaston, 1994; McCain and Colwell, 2011; Orme et al., 2005).

Despite the global conservation importance of tropical ecosystems, the majority of studies examining avian communities have focused on the Neotropics (Freeman et al., 2018; Jankowski et al., 2009, 2010; Loiselle and Blake, 1991; Robinson and Terborgh, 1995; Ruggiero and Hawkins, 2008; Terborgh et al., 1990). The Afromontane region of the Albertine Rift in East Africa supports more vertebrate and endemic species than any other region in the African continent, including over 50 % of Africa's bird species (Plumptre et al., 2007) and has been severely altered by anthropogenic land use changes (Carr et al., 2013); yet, this region has received little ecological study (but see Neate-Clegg et al., 2020; Rurangwa et al., 2021; van der Hoek et al., 2022; Romdal and Rahbek, 2009). There is evidence that the Albertine Rift avian community is threatened by interacting effects of climate change, habitat loss and fragmentation, and other anthropogenic factors (Carr et al., 2013; Phillipps and Seimon, 2010; Plumptre et al., 2021; Ponce-Reyes et al., 2017). Some bird species in this region are known exhibit incremental shifts in their elevational ranges (Neate-Clegg et al., 2020; Sekercioğlu et al., 2008; van der Hoek et al., 2022), yet the direction and magnitude of their responses is highly variable depending on extrinsic (e.g., precipitation, temperature, habitat type), and intrinsic (e.g., body size, life history) factors. However, we still know little about the factors and processes influencing spatio-temporal structure and composition of the Albertine rift avian community.

Using 11 years of point count data, we studied the structure and composition of the bird community across geographic regions and elevation gradients in Nyungwe National Park (NNP), Southwest Rwanda. NNP is located at the center of the Albertine Rift, and

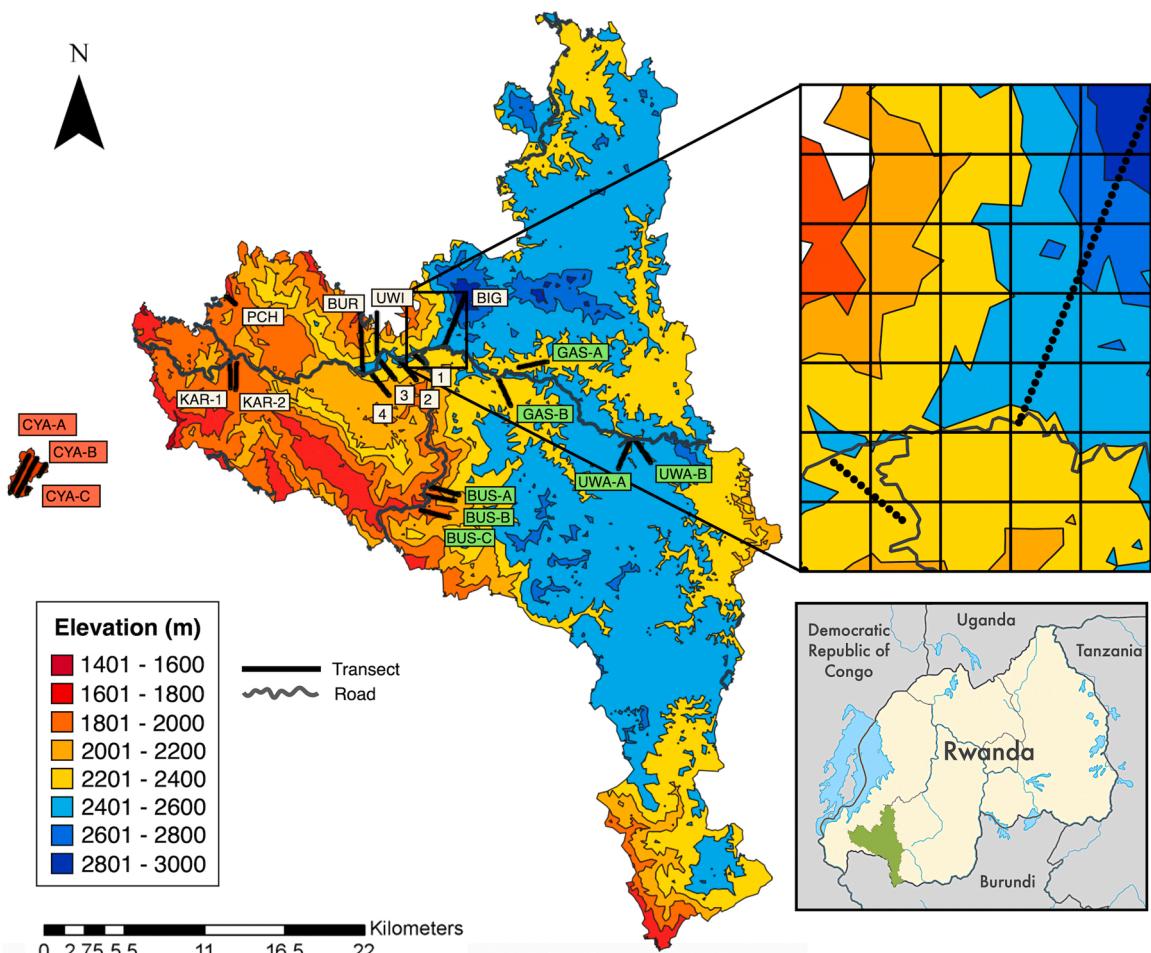


Fig. 1. Map of Nyungwe National Park, Rwanda colored by elevation (200-m bands). Roads and transects are indicated by gray and black lines, respectively. Transect abbreviations are noted in rectangular boxes adjacent to the transects (CYA = Cyamudongo; KAR = Karamba; PCH = Pchuelle; BUR = BURURI; UWI = Uwinka; BIG = Bigugu; BUS = Busoro; GAS = Gasare; and UWA = Uwasenkoko) and are color-coded based on the transect group (Red = Fragment; White = Transect group A; and Green = Transect group B).

combined with Kibira National Park of Burundi, forms the largest protected area of contiguous montane rainforest in East Africa, supporting close to 300 bird species of which 26 are endemics. Specifically, we tested the hypotheses that (1) the NNP bird community is structured by geographic region; (2) the structure and composition of NNP bird community is influenced by elevation, distance to edges, and vegetation; and (3) these factors have differentially influenced diversity and composition of NNP bird community over time.

Regional biodiversity levels are determined by species turnover along environmental and spatial gradients; organisms with narrow ranges, due to abiotic or biotic constraints (Buckley and Jetz, 2008; Tilman, 1982) or limited dispersal (Hubbell, 2011), exhibit higher rates of turnover. Based on the findings of prior studies (Blake and Loiselle, 2000; Loiselle and Blake, 1991; McCain and Grytnes, 2010; Montaño-Centellas et al., 2021; Rahbek, 1997), we expected the NNP bird community to be primarily structured regionally and along the elevational gradient with richness decreasing with elevation. Furthermore, we expected community composition to change with distance to the forest edge and a major road that passes through the forest Fig. 1. Effects of habitat edges on populations and communities are complex and influenced by habitat area and quality, landscape configuration, and species life history (Fletcher Jr, 2005; Gascon et al., 1999; Ries and Sisk, 2004; Sekercioglu, 2002). Studies examining edge effects in tropical bird communities have yielded mixed results, but changes in microclimatic variables (e.g., light intensity, humidity, temperature) with respect to distance from forest edges have been well documented, and can negatively impact some species (Khamcha et al., 2018; Laurance et al., 1998; Neate-Clegg et al., 2016; Wiens et al., 1985). Other studies have demonstrated positive edge responses for some taxa, often depending on habitat and resource requirements (e.g., foraging guild and stratum and degree of specialization) (Fonderlick et al., 2013; Ries and Sisk, 2008; Villard, 1998). Given that hard edges between forest habitat and exposed agricultural land characterize NNP, we predicted species richness to increase with distance from the forest edge.

