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1	Assessing tropical forest restoration after fire using birds as indicators: an Afrotropical case
2	study
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4	Journal: Forest Ecology and Management
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25 Abstract

The necessity to restore rainforest habitats degraded by anthropogenic fires is widely recognized, 26 27 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 28 recovery of the faunal diversity and features linked to key ecosystem functions. We assessed the 29 taxonomic diversity and functional trait structure of bird assemblages in undisturbed primary 30 forest and fire-affected habitats undergoing natural regeneration, as well as areas of assisted 31 natural regeneration, in Nyungwe National Park, Rwanda. We compiled bird occurrence data from 32 point-count sampling, and obtained morphological traits for all species in our assemblages using 33 measurements taken from wild birds and museum specimens. We found marked differences in 34 35 species composition between primary forest habitats and regenerating forest, with similarity 36 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 37 38 naturally regenerated habitats, although separate analyses within dietary guilds revealed no differences across habitats. Among desired restoration outcomes, tree species diversity was the 39 leading positive driver of avian species diversity, fern coverage exerted negative effects, while 40 41 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 42 are not easily reversed, as shown by the lack of improvement in avian diversity metrics under 43 assisted naturally regeneration in relation to natural regeneration. We stress the need to document 44 both floral and faunal recovery in order to aid informed decision-making on restoration methods. 45

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47 Key words: Afrotropics, assisted natural regeneration, avian diversity, ecological restoration,

48 functional traits, Nyungwe forest, passive restoration.

50

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, 51 1987; Sodhi et al., 2011; He et al., 2019). Nonetheless, its current frequency and intensity in less 52 fire-adapted wet forests present detrimental effects on ecological processes (King et al., 1997; 53 Cochrane, 2003). Large-scale fires in tropical rainforests have mostly anthropogenic origins, with 54 55 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 56 57 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 58 intensify under future climatic conditions (IPBES, 2019; IPCC, 2019). Where wildfires become 59 chronic and frequent, grasses or opportunistic ferns may occupy the degraded areas, fueling future 60 fires and hampering regeneration for decades (Cohen et al., 1995; Ashton et al., 2001). 61

Pteridium aquilinum (L.) Kuhn (bracken fern) is one of the most notorious plants responsible for 62 arrested succession. It is native to all continents and has a distribution spanning temperate and 63 tropical forests and grasslands (Dolling, 1996; Adie et al., 2011). The dominance and persistence 64 65 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, 66 67 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); 68 and v) toxic compounds that protect against grazing herbivores (Grime et al., 1988; Ssali et al., 69 2017). 70

In Bwindi Impenetrable National Park, Uganda, it was found that all sites dominated by the 71 bracken fern had been affected by fires (Ssali et al., 2017). In comparison to the undisturbed 72 forest, the few woody plants that were found within the bracken-dominated area were 73

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 81 tropics (Shono et al., 2007; Crouzeilles et al., 2017), has sparked the testing of a range of 82 alternative management techniques to accelerate regeneration processes. An experiment 83 conducted by Cohen et al. (1995) in the above-mentioned Sri Lankan lowland rainforest where 84 dominance of Dicranopteris linearis had become the stable state, found that techniques 85 comprising rhizome removal and tilling to mix top and mineral soils, eliminated the ferns and 86 enhanced the growth of herbs, shrubs and trees. In Chiapas, Mexico, the monthly removal of the 87 bracken ferns (Pteridium caudatum) and sowing or planting seedlings of balsa (Ochroma 88 pyramidale), a fast growing pioneer tree species, led to the total elimination of the ferns in 18 89 months in plots where balsa occupied at least $11m^2$ per ha (Douterlungne et al., 2013). 90

Due to the high cost associated with the planting of seeds or seedlings (active restoration), the 91 92 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 93 artificial perches to enhance propagule supply — has been preferentially applied (Shono et al., 94 2007; Shoo & Catterall, 2013; Elliott, 2016; Chazdon, 2017). Assisted natural regeneration was 95 found to be effective in increasing substantially the canopy cover, species richness, and stem 96 density of woody plants in an Australian subtropical forest that was previously cleared for grazing 97 (Uebel et al., 2017). 98

