

RESEARCH ARTICLE

Effects of land-use change on avian taxonomic, functional and phylogenetic diversity in a tropical montane rainforest

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Abstract

Aim: Although land use change is a leading cause of biodiversity loss worldwide, there is scant information on the extent to which it has affected the structure and composition of bird communities in the Afrotropical region. This study aimed to quantify the effects of habitat transformation on taxonomic, functional and phylogenetic diversity in Afrotropical bird communities.

Location: Nyungwe landscape, a montane rainforest with adjoining farmland in south-west Rwanda.

Methods: Data on bird occurrence, abundance and functional traits were collected in 2017/18 using point counts. We also collected data on habitat and morphological traits for all bird species recorded. We quantified bird diversity using a range of metrics, including the inverse Simpson index, functional dispersion and the standardized effect size of mean nearest taxon distance.

Results: In comparison with primary forest areas, even low levels of land use change altered species composition and reduced species diversity. Although overall functional diversity and phylogenetic diversity were similar across land use types, we found a significant contraction of trophic and locomotory trait structures of bird communities in restored areas and cultivated areas, respectively. Soil moisture, elevation and lower vegetation height were major factors influencing taxonomic, functional and phylogenetic dimensions of bird communities, although their effects varied across these dimensions.

Main conclusions: The sensitivity of forest species to minor habitat disturbance emphasizes the value of conserving primary vegetation. Long-term conservation of bird communities in Afrotropical ecosystems requires halting wide-scale destruction of primary forest, promoting vegetation heterogeneity in the ecological restoration of degraded habitats and adopting wildlife-friendly agricultural practices. Our results suggest that monitoring and conservation in these landscapes can be refined using taxonomic, functional and phylogenetic diversity metrics to provide complementary information about the current and likely future impacts of land use change.

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KEYWORDS

birds, functional diversity, land use change, Nyungwe forest, phylogenetic diversity, Rwanda, taxonomic diversity, tropical forest

1 | INTRODUCTION

Tropical ecosystems provide essential ecosystem services ranging from carbon sequestration to climate and water regulation, and they also harbour 91% of terrestrial avian species (Barlow et al., 2018; Diaz et al., 2019; Phillips et al., 2017). Tropical montane forest ecosystems in particular have distinct taxonomic and phylogenetic assemblages, reflecting their high environmental (especially climatic) diversity (Quintero & Jetz, 2018; Rahbek et al., 2019). Despite the multitude of services provided by tropical forests, they are facing increasing biodiversity loss due to land use change, mainly in the form of conversion of natural habitats to agricultural areas (Diaz et al., 2019; Turubanova et al., 2018). Global projections by Jetz et al. (2007), based on a low environmental degradation scenario, but incorporating the combined effects of climate change and land use change, showed that 900 land bird species (from a total of 8,750) will experience range contractions of at least 50% by the end of this century. The study indicated a particularly bleak future for tropical montane endemic species, due to accelerated anthropogenic habitat conversion (see also Ayebare et al., 2018; Plumptre et al., 2003, 2007).

At the habitat level, land use change often entails the modification of the physical environment and vegetation structure, with impacts on many bird species. For instance, the removal of mature trees (large and tall) affects canopy foragers and cavity nesters (Bonaparte et al., 2020; Lindenmayer, 2017), while changes in microclimatic and edaphic conditions, such as soil water content, affect the abundance of soil invertebrates, which avian insectivores consume (Cifuentes-Croquevielle et al., 2020; Sutherland & Green, 2004). The clearing of forest in the tropics is often concentrated at lower elevation habitats, leading to the loss of specific vegetation types and their associated bird assemblages (Franklin et al., 2019; Harris et al., 2014). For example, (a) in the montane rainforests of Rwanda, Neate-Clegg et al. (2020) reported the upslope shift of bird communities following anthropogenic habitat transformation over 15 years in Nyungwe National Park, while (b) in the Volcanoes National Park, Rwanda, where the vegetation stratification is well marked, extirpation of bird species such as *Cercococcyx montanus* (Barred long-tailed cuckoo) was documented after the clearance of the low-elevation mixed forest (Vande weghe & Vande weghe, 2011).

Although birds have been the focus of many land use change studies worldwide, research coverage in the Afrotropics remains poor and is dominated by the evaluation of taxonomic diversity, which is not always sufficiently informative about ecosystem processes and responses to environmental disturbances (Cadotte et al., 2011; Mouillot et al., 2013; Petchey & Gaston, 2002; Walker et al., 1999). To fill this gap, functional trait-based approaches are gaining prominence, wherein functional traits are defined as a quantifiable aspect

of an organism that influences its interaction with the environment (Flynn et al., 2009). A growing number of studies have used these approaches to investigate the impacts of habitat loss and fragmentation on tropical forest bird communities (e.g. Bregman et al., 2016; Cannon et al., 2019; Chapman et al., 2018), including preliminary studies in the Afrotropics (e.g. Ulrich et al., 2016). The use of measurable morphological traits, such as beak dimensions, can help to characterize the bird trophic niche and thus enables inferences concerning ecosystem functions of bird communities such as seed dispersal and pest control (Bregman et al., 2016; Pigot et al., 2020; Tobias et al., 2020). In the tropics, functional diversity has been found to decline with increasing intensity of land use change (Flynn et al., 2009; Şekercioğlu, 2012). Yet, comparatively little is known about how different forms of anthropogenic disturbances impact different trophic processes (but see Bregman et al., 2016; Trisos et al., 2014), especially in the Afrotropics.

Phylogenetic differences reflecting evolutionary divergence among taxa can potentially provide further information about a range of hidden ecological or behavioural properties that may not be evident from the morphological traits analysed (Mouquet et al., 2012). Thus, phylogenetic diversity (PD) is often estimated in conjunction with functional diversity and is increasingly used to determine community responses to environmental disturbances (e.g. Aguirre-Gutiérrez et al., 2020; Helmus et al., 2010; Rolland et al., 2012). Comprehensive assessment of the impacts of land use change should therefore make use of different facets of biodiversity—including both morphological and phylogenetic data—to guide conservation strategies (Cannon et al., 2019; Chapman et al., 2018; Devictor et al., 2010; Le Bagousse-Pinguet et al., 2019).

Here, we assess how land use change (modification from primary forest to other land use types) has affected bird communities within Nyungwe forest (a key landscape in the Albertine Rift) and adjoining agricultural farms in south-west Rwanda, a region that is underrepresented in ecological and biogeographical research. In particular, we ask how bird species composition and taxonomic, functional and phylogenetic diversity vary with land use and related environmental properties. Following the intermediate disturbance hypothesis (Connell, 1978), we predict that (a) taxonomic, functional and phylogenetic diversity levels will be highest in moderately disturbed secondary forests and lowest in habitats heavily degraded by fire or agriculture. Since the structural complexity of vegetation is known to drive species diversity (MacArthur & MacArthur, 1961) and anthropogenic disturbances may catalyse habitat filtering processes resulting in reduced avian diversity (Evans et al., 2018; Flynn et al., 2009), we also predict that (b) communities in highly degraded land uses will comprise sets of closely related species and (c) increased vegetation structural complexity will drive increases in each diversity component.

