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Assessing tropical forest restoration after fire using birds as indicators: an Afrotropical case study

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Abstract

The necessity to restore rainforest habitats degraded by anthropogenic fires is widely recognized, however, research on restoration approaches has mainly centred on the recovery of forest structural complexity. There is insufficient evidence on the efficacy of restoration methods in the recovery of the faunal diversity and features linked to key ecosystem functions. We assessed the taxonomic diversity and functional trait structure of bird assemblages in undisturbed primary forest and fire-affected habitats undergoing natural regeneration, as well as areas of assisted natural regeneration, in Nyungwe National Park, Rwanda. We compiled bird occurrence data from point-count sampling, and obtained morphological traits for all species in our assemblages using measurements taken from wild birds and museum specimens. We found marked differences in species composition between primary forest habitats and regenerating forest, with similarity increasing over time since perturbation. Taxonomic diversity was higher in primary forest, and similar between the two restoration approaches. Functional diversity was lower in assisted naturally regenerated habitats, although separate analyses within dietary guilds revealed no differences across habitats. Among desired restoration outcomes, tree species diversity was the leading positive driver of avian species diversity, fern coverage exerted negative effects, while canopy cover had a positive but weak influence. Our findings underscore the importance of preventing anthropogenic fires in tropical rainforest since their impacts on ecological processes are not easily reversed, as shown by the lack of improvement in avian diversity metrics under assisted naturally regeneration in relation to natural regeneration. We stress the need to document both floral and faunal recovery in order to aid informed decision-making on restoration methods.

Key words: Afrotropics, assisted natural regeneration, avian diversity, ecological restoration, functional traits, Nyungwe forest, passive restoration.

1. Introduction

Fire is a natural component of African landscapes, contributing to the formation and maintenance of grasslands and savannas, and the high diversification rate of the associated biota (Cowling, 1987; Sodhi et al., 2011; He et al., 2019). Nonetheless, its current frequency and intensity in less fire-adapted wet forests present detrimental effects on ecological processes (King et al., 1997; Cochrane, 2003). Large-scale fires in tropical rainforests have mostly anthropogenic origins, with agricultural and ranching activities being the leading factors (Juárez-Orozco et al., 2017; van Vliet et al., 2012). Indirect drivers, such as fragmentation and deforestation, also increase the occurrence and intensity of fires (Cochrane, 2001; Silva-Junior, 2018). Fire severity is amplified by drought and high temperatures, such as those associated with El Niño years, and is predicted to intensify under future climatic conditions (IPBES, 2019; IPCC, 2019). Where wildfires become chronic and frequent, grasses or opportunistic ferns may occupy the degraded areas, fueling future fires and hampering regeneration for decades (Cohen et al., 1995; Ashton et al., 2001).

Pteridium aquilinum (L.) Kuhn (bracken fern) is one of the most notorious plants responsible for arrested succession. It is native to all continents and has a distribution spanning temperate and tropical forests and grasslands (Dolling, 1996; Adie et al., 2011). The dominance and persistence of this fern is owed to: i) a dense frond canopy that shades out emerging seedlings; ii) deep ground litter that depletes the seed bank, and constrains colonisation by other species (den Ouden, 2000; Ghorbani et al., 2006); iii) a complex rhizome system that resprouts after fires (Ashton et al., 2001); iv) allelopathic effects that minimize plant competition (Gliessman & Muller, 1978); and v) toxic compounds that protect against grazing herbivores (Grime et al., 1988; Ssali et al., 2017).

In Bwindi Impenetrable National Park, Uganda, it was found that all sites dominated by the bracken fern had been affected by fires (Ssali et al., 2017). In comparison to the undisturbed forest, the few woody plants that were found within the bracken-dominated area were characterized by small seeds and thick bark. There were also fewer animal-dispersed tree species. Similar results were documented for *Dicranopteris linearis,* an introduced fern in a Sri Lankan rainforest, which proliferated after clearance for swidden agriculture, and repeated fires (Hafeel, 1991). In contrast, some other studies in the Neotropics and Afrotropics concluded that bracken ferns played facilitative roles towards late-successional tree species, filtering out pioneer species but providing favourable conditions for germination and establishment of shade-tolerant rainforest species (Gallegos et al., 2015; Ssali et al., 2019).

The generally slow performance of natural ("passive") regeneration in fern-infested areas in the tropics (Shono et al., 2007; Crouzeilles et al., 2017), has sparked the testing of a range of alternative management techniques to accelerate regeneration processes. An experiment conducted by Cohen et al. (1995) in the above-mentioned Sri Lankan lowland rainforest where dominance of *Dicranopteris linearis* had become the stable state, found that techniques comprising rhizome removal and tilling to mix top and mineral soils, eliminated the ferns and enhanced the growth of herbs, shrubs and trees. In Chiapas, Mexico, the monthly removal of the bracken ferns (*Pteridium caudatum*) and sowing or planting seedlings of balsa (*Ochroma pyramidale),* a fast growing pioneer tree species, led to the total elimination of the ferns in 18 months in plots where balsa occupied at least 11m^2 per ha (Douterlungne et al., 2013).

Due to the high cost associated with the planting of seeds or seedlings (active restoration), the assisted regeneration approach— a less intensive management intervention that often entails the removal of the herbaceous vegetation, the application of fertilizers or herbicides, and the use of artificial perches to enhance propagule supply — has been preferentially applied (Shono et al., 2007; Shoo & Catterall, 2013; Elliott, 2016; Chazdon, 2017). Assisted natural regeneration was found to be effective in increasing substantially the canopy cover, species richness, and stem density of woody plants in an Australian subtropical forest that was previously cleared for grazing (Uebel et al., 2017).

Although a range of techniques have long been practiced by indigenous communities to regenerate forests (Dugan et al., 2003; Douterlungne et al., 2010), there is scant information on their performance in the recovery of animal species diversity, and features linked to ecological functions. A search in the bibliographic database, ISI Web of Science employing the terms "fern or Pteridium & tropic* forest & restor*", for the period 2010 to 2020, covering Ecology, Environmental sciences, Forestry, Biodiversity Conservation, and related fields, gave 210 research items that contained the search terms in their topics but none that evaluated the effects of restoration approaches on the fauna. Instead, studies largely focused on distribution of the fern species, control methods, and the vegetation assessment following restoration interventions. It is thus too early to generalize as to the efficiency of a particular restoration technique in regard to the recovery of animal diversity, especially in the Afrotropics where there has been less research coverage (Reij & Garrity, 2016; Shoo & Catterall, 2013). This paucity of information also applies to the wider restoration field since many existing studies are based on comparisons of projects with different timeframes or end-goals (Larkin et al., 2019).

Our study aims to address this gap by comparing both naturally regenerated and assisted naturally regenerated habitats to primary forest (areas of no major disturbance) within the same landscape. The advantage of our method is that we are not comparing the outcome of restoration efforts to a pre-disturbance state, an approach which would not account for the dynamism of ecosystem processes, such as the variabilities induced by anthropogenic climatic changes (Holl & Aide, 2011). Instead, we are carrying out a spatial comparison using birds to assess the faunal recovery with particular reference to their functional roles within the ecosystem. Birds provide a well-established indicator group of the vitality of ecosystems that are highly relevant to restoration studies since the ecosystem services performed by birds, such as seed dispersal, pollination and herbivory control combine to accelerate the recovery of degraded forest landscapes (Şekercioğlu, 2012; Roels et al., 2019).

We conducted our study in Nyungwe National Park (Fig.1), a tropical montane rainforest in the southwest of Rwanda. In proportion to its surface area, Rwanda has made the largest pledge to the Bonn Challenge. A commitment of 2 Mha was made, representing an area larger than that currently supporting agricultural or forestry activities (Fagan et al., 2020). Rwanda has also been classified among the top restoration hotspots based on benefits and feasibility factors (Brancalion et al., 2019). One of the restoration projects undertaken includes the restoration of burnt areas within the Nyungwe National Park. The project has used assisted natural regeneration methods to increase tree cover and tree species diversity by combatting the opportunistic fern *Pteridium aquilinum,* which inhibits forest regeneration processes (Masozera & Mulindahabi, 2007).

In the present study, we asked two primary questions. First, how do avian species composition, diversity and functional trait structures vary across three different habitat types? We made three predictions regarding this question: i) the three habitats (naturally regenerated, assisted naturally regenerated and primary forest) will have distinct species composition, and different amounts of taxonomic and functional diversity; ii) avian diversity will be higher in assisted naturally regenerated than in naturally regenerated habitats; both will converge towards the composition and diversity of undisturbed primary forest habitats over time (Derhé, et al., 2016); and finally iii) there will be a difference in the recovery of major guilds occupying naturally regenerated and assisted naturally regenerated sites, with frugivores in both habitats slower to recover due to their preference for a continuous forest cover (Farwig et al., 2017). Second, to what extent do changes in vegetation generated by the assisted restoration project influence avian taxonomic and functional diversity across the habitat types? We hypothesized that: i) vegetation complexity and stature drive increasing avian diversity, and; ii) the proportion of ferns will be the major negative driver of avian taxonomic diversity and will lead to reduced avifaunal community trait structure, particularly for the regenerated habitats (cf. Gould & Mackey, 2015, Ikin et al., 2019).

2. Methods

2.1 Study site description

The study was conducted in Nyungwe National Park (Nyungwe NP), a tropical montane rainforest of 1,019 km^2 in south-western Rwanda. Its elevational range spans 1,600–2,950 m. The mean annual rainfall spans 1500 – 2500 mm, and the average minimum temperature is 10.9^{0}C, whilst the maximum is 19.6^0 C (Sun et al., 1996; Seimon, 2012).

In the last twenty-three years, anthropogenic fires in the Nyungwe forest have ravaged more than 12% of the forest (Weber et al., 2005; Nyungwe National Park, 2018, 2019). In most instances, the fires were set accidentally by people engaging in illicit activities, mainly honey collection, wood collection, hunting and mining (Barnett and Dardis, 2017). The fire management strategies implemented in the Nyungwe NP have considerably lowered the annual tally of burnt areas from 155.5 ha and 234.5 ha in 2003 and 2004, to 8.8 ha and 5 ha in 2018 and 2019, respectively (Nyungwe National Park, 2018, 2019). Nonetheless, in extensive parts of the forest, sites that were occupied by a tall canopy forest comprising late-successional forest species, dominated by *Syzygium guineense,* have been replaced by dense thickets of opportunistic ferns, typically *Pteridium aquilinum,* leading to arrested succession (Masozera & Mulindahi, 2007).