Although a range of techniques have long been practiced by indigenous communities to 99 regenerate forests (Dugan et al., 2003; Douterlungne et al., 2010), there is scant information on 100 their performance in the recovery of animal species diversity, and features linked to ecological 101 functions. A search in the bibliographic database, ISI Web of Science employing the terms "fern 102 or Pteridium & tropic* forest & restor*", for the period 2010 to 2020, covering Ecology, 103 Environmental sciences, Forestry, Biodiversity Conservation, and related fields, gave 210 104 105 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 106 107 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 108 the recovery of animal diversity, especially in the Afrotropics where there has been less research 109 110 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 111 with different timeframes or end-goals (Larkin et al., 2019). 112

113

Our study aims to address this gap by comparing both naturally regenerated and assisted naturally 114 regenerated habitats to primary forest (areas of no major disturbance) within the same landscape. 115 The advantage of our method is that we are not comparing the outcome of restoration efforts to a 116 pre-disturbance state, an approach which would not account for the dynamism of ecosystem 117 processes, such as the variabilities induced by anthropogenic climatic changes (Holl & Aide, 118 2011). Instead, we are carrying out a spatial comparison using birds to assess the faunal recovery 119 with particular reference to their functional roles within the ecosystem. Birds provide a well-120 established indicator group of the vitality of ecosystems that are highly relevant to restoration 121 studies since the ecosystem services performed by birds, such as seed dispersal, pollination and 122

herbivory control combine to accelerate the recovery of degraded forest landscapes (Şekercioğlu,
2012; Roels et al., 2019).

125

We conducted our study in Nyungwe National Park (Fig.1), a tropical montane rainforest in the 126 southwest of Rwanda. In proportion to its surface area, Rwanda has made the largest pledge to the 127 Bonn Challenge. A commitment of 2 Mha was made, representing an area larger than that 128 129 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 130 131 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 132 increase tree cover and tree species diversity by combatting the opportunistic fern Pteridium 133 aquilinum, which inhibits forest regeneration processes (Masozera & Mulindahabi, 2007). 134

135

In the present study, we asked two primary questions. First, how do avian species composition, 136 137 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 138 regenerated and primary forest) will have distinct species composition, and different amounts of 139 taxonomic and functional diversity; ii) avian diversity will be higher in assisted naturally 140 regenerated than in naturally regenerated habitats; both will converge towards the composition 141 and diversity of undisturbed primary forest habitats over time (Derhé, et al., 2016); and finally iii) 142 there will be a difference in the recovery of major guilds occupying naturally regenerated and 143 assisted naturally regenerated sites, with frugivores in both habitats slower to recover due to their 144 preference for a continuous forest cover (Farwig et al., 2017). Second, to what extent do changes 145 in vegetation generated by the assisted restoration project influence avian taxonomic and 146 functional diversity across the habitat types? We hypothesized that: i) vegetation complexity and 147 stature drive increasing avian diversity, and; ii) the proportion of ferns will be the major negative 148

149 driver of avian taxonomic diversity and will lead to reduced avifaunal community trait structure,

150 particularly for the regenerated habitats (cf. Gould & Mackey, 2015, Ikin et al., 2019).

151 **2.** Methods

152 **2.1 Study site description**

The study was conducted in Nyungwe National Park (Nyungwe NP), a tropical montane rainforest
of 1,019 km² 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°C, whilst
the maximum is 19.6° C (Sun et al., 1996; Seimon, 2012).

157 In the last twenty-three years, anthropogenic fires in the Nyungwe forest have ravaged more than

158 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,

160 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

162 155.5 ha and 234.5 ha in 2003 and 2004, to 8.8 ha and 5 ha in 2018 and 2019, respectively

163 (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

165 *Syzygium guineense,* have been replaced by dense thickets of opportunistic ferns, typically

166 *Pteridium aquilinum*, leading to arrested succession (Masozera & Mulindahi, 2007).