Concurrent with elevation and distance to edges, primary productivity has been shown to be a strong predictor of avian species richness (Bino et al., 2008; Cueto and de Casenave, 1999; Hurlbert and Haskell, 2003; Nieto et al., 2015). Vegetation indices including Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), and Potential Evapotranspiration (PET) have been shown to be reliable proxies for vegetative biomass and productivity (Huete et al., 2002). We predicted a positive relationship between these measures and species richness. Finally, based on changing weather patterns and ongoing human disturbance in the region, we predicted that species richness would have declined over the study period, with greater decreases at low and high elevations corresponding to more extreme shifts in weather at these elevations (Phillips and Seimon, 2010).

2. Methods

2.1. Study site

Located at the center of the Albertine Rift, Nyungwe National Park (NNP) is comprised of 1019 km² of montane forest located in Southwest Rwanda (2°15'–2°55'S, 29°00'–29°30'E) (Fig. 1). The forest acquired protected status as a national park in 2005. Elevation within the park ranges from 1600 to 2950-m. The climate is characterized by one dry season (June-August) and a long and variable wet season (September-May) with an average annual precipitation of 1500 mm. There is one major road that passes West-East through the park, and a secondary road that extends from the middle of the park to the South. These roads experience heavy traffic and serve as the primary route used for transport of goods between the Democratic Republic of Congo and Rwanda. The Congo-Nile Crest runs North-South through the main forest block demarcating distinct environmental conditions in the eastern and western regions, including differences in vegetation, waterflow, soil chemistry, and elevational range (Ghehi et al., 2011). Specifically, the western part of the

Table 1

Description of transects and points including transect name, length, number of points, elevation range, time frame over which transect was sampled, transect group, and region.

Transect	Transect Code	Transect Length (km)	Points (#)	Elevation Range (m)	Data Collection (Years)	Transect Group	Region
1	1	1.3	14	2240–2410	2001–2011	A	West
2	2	2	21	2200–2520	2001–2011	A	West
3	3	2	21	2100–2460	2001–2011	A	West
4	4	2	21	2000–2460	2001–2011	A	West
Uwinka	UWI	3.1	32	2070–2460	2001–2011	A	West
Bururi	BUR	4.5	46	1830–2470	2001–2011	A	West
Pchutte	PCH	2	21	1767–1848	2001–2011	A	West
Karamba 1	KAR-1	2	21	1848–1917	2001–2011	A	West
Karamba 2	KAR-2	2	21	1870–1964	2001–2011	A	West
Bigugu	BIG	4.5	46	2380–2940	2001–2011	A	East
Busoro A	BUS-A	2	21	1800–2180	2005–2011	B	West
Busoro B	BUS-B	2	21	1840–2150	2005–2011	B	West
Busoro C	BUS-C	2	21	1840–2180	2005–2011	B	West
Gasare A	GAS-A	2	21	2330–2340	2005–2011	B	East
Gasare B	GAS-B	2	21	2250–2330	2005–2011	B	East
Uwasenoko A	UWA-A	2	21	2380–2490	2005–2011	B	East
Uwasenoko B	UWA-B	2	21	2360–2420	2005–2011	B	East
Cyamudongo A	CYA-A	3	31	1910–2140	2005–2011	Fragment	Fragment
Cyamudongo B	CYA-B	3.1	32	1820–2140	2005–2011	Fragment	Fragment
Cyamudongo C	CYA-C	1.4	12	1760–2070	2005–2011	Fragment	Fragment

park is characterized by schists and denser forest, whereas the eastern part of the park is characterized by granitic soils and secondary forest. Based on IUCN habitat classification scheme, the majority of surveyed habitat in the western region of the park is characterized as subtropical-tropical moist montane forest (82.27 %) and tropical dry forest to a lesser extent (10.64 %) (Jung et al., 2020). Habitat types that were surveyed in the eastern region of the park are much more variable with 60.77 % subtropical-tropical moist montane forest, 23.08 % plantations, 9.23 % subtropical-tropical high elevation shrublands. The Cyamudongo Forest fragment, isolated from the rest of the park, is characterized as disturbed forest with different successional phases, dense vegetation, and few clearings (Kanyamibwa, 2001) and soils dominated by cambisols and ferralsols (Nsanzurwimo, 2021). The majority of surveyed habitat (90.54 %) in Cyamudongo is characterized as subtropical-tropical moist montane forest and a smaller percentage of pastureland (4.05 %). The elevation ranges for the Cyamudongo forest fragment and the western region of the main forest block are lower (1638 – 2125 m and 1717 – 2530 m, respectively) compared to the east (2262 – 2942 m).

Once contiguous with the main forest block, since the 1960 s the 4-km² Cyamudongo Forest fragment has been separated from the rest of NNP by 10 km of transformed land. This fragment is classified as a Key Biodiversity Area (IUCN, 2016), and supports species found in Guinea-Congo Forest biome that are not found in the main forest block. The entire park includes a wide range of habitats including primary and secondary cloud forests, highland swamps, grasslands, and bamboo forests. Characterized as an Endemic Bird Area (Stattersfield et al., 1998), NNP supports more than 295 bird species, of which at least 74 are biome-restricted, 31 are range-restricted, 26 are endemic, and eight are listed as globally threatened or endangered (Plumptre et al., 2007).

2.2. Avian sampling

Bird monitoring data in Nyungwe National Park were collected based on point count surveys along 20 line transects, conducted twice annually from 2001 to 2011 or 2005–2011 (Table 1). All surveys were carried out by the same two trained ornithologists. Transects ranged from 1.3 to 4.5 km in length and were designed to traverse the range of elevations (1767 – 2940 m) and habitats in the park (Fig. 1 and Fig. S1). At each survey point (every 200 m along each transect), observers waited for two minutes for birds to settle. Subsequently, the team recorded the number of individuals and the species identification of all birds observed or heard during a ten-minute period. Observers used a laser rangefinder to determine distances to birds that were visible and within 70 m of the observation point. Observers also estimated distances of birds that were visually identified farther than 70 m and those detected by calls. The majority of transects begin on a road or base camp and extend perpendicularly into the forest. The North and South of the park were not sampled due to limited access. For each observation, the detection cue was noted (vocal or visual). Sampling effort included 84 temporal replicates of 485 unique points generating 55,965 observations of 176 species (relative to 310 documented to occur in the park), 124 genera, and 53 families (IOC World Bird List) (Table S1).

2.3. Vegetation indices

To test for effects of vegetation on species richness, vegetation indices were generated using Moderate Resolution Imaging Spectroradiometer (MODIS) data obtained from NASA's Earth Observing System Data and Information System (<https://earthdata.nasa.gov/>). Terra Moderate Resolution Imagine Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1) were generated every 16 days at a spatial resolution of 250 m as a Level 3 product and include Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI), which partially corrects for canopy background noise and other inaccuracies in regions with increased biomass. MOD16A2 Version 6 Evapotranspiration/Latent Heat Flux data include Potential Evapotranspiration (PET) as an 8-day composite at a 500 m resolution. Seasonal (wet and dry) annual vegetation indices for each 500 m x 500 m grid cell were generated by averaging available 250 m x 250 m pixel values. The raw vegetation metrics were summarized using principal component analyses and the primary axis of variation (PC1) was used to examine the relationship between vegetation and patterns of species richness (factor loadings for PC1: PET = 0.67, NDVI = -0.71, and EVI = -0.24).