In early 2000, the park management and conservation partners initiated trials to determine the most efficient restoration method in terms of seedling establishment and cost-effectiveness between: 1) cutting the fern vegetation and planting indigenous forest tree seedlings from tree nurseries established outside of the forest, and 2) removing the ferns to facilitate germination of any viable seeds from the soil seed bank or seeds that were newly dispersed by various agents (assisted natural regeneration) (Weber et al., 2005). Trial results supported the latter method, and the systematic removal of the fern vegetation in every three months over a three-year period was recommended (Masozera and Mulindahabi, 2007). After this period, seedlings were strong and tall enough to survive, shade-out and outcompete the fern vegetation.

Clearing of restoration sites followed the nucleation technique to limit soil disturbances. Per hillside, only plots ranging from 250 to 500 m^2 were cleared. It was envisaged that with time, the restored canopy would expand outwards, and shade-off the remaining ferns. Since 2003, the assisted natural-regeneration method has been applied in all restoration interventions in the Nyungwe NP. Restoration sites were prioritized based on the scarcity of trees and the accessibility and visibility from the main road (Masozera & Mulindahabi, 2007). The total area of plots that have been treated amount to 250 ha (WCS, pers. comm). In most cases, the shade-intolerant pioneer species (particularly *Macaranga kilimandscharica*) grow immediately after the treatment was applied. The recruitment of shade-tolerant primary forest species follows after the canopy starts to close (P.N. pers. obs.). Although annual monitoring of the vegetation cover in the restored plots has been conducted as part of the management of the park, no scientific study has hitherto been conducted to assess the recovery of the avifauna.

2.2 Avian sampling

Sampling was conducted in naturally regenerated habitats (NR), assisted naturally regenerated habitats (AR), and in primary forest (PF), which is considered herein as the reference state. Sites were classified as primary forest if they contained old growth forest, i.e. late stages of stand development, with little human-induced degradation (Putz and Redford, 2010). In Nyungwe NP, such sites were characterized by tree species such as *Syzygium guineense*, *Strombosia schefflera*, and to a less extent *Entandophragma excelsum*. Both NR and AR were disturbed by anthropogenic fire events that occurred between 1996 to 2017. Most sites were burnt during the El Niño period of 1997–1998. A few sites experienced a second fire between 2004 and 2017. Sampling sites were predefined after a series of meetings with key researchers and managers involved in the fire management and restoration programs of the park. The criteria for site selection included safe road conditions and the general safety of the area.

To record birds, point-counts of 100 m radius were conducted in naturally regenerated habitats, assisted naturally regenerated habitats, and primary forest. At each point, bird species seen or heard were recorded for a duration of 10 minutes by one observer with 30 years of bird survey experience in the Nyungwe landscape. Ten point-counts were conducted within the same site (same habitat) per day, starting at 5:45 and finishing at 10:30 am.

A hundred point stations were sampled in each habitat from November 2017 to February 2018 (wet season), and they were repeat-sampled between June and August 2018 (dry season), bringing the total to 600 point-counts. Regenerating forests were further classified by age class, relating to the time since a fire incidence for NR habitats, and the year of restoration for AR habitats. Within NR, 30 point stations were established in young habitats (<10 years), and 70 point stations in mid-age habitats (10–20 years), while in AR, 50 points stations were established in each age class. Fewer points were conducted in young NR due to the low representation of this age class in the Nyungwe NP. A minimum distance of 200 m was maintained between points to reduce the risk of double counting of birds and to maintain statistical independence.

2.3 Vegetation assessment

At each plot, a smaller circular plot of 20 m radius was established to record vegetation attributes targeted by the restoration project. Trees of diameter at breast height (DBH) >5 cm were counted, identified to species level, and their height was measured using a laser range finder. The trees were then sorted into DBH classes of 5–14, 15–50, 51–100, 101–200, and > 200 cm. Canopy cover was estimated using a spherical densiometer. Four readings were taken from each cardinal direction, and the mean was used as the final record. The percentage of the fern coverage inside the plot was visually estimated, with 0% indicating absence and 100% signifying total occupation by the ferns. One botanist and an assistant conducted the vegetation survey, and they sampled one to two plots behind the bird survey team. As with the avian survey, sampling was carried out in the wet season, and a replication was done in the dry season.

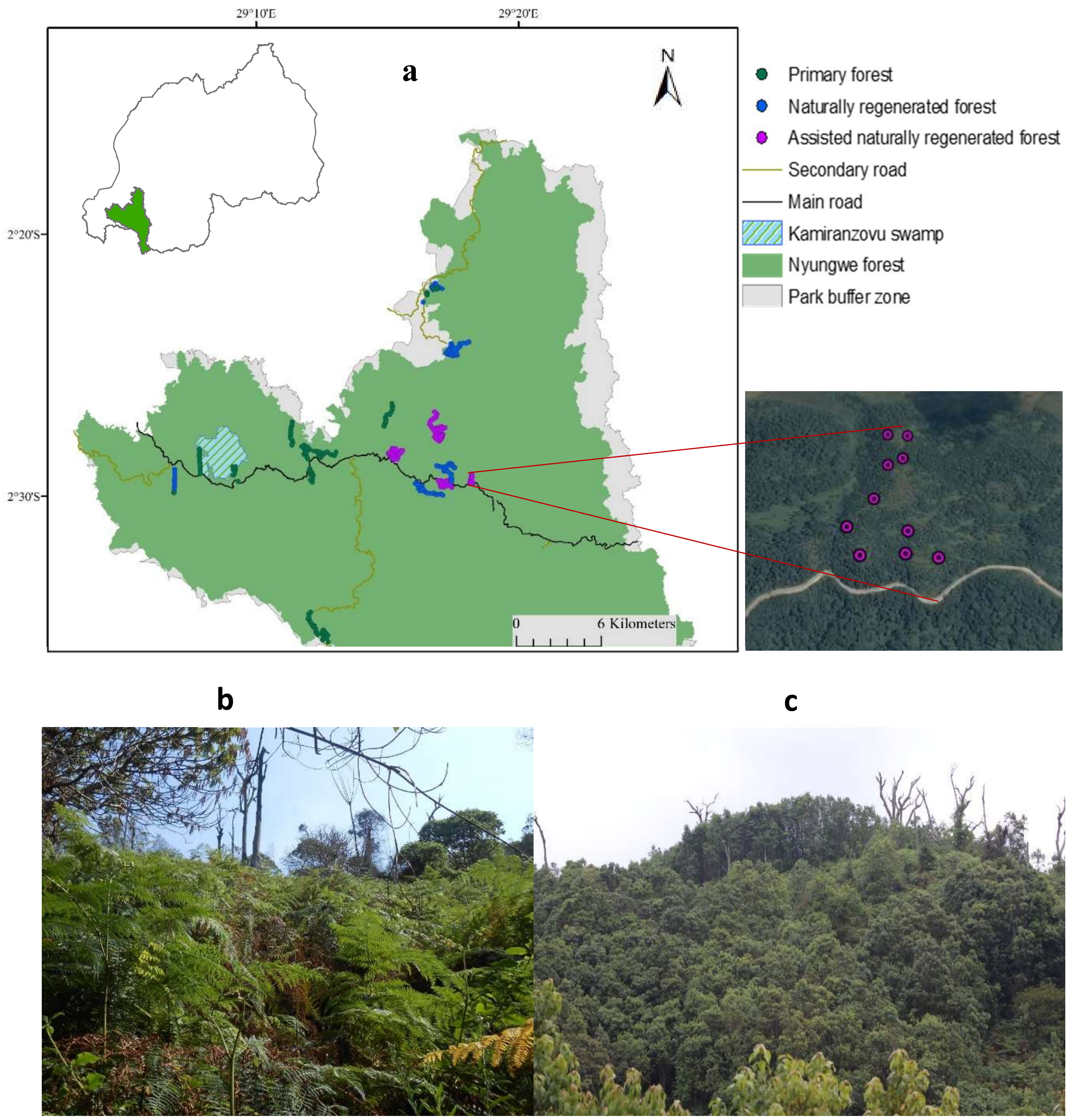

Figure 1 Geographic location of 300 point-counts conducted in Nyungwe National Park, Rwanda (**a**), within primary forest (PF), naturally regenerated forest dominated by *Pteridium aquilinum* (NR; **b**) and assisted naturally regenerated forest dominated by *Macaranga kilimandscharica* (AR; **c**). 10 points counts were conducted within the same site per day. Base map sources: WCS, Rwanda, Google Earth.

2.4 Functional traits collection

Biometric data of study birds were measured from wild birds or museum specimens following a standardized protocol elaborated in Bregman et al. (2016). The measurements included: bill length, width and depth, which are indicative of the trophic niche; tarsus length, hand wing index, tail length, which are indicative of locomotory and flight capabilities; and body size (measured as body mass in grams), which indicates energy requirements (Hutchinson, 1959; Grant & Grant, 2006; Sheard et al. 2020). Dietary data were obtained from Wilman et al. (2014), who grouped birds according to their preferred food items as follows: Fruit-Nectar, Invertebrates, Omnivore, Plant-Seed matter, Vertebrate-Fish-Scavengers. The foraging stratum was obtained from Vande weghe and Vande weghe (2011).

2.5 Data analysis

Except where mentioned, the sampling unit of analysis was five adjacent points within the same habitat. Twenty samples (100 points) were collected per habitat. The values are pooled for avian diversity and averaged for vegetation attributes. For analyses involving avian and vegetation data, avian diversity metrics were calculated based on birds recorded within 20 m radius of the point station instead of the 100 m radius, corresponding to the size of the vegetation assessment plots. A previous study based on the same dataset found no seasonality effects (Rurangwa et al., in review), hence data for the two sampling seasons were averaged to avoid pseudo-replication.