167 In early 2000, the park management and conservation partners initiated trials to determine the

168 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

170 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

172 (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 176 hillside, only plots ranging from 250 to 500 m² were cleared. It was envisaged that with time, the 177 restored canopy would expand outwards, and shade-off the remaining ferns. Since 2003, the 178 assisted natural-regeneration method has been applied in all restoration interventions in the 179 Nyungwe NP. Restoration sites were prioritized based on the scarcity of trees and the accessibility 180 and visibility from the main road (Masozera & Mulindahabi, 2007). The total area of plots that 181 have been treated amount to 250 ha (WCS, pers. comm). In most cases, the shade-intolerant 182 pioneer species (particularly Macaranga kilimandscharica) grow immediately after the treatment 183 was applied. The recruitment of shade-tolerant primary forest species follows after the canopy 184 starts to close (P.N. pers. obs.). Although annual monitoring of the vegetation cover in the 185 restored plots has been conducted as part of the management of the park, no scientific study has 186 hitherto been conducted to assess the recovery of the avifauna. 187

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190 2.2 Avian sampling

191 Sampling was conducted in naturally regenerated habitats (NR), assisted naturally regenerated

192 habitats (AR), and in primary forest (PF), which is considered herein as the reference state. Sites

193 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 207 (wet season), and they were repeat-sampled between June and August 2018 (dry season), bringing 208 the total to 600 point-counts. Regenerating forests were further classified by age class, relating to 209 the time since a fire incidence for NR habitats, and the year of restoration for AR habitats. Within 210 211 NR, 30 point stations were established in young habitats (<10 years), and 70 point stations in midage habitats (10–20 years), while in AR, 50 points stations were established in each age class. 212 213 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 214 double counting of birds and to maintain statistical independence. 215

216 **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

221	cover was estimated using a spherical densiometer. Four readings were taken from each cardinal
222	direction, and the mean was used as the final record. The percentage of the fern coverage inside
223	the plot was visually estimated, with 0% indicating absence and 100% signifying total occupation
224	by the ferns. One botanist and an assistant conducted the vegetation survey, and they sampled one
225	to two plots behind the bird survey team. As with the avian survey, sampling was carried out in
226	the wet season, and a replication was done in the dry season.
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240 **2.4 Functional traits collection**

Biometric data of study birds were measured from wild birds or museum specimens following a 241 standardized protocol elaborated in Bregman et al. (2016). The measurements included: bill 242 length, width and depth, which are indicative of the trophic niche; tarsus length, hand wing index, 243 tail length, which are indicative of locomotory and flight capabilities; and body size (measured as 244 body mass in grams), which indicates energy requirements (Hutchinson, 1959; Grant & Grant, 245 246 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, 247 248 Plant-Seed matter, Vertebrate-Fish-Scavengers. The foraging stratum was obtained from Vande weghe and Vande weghe (2011). 249

250 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).

278 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 279 community-weighted mean (CWM) were calculated for samples within each habitat. CWM was 280 281 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. 282 We used the FD package (Laliberté et al., 2014) and followed the analytical steps described in 283 284 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 10 285 000 randomizations for samples within each habitat. Separate analyses were conducted for data 286

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 291 292 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 293 were removed from further analyses due to the high correlation between the two and with tree 294 diversity (Pearson's R > 0.7; Fig.A.1). Vegetation attributes were standardized to mean of 0 and 295 standard deviation of 1. We checked for the extent of collinearity among vegetation attributes by 296 computing the variance inflation factor (VIF). VIF values for the model predictors ranged 297 between 1.2 and 2.0. 298

Since the assumptions of standard linear regression were met for the taxonomic diversity variable, 299 we performed a Gaussian multiple linear regression analysis for species diversity, while a 300 generalised linear model (Quasi-Poisson family) was used with the species abundance response 301 variable to account for overdispersion. We then performed model selection based on AIC_c 302 (Akaike Information Criterion corrected for sample size). QAIC_c, a modified AIC_c for Quasi-303 Poisson models with overdispersion, was used for the abundance model. Spatial autocorrelation 304 305 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 306 the most parsimonious model. The models were constructed using the Package "Ime4", and 307 "MuMin" (Bates, Maechler et al., 2014; Barton, 2019). 308 To explore the same relationship but with functional traits, a combination of the RLQ and Fourth-309

310 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 312 vegetation attributes, the L table from species abundance across samples, and the Q table from 313 314 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 315 three tables containing species abundance, traits and environmental attributes through ordination 316 scores (Dray et al., 2002), whereas the fourth-corner analysis focuses on the interaction between 317 318 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 319 320 pathways (Dray et al., 2014). Except where otherwise mentioned, all statistical analyses were performed using R version 3.6.1 (R CoreTeam, 2019). 321

322 3. Results

323 **3.1 Species composition**

The study recorded 4,565 bird individual sightings belonging to 122 species. The number of 324 individuals per sample ranged from four individuals and three species in the assisted naturally 325 regenerated habitats (AR) to 107 individuals and 34 species in the primary forest (PF). The 326 highest total numbers of individuals and of species were recorded in PF (n = 1,954; species = 327 102), followed by NR (n = 1,322, species = 83) and AR (n = 1,289, species: 58) (Table A1). 328 329 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 330 frequently encountered Albertine Rift endemic species. 331

332 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),

336 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).