2 | METHODS

2.1 | Study area

The study area of Nyungwe landscape in south-west Rwanda comprises Nyungwe National Park (Nyungwe NP) and surrounding agricultural areas (Figure 1). Nyungwe NP is a tropical montane rain-forest covering an elevational range of 1,600–2,950 m, with an area of 1,019 km², mean annual rainfall of 1,500–2,500 mm and average

minimum and maximum temperature of 10.9 and 19.6°C, respectively (Seimon, 2012; Sun et al., 1996). Nyungwe NP was gazetted as a forest reserve in 1933, gaining National Park status in 2004. The forest is considered one of the six key landscapes of the Albertine Rift in terms of the number of plant and animal species that are endemic to this region, and those that are considered globally threatened based on the IUCN Red List (Plumptre et al., 2007).

Changes to the Nyungwe landscape within the past 50 years have involved clearance for agriculture, settlements and roads, gold and

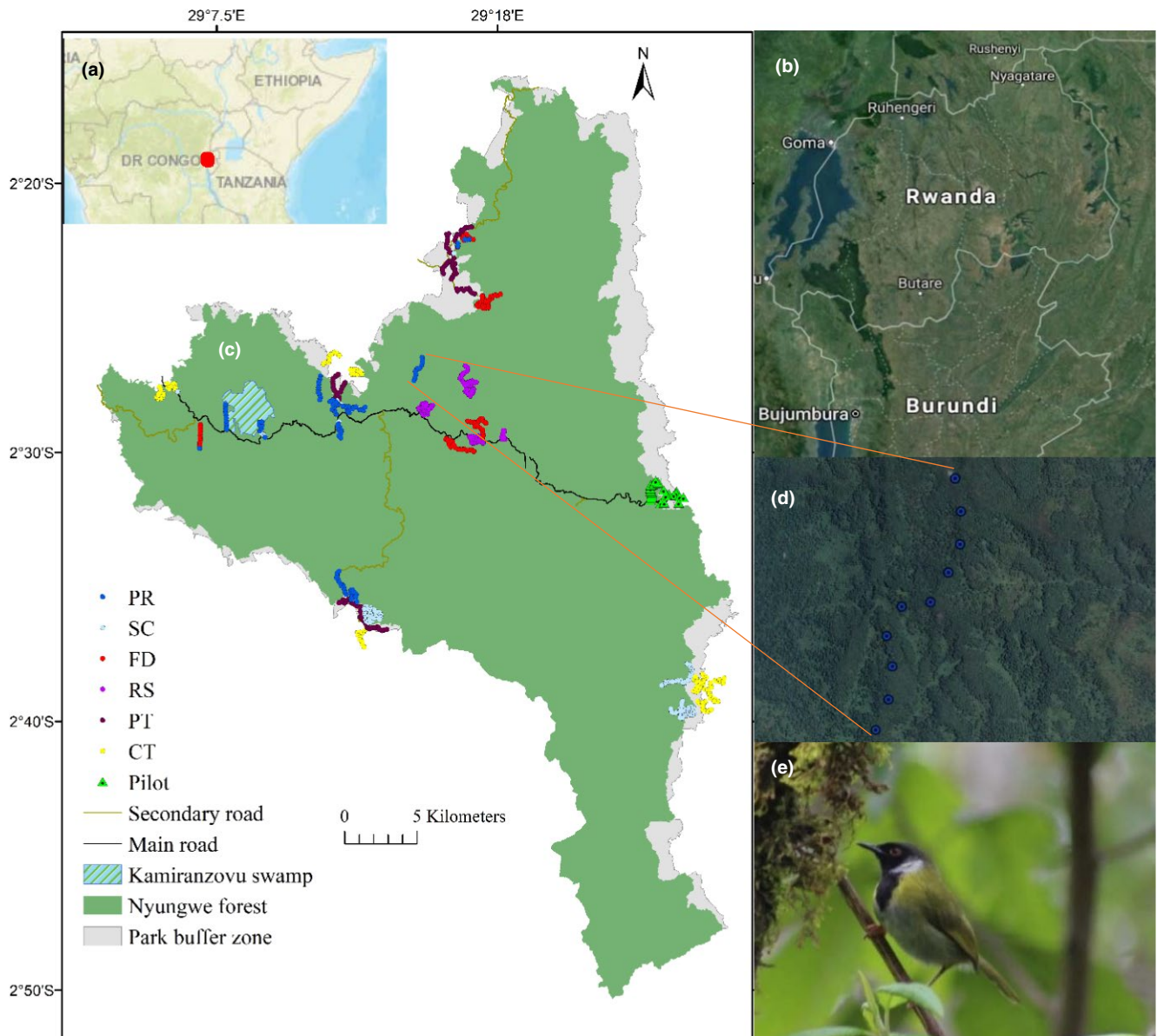


FIGURE 1 Location of the Nyungwe landscape within Central and Eastern Africa (a). Nyungwe forest (the dark shaded area towards the left of the image) lies in south-west Rwanda and is contiguous to Kibira National Park, Burundi (b). The distribution of points sampled in six different land use types within the Nyungwe landscape, Rwanda (c). PR: primary forest, SC: secondary forest, FD: fire-disturbed area, RS: restored areas, PT: plantation of non-native tree species and CT: cultivated areas. The points were separated by 200 m. Each point was sampled in both wet and dry seasons. Ten plots sampled within primary forest at Mt. Bigugu within Nyungwe NP (d). A high number of points in restored areas are close to the main road because one of the criteria considered by the restoration project was visibility from the road for tourism and aesthetic purposes (Masozera & Mulindahabi, 2007). *Apalis personata*, an Albertine Rift endemic bird that is commonly encountered in the Nyungwe forest (e). Base map source: WCS-Rwanda and Google Earth

sand mining, and the harvesting of trees and non-timber products, such as medicinal herbs and honey (Masozera & Alavalapati, 2004). To delineate the forest from community land holdings, a buffer zone of non-indigenous trees was established in the 1980s, creating a pine and *Eucalyptus*-dominated forest clearly distinct from the native forest. Fires largely resulting from honey collection and hunting practices have contributed to the degradation of at least 12% of the forest, in some areas impeding tree growth for decades due to the colonization of opportunistic ferns (Masozera & Mulindahabi, 2007). Assisted-natural regeneration activities were initiated in 2003 by the Nyungwe NP management and key conservation stakeholders to restore extensively fire-degraded areas.

2.2 | Study design

Based on the land use history, largely recorded through the park's ranger-based monitoring programme since the late 1990s, we identified six major land use categories: (a) primary forest (PR): mature and old-growth forest whose vegetation structure and composition have not been substantially disturbed and appear relatively intact; (b) secondary forest (SC): forest regrowth after non-fire disturbances, such as mining and cultivation; (c) fire-disturbed areas (FD): parts of the forest affected by fires; (d) restored areas (RS): forest regrowth after human-assisted natural regeneration of burnt areas; (e) non-native forest (NF): non-indigenous plantations of largely pine and *Eucalyptus* trees serving as a buffer zone; and (f) cultivated areas (CT): tea estates and mixed-crop farms adjacent to the park. For further details, see Appendix S1. A series of meetings with key people involved in the park management and monitoring enabled identification of safe and accessible sampling sites within each land use. We conducted a four-day pilot study to test bird and plant sampling methods and to train three field assistants. Sampling was conducted in two phases: 14/11/17–09/02/18 and 06/06/18–25/8/18, corresponding to a short-wet and a long-dry season, respectively. We sampled 10 days per land use type, bringing the total to 60 days in each season.