To explore the similarity in species composition across habitat type and age, a nonmetric multidimensional scaling (NMDS) ordination analysis based on the Bray-Curtis similarity measure was used, followed by an ANOSIM test which reveals the degree of significance of the similarities among the habitat groups. Both analyses were performed using the Community Analysis Package 5 (Seaby et al., 2014).

To measure the taxonomic diversity within each habitat, the exponential of Shannon entropy and pairwise beta diversity (measured using Sørensen dissimilarity, and partitioned into spatial turnover and nestedness-resultant dissimilarity, based on a presence and absence matrix: Baselga (2012)) were computed using the iNext, Vegan and Betapart R packages (Oksanen et al., 2010; Baselga and Orme 2012; Hsieh et al., 2016).

To assess the within-habitat variations of beta diversity components, a permutation analysis of multivariate dispersions (PERMDISP; Anderson et al., 2006) using 999 iterations was also performed, followed by an ANOVA, and a Tukey's test.

To investigate how total beta diversity and its components change with the habitat regeneration time between pairs of the samples within AR and NR habitats (a sample here was based on the average of two replicates of 10 adjacent points belonging to the same site, and hence same regeneration time, amounting to 20 samples and 190 pairwise comparisons), three separate correlation analyses were conducted. Since the variables were pairwise distance matrices that violated the linear regression assumption of independence, Pearson correlations were obtained using Mantel tests (Baselga, 2010; Aspin et al., 2018).

To quantify functional diversity, functional dispersion (FDis), a distance-based multivariate metric that measures the spread of species in a trait space (Laliberté & Legendre, 2010), and the community-weighted mean (CWM) were calculated for samples within each habitat. CWM was calculated for the traits that are indicative of energy requirements, feeding, locomotion and dispersal functions. Gower's distance was used as a measure of distance as some of the traits were categorical. We used the FD package (Laliberté et al., 2014) and followed the analytical steps described in Bregman et al. (2016). We determined differences in taxonomic and functional diversity metrics across habitat types by bootstrapping the mean and confidence intervals (bias corrected) using 10 000 randomizations for samples within each habitat. Separate analyses were conducted for data subsets containing invertivorous (invertebrates constitute at least 60% of the diet), and frugivorous guilds (fruit constitutes at least 60% of the diet), following Wilman et al. (2014). The two guilds were selected to evaluate maintenance of herbivory control, and seed dispersal functions under the two regeneration methods.

We modelled separately the influence of the extent of ferns, canopy cover, and tree diversity on avian species diversity (measured as the exponential of the Shannon entropy), and abundances across the three habitat types. Although tree size (DBH), and canopy height were recorded, they were removed from further analyses due to the high correlation between the two and with tree diversity (Pearson's $R > 0.7$; Fig.A.1). Vegetation attributes were standardized to mean of 0 and standard deviation of 1. We checked for the extent of collinearity among vegetation attributes by computing the variance inflation factor (VIF). VIF values for the model predictors ranged between 1.2 and 2.0.

Since the assumptions of standard linear regression were met for the taxonomic diversity variable, we performed a Gaussian multiple linear regression analysis for species diversity, while a generalised linear model (Quasi-Poisson family) was used with the species abundance response variable to account for overdispersion. We then performed model selection based on AIC_c (Akaike Information Criterion corrected for sample size). $QAIC_c$, a modified AIC_c for Quasi-Poisson models with overdispersion, was used for the abundance model. Spatial autocorrelation was diagnosed on model residuals using Moran's I test and was not significant for both taxonomic diversity and abundance metrics ($P > 0.05$). We averaged all models within ΔAIC or $\Delta AIC_c < 2$ of the most parsimonious model. The models were constructed using the Package "lme4", and "MuMin" (Bates, Maechler et al., 2014; Barton, 2019).

To explore the same relationship but with functional traits, a combination of the RLQ and Fourth-corner analyses (Dolédec et al., 1996) was performed using the R package "ADE4" (Dray et al., 2007). Both the RLQ and Fourth-corner analyses hinge on the analysis of a fourth-corner matrix obtained by crossing variables from three tables. In this case the R table was derived from vegetation attributes, the L table from species abundance across samples, and the Q table from species traits. Although the two methods' inputs are similar, their outputs differ substantially (Dray et al., 2014). The RLQ is a multivariate approach and explains the interaction between the three tables containing species abundance, traits and environmental attributes through ordination scores (Dray et al., 2002), whereas the fourth-corner analysis focuses on the interaction between an individual trait and one environment attribute at a time (Dray and Legendre, 2008). Combining the two methods helps to unveil which traits have changed as a result of the regeneration pathways (Dray et al., 2014). Except where otherwise mentioned, all statistical analyses were performed using R version 3.6.1 (R CoreTeam, 2019).

3. Results

3.1 Species composition

The study recorded 4,565 bird individual sightings belonging to 122 species. The number of individuals per sample ranged from four individuals and three species in the assisted naturally regenerated habitats (AR) to 107 individuals and 34 species in the primary forest (PF). The highest total numbers of individuals and of species were recorded in PF (n = 1,954; species = 102), followed by NR (n = 1,322, species = 83) and AR (n= 1,289, species: 58) (Table A1). *Bradypterus cinnamomeus, Zosterops senegalensis,* and *Apalis personata* were well represented across all habitat types and constituted 17% of all individuals. *A. personata* was the most frequently encountered Albertine Rift endemic species.

The dominant dietary guild in terms of species richness and individual sightings was invertivores, with 72 species and 2,675 individuals, followed by omnivores, with 15 species and 681 individuals, and frugivores, with 14 species and 578 individuals. The top three recorded species among invertivores were: *B. cinnamomeus, A. personata*, and *Phylloscopus laetus* (endemic), frugivores: *Z. senegalensis*, *Ruwenzornis johnstonii* (endemic), *Arizerocicla nigriceps*, and omnivores: *Onychognathus walleri, Eurillas latirostris,* and *Cinnyris regius* (endemic). Although rarefaction curves based on species richness did not level off in any of the habitats, those based on species diversity plateaued, particularly in AR habitats, showing the adequacy of sampling efforts (Fig. A.2).

NMDS revealed high segregation of PF from the other two habitat types, and considerable overlap between NR and AR samples (Fig. 2). The ANOSIM test (Table A.2) concurred with the NMDS ordination, showing significant differences between most habitat types (r = 0.3, *P* = 0.001). As expected, mid-aged regenerating communities (MNR, and MAR) were more similar to PF communities than young ones (YNR, and YAR). The lowest similarity was between PF and young NR (r = 0.68, *P* = 0.001). All pairwise comparisons were significant at *P* = 0.05, except for MNR–MAR, and MNR–YNR.

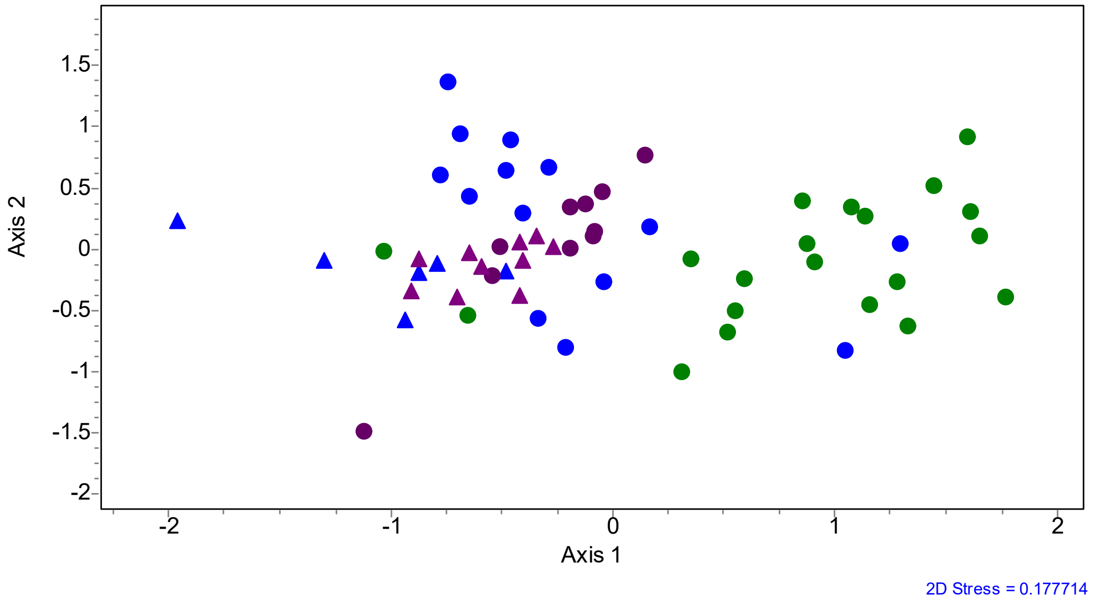

Figure 2 Two dimensional non-metric multidimensional scaling (NMDS) based on species raw abundances within primary forest (green circles; N = 20), young naturally regenerated (blue triangle; N= 6), mid-aged naturally regenerating (blue circles, N = 14), young assisted naturally regenerated (purple triangles; N = 10), and mid-aged assisted naturally regenerated (purple circles; N=10). The left-most blue triangle represents a sample with rare species: *Dendropicos griseocephalus* which was recorded once, and *Buteo buteo,* which was only recorded twice. The most negative sample on Axis 2 contains the fewest individuals (11; the mean is 42). The two blue samples with the highest score on axis 1 were located in close proximity to PF habitats. Each sample is an aggregate of 5 adjacent point counts sampled twice (in the wet and dry seasons) and then averaged.

3.2 Beta diversity

The within-habitat variation was only significant for total beta diversity βsor ($F_{2,27}$=5.37, *P* = 0.01), and the difference was highest between NR and AR (*P* = 0.0079). Using Mantel tests for samples within AR and NR habitats, we found a moderate positive correlation between difference in the regeneration time (time since a fire incidence or since restoration interventions) and the total beta diversity (R = 0.35, *P* = 0.0002), a weak positive relationship with species turnover (R

= 0.23, *P* = 0.01) and no significant relationship with nestedness-resultant dissimilarity (R = 0.11, *P* = 0.11, Fig. 3a-c).