342	NMDS revealed high segregation of PF from the other two habitat types, and considerable overlap
343	between NR and AR samples (Fig. 2). The ANOSIM test (Table A.2) concurred with the NMDS
344	ordination, showing significant differences between most habitat types (r = 0.3 , P = 0.001). As
345	expected, mid-aged regenerating communities (MNR, and MAR) were more similar to PF
346	communities than young ones (YNR, and YAR). The lowest similarity was between PF and
347	young NR (r = 0.68, P = 0.001). All pairwise comparisons were significant at P = 0.05, except for
348	MNR–MAR, and MNR–YNR.
349	
350	



Figure 2 Two dimensional non-metric multidimensional scaling (NMDS) based on species raw 353 354 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 355 356 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 357 Buteo buteo, which was only recorded twice. The most negative sample on Axis 2 contains the fewest 358 individuals (11; the mean is 42). The two blue samples with the highest score on axis 1 were located in 359 360 close proximity to PF habitats. Each sample is an aggregate of 5 adjacent point counts sampled twice (in 361 the wet and dry seasons) and then averaged.

363 **3.2 Beta diversity**

The within-habitat variation was only significant for total beta diversity β sor (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 369 = 0.23, P = 0.01) and no significant relationship with nestedness-resultant dissimilarity (R = 0.11, 370 P = 0.11, Fig. 3a-c).

371



372

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 (β sor), **b**: turnover (β sim), and **c**: nestedness-resultant dissimilarity (β sne). 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.

380

381 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
- 388 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
- 390 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.

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	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

399 Note. Taxonomic diversity was measured as the exponential of the Shannon diversity index. FDis: Functional dispersion, and CWM: Community weighted

400 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

401 are assigned the same letter. Bold values signify statistically significant differences.

402 **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). 403 An average of the most parsimonious model and a supporting model within $\Delta AIC_c < 2$ for PF, NR 404 and AR habitats explained a moderate amount of variation (AdjR²: 0.38) and showed tree 405 diversity as the leading driver of avian taxonomic diversity with a higher Beta coefficient and 406 relative importance values of 0.82, and 0.96, respectively, followed by the extent of ferns, which 407 had a Beta coefficient of -0.68 and an importance of 0.75. Canopy cover exerted a weak positive 408 influence, with a Beta coefficient of 0.23 and an importance value of 0.37 (Table 2, Fig. A3). The 409 pattern was consistent for species abundance, however, tree diversity and the extent cover of ferns 410 had lower importance values of 0.74, and 0.51, respectively (Table A4). 411 412 413 **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 414 forest, naturally regenerated forest and restored forest in Nyungwe National Park, Rwanda. The average 415 and relative importance of model parameters of the linear regression models within $\Delta QAIC_c < 2$ are given 416 417 for each metric. The relative importance is computed as the total of Akaike weights over all selected 418 models containing the explanatory attribute. Importance values close to one indicate a stronger effect 419 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					

420 Note. Cnp.cover = Canopy cover, Ferns = cover of ferns, Tree.div = tree diversity, and it is computed as

421 the exponential of the Shannon diversity index.

422

424 **3.5** The relationship between avian traits and vegetation attributes

425 The RLQ analysis showed on the first axis a gradient from primary forest sites (PF) with tall,

426 large trees and a high diversity of trees, to sites with low values for each and with higher fern

427 coverage (Fig. 4a). By this analysis, the PF habitat is associated with species of birds whose traits

- 428 indicate mid-strata and canopy use (strat.Mid, strat.Cnp), and fruit-nectar and omnivore diets (Fig.
- 429 4b-c). Typical species include *Bycanistes subcylindricus, Lophoceros alboterminatus,*
- 430 *Corythaeola cristata* (Fig. 4c, and Table A.1). The second axis is largely structured by the

431 naturally regenerated habitat (NR) and the assisted naturally regenerated habitat (AR). The NR

432 habitat is associated with the right upper quadrant and low canopy heights and high fern cover,

433 and the AR habitat occupies the bottom right quadrant, featuring sites of low tree diversity, and

434 low canopy cover. NR sites feature birds with a plant-seed diet such as *Pternistis nobilis*, and

435 Turtur tympanistria, and Cryptospiza jacksoni (ARE), while AR sites feature in particular,

436 invertivores and species that forage across multiple strata (Strat Gen).