2.4. Analyses of community structure

To determine which variables best explained variation in our sampled bird community, principal coordinate analysis (PCoA) was performed on a Bray-Curtis dissimilarity matrix of point count data (Bray and Curtis, 1957). All observations were grouped based on grid cell identity (defined above) and season. Abundances (counts) were standardized and a distance matrix was generated using the *decostand* (method = 'hellinger') and *vegdist()* functions, respectively, in the vegan package in R (Oksanen et al., 2016). The variation in the NNP bird community explained by season, year, elevation category, and region were tested using a permutational multivariate analysis of variance (PERMANOVA) on the Bray-Curtis distance matrix with site as a random effect (Anderson and Walsh, 2013). Analysis of similarities (ANOSIM) was used to calculate within vs. among group differences. All PERMANOVAs and ANOSIMs were implemented using the vegan package *adonis()* and *anosim()* functions, respectively, with 1000 permutations. To test for homogeneity of multivariate dispersion between elevational groups and regional assemblages, we used the *betadisper()* function, also included in the *vegan* package.

Dissimilarity among bird assemblages as a function of geographic distance (Euclidian distance), elevational distance (difference in elevation in meters), and relative distance to the forest edge (difference in distance to the edge in meters) between sites (grid cells) was examined using pairwise Sørensen (incidence-based beta-diversity: $\beta_{\text{sø}}$) dissimilarities, which can be partitioned into two major components including nestedness (species gains/losses: β_{sne}) and species turnover (species replacement: β_{sim}) (Baselga, 2010; Legendre, 2014). For each comparison, incidence data were grouped by grid cell and season. This analysis was carried out using the *beta*.

pair() function in the *betapart* package in R (Baselga and Orme, 2012). To test for predicted differences in estimates of beta diversity among groups, we used the Wilcoxon rank-sum test. To assess turnover rates over time and with respect to gradients of geographic distance, elevation, and distance to edges we fitted exponential distance-decay models using the *decay.model()* function. These models describe how dissimilarity in species assemblages between sites varies with the temporal, environmental, or geographic distances that separate them. Geographic distances between sites were calculated as Euclidian distances using the *dist()* function in R. Elevational and edge distances were calculated as absolute differences in these measurements between sites. To test for effects of geographic and environmental distances on dissimilarity between bird assemblages, we performed Mantel tests using dissimilarity matrices (described above) which were averaged over the study period for each grid cell, and corresponding matrices of geographic distances or differences between elevation or distance to edges between grid cells. Mantel tests were performed using the *mantel.rtest()* function in the *ade4* package with 10,000 permutations (Dray and Dufour, 2007).

2.5. Estimating species richness

To estimate species richness, data were grouped based on location within a 500 m x 500 m grid framework. The reason for this was two-fold: (1) to provide adequate spatial replication for estimating richness and (2) to define a consistent spatial framework for covariate data. Within each of the 85 grid cells, every point was treated as a sampling unit. Richness was then estimated for each grid cell and survey replicate ($n = 495$) with an average and median of six points per grid cell. Species richness was estimated using the non-parametric Abundance-based Coverage Estimator (ACE) developed by Chao et al. (Chao et al., 2005; Chao and Chiu, 2016) which uses the proportion of rare species that are not singletons to estimate richness. Specifically, this continuous sampling approach provides estimates of species richness without making any assumptions about the underlying distribution, only that rare species contribute the most information about undetected species. We chose this method because it has been shown to be more precise and less biased than other richness estimators under low to intermediate sampling intensity (Brose and Martinez, 2004; Hortal et al., 2006; Reese et al., 2014).

Estimates of sample completeness for each elevation group (low = 1750 – 2100 m; middle = 2101 – 2450 m; and high = 2451 – 2950 m) and each season (wet and dry) were generated using a coverage-based rarefaction method (Chao and Jost, 2012) which estimates the fraction of the community that remains undiscovered. Confidence intervals were generated based on 1000 bootstrap samples. Estimation of species richness and sample completeness were implemented using the iNext package (Hsieh et al., 2016) in the R computing environment (R Core Team 2021).

2.6. Statistical analyses of species richness

We constructed generalized linear mixed models (GLMMs) to test our hypotheses that elevation, distance to roads, and primary productivity would predict spatio-temporal pattern in species richness. Our response variable in all models included scaled and centered square root transformed grid and survey specific estimates of species richness (ACE) described above. Elevation was tested separately as either a continuous variable and also categorical variable, for which sites were categorized as either low (1750 – 2100 m), middle (2100 – 2450 m) or high (2450 – 2950 m) elevation sites. All linear explanatory variables were also centered and scaled to zero mean and unit variance. To avoid potentially erroneous interpretations of seasonal differences in richness caused by altitudinal migration and expected differences in detection, we analyzed the species richness patterns for wet and dry seasons separately. To control for differences in sampling effort, including spatial extent, we further divided our analyses of transects surveyed in the main forest block from 2000 to 2011 (Transect group A), those surveyed 2005–2011 in the main forest block (Transect group B), and those surveyed in the Cyamudongo forest fragment from 2005 to 2011 (Fragment). Grid cell identity and survey replicate were both specified as random effects in all models (Zuur et al., 2009). For model comparison and statistical inference, we used an information-theoretic approach using the Akaike's information criterion (AIC) (Burnham and Anderson, 2002). All statistical analyses were performed using the *lme4* package in R (Bates et al., 2014).

3. Results

3.1. General description of the NNP bird community

Over the course of this study, 176 species belonging to 53 families and 17 orders were detected (Table S1). Based on IUCN habitat classifications for the park and the bird community (Jung et al., 2021) species range from being specialized on a single habitat (38 species) to those associating with all seven habitat types found in NNP (28 species) (Fig. S2A). The majority of species that were specialized (32/38) were only detected in tropical moist montane forest habitat. Among those associated with drier and more open habitats (e.g., arable land, pastureland, and shrubland) the majority of species were associated with five or more other habitats indicating a greater association of generalists with this type of environment (Table S2). This is also reflected in the amount of overlap observed in each habitat type such that tropical moist montane forest, tropical dry forest, and plantations share the most species (Fig. S2B). Inland alpine wetlands habitat characterizes the Kamiranzovu swamp; only generalists were detected in this environment.

3.2. Avian community structure

Bray-Curtis dissimilarity principal coordinate analysis (PCoA) revealed clear differences based on both the geographic region of the

park and elevation, with the first two axes explaining 16.79 % and 13.21 % of the variation, respectively (Fig. 2). Based on PERMANOVA analyses, we found that NNP bird community was structured with respect to geographic regions of the park ($F = 47.43$, $df = 2$, $R^2 = 0.28$, $p = 0.001$) and elevation categories ($F = 33.87$, $df = 2$, $R^2 = 0.20$, $p = 0.001$). The community also varied with season ($F = 7.61$, $df = 1$, $R^2 = 0.023$, $p = 0.001$) and year ($F = 5.01$, $df = 1$, $R^2 = 0.015$, $p = 0.001$), indicating that bird assemblages at grid cells differed between the wet and dry seasons and changed over the study period.

Separation between sites within the Cyamudongo forest fragment, the western, and eastern transects indicated regionally distinct bird assemblages (Fig. 2 A) and between-site differences among regions exceeded those within each region (ANOSIM: $R = 0.497$, $p = 0.001$) (Fig. 3A and Table S3). This was also reflected in differences in the relative abundances among species with some species unique to each region (Table S4). Specifically, 2.84 %, 15.91 %, and 6.82 %, of the detected species pool were unique to the Cyamudongo forest fragment, the western, and the eastern regions of the main forest block, respectively. Regional dissimilarity estimates revealed the largest differences were between the Cyamudongo forest fragment and the eastern region of the main forest block, with turnover contributing the most to those differences (Fig. 3A and Table S3).