2.3 | Avifaunal sampling

A point-count transect method was used to record the occurrence and abundance of birds in the Nyungwe Landscape. We selected random starting points in a predefined site and set up 10 circular stations (plots) of 100 m radius. The distance between plots was at least 200 m to minimize the risk of double counts and to maintain statistical independence (Ralph et al., 1995). 100 points per land use type were established, collectively surpassing the 300 points recommended when sampling rainforests (Ralph et al., 1995). At sites where trails were present, they were followed for practical reasons due to the rough and steep relief of the sites. Establishing points along reconnaissance trails gives maximum attention to bird observation, while inducing little disturbance to habitats (Bibby et al., 2000). Where possible plots were positioned at right angles to the path and 30 m into the habitat (Gregory et al., 2004). Sampling of the same

set of points was replicated in the second season, amounting altogether to 1,200 point counts. At each point, 1 min was allowed to elapse, in a bid to let birds settle before taking records of birds seen or heard. Their distance from the centre of the station was measured using a laser range finder. The count period was of 10 min duration (Buskirk & McDonald, 1995). All bird recordings were conducted by one observer with 30 years' experience of bird monitoring in the Nyungwe landscape. Sampling usually started at 5:45 and finished at 10:30 a.m. and covered 10 point counts in one land use type.

2.4 | Functional traits

For all species recorded on surveys, we collected eight biometric measurements, including four bill dimensions (length from tip to skull along culmen, length from tip to nares, width at anterior nares and depth at anterior nares), tarsus length, tail length, wing length and Kipp's distance (the length from the tip of the longest primary and the first secondary, on a folded wing). The size and shape of the bill are associated with the trophic niche in birds, while wing, tail and tarsus are indicative of locomotory, flight and foraging strategies (Grant & Grant, 2006; Hutchinson, 1957; Pigot et al., 2020; Schoener, 1965). Kipp's distance provides additional information on the wing morphology relevant to flight and dispersal abilities (Baldwin et al., 2010; Sheard et al., 2020). See Appendix S1 for further details on the link between avian traits and vegetation attributes.

Morphological traits were measured from specimens using a standardized protocol described in Pigot et al. (2020), sampling a minimum of two adult male and two adult female specimens per species where possible (average number of specimens measured per species: 5). The specimens were accessed in numerous museums and research collections worldwide, primarily the Natural History Museum at Tring (see Pigot et al., 2020).

The preferred foraging stratum of each bird was recorded from the field, although in cases of few observations we retrieved the information from the *Handbook and Atlas of Birds of Rwanda* (Vandeweghe & Vandeweghe, 2011). The foraging stratum was classified into lower stratum: 3 metres and below, middle stratum: 4–7 m and upper stratum: >7 m. Data on diet for all species recorded were extracted from Wilman et al. (2014), a global dataset containing literature-based estimates of dietary proportions for ten different food categories, which we combine to form the following five dietary categories: invertivores (consuming terrestrial and aquatic invertebrates), herbivores (consuming plant matter and seeds), frugivores/nectarivores (consuming fruits and nectar), carnivores/scavengers (consuming vertebrates, fish and carrion) and omnivores (none of the four categories exceeds 50% of the bird's total diet).

2.5 | Habitat assessment

For each point count location, a smaller plot of 20 m radius was demarcated to record vegetation structure and composition, soil and weather in order to capture fine-scale habitat conditions. Elevation

was recorded using a GPS. The ground cover (the extent of the ground covered with vegetation) was visually estimated and recorded in percentages. The depth of the litter was measured with a thin metallic ruler, and samples were taken and averaged from 4 different random points. The height of undergrowth <3 m (lower vegetation height) was measured with a 3-m folding rule. Tree species (for individuals with diameter at breast height (DBH, 1.3 m) >5 cm) were identified and counted, and their DBH was recorded in classes of 5–14, 15–50, 51–100, 101–200 and >200 cm. Tree height was measured with a laser range finder. Canopy cover was estimated from the average of four readings, all taken with a spherical canopy densiometer from the four cardinal directions (Cook et al., 1995; Jennings et al., 1999; Strickler, 1959). Temperature and soil moisture were recorded using a portable data logger and a soil moisture probe, respectively.

2.6 | Statistical analysis

All analyses were conducted at the site level, where each site comprised 10 point counts. To explore differences in species composition across land use types, a detrended correspondence analysis (DCA)—a multivariate technique that explores the model responses of species along predominant ecological gradients (Hill, 1979)—was conducted (Figure 2). The strength of DCA lies in its ability to correct distortions in ordination axes that are generated by other ordination methods, and it also provides an option to downweight the influence of rare species (Hill, 1979; Hill & Gauche, 1980). To test whether sites within each land use category exhibited greater

species compositional similarity than expected by chance, we performed an analysis of similarity (ANOSIM) in the CAP program (Seaby et al., 2014).

To determine how land use change affected taxonomic, functional and phylogenetic diversity of bird communities, we computed the inverse Simpson diversity index, functional dispersion index (Laliberté & Legendre, 2010) and the standardized effect size of mean nearest taxon distance (ses.MNTD) using the “Vegan,” “FD” and “Picante” R packages, respectively (Kembel et al., 2010; Laliberté et al., 2014; Oksanen et al., 2010). These three metrics were chosen on the basis of a low correlation between them (Pearson's $r < .35$) and because they allowed the incorporation of abundances. FDis and ses.MNTD were weakly correlated with species richness (Pearson's $r = .25$, and $.27$, respectively), while the inverse Simpson diversity index was strongly positively correlated with species richness (Pearson's $r = .89$). Additional metrics were used for comparison (below).

The inverse Simpson index is a derivative of the Simpson's index that measures the probability that two individuals drawn randomly from a large community belong to the same species. It is weighted by the abundances of the most common species, and it is thus less sensitive to rare species, which frequently occur in rainforest systems. A high value of the inverse Simpson index denotes higher diversity. The inverse Simpson index is more robust, intuitive and mathematically sound in comparison with many other species diversity indices (Chao et al., 2014; Magurran, 2004).