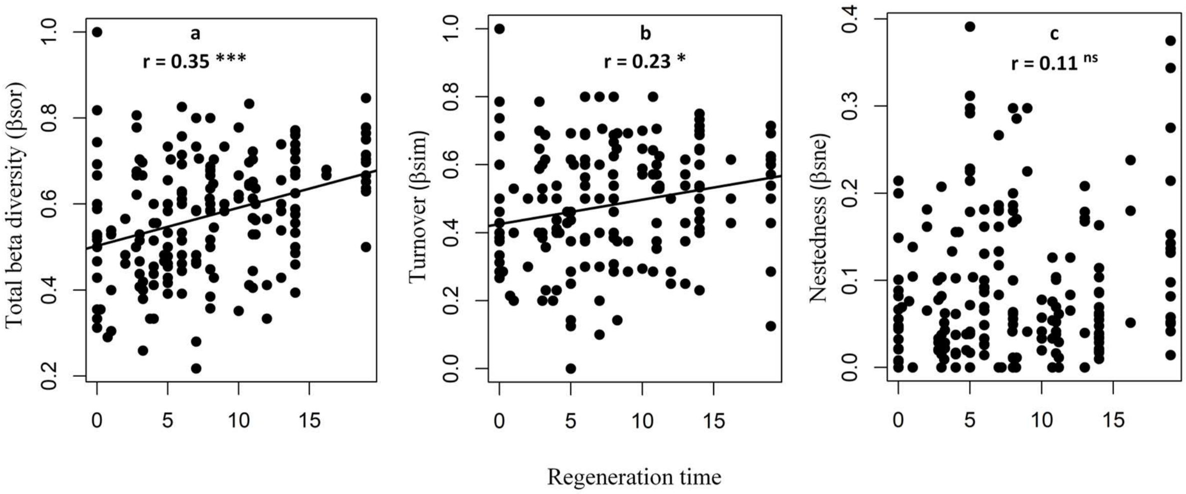

Figure 3. Correlation of pairwise dissimilarities in species composition of avian communities (species = 91) and habitat regeneration time (difference in time since fire or since restoration activites) of naturally regenerated and assisted naturally regenerated habitats within Nyungwe National Park, Rwanda. **a**: Total beta diversity (βsor), **b**: turnover (βsim), and **c**: nestedness-resultant dissimilarity (βsne). The correlation coefficients and p-values were generated by Mantel tests. Asterisks indicate statistically significant differences: '*' 0.05, '**' 0.01, '***' 0.001. The analysis is based on 20 samples, whereby a sample constitutes 10 adjacent points within the same habitat sampled twice (once in each season) and averaged.

3.3 Avian richness and diversity estimates across habitat types and dietary guilds

Taxonomic and trait-based metrics differed across habitat types except for community weighted mean (CWM) of the dispersal traits (Table 1). For the overall category (all birds combined) and within major dietary guilds, Taxonomic diversity (exponential of Shannon entropy) was significantly different between PF and NR, and PF and AR, but did not differ between NR and AR. For the trait-based metrics, variation within the invertivores was similar to the overall pattern except for the functional dispersion index (FDis). FDis values were significantly lower in AR when data for all birds were combined (Table 1). A shift towards higher mean values in AR than in PF was registered for the traits indicative of body size within invertivores, and the trophic axis within frugivores.

Table 1. Comparisons of Taxonomic diversity and functional diversity metrics for bird communities sampled in primary forest (PF), naturally regenerated sites (NR), and assisted naturally regenerated sites (AR) in Nyungwe National Park, Rwanda. Sample sizes (N = 20) are equal among habitat types. Each sample is a pool of 5 adjacent point counts, each sampled twice over the wet and dry seasons and averaged. Statistical significance was tested using bootstrap analysis with 10 000 randomisations (see text). Confidence intervals are not included in the table for readability purposes. Overall, the range of the metrics were as follows: Taxonomic diversity: 10.9–18.46; FDis: 0.177–0.21; CWM.Trophic: 0.027–0.129; CWM.Dispersal: 12.85–16.26; CWM.Locomotion: -0.097–0.076; CWM.Size: 0.196–0.581.

	Overall			**Invertivores**			**Frugivores**		
	PF	NR	AR	PF	NR	AR	PF	NR	AR
Taxonomic diversity	**17.03**^{a}	**11.72**^{b}	**12.00**^{b}	**11.04**^{a}	**7.36**^{b}	**8.45**^{b}	**2.54**^{a}	**1.46**^{b}	**1.49**^{b}
FDis	**0.20**^{a}	**0.20**^{a}	**0.18**^{b}	0.13	0.14	0.13	0.06	0.09	0.07
CWM.Trophic	0.09	0.08	0.06	0.26	0.26	0.23	**-0.01**^{a}	**0.05**^{ab}	**0.06**^{b}
CWM.Dispersal	15.35	14.05	13.74	12.89	11.86	11.97	15.10	12.44	12.15
CWM.Locomotion	**-0.05**^{a}	**0.03**^{b}	**0.04**^{b}	**0.04**^{a}	**0.29**^{b}	**0.22**^{ab}	0.06	0.12	0.13
CWM.Size	**0.31**^{a}	**0.42**^{ab}	**0.53**^{b}	**0.30**^{a}	**0.34**^{ab}	**0.50**^{b}	-0.05	0.05	-0.20

Note. Taxonomic diversity was measured as the exponential of the Shannon diversity index. FDis: Functional dispersion, and CWM: Community weighted mean of traits indicative of key ecological functions. The metric values are ranked from a-c; in the absence of significant differences at a = 0.05, they are assigned the same letter. Bold values signify statistically significant differences.

3.4 The relationship between avian taxonomic diversity and vegetation attributes

Vegetation attributes were in most cases higher in PF, and mostly lowest in AR (Table A3). An average of the most parsimonious model and a supporting model within $\Delta AIC_c < 2$ for PF, NR and AR habitats explained a moderate amount of variation ($AdjR^2$: 0.38) and showed tree diversity as the leading driver of avian taxonomic diversity with a higher Beta coefficient and relative importance values of 0.82, and 0.96, respectively, followed by the extent of ferns, which had a Beta coefficient of -0.68 and an importance of 0.75. Canopy cover exerted a weak positive influence, with a Beta coefficient of 0.23 and an importance value of 0.37 (Table 2, Fig. A3). The pattern was consistent for species abundance, however, tree diversity and the extent cover of ferns had lower importance values of 0.74, and 0.51, respectively (Table A4).

Table 2 A multiple regression analysis showing the relationship between vegetation parameters and avian species diversity (exponential of Shannon entropy) for sample plots (n= 20 per habitat) within primary forest, naturally regenerated forest and restored forest in Nyungwe National Park, Rwanda. The average and relative importance of model parameters of the linear regression models within $\Delta QAIC_c < 2$ are given for each metric. The relative importance is computed as the total of Akaike weights over all selected models containing the explanatory attribute. Importance values close to one indicate a stronger effect whilst those close to 0 indicate weaker effects.

			Species diversity					
Models	Cnp.cover	Ferns	Tree.div	$adjR^2$	logLik	AICc	delta	weight
1		-0.71	0.80	0.37	-120.74	250.20	0.00	0.46
2	0.23	-0.60	0.86	0.38	-120.32	251.76	1.55	0.21
Average	**0.23**	**-0.68**	**0.82**					
Importance	**0.37**	**0.75**	**0.92**					

Note. Cnp.cover = Canopy cover, Ferns = cover of ferns, Tree.div = tree diversity, and it is computed as the exponential of the Shannon diversity index.

3.5 The relationship between avian traits and vegetation attributes

The RLQ analysis showed on the first axis a gradient from primary forest sites (PF) with tall, large trees and a high diversity of trees, to sites with low values for each and with higher fern coverage (Fig. 4a). By this analysis, the PF habitat is associated with species of birds whose traits indicate mid-strata and canopy use (strat.Mid, strat.Cnp), and fruit-nectar and omnivore diets (Fig. 4b-c). Typical species include *Bycanistes subcylindricus, Lophoceros alboterminatus, Corythaeola cristata* (Fig. 4c, and Table A.1). The second axis is largely structured by the naturally regenerated habitat (NR) and the assisted naturally regenerated habitat (AR). The NR habitat is associated with the right upper quadrant and low canopy heights and high fern cover, and the AR habitat occupies the bottom right quadrant, featuring sites of low tree diversity, and low canopy cover. NR sites feature birds with a plant-seed diet such as *Pternistis nobilis,* and *Turtur tympanistria,* and *Cryptospiza jacksoni* (ARE), while AR sites feature in particular, invertivores and species that forage across multiple strata (Strat Gen).