Replacing region with habitat type in the PERMANOVA analysis ($F = 4.40$, $df = 6$, $R^2 = 0.11$, $p = 0.001$), although statistically significant, explained less variation in the NNP bird community. Distance-decay models demonstrated increasing dissimilarity between sites as a function of the geographic distance between them (Fig. 4A and Table 2). Mantel tests revealed a strong correlation between geographic distance and community dissimilarities among bird assemblages across the park, and differences were better explained by turnover (β_{sim} : species replacement) than nestedness (β_{sne} : species gains and losses) (Table 3). Notably, turnover also contributed more than nestedness to inter-regional estimates of beta diversity, and this ratio increased with distance between sites (Fig. 3A and Table S3).

Elevation also explained a significant portion of the observed variation in the NNP bird community with significant differences in species composition among low, middle, and high elevation assemblages (Fig. 2B). Differences in turnover between the bird assemblages at sites associated with each elevation category were greater than the differences observed between sites within the same elevation category (ANOSIM: $r = 0.147$, $p = 0.001$; Fig. 3B and Table S3). This is further demonstrated by distance-decay model results showing that dissimilarity between sites increases as a function of elevational distance (Fig. 4B and Table 2), with turnover contributing more than nestedness to differences between bird assemblages as the difference in site elevation increased.

As predicted, among-group comparisons of dissimilarity indices for assemblages associated with each elevational band demonstrated greater similarity between bird assemblages at high elevations compared to low or middle elevations (Fig. 3B and Table S3), although only the turnover component was significant. Middle elevation assemblages were more similar to those of high elevations than low elevations, which again, was a pattern driven mostly by turnover. Although dissimilarity was greater between middle and low elevation assemblages, nestedness was highest between middle and high elevations, indicating species replacement contributed more to differences in species assemblages at low and middle elevations and species losses contribute more to difference between middle and high elevations.

The amount of variation in the NNP bird community explained by distance to the nearest edge, either the primary road traversing the forest block or the perimeter of the forest, was also significant. Distance-decay models (Fig. 4C and Table 2) and Mantel tests (Table 3) indicated that dissimilarity between bird assemblages is correlated with their distance from the forest edge, differences that are driven more by turnover than nestedness.

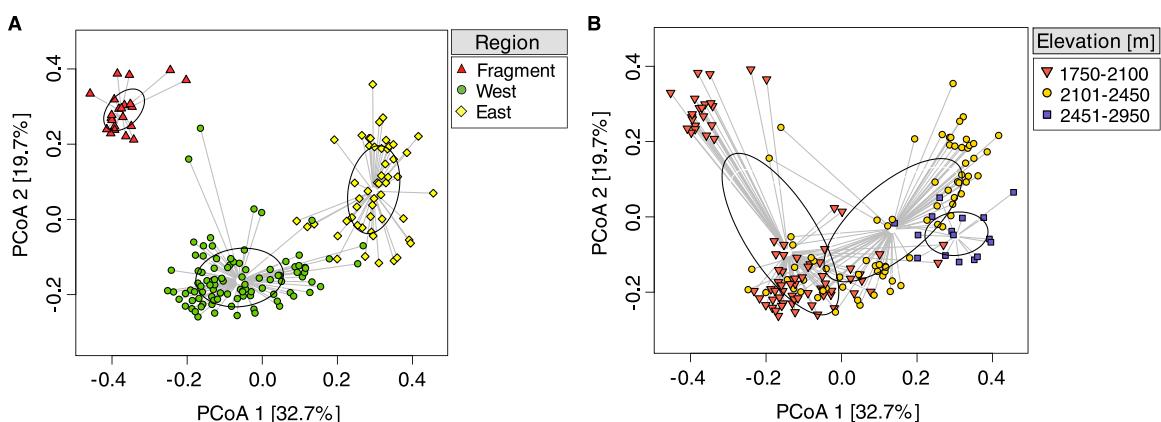


Fig. 2. Bray-Curtis dissimilarity principal coordinate analysis (PCoA) of the bird community in Nyungwe National Park. Each point represents a grid cell (500 m x 500 m) and season ($n = 170$) and is colored based on (A) region of the park: Cyamudongo forest fragment = red; western transects = green; and eastern transects = yellow, and (B) elevation: 1750–2100 m (low) = red; 2101–2450 m (middle) = yellow; and 2451–2950 m (high) = blue. The first two axes explain 32.73 % and 19.72 % of the variation, respectively. Ellipses represent 75 % CI around the cluster centroid for each region (A) or elevation group (B).

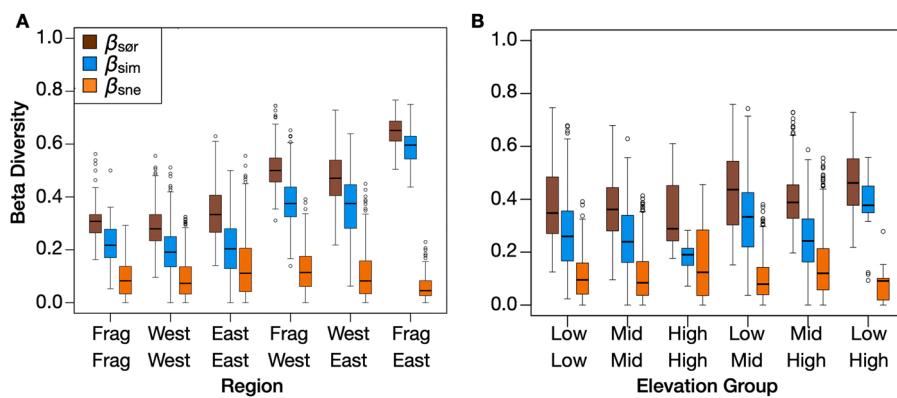


Fig. 3. Estimates of beta diversity for avian assemblages between sites within and among (A) regions of Nyungwe National Park (Frag = Fragment, West, and East) and (B) elevation groups (Low, Mid, and High). Sørensen dissimilarities (β_{sor} : brown) were decomposed into components of turnover (β_{sim} : blue) and nestedness (β_{sne} : orange).

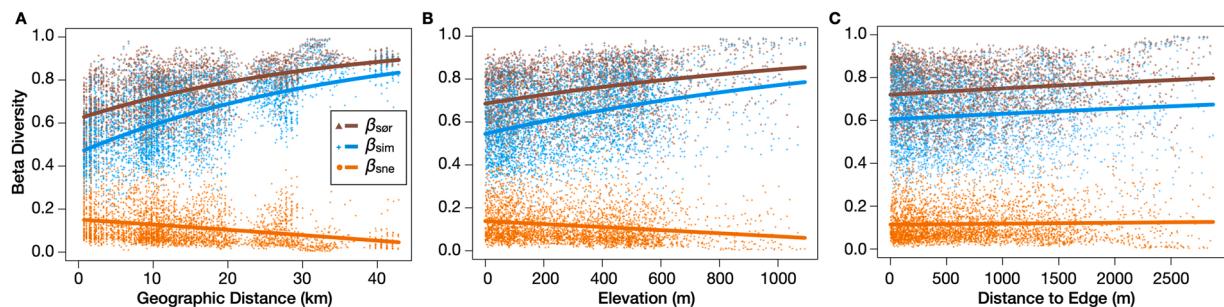


Fig. 4. Distance decay patterns for beta diversity with respect to (A) geographic distance, (B) elevation, and (C) distance to the forest edge. Sørensen dissimilarities (β_{sor} : brown) were decomposed into components of turnover (β_{sim} : blue) and nestedness (β_{sne} : orange).