Functional dispersion measures the overall spread of species trait values in a multi-dimensional space (Laliberté & Legendre, 2010). The functional dispersion index (FDis) is less sensitive to species

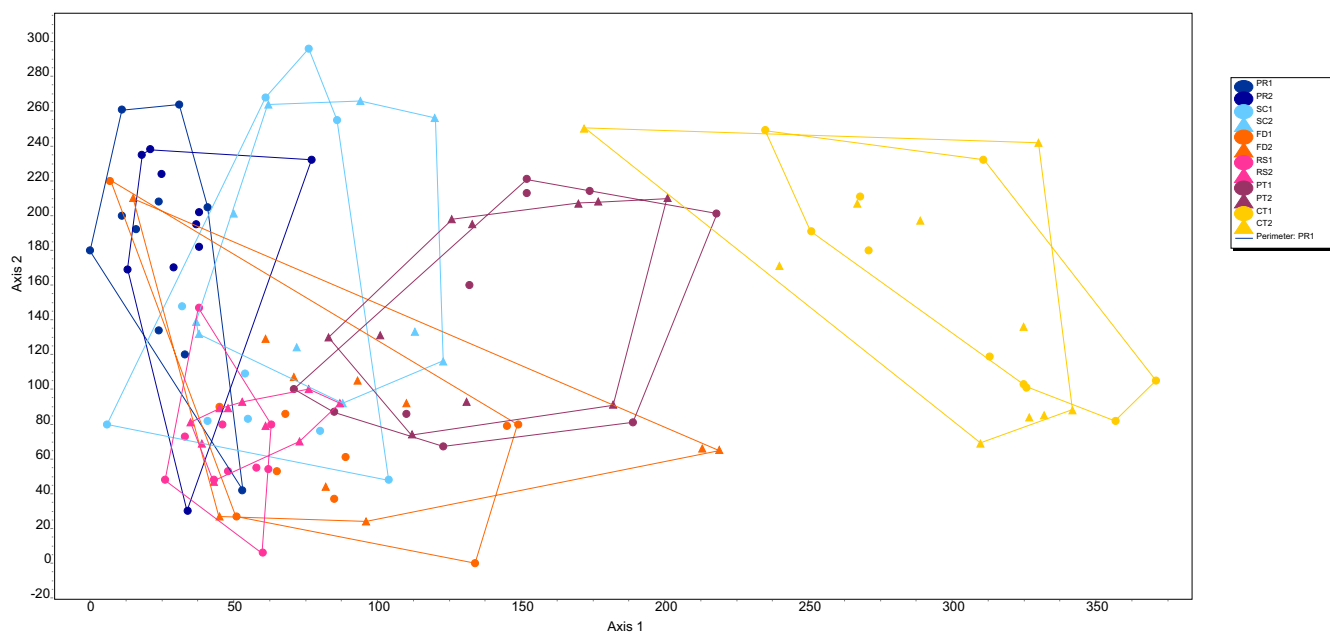


FIGURE 2 Detrended correspondence analysis (DCA) of bird community composition showing the distribution of sites (samples) ($N = 120$) belonging to the six land use types within the Nyungwe Landscape, Rwanda, along the first and second ordination axes. The categories were primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), restored areas (RS), plantation of non-native tree species (PT) and cultivated areas (CT). The first sampling was conducted over the wet season, and a replication was done over the dry season. Circles and diamonds denote the first (wet) and second (dry) seasons, respectively. The plot was generated using the CAP 5 program (Seaby et al., 2014). The units are standard deviations of species turnover $\times 100$

richness than many other functional diversity metrics and allows the comparison of samples with less than three observations, which can occur within avian point counts (Laliberté & Legendre, 2010). Higher levels of FDis correspond to assemblages with greater functional dissimilarity. To circumvent the problem of considerable intra-specific trait variations, and correlation among avian morphological traits influenced largely by body size, a two-step principal components analysis (PCA) was performed using the eight morphological traits (Trisos et al., 2014). Following Trisos et al. (2014) and Bregman et al. (2016), the first PCA was conducted on bill variables, and its second component was retained as an index of trophic processes. The second PCA was performed on tarsus, wing and tail variables, and its second component was retained as an index of locomotive abilities. To obtain an index of body size, a third PCA was performed on the first axes obtained from the previous PCAs. The hand-wing index, an additional index associated with flight and dispersal abilities, was computed from the wing measurements as described in Sheard et al. (2020). These indices, the dietary classification, and foraging strata were then used to compute the overall functional diversity metrics in the R package “FD” (Laliberté et al., 2014). Due to the presence of categorical data, we used Gower's distance, and we standardized avian traits by the range. We also assessed the functional diversity indices indicative of the trophic, dispersal (hand-wing index), locomotory and size niche axes separately.

To perform phylogenetic analyses, we extracted a set of 1,000 avian phylogenies from birdtree.org (Jetz et al., 2012; downloaded on 14/12/2018), based on the Ericson backbone (Ericson et al., 2006). The phylogenetic trees were pruned to match our study species. We then built a consensus tree and converted it into a distance matrix from which phylogenetic diversity measures were calculated using the “ape” and “picante” R packages (Kembel et al., 2010; Paradis et al., 2004). We calculated the standardized effect size of mean nearest taxon distance (ses.MNTD), which quantifies the average phylogenetic distance separating individuals from their closest relatives, corrected for species richness using a null model that randomizes the tip labels of the phylogeny (999 iterations) (Webb et al., 2002). Low ses.MNTD values indicate high phylogenetic clustering of closely related individuals.

For comparison purposes, we computed additional metrics, including (a) the functional richness metric (FRic), which measures the volume of functional trait space occupied by a species assemblage (Villéger et al., 2008); (b) Faith's (1992) phylogenetic diversity metric (PD), which is the sum of branch lengths of a phylogenetic tree encompassing a given sample; and (c) the standardized effect size of mean pairwise distance (ses.MPD), which is the average pairwise phylogenetic distance among individuals in an assemblage (Webb et al., 2002), corrected for species richness using the same null as for ses.MNTD.

Statistical significance of differences in diversity between primary forest and other land use types was tested with analysis of variance (ANOVA) where the metrics fulfilled the test assumptions, otherwise with the Kruskal–Wallis test. The tests were followed by a Tukey's post hoc test and Dunn's tests, respectively. Due to the

repeated measure nature of the study (temporal replication) and the randomness of site placements, three linear mixed-effects models were first conducted to determine the influence of habitat attributes on inverse Simpson diversity index, FDis and ses.MNTD. Site identity was used as the random variable. A likelihood-ratio test showed no significant contribution of the random variable (Kuznetsova et al., 2017). Additionally, a test for spatial autocorrelation of the model residuals, using Moran's *I* coefficient, was non-significant for the metrics considered; hence, a standard multiple linear regression analysis was performed instead. Canopy height, litter and temperature were not included in the analysis due to their high correlation with other habitat attributes (Pearson's $r > .7$) (see Appendix S2 for further details on their exclusion). The regression analyses contained the following habitat variables: elevation, canopy cover, number of trees, DBH, lower vegetation height, ground cover and soil moisture. Model selection was carried out based on BIC, due to the high number of predictors, using the “MuMIn” R package (Barton, 2019). Models within $\Delta\text{BIC} < 2$ of the model with the lowest BIC value were then averaged. All analyses, except where otherwise mentioned, were performed in the R 3.6.1 environment (R Core Team, 2019).

3 | RESULTS

We recorded a total of 8,656 individuals belonging to 170 species of birds across the 1,200 point counts, which were evenly subdivided across our six land uses (Figure 1). Per land use type, the number of individuals encountered was as follows: primary forest: 1,954, secondary forest: 1,471, fire-disturbed areas: 1,322, restored areas: 1,289, non-native forest: 1,093 and cultivated areas: 1,527. Although the rarefaction curves for species richness did not plateau in any of the habitats, those based on species diversity (Shannon entropy index and the inverse of Simpson diversity index) levelled off in each of the land use types, supporting the adequacy of the point-count sampling effort (Appendix S3).