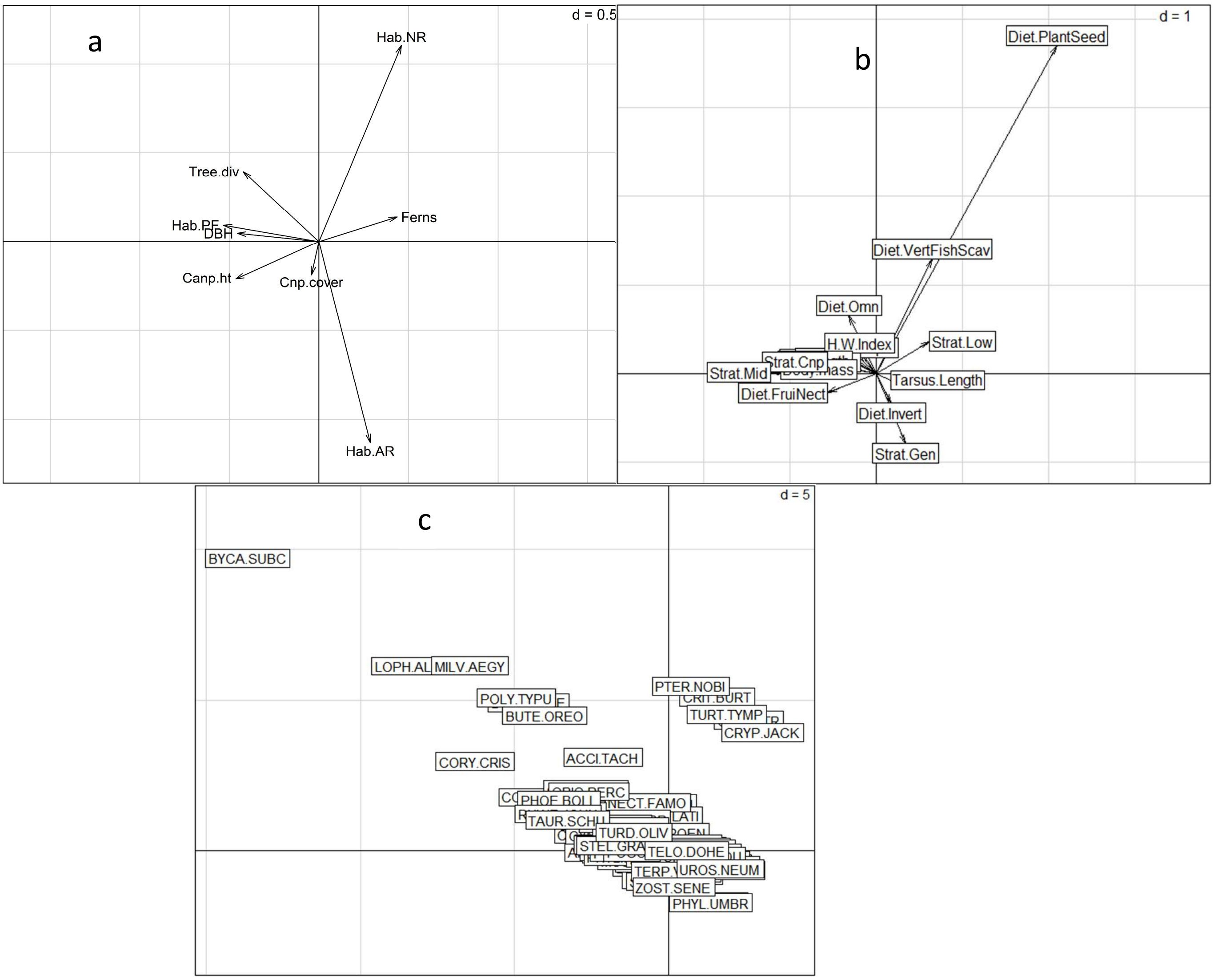

Figure 4 RLQ analysis showing relationships between avian traits and habitat variables related to restoration activities of fire-degraded sites within Nyungwe NP, Rwanda. **a**: Coefficients for the habitat variables, **b**: coefficients for the avian trait variables, **c**: scores of bird species. The “d” values in the upper right corner indicates the scale grid dimension for comparison across the three plots. Axes 1 and 2 accounted for 85.6% and 12% of the projected inertia, respectively. Hab: Habitat, Cnp.cover: Canopy cover, Tree.div: Tree diversity, DBH: Diameter at Breast height, Canp.ht: Canopy height, FruiNect: Fruit/Nect, Invert: Invertivore; VertFishScav: Vertebrate/Fish/Scavenger, Strat.Low: Lower stratum, Strat.Mid: Medium stratum, Strat.Gen: multiple strata, Omn: Omnivore; H.W.Index : Hand Wing Index. Full names of species and their scores are given in Table A.1.

The fourth corner analysis did not reveal any significant associations between traits and environmental attributes when the p-values are adjusted for multiple comparisons using the Benjamini and Hochberg method (without this adjustment, PF and AR are significantly associated with fruit-nectar diet, and multiple strata, respectively). The multivariate permutation test combining both the RLQ and Fourth-corner approaches, which was performed to determine the overall significance of the traits-environment relationships, showed a significant relationship for model 2— permutation of sites ($P = 0.00002$), and a non-significant relationship for model 4— permutation of species ($P = 0.50$).

4. Discussion

4.1 Dynamism of avian taxonomic diversity with forest regeneration

As predicted, primary forest (PF), naturally regenerated (NR), and assisted naturally regenerated habitats (AR) had distinct avian species assemblages. Although there was a degree of overlap in composition between the regenerated habitats and across age classes, bird assemblages of mid-aged habitat were more similar to those within primary forest habitats than young ones. The role of fire in creating different bird communities from those of undisturbed forest has also been observed in the Amazon forest (Barlow and Peres, 2004; Barlow et al., 2006). Similarly, Gould and Mackey (2015), in their study in tropical northern Australia, noted differences in avian assemblages between undisturbed woodlands and revegetated sites that had been cleared for mining, and also between age categories of the revegetated habitats.

The tendency of increased similarity in species composition with time between regenerated habitats and the primary forest noted by this study is reaffirmed by the correlation of pairwise beta diversity with difference in time since fire disturbances. The increase in similarity was principally driven by the turnover of species, however, the relationship was of only moderate strength, probably due to the fact that the assessment was carried out within a short time interval, since the longest regeneration time was two decades. Another explanation could be the high within-habitat variation in avian species composition exhibited by naturally regenerated habitats, which may reflect the varying intensity and recurrence of the fires resulting in habitats of different forest textures. The slow recovery of disturbed habitats was also noted in a study by Shoo et al. (2016) in the wet tropics of Australia, where they found that regenerated sites recovered forest structure attributes such as canopy cover of old growth levels within 40 years, but that at this point the wood volume, the richness of plant species and functional diversity levels were each less than half those found in the old-growth forest.

4.2 Mixed responses of avian diversity features linked to ecosystem functions

The species diversity of both invertivores and frugivores were comparable between the naturally regenerated and assisted regenerated habitats, but lower than the levels in primary forest, which implies reduced invertebrate herbivory regulation and seed dispersal services in the regenerated habitats. This might have more consequences in young naturally regenerated habitats, which were structurally and compositionally simplified due to the high coverage of ferns and a paucity of remnant trees, leading to reduced ecological niche space within these habitats. Although tree cover and fruiting were much more restored in assisted regenerated sites, the fact that restoration was done in patches of typically around 500m^2 may deter frugivores whose reliance on a continuous forest cover has been noted (Farwig and Berens, 2012; Farwig et al., 2017). The high density of young trees within restored patches and little herbaceous understorey may also reduce the permeability of these patches to invertivore birds with gap preferences such as *Caprimulgus poliocephalus* and *Bathmocercus rufus* (Vande weghe & Vande weghe, 2011). These species were only recorded in NR and PF, illustrating why AR sites were associated with generalists in terms of foraging stratum.

The lower levels of avian taxonomic diversity in regenerating habitats did not much affect the functional dispersion when the analysis was conducted for separate dietary guilds. One reason could be the functional redundancy exhibited by tropical forests (Cooke et al., 2019). For instance, species exclusive to primary forest in this study had a similar trait structure to those found in naturally regenerated and assisted regenerated habitats, including: *Tauraco schuetti*, a frugivorous large-bodied species which is sympatric to the *Ruwenzorornis johnstoni* commonly found in all habitats, and *Stelgidillas gracilirostris,* which belongs to the same family (Pycnonotidae) as *Arizelocicla nigriceps*, a species abundant in all three habitats. A similar pattern of stable functional traits between birds of regenerated habitats previously disturbed by fire and those of clearings and old growth forests, was reported by Ikin et al. (2019) in a temperate landscape of the South West Slopes bioregion, in Australia.

Although the birds recorded in the assisted natural regeneration habitats were essentially a subset of the birds of the primary forest, the shift towards higher mean values for traits related to the body size in the former habitats contradicts what is often documented in fragmented habitats, where small-bodied birds dominate the avian communities (Poulsen et al., 2011). In the absence of substantial hunting of birds in the Nyungwe NP, the dominance of large-sized birds corroborates the landscape texture hypothesis. This concept postulates that smaller bodied organisms are more associated with landscapes with a complex texture, whilst large-bodied ones are associated with simple textures (Holling, 1992; Fischer et al., 2008). The varying restoration interventions create discontinuities in the landscape, which in turn generates different assemblages of birds (Lindenmayer et al., 2012). The filtering of the discontinued vegetation systems along avian body size traits has been documented from habitat to continental scales (Allen and Holling, 2008; Thibault et al., 2011; Nash et al., 2014).

4.3 Efficacy of the restoration project actions in benefiting birds

In comparison to natural regeneration, the present study did not find a higher impact of the assisted natural regeneration intervention in terms of recovering the avian diversity. In the course of 20 years, bird communities of the two regenerating habitats remained distinct and had lower diversity levels relative to undisturbed primary forest. Although some trophic niche axes were more associated with certain habitats, there was no proof of filtering out of specific traits by a given habitat type.

The lack of pronounced efficacy of the assisted natural regeneration approach in recovering avian species and functional diversity might be due to the early phase of regeneration process within restored sites. The vegetation was characterized by a low tree diversity and dominance of pioneer woody species, particularly *Macaranga kilimandscharica* and *Hagenia abyssinica.* How long it may take for the restored vegetation to resemble the old growth and to regain an avian assemblage similar to that of old growth remain outstanding questions. The possibility of not attaining old growth levels and the development instead of a novel assemblage is another possible outcome (Catterall et al., 2012). Further studies and experiments will be needed to address these questions.

An important factor that was not incorporated in this study, owing to a lack of fine-scale data, is fire severity. Fire severity can dictate the degree of damage experienced by a habitat and thus may influence the speed of recovery of the vegetation structure and composition and associated fauna (Franklin et al., 2000; Roberts et al., 2020). With better fire monitoring tools being introduced in the Nyungwe NP, such data will allow improved inferences to be made in the future.

The restoration project in the Nyungwe NP deliberately chose to rehabilitate sites deprived of all trees and covered in ferns. It was hoped that with the elimination of ferns, a diversified tree cover would develop, and the canopy cover of the restored nuclei would progressively shade out ferns in neighbouring sites, eventually becoming a fully forested landscape supporting a range of ecosystem processes (Masozera and Mulindahabi, 2007). This study confirms the validity of the project's assumptions, in respect to the roles of tree species diversity in supporting a high avian diversity, and fern coverage in hindering it.

Although tree cover can be indispensable for a high avian diversity (especially of insectivores and canopy foragers) in forested habitats (Şekercioḡlu et al., 2002; Ikin et al., 2019), to accommodate both dense-forest interior birds and those with other habitat affinities will require the maintenance of diverse habitats (Kupsch et al., 2019). As a montane ecosystem, the physiognomy of the Nyungwe NP prior to burning differed from other rainforests, which are typically characterized by an enclosed canopy. Nyungwe NP comprised a mosaic of forest habitats owing to the dispersal barriers presented by valleys and ridges and steep cliffs. Longitudinal studies will reveal whether the restored sites will maintain the variation in forest structure (e.g. canopy openness), or whether further management interventions will be needed to recreate the variety of habitats.