Table 3

Mantel correlations between community dissimilarity and geographic, elevational, and edge distances. Statistical significance for each Mantel correlation value is given in parentheses. Sørensen dissimilarities (β_{sor}) were decomposed into components of turnover (β_{sim}) and nestedness (β_{sne}).

Beta Diversity	Geographic Distance	Elevation	Distance to Edge
β_{sor}	0.689 (< 0.001)	0.424 (< 0.001)	0.195 (0.002)
β_{sim}	0.684 (< 0.001)	0.367 (< 0.001)	0.201 (0.001)
β_{sne}	-0.067 (0.921)	0.056 (0.092)	0.063 (0.113)

Table 2

Distance-decay relationships between community dissimilarity and geographic, elevational and edge distances. Sørensen dissimilarities (β_{sor}) were decomposed into components of turnover (β_{sim}) and nestedness (β_{sne}).

Variable	Beta Diversity	Pseudo-r ²	Slope	y-intercept	p-value
Geographic Distance (km)	β_{sor}	0.322	0.030	0.030	< 0.01
	β_{sim}	0.357	0.027	0.462	< 0.01
	β_{sne}	0.083	-0.003	0.152	< 0.01
Elevation (100 m)	β_{sor}	0.127	0.080	0.685	< 0.01
	β_{sim}	0.146	0.073	0.544	< 0.01
	β_{sne}	0.057	-0.014	0.138	< 0.01
Distance to Edge (100 m)	β_{sor}	0.101	0.071	0.720	< 0.01
	β_{sim}	0.123	0.069	0.606	< 0.01
	β_{sne}	0.036	-0.008	0.114	< 0.01

3.3. Patterns of species richness

Species richness for all three elevation groups were close to their respective asymptotes, indicating that bird assemblages were almost fully sampled during both the wet and dry seasons (Fig. 5). Extrapolating each curve to double the sampling depth increased the wet season species richness estimates by 4.89 %, 11.00 %, and 9.76 % for low, mid, and high elevation groups, respectively; dry season species richness estimates were increased by 5.77 %, 9.76 % and 11.15 %.

As expected, estimated species richness (ACE) was higher than raw species counts, but patterns of community structure were consistent between the two with respect to the variables that we examined (Table 4 and Fig. S3). Species richness estimates were higher during the dry season, despite less sampling (t -test: $t = 2.915$, $df = 903$, $p = 0.004$). Examining spatio-temporal patterns of species richness, the most parsimonious generalized linear mixed models revealed that species richness ($\Delta AIC < 2$) differed between wet and dry season, and among transect groups (Table 5).

Consistent across all transects and seasons was a pattern of decreasing species richness with elevation (Figs. 6A, 6C, and 6E) and increasing species richness with survey effort. For transect group A, the best model during the wet season included additive and interactive effects of elevation category and temporal trend, distance to road, and survey effort (Table 5 A). Although there was no evidence for an overall temporal trend in species richness, middle and high elevation sites experienced a significant increase in species richness over the eleven-year period that was specific to the wet season (Table 6A and Fig. 7A). In contrast, high elevation sites during the dry season showed a pattern of decreasing richness, but this effect was not significant. Distance to roads was included as an additive effect in the top models for both seasons but was only significant during the dry season (Fig. 6B). For both seasons, richness declined with increasing distance to the road. For the dry season, the best model included an interactive effect of distance to road and temporal trend, specifically, an overall negative but non-significant trend in species richness, with an increase in richness further from the main road and a decrease in richness closer to the road over time (Tables 5B and 6B and Fig. 7B).

In addition to the additive effects of elevation (Fig. 6C) and survey effort for both seasons for transect group B (Table 5 C and 5D), the top model for the wet season also included distance to roads as an additive effect and as an interactive effect with elevation; however, neither of these were significant (Tables 6C and 6D and Fig. 6D). The data collected for the Cyamudongo forest fragment were more limited in terms of timespan and elevational range and the top model for both the wet and dry seasons was the intercept-only model (Tables 5E and 5 F). However, the second-best model for Cyamudongo during the wet season included additive effects of elevation and distance to the fragment boundary, the latter showing a positive effect on richness (Table 6E and Fig. 6F).

4. Discussion

Understanding the spatiotemporal diversity patterns that characterize tropical montane forest communities is of critical importance in determining how to maximize the effectiveness of protected areas to conserve biodiversity. Our study revealed that the Afromontane tropical forest bird community of Nyungwe National Park is geographically structured with strong compositional turnover along the elevational gradient, and with respect to geographic distance, despite the lack of geographic barriers. Supporting our predictions, we found a pattern of decreasing richness with increasing elevation that is consistent with other studies (Blake and Loiselle, 2000; Herzog et al., 2005; Terborgh, 1977). We also found that richness was overall stable during the 11-year study period, but that temporal changes in richness differed depending on elevation and distance to the forest edge, and that these patterns were season-specific. These results suggest that sensitivity to anthropogenic factors may be elevation- and site-specific, and that tropical diversity patterns should be evaluated seasonally to fully understand local community dynamics. Above all, we argue that the strong temporal and spatial structure of these communities suggest that large reserves such as NNP may be necessary to conserve the full Afromontane bird community.

Previous studies indicate that while environmental and neutral dispersal processes are not mutually exclusive in structuring

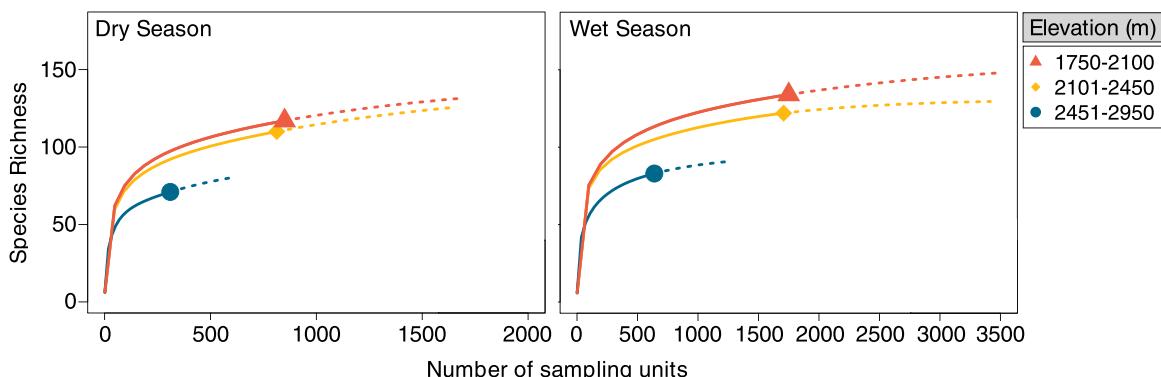


Fig. 5. Results of integrated coverage-based rarefaction-extrapolation of richness for each elevation group with randomized avian species accumulation curves in Nyungwe National Park, Rwanda. Solid portions of the lines represent interpolation whereas the dashed portions of the lines represent extrapolation beyond observed samples; 95 % confidence intervals are indicated by the shaded areas.

Table 4

Summary statistics of estimated (ACE = Abundance-based Coverage Estimator) and raw species richness for covariates of interest for each grid cell and season. Wet and Dry seasons were analyzed separately in order to account for potential seasonal altitudinal migration.