Among the most encountered species were *Zosterops senegarensis*, a small flocking invertivorous species mostly recorded in forested sites; *Bradypterus cinnamomeus*, a small understorey invertivore mostly associated with forest edges and clearings; *Apalis personata* and *Phylloscopus laetus*, two small invertivores exclusively recorded inside the forest; *Onychognathus walleri*, a small flocking frugivorous species mostly recorded in the primary forest; *Crithagra citrinelloides*, 90% of which were recorded in open areas; and *Cinnyris regius*, a sunbird which mostly occurred in forested areas (Appendix S4). The ten most abundant species provided 40% of the records.

Albertine Rift Endemic (AR endemic) species—most commonly including *Apalis personata*, *Phylloscopus laetus*, and *Cinnyris regius*—constituted 17.6% of all encountered individuals ($N = 8,656$) in our data. Of the 27 AR endemic species recorded in this study (Appendix S5), the primary forest featured the most species and individuals (20 and 406, respectively), followed by the secondary forest (18 and 304, respectively). Fire-disturbed areas had more AR endemic species (18), but fewer individuals (296) than restored areas

(14 and 405, respectively). The lowest counts were in non-native forest (11 and 104, respectively) and cultivated areas (4 and 13, respectively). One-third of AR endemics were at least twice as abundant in the primary forest as in other land use types. However, a few species were found only in other habitat types, notably *Caprimulgus ruwenzorii*, which was recorded in the secondary forest and in fire-disturbed forest, and *Geokichla tanganicae*, which was only recorded in the fire-disturbed forest. Two individuals of the rare species *Apalis argentea* were only recorded in the primary forest. *Phylloscopus laetus* was mostly found in the restored areas ($N = 107$), where its abundance was at least double compared to the other land uses. We encountered most endemic species expected to occur in the Albertine Rift forest belt, with the exception of *Glaucidium albertinum*, *Indicator pumilio*, *Cinnyris rockefelleri* and *Cryptospiza shelleyi*.

3.1 | Species composition

A forest-to-open area gradient is evident on the first DCA axis, with the primary forest samples on the leftmost side and the cultivated areas dominating the right side (Figure 2). The ordination shows overlap in composition between several of the land uses but a clear separation of the bird communities of the cultivated areas from all forested or partially forested areas and separation of the bird community in the primary forest from forest plantations. The span of 3.7 SD along this axis indicates near-complete species replacement of birds across this gradient (4 SD being the threshold of complete replacement generally recognized; Jongman et al., 1995). The second axis relates to the elevational gradient, with fire-degraded areas and restored areas occupying higher elevations and primary forest at the lower extreme. Sample positions shift with seasons; however, the clustering pattern per land use type persists, indicating little variation in species composition across sampling seasons (Figure 2).

Notwithstanding the compositional overlap between some land uses shown in the ordination (Figure 2), ANOSIM returned an overall sample statistic (R) of 0.49, ($p = .01$), indicating that samples within each land use type were more similar in composition than samples in other land uses. Pairwise comparisons among the land use types were also statistically significant ($p = .01$), indicating varying degrees of separation of the defined land use types (Table 1). The primary forest harboured species that were not observed in other land uses, particularly in cultivated areas and restored areas. These two land uses shared only 49% and 28% of their species with the primary forest. The closest land use to primary forest, in terms of similarity of species composition, was the secondary forest. Nonetheless, unshared species account for 34% ($N = 122$) of all the species recorded in the two habitats (Table 1).

3.2 | Species diversity

Species diversity, as measured by the inverse Simpson diversity index, decreased with increasing anthropogenic modification (Figure 3).

TABLE 1 Pairwise comparisons of similarity of bird communities among study land use types in the Nyungwe landscape, Rwanda. Sample size is 20 per land use. A sample comprised 10 point counts conducted within the same land use type. Raw shared species numbers are below the diagonal, and ANOSIM sample R above. Theoretically, R values range from +1 to -1. Values close to +1 indicate high within group similarity and therefore a highly dissimilar pair. All the R values for each pairwise comparison were significant ($p = .001$), reflecting compositional differences among land use types

	PR	SC	FD	RS	PT	CT
PR		0.21	0.47	0.65	0.63	0.92
SC	81		0.18	0.33	0.27	0.83
FD	67	69		0.14	0.35	0.8
RS	53	51	50		0.53	0.92
PT	63	67	58	44		0.63
CT	43	49	40	29	51	

Note: PR: primary forest (number of species (N) = 102); SC: secondary forest ($N = 101$); FD: fire-disturbed area ($N = 83$); RS: restored area ($N = 58$); PT: plantation forestry of non-native tree species ($N = 83$); and CT: cultivated area ($N = 92$). The blue shade denotes the most dissimilar land use types, while the red shade denotes the most similar land use types.

Species diversity in primary forest was statistically different from that of other land use categories ($F(5, 114) = 14.11$, $p < .001$), as revealed by ANOVA followed by Tukey's post hoc test. Sharp declines in diversity were registered in fire-disturbed areas, restored areas and monocultures of non-native forest and cultivated areas (Figure 3). The decline in diversity with land use change intensity was equally observed when other taxonomic diversity metrics were analysed, such as species richness (Kruskal-Wallis ($H(5) = 23.21$, $p < .001$) and rarefied species richness (Kruskal-Wallis ($H(5) = 27.60$, $p < .001$; Appendix S6).

3.3 | Functional diversity

The pooled functional diversity, measured by mean functional dispersion (FDis), remained fairly stable across the land use types (Figure 3), while functional richness (FRic) declined in restored and cultivated areas relative to primary forest (Kruskal-Wallis ($H(5) = 19.48$, $p = .002$; Dunn's test, $p = .006$ and $p = .016$, respectively). Separate analyses of niche axes revealed statistically significant differences in FDis levels for the trophic axis only in restored areas relative to primary forest (Kruskal-Wallis ($H(5) = 21.85$, $p = .0006$; Dunn's test, $p = .006$; Appendix S7), and a similar pattern was observed with FRic (Kruskal-Wallis ($H(5) = 16.37$, $p = .006$; Dunn's test, $p = .002$). There were no evident differences in FDis among land uses for the dispersal and body size axes, but FRic of body size was significantly lower in restored areas compared to primary forest (Kruskal-Wallis ($H(5) = 15.21$, $p = .009$; Dunn's test, $p = .01$; Appendix S7). Changes in FDis values across the land uses for the locomotion axis were only discerned in cultivated areas,