4.5 Study contribution to global restoration frameworks

This study contributes to the documentation of empirical evidences of restoration activities in Rwanda and similar tropical landscapes. Advancing the field of tropical forest necessitates the wide sharing of steps of restoration projects, including both desired outcomes and failures (Holl, 2017). Such knowledge-sharing is particularly important since despite the increasing national and global commitments to restore degraded forest through frameworks such as the Bonn challenge and the complementary New York declaration on forests, since 2000, only 26.7 Mha of forests have been reported as restored, representing just 18% of the 2020 goal (NYDF Assessment Partners, 2019). Moreover, many restoration projects commence without well-defined ecological goals, have conflicting end-goals, lack scientific-based guidance and monitoring, and have resulted in forests providing low biodiversity and reduced ecosystem services (Li et al., 2014; Jacobs et al., 2015). Countries like Rwanda have shown high willingness to restore degraded forests. However, current conflicting policies in the forestry and agriculture sectors (Fagan et al., 2020; Rurangwa and Whittaker, 2020), may result in forest ecosystems that do not contribute substantially to global restoration goals. Studies like ours are important in documenting restoration processes and can serve to guide decision-making on the conservation of intact rainforest systems and future restoration management plans and actions.

Authors' contributions

Marie Laure Rurangwa: Conceptualization; Methodology, fieldwork funding acquisition and Writing; Marie Laure Rurangwa: Formal analysis; Robert J. Whittaker: Supervision; Joseph A. Tobias, and Protais Niyigaba: Data resources; All authors: Reviewing and editing.

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Assessing tropical forest restoration after fire using birds as indicators: an Afrotropical case study

Appendix 1

Table A.1 Species list of bird species recorded in 100 m radius points (N=600) in Nyungwe National Park, Rwanda. Habitat preference, dietary guild, foraging stratum and species loadings for Axes 1 and 2 of the RLQ ordination (Fig. 4c) are provided. The RLQ analysis involves species recorded within 20 m radius plots. PF: Primary forest; NR: Naturally regenerated; AR: Assisted naturally regenerated. A habitat is marked as preferred if it encompassed at least 50% of a species' recordings in this study. Two habitats are assigned, if they were used equally by the species, and their combined proportions constituted at least 80% of all recordings. Generalist species (GEN) exhibited no preference to a particular habitat. FruiNect: Fruit/Nect (Frugivore), Invert: Invertivore; VertFishScav: Vertebrate/Fish/Scavenger, Strat.Low: Lower stratum, Strat.Mid: Medium stratum, Strat.Gen: multiple strata, Omn: Omnivore. Dietary information is obtained from Wilman et al. (2014). Nomenclature follows the IOC world bird list, version 8.2. Doi: 10.14344/IOC.ML.8.2.

Abbreviation	**Scientific name**	**Common name**	**Habitat**	**Diet**	**Stratum**	**AxcQ1**	**AxcQ2**
ACCI.MELA	*Accipiter melanoleucus*	Great Sparrowhawk	PF	VertFishScav	Cnp		
ACCI.TACH	*Accipiter tachiro*	African goshawk	PF	VertFishScav	Cnp	-2.122	3.099
APAL.ARGE	*Apalis argentea*	Kungwe Apalis	PF	Invertebrate	Cnp	0.209	-0.644
APAL.CINE	*Apalis cinerea*	Grey Apalis	PF	Invertebrate	Cnp	0.302	-0.739
APAL.JACK	*Apalis jacksoni*	Black-throated Apalis	GEN	Invertebrate	Cnp	0.306	-0.688
APAL.NARI	*Apaloderma narina*	Narina Trogon	GEN	Invertebrate	Mid		
APAL.PERS	*Apalis personata*	Black-faced Apalis	GEN	Invertebrate	Cnp	0.407	-0.826
APAL.PORP	*Apalis porphyrolaema*	Chestnut-throated Apalis	GEN	Invertebrate	Cnp	0.347	-0.744
APAL.VITT	*Apaloderma vittatum*	Bar-tailed Trogon	PF	Invertebrate	Mid		
APUS.APUS	*Apus apus*	Common Swift	AR	Invertebrate	Mid		
APUS.CAFF	*Apus caffer*	White-rumped Swift	PF, NR	Invertebrate	Mid	-2.790	1.446
AQUI.AFRI	*Aquila africana*	Cassin's Hawk-eagle	PF	VertFishScav	Cnp		
ARIZ.NIGR	*Arizelocichla nigriceps*	Eastern Mountain Greenbul	GEN	FruiNect	Mid	-2.223	-0.040
BATH.RUFU	*Bathmocercus rufus*	Black-faced Rufous Warbler	PF	Invertebrate	Low	1.362	-0.416
BATI.DIOP	*Batis diops*	Ruwenzori Batis	GEN	Invertebrate	Mid	-0.666	-0.551
BATI.MOLI	*Batis molitor*	Chinspot Batis	AR	Invertebrate	Cnp	-0.082	-0.378
BOST.HAGE	*Bostrychia hagedash*	Hadada Ibis	PF	Invertebrate	Low		
BRAD.CINN	*Bradypterus cinnamomeus*	Bracken Warbler	NR, AR	Invertebrate	Low	1.284	-0.430
BRAD.GRAU	*Bradypterus graueri*	Grauer's Swamp-warbler	NR	Invertebrate	Low	1.243	-0.366
BUTE.BUTE	*Buteo buteo*	Common Buzzard	NR	VertFishScav	Cnp	-4.550	4.921
BUTE.OREO	*Buteo oreophirus*	Mountain Buzzard	GEN	VertFishScav	Cnp	-4.029	4.483
BYCA.SUBC	*Bycanistes subcylindricus*	Black-and-white-casqued Hornbill	PF	FruiNect	Cnp	-13.683	9.710

Abbreviation	**Scientific name**	**Common name**	**Habitat**	**Diet**	**Stratum**	**AxcQ1**	**AxcQ2**
CAMA.BRAC	*Camaroptera brachyura*	Green-backed Camaroptera	PF	Invertebrate	Low	1.712	-0.645
CAMP.ABIN	*Campethera abingoni*	Golden-tailed Woodpecker	PF	Invertebrate	Mid	-2.406	0.552
CAMP.NIVO	*Campethera nivosa*	Buff-spotted Woodpecker	NR	Invertebrate	Mid	-1.486	-0.098
CAPR.POLI	*Caprimulgus poliocephalus*	Ruwenzori Nightjar	NR	Invertebrate	Low	-1.152	1.516
CENT.MONA	*Centropus monachus*	Blue-headed Coucal	NR	VertFishScav	Low		
CERC.MONT	*Cercococcyx montanus*	Barred Long-tailed Cuckoo	PF	Invertebrate	Cnp		
CHAM.POLI	*Chamaetylas poliophrys*	Red-throated Alethe	PF	Invertebrate	Low	0.500	0.159
CHRY.CUPR	*Chrysococcyx cupreus*	African Emerald Cuckoo	PF	Invertebrate	Gen		
CINN.REGI	*Cinnyris regius*	Regal Sunbird	GEN	Omnivore	Cnp	-0.472	0.564
CINN.STUH	*Cinnyris stuhlmanni*	Ruwenzori double-collared sunbird	PF	Omnivore	Cnp	-0.861	0.750
CINN.VENU	*Cinnyris venustus*	Variable Sunbird	NR	Omnivore	Cnp	-0.405	0.549
CIST.CHUB	*Cisticola chubbi*	Chubb's Cisticola	GEN	Invertebrate	Low	1.293	-0.430
COLI.STRI	*Colius striatus*	Speckled Mousebird	NR	FruiNect	Gen		
COLU.ARQU	*Columba arquatrix*	African Olive-pigeon	NR	FruiNect	Cnp	-4.122	1.778
CORA.CAES	*Coracina caesius*	Grey Cuckooshrike	PF	Invertebrate	Cnp	-2.058	0.983
CORV.ALBI	*Corvus albicollis*	White-necked Raven	PF	VertFishScav	Low		
CORY.CRIS	*Corythaeola cristata*	Great blue turaco	PF	FruiNect	Cnp	-6.272	2.962
COSS.ARCH	*Cossypha archeri*	Archer's Robin-chat	GEN	Invertebrate	Low	1.216	-0.316
CRIT.BURT	*Crithagra burtoni*	Thick-billed Seedeater	PF	PlantSeed	Low	1.585	5.104
CRIT.CITR	*Crithagra citrinelloides*	African Citril	NR	PlantSeed	Low	2.602	4.330
CRIT.STRI	*Crithagra striolata*	Streaky Seedeater	NR	Omnivore	Low	-0.193	1.564
CRYP.JACK	*Cryptospiza jacksoni*	Dusky Crimson-wing	GEN	PlantSeed	Low	3.061	3.928
CUCU.CLAM	*Cuculus clamosus*	Black Cuckoo	PF	Invertebrate	Cnp		
CUCU.SOLI	*Cuculus solitarius*	Red-chested Cuckoo	NR	Invertebrate	Cnp		
CYAN.ALIN	*Cyanomitra alinae*	Blue-headed Sunbird	PF	Invertebrate	Low	0.550	0.156
CYAN.OLIV	*Cyanomitra olivacea*	Olive Sunbird	PF	FruiNect	Gen	-0.280	-0.969
DEND.GRIS	*Dendropicos griseocephalus*	Olive Woodpecker	NR	Invertebrate	Cnp	-1.604	0.623
DRYO.GAMB	*Dryoscopus gambensis*	Northern Puffback	GEN	Invertebrate	Cnp	-1.061	0.218
ELMI.ALBI	*Elminia albiventris*	Elminia albiventris	PF	Invertebrate	Low	1.099	-0.178
EURI.LATI	*Eurillas latirostris*	Yellow-whiskered Greenbul	PF	Omnivore	Low	-0.007	1.160