438

Figure 4 RLQ analysis showing relationships between avian traits and habitat variables related to 439 440 restoration activities of fire-degraded sites within Nyungwe NP, Rwanda. a: Coefficients for the habitat 441 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 2 442 accounted for 85.6% and 12% of the projected inertia, respectively. Hab: Habitat, Cnp.cover: Canopy 443 444 cover, Tree.div: Tree diversity, DBH: Diameter at Breast height, Canp.ht: Canopy height, FruiNect: 445 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. 446 Full names of species and their scores are given in Table A.1. 447

The fourth corner analysis did not reveal any significant associations between traits and 449 environmental attributes when the p-values are adjusted for multiple comparisons using the 450 451 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 452 453 combining both the RLQ and Fourth-corner approaches, which was performed to determine the 454 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— 455 permutation of species (P = 0.50). 456

457

458 **4. Discussion**

459 **4.1 Dynamism of avian taxonomic diversity with forest regeneration**

As predicted, primary forest (PF), naturally regenerated (NR), and assisted naturally regenerated 460 habitats (AR) had distinct avian species assemblages. Although there was a degree of overlap in 461 composition between the regenerated habitats and across age classes, bird assemblages of mid-462 463 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 464 observed in the Amazon forest (Barlow and Peres, 2004; Barlow et al., 2006). Similarly, Gould 465 and Mackey (2015), in their study in tropical northern Australia, noted differences in avian 466 assemblages between undisturbed woodlands and revegetated sites that had been cleared for 467 mining, and also between age categories of the revegetated habitats. 468

469 The tendency of increased similarity in species composition with time between regenerated

470 habitats and the primary forest noted by this study is reaffirmed by the correlation of pairwise beta

471 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, 472 probably due to the fact that the assessment was carried out within a short time interval, since the 473 longest regeneration time was two decades. Another explanation could be the high within-habitat 474 variation in avian species composition exhibited by naturally regenerated habitats, which may 475 reflect the varying intensity and recurrence of the fires resulting in habitats of different forest 476 textures. The slow recovery of disturbed habitats was also noted in a study by Shoo et al. (2016) 477 478 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 479 480 wood volume, the richness of plant species and functional diversity levels were each less than half those found in the old-growth forest. 481

482 4.2 Mixed responses of avian diversity features linked to ecosystem functions

483

The species diversity of both invertivores and frugivores were comparable between the naturally 484 485 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 486 487 habitats. This might have more consequences in young naturally regenerated habitats, which were 488 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 489 cover and fruiting were much more restored in assisted regenerated sites, the fact that restoration 490 was done in patches of typically around 500m² may deter frugivores whose reliance on a 491 continuous forest cover has been noted (Farwig and Berens, 2012; Farwig et al., 2017). The high 492 density of young trees within restored patches and little herbaceous understorey may also reduce 493 the permeability of these patches to invertivore birds with gap preferences such as *Caprimulgus* 494 poliocephalus and Bathmocercus rufus (Vande weghe & Vande weghe, 2011). These species were 495 496 only recorded in NR and PF, illustrating why AR sites were associated with generalists in terms of foraging stratum. 497

The lower levels of avian taxonomic diversity in regenerating habitats did not much affect the 498 functional dispersion when the analysis was conducted for separate dietary guilds. One reason 499 500 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 501 naturally regenerated and assisted regenerated habitats, including: Tauraco schuetti, a frugivorous 502 large-bodied species which is sympatric to the Ruwenzorornis johnstoni commonly found in all 503 504 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 505 506 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 507 South West Slopes bioregion, in Australia. 508

509 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 510 body size in the former habitats contradicts what is often documented in fragmented habitats, 511 where small-bodied birds dominate the avian communities (Poulsen et al., 2011). In the absence 512 of substantial hunting of birds in the Nyungwe NP, the dominance of large-sized birds 513 514 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 515 516 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 517 of birds (Lindenmayer et al., 2012). The filtering of the discontinued vegetation systems along 518 avian body size traits has been documented from habitat to continental scales (Allen and Holling, 519 520 2008; Thibault et al., 2011; Nash et al., 2014).