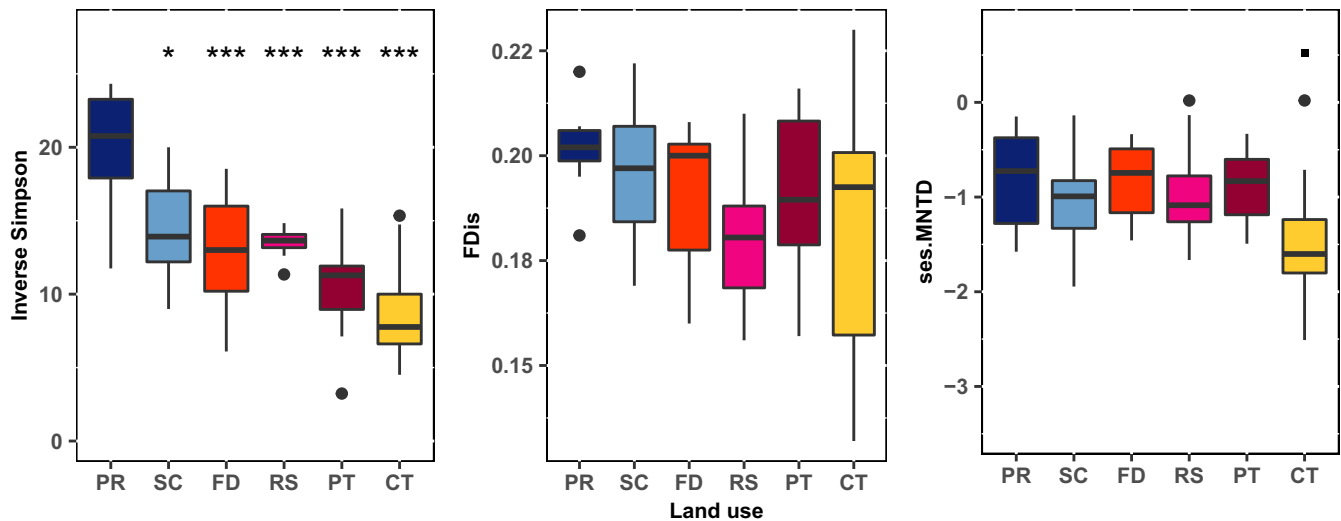


FIGURE 3 Effects of land use change on the inverse Simpson diversity index (inverse Simpson), functional dispersion index (FDIs) and phylogenetic diversity (ses.MNTD) for bird communities in the Nyungwe landscape across six land use types: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), restored areas (RS), plantation of non-native tree species (PT) and cultivated areas (CT). Sample sizes ($N = 10$) are equal among categories, and each site comprised 10 summed point counts sampled in a patch within the same land use type. Each point count was sampled in both wet and dry seasons, with bird counts averaged across the two sample seasons. Asterisks indicate statistically significant differences in comparison with diversity in primary forest: “*” 0.05, “***” 0.01 and “****” 0.001. Statistical significance was tested using an ANOVA followed by a Tukey’s post hoc test

TABLE 2 (a–c) Relationship between avian diversity and habitat parameters across sample plots ($N = 60$) in the Nyungwe landscape, Rwanda. The average of the models and the relative importance of predictors are indicated for each diversity metric. The relative importance is computed by summing Akaike weights over all models containing a given predictor and ranges from 0 to 1. Values close to 1 represent a strong importance, while those close to 0 represent a weak importance. DBH is not included because only models within $\Delta BIC < 2$ are presented

Models	Canopy cover (%)	Elevation (m)	Ground cover (%)	L. Veg. Height (m)	Soil moisture (%)	Tree number	AdjR ²	BIC	Delta	Weight
(a) Inverse Simpson diversity index										
1		-1.166		0.762	1.328	0.657	0.537	254.101	0.000	0.68
2		-1.193	0.381	0.672	1.388	0.803	0.557	255.641	1.541	0.32
Average		-1.174	0.381	0.734	1.347	0.703				
Importance		1.00	0.32	0.93	1.00	0.88				
(b) Functional dispersion index										
1		-0.009					-0.001	-302.199	0.00	0.16
2		-0.009				0.004	-0.002	-301.527	0.67	0.11
3		-0.009		0.004			-0.002	-300.523	1.68	0.06
Average		-0.009		0.004		0.004				
Importance		0.99		0.35		0.45				
(c) Standardized effect size of the mean nearest taxon distance										
1				-0.169	-0.259		0.234	108.185	0.00	0.5
2					-0.200		0.143	109.459	1.27	0.26
3	0.110				-0.272		0.276	109.632	1.44	0.24
Average	0.110			-0.169	-0.247					
Importance	0.34			0.60	0.95					

Note: L. Veg. Height denotes lower vegetation height.

The model average and relative importance are written in bold for greater legibility.

where the changes were negative relative to levels in primary forest (Kruskal-Wallis ($H(5) = 12.32$, $p = .03$; Dunn's test, $p = .029$), and the pattern persisted for FRic (Kruskal-Wallis ($H(5) = 16.22$, $p = .006$; Dunn's test, $p = .02$ and $p = .013$, respectively).

3.4 | Phylogenetic diversity

Values of ses.MNTD (Figure 3) and ses.MPD were comparable across land uses. Faith's (1992) Phylogenetic diversity metric (PD), which does not incorporate abundances, showed declines in fire-disturbed areas, restored areas and non-native forests, and steeper losses in cultivated areas compared to primary forest (Appendix S8).

3.5 | Habitat attributes

The regression model selection analyses revealed elevation as a primary negative influence on taxonomic diversity and FDis (Table 2a; Figure 4a). Soil moisture and the lower vegetation height had contrasting effects, in that they influenced taxonomic diversity positively and phylogenetic diversity (ses.MNTD) negatively (Table 2a–c; Figure 4b, d–f). The number of trees was only important for taxonomic diversity (Figure 4c). Ground cover and canopy cover had weak positive effects on taxonomic and phylogenetic diversity, respectively, while DBH did not exert much effect (Table 2a–c). The models explained a reasonable amount of variation except for FDis

(Table 2b; highest $\text{adj}R^2$ for inverse Simpson diversity index: 0.56; ses.MNTD: 0.28; and FDis: 0).

4 | DISCUSSION

4.1 | Altered patterns of species composition and diversity

Our analyses reveal that increasing levels of land use change alter species composition and reduce taxonomic diversity. In general, the patterns detected align with those reported by previous studies that have concluded that bird species diversity within tropical forested landscapes is reduced with intense human habitat transformations, particularly from primary forest to agricultural uses (Albanesi et al., 2014; Bregman et al., 2016). The bird diversity patterns noted here are also consistent with the predictions of the intermediate disturbance hypothesis (Connell, 1978), which is a relevant theoretical construct given that it describes diversity responses at the patch scale across landscapes.

Although primary and secondary forest had almost equal species richness, there were differences in species composition between the plots from the two land use types, highlighting the sensitivity of some forest species, even to low levels of disturbances, and the crucial roles that primary vegetation plays in maintaining distinct communities, particularly of forest specialist (often locally endemic) species (Barlow et al., 2007; Gibson et al., 2011; O'Dea &