Abbreviation	**Scientific name**	**Common name**	**Habitat**	**Diet**	**Stratum**	**AxcQ1**	**AxcQ2**
GEOK.PIAG	*Geokichla piaggiae*	Kivu Ground-thrush	NR	Omnivore	Low		
GRAU.VITT	*Graueria vittata*	Grauer's Warbler	PF	Invertebrate	Low	1.034	-0.221
GYMN.BONA	*Gymnobucco bonapartei*	Grey-throated Barbet	PF	FruiNect	Cnp	-1.934	0.526
HEDY.COLL	*Hedydipna collaris*	Collared Sunbird	PF	Invertebrate	Cnp	0.241	-0.570
IDUN.SIMI	*Iduna similis*	Mountain Flycatcher-warbler	AR	Invertebrate	Low	1.190	-0.209
ILLA.PYRR	*Illadopsis pyrrhoptera*	Mountain Illadopsis	GEN	Invertebrate	Low	1.050	-0.252
INDI.EXIL	*Indicator exilis*	Least Honeyguide	PF	FruiNect	Cnp		
KAKA.POLI	*Kakamega poliothorax*	Grey-chested Babbler	PF	Invertebrate	Low	0.788	-0.101
KUPE.RUFO	*Kupeornis rufocinctus*	Red-collared Mountain-babbler	PF	Invertebrate	Cnp	-0.635	-0.213
LANI.LUEH	*Laniarius luehderi*	Luehder's Bush-shrike	PF	Invertebrate	Mid	-1.662	-0.037
LANI.MACK	*Lanius mackinnoni*	Mackinnon's Shrike	PF	Invertebrate	Gen	-0.457	-0.406
LANI.POEN	*Laniarius poensis*	Mountain Boubou	GEN	Invertebrate	Mid	-1.471	-0.141
LOPH.ALBO	*Lophoceros alboterminatus*	Crowned Hornbill	NR, AR	Omnivore	Cnp	-8.286	6.130
LOPH.OCCI	*Lophaetus occipitalis*	Long-crested Eagle	PF	VertFishScav	Low		
MELA.ARDE	*Melaenornis ardesiacus*	Yellow-eyed Black Flycatcher	PF	Invertebrate	Low	0.483	0.147
MELA.FASC	*Melaniparus fasciiventer*	Stripe-breasted Tit	AR	Invertebrate	Cnp	-0.284	-0.233
MELA.FISC	*Melaenornis fischeri*	White-eyed Slaty Flycatcher	PF, NR	Invertebrate	Cnp	-0.608	-0.135
MERO.OREO	*Merops oreobates*	Cinnamon-chested Bee-eater	PF	Invertebrate	Cnp	-2.166	1.018
MILV.AEGY	*Milvus aegyptius*	Black Kite	AR	VertFishScav	Cnp	-6.439	6.137
MUSC.ADUS	*Muscicapa adusta*	African Dusky Flycatcher	PF	Invertebrate	Mid	-0.876	-0.337
NECT.FAMO	*Nectarinia famosa*	Malachite Sunbird	NR	Omnivore	Low	-0.676	1.598
NECT.PURP	*Nectarinia purpureiventris*	Purple-breasted Sunbird	PF	Omnivore	Cnp	-1.284	1.039
NEOC.POEN	*Neocossyphus poensis*	White-tailed Ant Thrush	NR	Invertebrate	Low	-0.085	0.601
NIGR.CANI	*Nigrita canicapillus*	Grey-headed Negrofinch	PF	Omnivore	Mid	-1.708	0.896
ONYC.TENU	*Onychognathus tenuirostris*	Slender-billed Starling	PF	FruiNect	Cnp	-3.354	1.305
ONYC.WALL	*Onychognathus walleri*	Waller's Starling	PF	Omnivore	Cnp	-2.678	2.033
OREO.RUWE	*Oreolais ruwenzorii*	Collared Apalis	PF, AR	Invertebrate	Low	1.523	-0.487
ORIO.PERC	*Oriolus percivali*	Black-tailed Oriole	PF	Omnivore	Cnp	-2.580	1.971
PHOE.BOLL	*Phoeniculus bollei*	White-headed Woodhoopoe	PF	Invertebrate	Cnp	-3.548	1.694
PHYL.FLAV	*Phyllastrephus flavostriatus*	Yellow-streaked Greenbul	PF	Invertebrate	Mid	-1.464	-0.200

Abbreviation	**Scientific name**	**Common name**	**Habitat**	**Diet**	**Stratum**	**AxcQ1**	**AxcQ2**
PHYL.LAET	*Phylloscopus laetus*	Red-faced Woodland-warbler	AR	Invertebrate	Gen	1.329	-1.686
PHYL.PLAC	*Phyllastrephus placidus*	Placid Greenbul	PF	Invertebrate	Low	0.482	0.058
PHYL.TROC	*Phylloscopus trochirus*	Willow Warbler	NR	Invertebrate	Cnp	-0.054	-0.255
PHYL.UMBR	*Phylloscopus umbrovirens*	Brown Woodland-warbler	NR	Invertebrate	Gen	1.383	-1.722
PLAT.CONC	*Platysteira concreta*	Yellow-bellied Wattle-eye	PF	Invertebrate	Low		
PLAT.PELT	*Platysteira peltata*	Black-throated Wattle-eye	PF	Invertebrate	Low		
PLOC.ALIE	*Ploceus alienus*	Strange Weaver	PF	Invertebrate	Low	0.509	0.244
PLOC.BAGL	*Ploceus baglafecht*	Baglafecht Weaver	NR	Invertebrate	Gen		
PLOC.BICO	*Ploceus bicolor*	Dark-backed Weaver	PF	Invertebrate	Mid	-1.742	0.220
PLOC.INSI	*Ploceus insignis*	Brown-capped Weaver	PF	Invertebrate	Mid	-1.385	-0.056
PLOC.MELA	*Ploceus melanogaster*	Black-billed Weaver	PF	Invertebrate	Low	0.641	0.114
POEO.SHAR	*Poeoptera sharpii*	Sharpe's Starling	NR	FruiNect	Mid		
POGO.BILI	*Pogoniulus bilineatus*	Yellow-rumped Tinkerbird	PF	FruiNect	Cnp	-0.933	-0.043
POGO.CORY	*Pogoniulus coryphaeus*	Western Tinkerbird	AR	FruiNect	Gen		
POGO.STEL	*Pogonocichla stellata*	White-starred Robin	AR	Invertebrate	Low	0.812	0.079
POLY.TYPU	*Polyboroides typus*	African harrier-hawk	PF	VertFishScav	Cnp	-4.935	5.069
PRIN.BAIR	*Prinia bairdii*	Banded Prinia	PF	Invertebrate	Low	1.205	-0.342
PSAL.PRIS	*Psalidoprocne pristoptera*	Black Saw-wing	PF	Invertebrate	Cnp	-1.241	0.798
PSEU.ABYS	*Pseudoalcippe abyssinica*	African Hill Babbler	GEN	Invertebrate	Low	1.118	-0.290
PTER.NOBI	*Pternistis nobilis*	Handsome Francolin	NR	PlantSeed	Low	0.729	5.467
PYCN.BARB	*Pycnonotus barbatus*	Common Bulbul	GEN	FruiNect	Cnp	-1.718	0.195
RALL.CAER	*Rallus caerulescens*	African Water Rail	PF	Omnivore	Low		
RUWE.JOHN	*Ruwenzorornis johnstoni*	Ruwenzori Turaco	NR, AR	FruiNect	Cnp	-3.590	1.222
SARO.RUFA	*Sarothrura rufa*	White-spotted Flufftail	NR	Invertebrate	Low		
SAXI.TORQ	*Saxicola torquatus*	Common Stonechat	NR	Invertebrate	Low	1.100	-0.074
SCHI.LEUC	*Schistolais leucopogon*	Tawny-flanked Prinia	PF	Invertebrate	Low		
SHEP.AEQU	*Sheppardia aequatorialis*	Equatorial Akalat	PF	Invertebrate	Low	1.117	-0.189
SMIT.CAPE	*Smithornis capensis*	African Broadbill	NR, AR	Invertebrate	Mid		
STEL.GRAC	*Stelgidillas gracilirostris*	Slender-billed Greenbul	PF	FruiNect	Cnp	-1.642	0.174
STEP.CORO	*Stephanoaetus coronatus*	African Crowned eagle	PF	VertFishScav	Gen		

Abbreviation	**Scientific name**	**Common name**	**Habitat**	**Diet**	**Stratum**	**AxcQ1**	**AxcQ2**
STRE.SEMI	*Streptopelia semitorquata*	Red-eyed Dove	PF	PlantSeed	Low		
SYLV.LEUC	*Sylvietta leucophrys*	White-browed Crombec	PF	Invertebrate	Mid	-0.055	-1.024
TAUR.SCHU	*Tauraco schuetti*	Black-billed turaco	PF	FruiNect	Cnp	-3.276	1.019
TELO.DOHE	*Telophorus dohertyi*	Doherty's Bush-shrike	NR, AR	Invertebrate	Low	0.601	0.005
TERP.VIRI	*Terpsiphone viridis*	African Paradise-flycatcher	PF	Invertebrate	Gen	-0.073	-0.677
TRER.CALV	*Treron calvus*	African Green-pigeon	PF	FruiNect	Cnp		
TURD.OLIV	*Turdus olivaceus*	Olive Thrush	PF, NR	Omnivore	Gen	-1.122	0.618
TURT.TYMP	*Turtur tympanistria*	Tambourine Dove	GEN	PlantSeed	Low	1.887	4.535
UROS.NEUM	*Urosphena neumanni*	Neumann's Warbler	PF	Invertebrate	Low	1.688	-0.601
ZOST.SENE	*Zosterops senegalensis*	African Yellow White-eye	GEN	FruiNect	Gen	0.181	-1.206

Table A.2 Results of analysis of similarity (ANOSIM) based on the Bray-Curtis distance for bird communities within Nyungwe NP, Rwanda. The sample statistic r ranges theoretically from -1 to +1. Values close to +1 signal a high degree of similarity between samples belonging to the same group, and thus greater dissimilarity with the compared group.