Season:	WET				DRY					
	Richness Estimate:		ACE		Raw		ACE		Raw	
Variable	N	Mean	SD	Mean	SD	N	Mean	SD	Mean	SD
Season	1039	26.9	10.4	18.1	6.88	509	28.7	11.8	19.2	7.56
Year	2001	107	27	10.8	17.5	6.49	38	29.2	11.5	19.1
	2002	72	26.7	9.37	18.5	6.41	37	30.4	11.1	19.9
	2003	112	27.8	10.6	18.8	6.81	36	31.5	12.1	20.5
	2004	104	26.9	10.1	18	6.85	34	26.4	9.84	17.4
	2005	126	26	9.89	17.2	6.86	61	30.2	12.6	19.3
	2006	192	27.8	10.8	18.2	7.01	64	28.5	10.8	19.3
	2007	29	25.1	9.48	17.4	6.9	32	27.7	12.7	18.8
	2008	90	24.9	11	17	6.8	69	26.6	11.5	18.7
	2009	65	26.5	10.1	19.2	7
	2010	68	28.1	11.4	19.9	7.85	70	30.8	13.4	19.9
	2011	74	26.8	9.66	18.4	6.53	68	26.2	11	19.1
Elevation Group	Low	500	26.5	10.8	17.4	6.92	246	28.2	12.8	18.5
	Mid	431	28.9	9.99	19.9	6.8	210	31.2	10.5	21.2
	High	108	20.7	7.07	14.4	4.54	53	20.6	7.33	15.2
Region	Cya	108	19.5	9.96	12.1	3.9	54	18.5	10.5	11.9
	West	704	29	10.1	19.6	6.93	334	31.8	11.4	21.2
	East	227	23.8	8.93	16.5	5.82	121	24.6	9.42	17.1
Transect Group	Frag	108	19.5	9.96	12.1	3.9	54	18.5	10.5	11.9
	A	688	27.3	10.1	18.4	6.72	317	29	11.2	19.4
	B	243	29	9.93	20.1	6.88	138	31.9	11.4	21.7

communities, the former is the predominant force (Cottenie, 2005; Silva and Hernández, 2014). Despite continuity of the forest between the west and east of the main forest block, NNP community was strongly structured with respect to region (Fig. 2A and Table S3), which differ in terms of age, disturbance, habitat type, soils, and size (Ghehi et al., 2011; Nsanjurwimo, 2021). Compositional turnover contributed more to average regional dissimilarity than did differences in richness (Fig. 3A and Tables 2 and 3). As species composition of bird assemblages largely overlapped at the regional scale, these differences can be primarily attributed to turnover between sites at the scale of the grid cell. Some species were however unique to each region. Specifically, the number of species detected was higher in the western part of the main forest block (158 detected species; 89.77 % of the regional assemblage, defined as all species detected in the park over the entire study period) compared to the east (121; 68.75 % of the regional assemblage), the former of which represents a larger area of the park, is less disturbed, and was surveyed over a longer time period. Taken together, these results suggest that larger parks will be more likely to support the full avian diversity of the birds of this region.

Twenty-eight and twelve species (corresponding to 15.91 % and 6.82 % of the detected species pool) were unique to the western and eastern parts of the park, respectively. Although heavily surveyed, the Cyamudongo forest fragment exhibited lower regional species richness with only 98 species (55.68 % of the regional pool) and five unique species detected there (*Bubo lacteus*, *Bubo poensis*, *Falco biarmicus*, *Anaplectes rubriceps*, and *Pternistis squamatus*). Other species such as the Ross's turaco (*Musophaga rossae*) was rarely detected in the main forest block but was one of the most frequently detected species in the Cyamudongo forest fragment. Reduced regional richness in the fragment could be a consequence of environmental variables that were not accounted for, or smaller area (4-km²) compared to the main forest block (1019-km²). The negative relationship frequently observed between avian species richness and fragment size (Ferraz et al., 2003; Kattan et al., 1994; Turner et al., 1996) has been attributed to changes in forest dynamics (Laurance et al., 2002), limited immigration (Bierregaard et al., 1992), edge effects (Banks-Leite et al., 2010; Jones et al., 2021), and disruption of ecological and/or trophic networks (Lovejoy et al., 1986; Willis, 1974). These fragmentation effects provide further evidence for the value of larger reserves, but the Cyamudongo fragment also contains some endemic species, which suggests that fragments near larger reserves also hold conservation value.

High beta diversity between regions is also reflected in the steep distance-decay pattern of dissimilarity for geographic distance (Fig. 4). Strong independent effects of geographic distance have been observed in birds at continental (Keil et al., 2012) and regional (Fluck et al., 2020; Wayman et al., 2021) scales and in plants (Qian et al., 2008; Tuomisto et al., 2003), but at finer scales climate and habitat characteristics have been shown to contribute more to avian beta diversity patterns (Hu et al., 2018), particularly in the tropics (Jankowski et al., 2009), highlighting the need for high resolution climate and habitat data in evaluating diversity patterns. The significant correlation that we found between turnover and spatial separation between sites Table 3 is likely indicative of uncaptured environmental gradients that differentiate regions of the park. Although dispersal limitation is generally more limited for animals that can fly (Soininen et al., 2018), tropical montane bird species typically have small home ranges and will not traverse short distances of unsuitable habitat (Hawkins and Felizola Diniz-Filho, 2006; Moore et al., 2008; Ruggiero and Hawkins, 2008). Once again, these data suggest that larger connected reserves will be better than smaller disconnected reserves.

The structuring of avian communities along elevational gradients is ubiquitous (Blake and Loiselle, 2000; Lomolino, 2001; McCain and Grytnes, 2010), yet rates of turnover and species richness patterns along elevational gradients differ regionally and among taxa. As predicted the NNP bird community was structured along the existing elevation gradient (Fig. 2) and among site dissimilarities

Table 5

Model comparison statistics for generalized linear mixed models testing the effects of covariates on species richness (ACE) for transects surveyed in the main forest block from 2001 to 2011 (Transect Group A; A and B), 2005–2011 (Transect Group B; C and D) and in the Cyamudongo forest fragment from 2005 to 2011 (Fragment; E and F) during the wet season (A, C, and E) and the dry season (B, D, and F). Covariates include median elevation (Elevation) which was treated as a factor (Low, Middle, or High) for Transect Group A (wet season) and as a continuous variable for all other analyses; distance to the road in the main forest block (Roads); distance to the fragment boundary (Boundary); sampling effort (Effort); vegetation (principal component 1 of NDVI, EVI, and ET); and annual trend. Grid and survey replicate were included as random effects in each model. The top five models for each analysis are shown.

Model	K	AICc	ΔAICc	Weight
(A) Transect Group A - Wet Season				
Elevation x Trend + Roads x Effort	12	1549.425	0.000	0.383
Elevation x Trend + Roads x Effort + Roads:Elevation	14	1550.921	1.497	0.181
Elevation x Trend + Effort	10	1551.357	1.932	0.146
Elevation x Trend + Roads x Effort + Vegetation	13	1551.364	1.940	0.145
Elevation + Trend + Roads x Effort	10	1551.370	1.946	0.145
(B) Transect Group A - Dry Season				
Elevation + Roads x Trend + Effort	9	785.914	0.000	0.387
Elevation x Trend + Roads + Effort	9	787.394	1.479	0.185
Roads x Trend + Elevation + Vegetation + Effort	10	787.638	1.724	0.163
Roads + Trend + Roads x Effort + Elevation	10	788.047	2.132	0.133
Roads x Trend + Effort	8	788.056	2.141	0.133
(C) Transect Group B - Wet Season				
Elevation x Roads + Effort	8	583.739	0.000	0.382
Elevation x Roads + Vegetation + Effort	9	584.861	1.122	0.218
Elevation + Effort	6	584.879	1.140	0.216
Elevation + Roads + Vegetation + Effort	8	586.295	2.556	0.106
Elevation + Roads + Effort	8	586.927	3.188	0.078
(D) Transect Group B - Dry Season				
Elevation + Effort	6	313.945	0.000	0.267
Elevation x Effort + Roads	8	314.138	0.192	0.243
Roads + Elevation + Effort	7	314.903	0.957	0.165
Elevation + Vegetation + Effort	7	314.912	0.967	0.165
Elevation x Effort + Trend	8	314.963	1.018	0.160
(E) Fragment - Wet Season				
Intercept-only	6	301.197	0.000	0.369
Elevation + Boundary + Effort	7	302.186	1.890	0.225
Elevation + Boundary x Effort + Vegetation	8	303.143	2.190	0.139
Elevation x Effort + Boundary	8	303.222	3.136	0.134
Elevation + Boundary x Effort + Trend	8	303.230	3.857	0.133
(F) Fragment - Dry Season				
Intercept-only	6	159.951	0.000	0.347
Elevation + Trend + Effort	7	161.040	1.089	0.202
Elevation + Effort	7	161.101	1.150	0.196
Trend + Effort	7	161.876	1.925	0.133
Elevation + Trend + Boundary + Effort	11	162.033	2.082	0.123