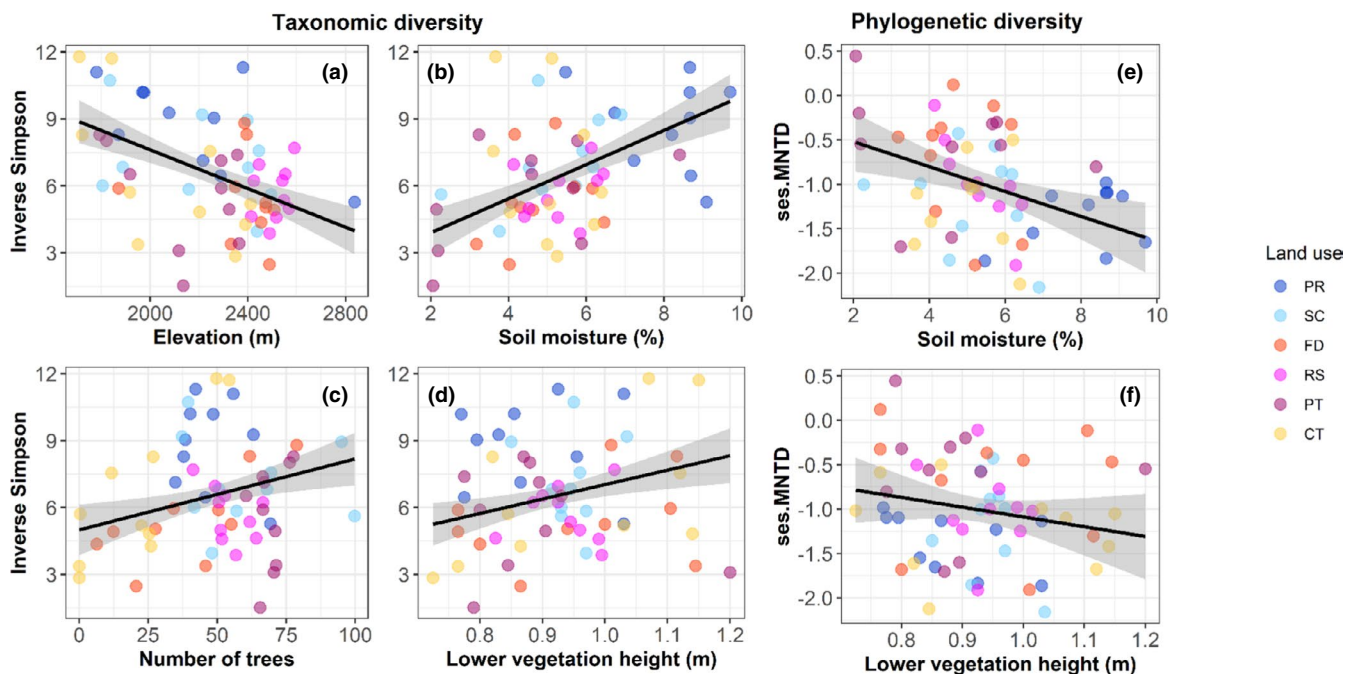


FIGURE 4 Relationships between bird taxonomic diversity (a–d) and phylogenetic diversity (e–f) and habitat parameters of study samples ($N = 10$ per land use) in the Nyungwe landscape. Taxonomic diversity and phylogenetic diversity are quantified using inverse Simpson diversity index (inverse Simpson index) and standardized effect size of mean nearest taxon distance (ses.MNTD), respectively. Results were obtained from a linear model fitted on unscaled raw data. Model estimates obtained from scaled data are given in Table 2. The grey band represents $\pm 95\%$ confidence interval. Habitat attributes with lower relative importance values (<0.5) and only found in models with low $\text{adj}R^2$ (<0) are not displayed

Whittaker, 2007). Although a higher species diversity is often reported in secondary forests, the gain usually originates from the influx of generalists and gap-tolerant species (Coetzee & Chown, 2016; Foord et al., 2018; Moura et al., 2013). For instance, in this study, *Platysteira concreta* and *Ploceus insignis*, known closed-forest species, were only recorded in primary areas, while open habitat and generalist species in the genera *Estrilda*, *Crithagra* and *Ploceus* were mostly recorded in secondary forests. The degree of disturbance and the time elapsed since release from disturbance may also determine the avian diversity supported by secondary forests. Areas restored following burning within the last 1–20 years supported only slightly more than half the taxonomic diversity found in the primary areas. Similar findings were noted in restored Australian tropical rainforest, where the rapid recovery of certain vegetation attributes, such as the stem density and canopy closure, led to the attainment of half the number of forest-dependent species supported by old-growth rainforests within a decade, and the similarity in species composition increased with the age of the restored habitat (Catterall et al., 2012; Dunn, 2004).

4.2 | Differential response of functional diversity to land use change

Overall functional diversity (measured using the FDis index) failed to produce clear patterns of difference between land uses (Figure 3); however, analysis at the level of individual trait axes revealed effects of varying magnitude (Appendix S7). Restored areas were the most affected land use type. The registered declines in the trophic and size axes in restored areas relative to primary forest can be explained by the absence of large-bodied birds such as those in the Accipitridae family, typical forest raptors such as *Aquila africanus*, as well as large invertivores (e.g. *Apaloderma vittatum*), and large frugivores (e.g. *Bycanistes subcylindricus*). Reforested areas tended to be dominated by small-sized insectivorous birds and exhibited poor representation of other guilds (Appendix S9); granivores were the least-represented guild, as exemplified by the absence of any of the eight forest and non-forest *Ploceus* species recorded within the study. The reduced niche breadth in restored areas can be attributed to the high degradation of the sites by anthropogenic fires before the restoration activities started (Masozera & Mulindahabi, 2007). Fire-disturbed sites sampled in our study had experienced fires of varying severity, and some old sites supported a fully established continuous canopy cover, likely explaining the relatively high mean FD value for this land use type compared to restored sites.

Cultivated areas in particular and non-native plantations to some degree featured communities of reduced locomotory niche occupancy (Appendix S7). These changes can be attributed to the homogenous vegetation of these land use types. The plantations constituted mainly mature monoculture stands of *Eucalyptus* and *Pinus* species, while half of the cultivated areas contained monocultures of tea plantations (*Camellia sinensis*). The simplified vegetation of these land uses limits the need for higher locomotory capacities.

Contrary to what is often reported (Bregman et al., 2016; Flynn et al., 2009; Frishkoff et al., 2014), there was no decline in avian body size in cultivated areas. Species only encountered in cultivated areas included medium and large birds of prey, insectivorous birds and large wading birds. The unexpected adaptation of several large-sized wetland birds, particularly those in the Ciconiidae, Ardeidae and Threskiornithidae families, to agricultural transformations in Rwanda, has been documented in previous work (Vandeweghe & Vandeweghe, 2011).

The maintenance of functional diversity in secondary forests and fire-disturbed areas, despite the loss of taxonomic diversity, could be explained by the functional redundancy of tropical forest ecosystems (Cooke et al., 2019). In our study, half of the species ($N = 85$) were small-sized (<28.3 g), and about three-quarters of these were invertivores. Feng et al. (2020) also noted that functional redundancy characterized the avian assemblages of the Amazon and Andean forests. Our findings in this regard agree with patterns often observed in other studies in tropical regions, showing stable functional diversity of forest species in moderately disturbed habitats, but steep declines in highly disturbed habitats, such as agricultural land (Bregman et al., 2016; Flynn et al., 2009; Sayer et al., 2017; Şekercioğlu, 2012).

4.3 | Stable community phylogenetic structure across the land use types

Although the loss of species with land use change culminated in lower phylogenetic diversity (Faith's PD) compared to primary forest levels, the phylogenetic structure (ses.MNTD and ses.MPD) remained stable. The decreases in Faith's PD are thus attributed to the decline in species richness and abundance along the disturbance gradient. Bird communities across the land use types including primary forest were characterized by shorter average phylogenetic distances between species than expected, as shown by negative values of ses.MNTD and ses.MPD, which imply high co-occurrence of closely related lineages. An explanation for the general phylogenetic clustering in the study area may be environmental filtering due to historical disturbances. The Nyungwe landscape forms part of the Albertine Rift, which has served as a refugium for rainforest birds during the alternating extreme climatic cycles over the Pleistocene (Kahindo et al., 2017; Lyons et al., 2015; Prigogine, 1988). Historical anthropogenic disturbances of the Nyungwe landscape may also have left legacy effects on the vegetation and associated fauna, resulting in phylogenetic clustering.