Habitats (sample size)			
1st Group	2nd Group	P Value	Sample Stat. (r)
PF (20)	MNR (14)	0.001	0.435
PF (20)	YNR (6)	0.001	0.681
PF (20)	MAR (10)	0.001	0.422
PF (20)	YAR (10)	0.001	0.522
MNR (14)	YNR (6)	0.136	0.137
MNR (14)	MAR (10)	0.396	0.011
MNR (14)	YAR (10)	0.023	0.152
YNR (6)	MAR (10)	0.004	0.389
YNR (6)	YAR (10)	0.001	0.476
MAR (10)	YAR (10)	0.004	0.235

Note. PF: Primary forest, MNR: Mid-age naturally regenerated sites, YNR: young naturally regenerated sites, MAR: Mid-aged assisted naturally regenerated sites, YAR: young assisted naturally regenerated sites.

Table A.3 Mean and standard deviation of elevation and vegetation attributes of study area samples averaged per habitat type and across two sampling seasons (2017/2019) within Nyungwe NP, Rwanda. The attributes were recorded in 20m radius plots. 100 plots were sampled in each habitat. 5 adjacent points were aggregated to form a sample.

Habitat	Elevation (m)	Canopy cover (%)	Ferns (%)	Tree diversity	DBH (cm)	Canopy height (m)
AR	2503.6±67	64.4±6	29.7±11	2.3±1	22.8±4	13.6±2
NR	2374.8± 186	56.3±13	42.4±22	5.3±3	27.5±9	11.4±3
PF	2174.1±305	62±7	1.5±3	10.2±3	52.1±14	22±4

DBH = Diameter at breast height measured at 1.3 m.

Table A.4 The relationship between vegetation attributes for sample plots (n= 20 per habitat) within primary forest, naturally regenerated forest and restored forest in Nyungwe NP, Rwanda. The average and importance of the models within $\Delta QAIC_c < 2$ is given. Importance values close to one indicate a stronger effect whilst those close to 0 indicate weaker effects.

			Abundance					
	Cnp.cover	Ferns	Tree.div	adjR^2	logLik	QAICc	delta	weight
1			0.17	0.37	-216.58	159.13	0.00	0.27
2	0.08		0.16	0.42	-214.21	159.75	0.63	0.20
3		-0.09	0.11	0.41	-214.56	160.00	0.87	0.18
4		-0.17		0.34	-217.85	160.02	0.90	0.18
Average	**0.08**	**-0.13**	**0.15**					
Importance	**0.37**	**0.51**	**0.74**					

Note: Cnp.cover = Canopy cover, Ferns = cover of ferns, Tree.div =Tree species diversity, measured as exponential of Shannon entropy. QAICc, is a modified AICc (Akaike information Criterion for small samples) for models with overdispersion.

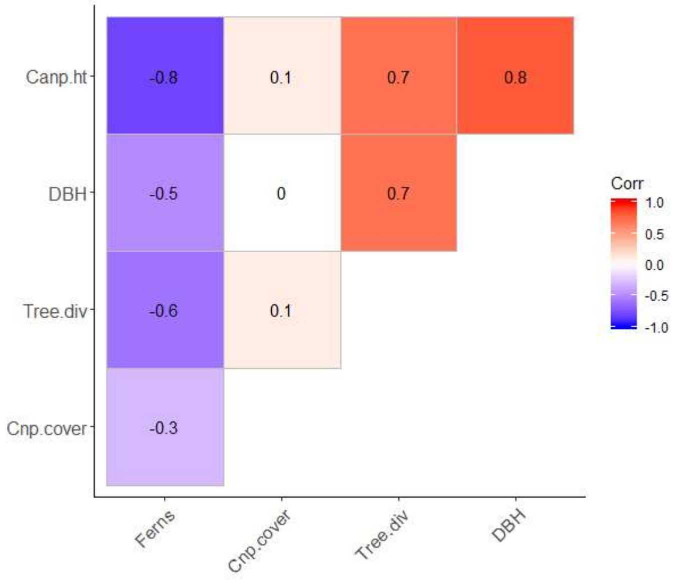

Figure A.1 Correlation plot of vegetation attributes and corresponding Pearson R correlation coefficients for study samples (N= 60) within naturally regenerated, assisted-naturally regenerated and primary forest within Nyungwe NP, Rwanda. A sample comprised 5 adjacent plots. Each attribute was measured twice: in the wet season, and the dry season of 2017/2018. DBH and Canopy height (Cnp.ht) were excluded from further analysis.

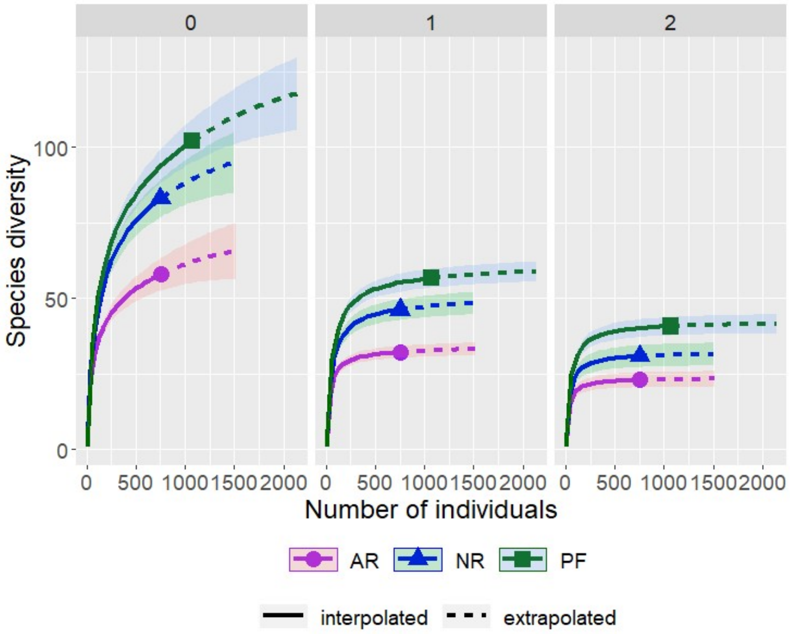

Figure A.2 Species rarefaction curves computed for each habitat to evaluate the exhaustiveness of sampling efforts. The species diversity of birds is calculated for the Hill numbers, where q=0 is based on the Chao 1 species richness estimator, q=1: the Shannon entropy index, and q=2: the Simpson diversity index. The shaded areas represent 95% Confidence intervals. The graph and estimates were obtained using the R package “iNext” (Hsieh et al., 2016).

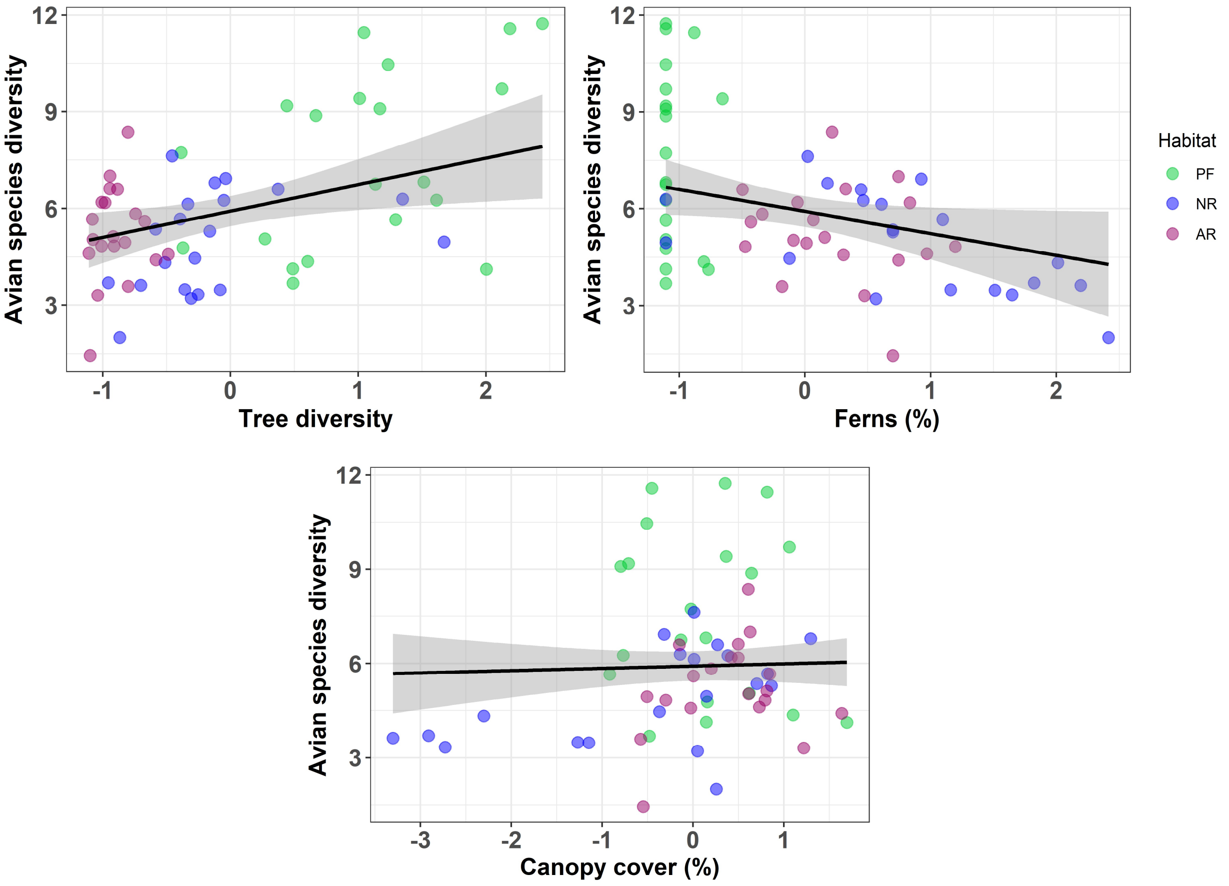

Figure A.3 Relationships between avian species diversity (exponential of Shannon entropy), functional diversity, and vegetation attributes of study samples (N=20 per habitat) in the primary forest (PF), Naturally regenerated sites (NR), and assisted naturally regenerating sites within Nyungwe National Park, Rwanda. Results were obtained from a multiple linear regression analysis. Attributes were first standardized to mean of 0 and standard deviation of 1. The grey band represents ± 95% confidence interval. Further details are presented in Table 2.