521 **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 528 species and functional diversity might be due to the early phase of regeneration process within 529 restored sites. The vegetation was characterized by a low tree diversity and dominance of pioneer 530 woody species, particularly Macaranga kilimandscharica and Hagenia abyssinica. How long it 531 may take for the restored vegetation to resemble the old growth and to regain an avian assemblage 532 similar to that of old growth remain outstanding questions. The possibility of not attaining old 533 534 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. 535 An important factor that was not incorporated in this study, owing to a lack of fine-scale data, is 536 fire severity. Fire severity can dictate the degree of damage experienced by a habitat and thus may 537 influence the speed of recovery of the vegetation structure and composition and associated fauna 538 539 (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. 540 The restoration project in the Nyungwe NP deliberately chose to rehabilitate sites deprived of all 541 542 trees and covered in ferns. It was hoped that with the elimination of ferns, a diversified tree cover

543 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 548 canopy foragers) in forested habitats (Sekercioglu et al., 2002; Ikin et al., 2019), to accommodate 549 550 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 551 Nyungwe NP prior to burning differed from other rainforests, which are typically characterized by 552 an enclosed canopy. Nyungwe NP comprised a mosaic of forest habitats owing to the dispersal 553 barriers presented by valleys and ridges and steep cliffs. Longitudinal studies will reveal whether 554 the restored sites will maintain the variation in forest structure (e.g. canopy openness), or whether 555 further management interventions will be needed to recreate the variety of habitats. 556

557 4.5 Study contribution to global restoration frameworks

This study contributes to the documentation of empirical evidences of restoration activities in 558 Rwanda and similar tropical landscapes. Advancing the field of tropical forest necessitates the 559 wide sharing of steps of restoration projects, including both desired outcomes and failures (Holl, 560 2017). Such knowledge-sharing is particularly important since despite the increasing national and 561 global commitments to restore degraded forest through frameworks such as the Bonn challenge 562 563 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 564 Partners, 2019). Moreover, many restoration projects commence without well-defined ecological 565 566 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; 567 Jacobs et al., 2015). Countries like Rwanda have shown high willingness to restore degraded 568 forests. However, current conflicting policies in the forestry and agriculture sectors (Fagan et al., 569

- 570 2020; Rurangwa and Whittaker, 2020), may result in forest ecosystems that do not contribute
- 571 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
- 573 rainforest systems and future restoration management plans and actions.

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576	Marie Laure Rurangwa: Conceptualization; Methodology, fieldwork funding acquisition and
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871	Appendix 1
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869	indicators: an Afrotropical case study
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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

- 881 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.
- 883 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.
- 885

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				

886 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

888 sites.

889

- 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.
- 894

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	$2374.8{\pm}\ 186$	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

BH = Diameter at breast height measured at 1.3 m.

898 Table A.4 The relationship between vegetation attributes for sample plots (n= 20 per habitat) within

899 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

901 stronger effect whilst those close to 0 indicate weaker effects.

- 902
- 903

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					

904

905 Note: Cnp.cover = Canopy cover, Ferns = cover of ferns, Tree.div =Tree species diversity, measured as

906 exponential of Shannon entropy. QAICc, is a modified AICc (Akaike information Criterion for small

samples) for models with overdispersion.

908



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.





922 Figure A.2 Species rarefaction curves computed for each habitat to evaluate the exhaustiveness of

923 sampling efforts. The species diversity of birds is calculated for the Hill numbers, where q=0 is based on

924 the Chao 1 species richness estimator, q=1: the Shannon entropy index, and q=2: the Simpson diversity

925 index. The shaded areas represent 95% Confidence intervals. The graph and estimates were obtained using

926 the R package "iNext" (Hsieh et al., 2016).



928

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,

951 Naturally regenerated sites (NK), and assisted naturally regenerating sites within hydrig we National Park

932 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 \pm 95% confidence
- 934 interval. Further details are presented in Table 2.

935