We were expecting to find filtering of certain clades with increasing intensity of habitat change, and especially in agriculture areas, as reported by other studies focusing on an array of taxa (Egorov et al., 2014; Frishkoff et al., 2014; Prescott et al., 2016). For instance, Frishkoff et al. (2014) compared bird communities in forest reserves with those in agricultural sites in Costa Rica and showed that although a wide spread of clades were using agricultural sites, closely related species tended to have similar habitat affinities, especially in intensive monocultures. The lack of such effects in our study may

result from the proximity of the cultivated areas to the forest, coupled with the low intensity farming practised. Although half of the surveyed farms contained tea plantations, the other half consisted of mixed-crop farming with moderate amounts of agroforestry.

A study by Cosset and Edwards (2017), conducted in Borneo using point counts and mist netting, found comparable ses.MPD values in naturally regenerating forests and unlogged forests, but significantly lower values in restored forests. For understorey birds, both restored and logged forests had significantly lower ses.MNTD values than naturally regenerating forests. The authors attribute the low phylogenetic diversity in restored forests to restoration practices that involved clearing shrubs and lianas, which are important foraging and nesting elements for a range of bird species. The contrast with this study's findings may result from differences in the land use histories of the two study systems, since the main disturbance investigated by Cosset and Edwards was logging, rather than fire and agriculture as in our study.

4.4 | Habitat attribute effects on taxonomic, functional and phylogenetic diversity

Fine-scale habitat heterogeneity, particularly in terms of the vegetation structure, has been reported to drive species, functional and phylogenetic diversity patterns in tropical birds (Foord et al., 2018; Karp et al., 2012; Maseko et al., 2019; Prescott et al., 2016). As expected, attributes linked to vegetation structure were important determinants of avian diversity here. Tree density positively drove taxonomic diversity, likely by creating favourable conditions for forest specialists, canopy dwellers and frugivores. Our results also indicate varying effects of habitat attributes on the three avian diversity components. Lower vegetation height and soil moisture positively affected inverse Simpson index values, but adversely affected ses.MNTD values. These attributes may provide suitable conditions for closely related understorey insectivorous and ground-nesting species, but negatively affect canopy dwellers and clades with bare-ground affinities (Maseko et al., 2019).

The modification of the soil water content through land use conversion, such as from primary forest to agriculture and forest plantations, has been documented across a range of tropical and temperate systems (Anamulai et al., 2019; Cifuentes-Croquevielle et al., 2020). For example, Cifuentes-Croquevielle et al. (2020) found that plantations of non-native *Pinus radiata* in central Chile had significantly lower soil water content and lower diversity of soil invertebrate communities than the remnant native forest. In our study, plots in non-native forests often had considerably lower values of soil moisture than adjacent primary forest, notwithstanding the plots being sampled very close together in time during a period of unchanging weather. The high soil moisture values in primary forest may help explain the high avian taxonomic diversity relative to other land uses, particularly the non-native monocultures of *Pinus* and *Eucalyptus* species.

Elevation was a strong negative driver of taxonomic diversity. This finding can be attributed to the fact that high elevation areas

are often characterized by extreme climate conditions, which in turn inhibit complex vegetation stature and heterogeneity that might otherwise support a range of species from different lineages, exhibiting varying functional traits (Hanz et al., 2019; Jankowski et al., 2013; Quintero & Jetz, 2018). However, we did not find such pronounced effects of elevation on the avian functional and phylogenetic structure as some studies have done. The reduced elevational gradient of the Nyungwe landscape (1,600–2,950 m) as compared to that covered by Hanz et al. (2019) in the Ecuadorian Andes (970–2,898 m) and on Mt. Kilimanjaro (1,169–3,060 m) may translate into reduced variation in biotic and abiotic factors. Their study also found that the availability of food resources, such as ripe fleshy fruits, an attribute that was not recorded by this study, was a major driver of avian functional diversity. More generally, the low explanatory power of our regression models when using FDis as the response variable is likely due, at least in part, to the comparatively high variation in FDis between sites of the same land use in relation to the mean differences between land uses (Figure 3). For instance, the three samples that supported the highest FDis values, and the two that supported the lowest, in the whole study belonged to the cultivated areas, specifically mixed-crop farms and tea plantations, respectively.

4.5 | Conservation implications

This study has shown how land use change, particularly in the form of fires, agriculture and plantation establishment in the Nyungwe landscape, has modified the species composition and led to declines in taxonomic diversity. The Nyungwe forest landscape is particularly rich in Afromontane and Albertine Rift endemic species (Vandeweghe & Vandeweghe, 2011), and the transformation of intact habitats is detrimental to these narrowly distributed species. The present expansion of monocultures of crops and trees across the Tropics will inevitably result in bird assemblages characterized by lower diversity of functional strategies, potentially reducing ecosystem function.

Our analyses also demonstrate the predicament of ecological restoration processes. The low species and functional diversity levels found in restored areas might be misinterpreted as failures in the eyes of stakeholders in need of fast results. There is a need to shift the restoration approach from tree-based to promoting vegetation heterogeneity, including a well-developed understorey herbaceous layer, for a full recovery of a diversified montane avifauna (Rurangwa et al., 2020). Further work should explore factors underlying the different recovery trajectories of sites affected by fires within the Nyungwe landscape for informed restoration policies in Rwanda and in similar tropical landscapes.

The conversion of natural habitats within the Nyungwe landscape mirrors what is happening in many parts of Africa. With the current rising population density, further adverse effects may persist. Montane forests continue to serve as biological refuges for both climatic and land use change events. Several bird species that used to be widespread in Rwanda are now confined within these forests, as suitable habitats (mostly at lower elevations) have been

lost (Vande weghe & Vande weghe, 2011). Conservation efforts should be steered into preventing further degradation of existing natural ecosystems (particularly through fires), adopting a holistic restoration approach that prioritizes both flora and fauna, working with local communities to find alternative sources of livelihoods and devising management plans that account for dynamic threats under present and future environmental conditions, such as the practising of ecofriendly agriculture.

This study has shown how varying degrees of land use change differentially impact the taxonomic, functional and phylogenetic diversity components of avian communities in the Nyungwe landscape. Based on the relationship of taxonomic diversity and habitat conditions found in this study, we recommend the use of species-based approaches as an early detection system in Afromontane forests. However, complementary approaches based on functional traits and phylogenies may provide useful insights into the maintenance of key ecosystem functions and services and enable the conservation of a more complex biodiversity, with greater resilience to environmental changes.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support findings of the functional diversity component of this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.41ns1rddd> Restrictions apply to the availability of the rest of the data due to co-ownership with a third party, so the data are not publicly available.

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BIOSKETCH

The authors share an interest in studying human-induced habitat changes using approaches spanning from community ecology to biogeography for potential applications in conservation strategies.

Author contributions: M.L.R. conceived the study and designed the methodology with input from RJW. M.R.L. and P.N. coordinated data collection. J.A.T. provided the avian functional trait data. M.L.R. and J.A.G. analysed the data. J.P.W. conducted the random forest analysis. M.L.R. led the manuscript write-up process with input from R.J.W. All authors commented on and approved the manuscript before submission.

SUPPORTING INFORMATION

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

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