increased with the elevational difference between them (Figs. 3 and 4). This pattern is consistent with a number of other studies which have also shown turnover to be steeper at lower latitudes (Burgess and Mlingwa, 2000). We found that parkwide, higher turnover was responsible for observed differences in assemblages between middle and high elevations and species losses contributed more to differences between middle and high elevations (Fig. 3), a pattern that is consistent with the observed decrease in richness with increasing elevation (Figs. 5 and 6). The monotonic decline in richness has been predicted for wet mountains with decreasing temperature along the elevational gradient positively associated with species richness in humid environments (McCain, 2009a). The greatest percentage of the regional species assemblage was detected within the low and middle elevation groups (84.09 % and 91.48 %, respectively) for both the wet and dry seasons (Table S5). However, few species were restricted to a single elevational band indicating extended elevational ranges for the detected species and potential seasonal migration. There are published observations of the White-starred Robin (*Pogonochichla stellata*) and the Barred Long-tailed Cuckoo (*Cercococcyx montanus*) moving to lower elevations to breed during the dry season in Tanzania (Burgess and Mlingwa, 2000) but this is an area of research that demands further study. Only thirteen and sixteen species were exclusively detected at low and middle elevations, respectively (corresponding to 7.39 % and 9.09 % of regional pool). Twenty-eight, fifteen, and sixty-seven species (corresponding to 15.91 %, 8.52 %, and 38.07 % of the regional assemblage, respectively) were undetected in the lower, middle, and high elevation ranges of the surveys. Notably, low and middle elevation sites exhibited significantly greater dissimilarity compared to higher elevation sites (Fig. 3), likely reflecting higher variability in habitat for lower and middle elevations spanning a larger area. These results suggest that conserving complete elevation gradients will provide better connectivity and allow birds to move freely up and downslope.

Although we anticipated vegetation to be a strong predictor of community structure and species richness in NNP, our results did not support this prediction. One possible explanation for this result is that differences in other biodiversity metrics such as localized flora are more important determinants of avian community structure than vegetation indices alone; we could not test this possibility due to

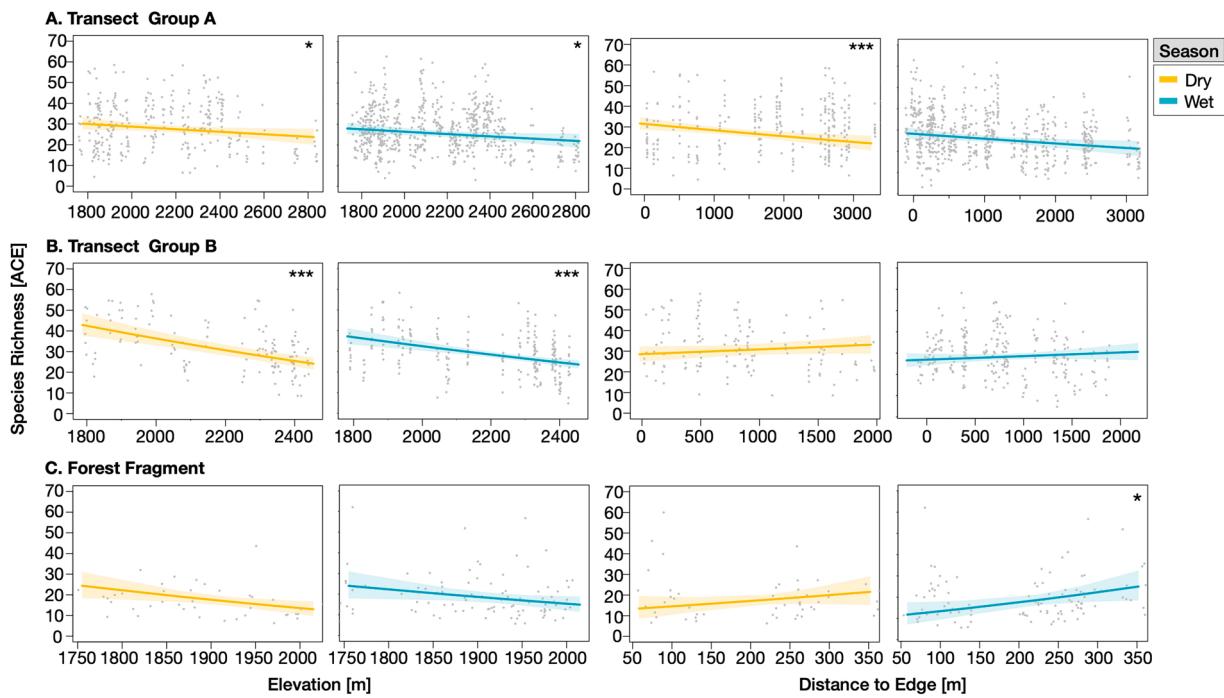


Fig. 6. Relationship between species richness using the non-parametric Abundance-based Coverage Estimator (ACE) and elevation (left panels: A, C, and E) and distance to the forest edge (right panels: B, D, and F) during the dry season (yellow) and wet season (blue) for sites in transect group A (A and B), transect group B (C and D) and the Cyamudongo forest fragment (E and F), Nyungwe National Park, Rwanda. Shaded areas show the 95 % confidence intervals of the regression lines.

the lack of data.

In addition to understanding how the Afrotropical montane bird community of Nyungwe National Park is structured, it is important to know if and how diversity patterns might change over time. We predicted that anthropogenic pressures affecting NNP (Crawford, 2012) would have caused decrease in species richness over the study period with steeper declines at high and low elevations. Although we did not expect richness trends to differ seasonally or regionally, accounting for them revealed significant differences (Table 6 and Fig. 7), with high elevation assemblages showing an increase in richness during the wet season, but a decrease during the dry season in the western region of the park. This partially supports findings by Neate-Clegg et al. (2020) demonstrating shifts in elevational ranges for NNP bird species. These were predominantly upslope shifts in mean elevation range and lower range limits; however, a few species exhibited reductions in the upper limits of their elevational ranges. These shifts were not strongly correlated with temperature or precipitation except that larger-bodied birds and species with lower dietary breadth tended to expand their ranges during warmer and wetter years, respectively. One recent study conducted by Hoek et al. (van der Hoek et al., 2022) in Volcanoes National Park, Rwanda, showed that for 35 focal species, the upper and lower elevational range limits were affected by habitat, temperature, and precipitation. Interestingly, temperature and habitat had a more ubiquitous effect on upper limits whereas precipitation exhibited similar effects on upper and lower limits for about half of the species examined. These differing responses likely reflect complex interactions between climate, weather, habitat and diet in determining the limits of species' elevational ranges and highlight the need for investigating the relationship between the phenology of altitudinal migration, local weather patterns, and habitat.

The relationship between species richness and edges is context- and taxon-dependent (Kroeger et al., 2021; Ries and Sisk, 2004). Roads have been shown to affect avian species richness more negatively in areas with denser tree cover and to be effective barriers to movements of understory bird species and exhibit guild-specific effects (Cros et al., 2020; Khamcha et al., 2018; Laurance et al., 2004; Lees and Peres, 2009). Although our sampling design did not allow for rigorous tests of the influence of these variables, we observed that for transect group A (predominantly western region transects) species richness decreased with increasing distance to roads, an effect that was stronger during the dry season. Several studies have documented that classic edge effects characterized by increasing rates of nest predation and parasitism with decreasing distance to forest edges (Robinson et al., 1995) are less common in Afrotropical forests compared to the Neotropics. In contrast, it has been shown that nest predation rates are relaxed in fragments with higher edge: area ratios and with decreasing distance from the forest edge (Spanhove et al., 2009, 2014). Decreasing richness farther from the forest edge observed in our study could arise due to reduced nest predation, and open and diverse habitat suitable for a more diverse group of species closer to the edge.

The top model for the dry season and Transect Group A includes an interaction between trend and distance to roads such that richness appears to be decreasing in areas in closer proximity to the main road and increasing further away. This may indicate increasing human impacts, heightened sensitivity to climate change, potentially positive effects of habitat protection on richness in the

Table 6

Coefficients for the most parsimonious generalized linear mixed model for species richness for transect group A (A and B), transect group B (C and D), and the Cyamudongo forest fragment (E and F) during the wet season (A, C, and E) and the dry season (B, D, and F).

A. Transect Group A - Wet Season						
Variable	b	SE	z	Sig.	0.025	0.975
Elevation(Low)	0.159	0.120	1.322	0.192	-0.084	0.396
Elevation(Middle)	-0.042	0.135	-0.309	0.759	-0.316	0.227
Elevation(High)	-0.438	0.202	-2.170	0.035	-0.843	-0.036
Roads	-0.160	0.091	-1.749	0.088	-0.344	0.023
Effort	0.432	0.067	6.477	< 0.001	0.299	0.565
Elevation(Low):Trend	-0.055	0.058	-0.949	0.347	-0.170	0.060
Elevation(Middle):Trend	0.144	0.074	1.954	0.051	0.000	0.288
Elevation(High):Trend	0.237	0.104	2.283	0.023	0.033	0.441
Roads:Effort	-0.171	0.075	-2.282	0.027	-0.326	-0.024
B. Transect Group A - Dry Season						
Variable	b	SE	z	Sig.	0.025	0.975
(Intercept)	0.145	0.076	1.892	0.074	-0.013	0.302
Elevation	-0.147	0.069	-2.131	0.040	-0.285	-0.008
Effort	0.362	0.069	5.276	< 0.001	0.226	0.502
Trend	-0.126	0.060	-2.088	0.070	-0.259	0.008
Roads	-0.294	0.076	-3.878	< 0.001	-0.445	-0.143
Trend:Roads	0.126	0.055	2.273	0.024	0.017	0.235
C. Transect Group B - Wet Season						
Variable	b	SE	z	Sig.	0.025	0.975
(Intercept)	-0.119	0.071	-1.680	0.106	-0.266	0.025
Elevation	-0.408	0.074	-5.533	< 0.001	-0.565	-0.261
Roads	0.088	0.074	1.187	0.246	-0.061	0.242
Elevation:Roads	-0.132	0.072	-1.835	0.078	-0.283	0.011
Effort	0.511	0.068	7.539	< 0.001	0.377	0.657
D. Transect Group B - Dry Season						
Variable	b	SE	z	Sig.	0.025	0.975
(Intercept)	-0.129	0.118	-1.062	0.304	-0.394	0.132
Elevation	-0.526	0.074	-7.002	< 0.001	-0.677	-0.374
Effort	0.426	0.070	6.535	< 0.001	0.285	0.568
E. Fragment - Wet Season						
Variable	b	SE	z	Sig.	0.025	0.975
(Intercept)	-0.148	0.225	-0.657	0.519	-0.676	0.298
Elevation	-0.334	0.163	-2.054	0.074	-0.692	0.027
Boundary	0.465	0.202	2.298	0.040	0.064	0.947
Effort	-0.226	0.306	-0.739	0.464	-0.916	0.392
F. Fragment - Dry Season						
Variable	b	SE	z	Sig.	0.025	0.975
(Intercept)	0.099	0.213	0.466	0.651	-0.382	0.538
Elevation	-0.289	0.138	-2.086	0.062	-0.580	0.018
Trend	0.211	0.126	1.679	0.091	-0.042	0.463
Effort	0.168	0.274	0.612	0.551	-0.442	0.726

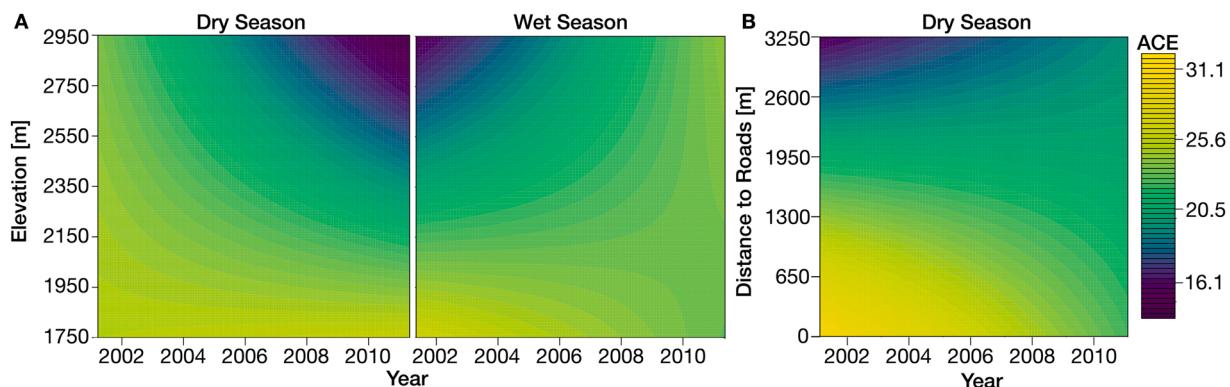


Fig. 7. Interaction plots showing patterns of species richness (ACE) in Nyungwe National Park, Rwanda over time with respect to elevation during the wet and dry seasons (A) and distance to roads during the dry season (B) for transect group A. Contour lines represent Abundance-based Coverage Estimator (ACE) estimates of species richness. Values are indicated by color ranging from 14 (purple) to 32 (yellow).

forest interior, and/or emigration of species from edges to the interior. Interestingly, although data for the Cyamudongo forest fragment were temporally limited compared to the main forest block, the second-best model for Cyamudongo during the wet season included an additive effect distance to the fragment boundary. In contrast to the distance to road effect that we found for the main forest block, the effect of distance to fragment boundary showed a positive relationship with species richness indicating the road and forest edge might have differing effects on richness, or that differences in habitat in the main forest block and the forest fragment might lead to differences in edge effects.

The relative stability in species richness over this eleven-year period demonstrates the immense value of large, protected areas, such as Nyungwe National Park, as essential refuges for the full Afromontane bird community. These large reserves will become increasingly important as climate rapidly continues to change and pressures from human activities intensify. Our observation that species richness trends differed with respect to elevational band, distance to the forest edge, and season highlight the need to better understand the factors influencing bird diversity patterns at fine temporal and geographic scales. All of our results, however, support the need to protect large reserves.

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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.

Data Availability

The authors do not have permission to share data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02333](https://doi.org/10.1016/j.gecco.2022.e02333).

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