Impact of land-use change on bird communities of a Rwandan biodiversity hotspot



DPhil Thesis

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Abstract

Although land-use change is increasingly flagged as the top driver of biodiversity loss in the tropics, there are important information gaps on its effects on particular facets of biodiversity, particularly in the Afrotropics. To contribute to this research agenda, and with a focus on birds, this study explores how the varying degrees of anthropogenic habitat transformations have affected the patterns of species composition, species diversity, functional and phylogenetic diversity. The study employed a range of methods, however, the core results are based on avian point-count sampling and habitat assessment conducted within major land-use types in the Nyungwe landscape, a tropical montane rainforest and adjacent croplands in Rwanda. Further data on avian functional traits were obtained from museum specimens. The study shows the following in relation to relatively undisturbed forest habitats of the Nyungwe landscape. 1) Species composition was altered and species diversity levels declined in all alternative land-uses. 2) Restored and cultivated areas experienced loss of functional diversity, with steeper falls for the trophic-related traits in the former land-use. 3) Phylogenetic diversity was stable across land-uses, except for cultivated areas, which registered marked declines, particularly in monoculture farms of tea. 4) At the landscape scale, avian diversity was influenced by elevation, soil moisture and the lower vegetation height, however, within cultivated areas and regenerating forests, vegetation composition, and tree cover extent were of high importance. 5) There was no evident superiority of the assisted natural regeneration approach over the passive restoration approach with respect to supported avian diversity, reflecting the long time needed for a full recovery. This study provides evidence of the irreplaceability of primary forests in the tropics, and the crucial roles habitat heterogeneity plays in maintaining avian diversity. The thesis also considers how these findings may inform the conservation planning of multiple-use landscapes in Rwanda, and similar landscapes in the tropics, with attention also to the use of birds as flagships for conservation.

Dedication

This thesis is dedicated to Father Jean-Paul Lebel, my spiritual guide and the greatest bird watching companion. I have learnt so much from him, from distinguishing identical-looking cisticolas to keeping a good record of observations for future scientific consultations.

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My eternal gratitude goes to *Imana y'i Rwanda* for the promises fulfilled beyond expectation, for infinite second chances, and above all, for the love that endures forever.

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Last, but not least, I am grateful for the natural landscapes of Rwanda, in particular, the Nyungwe forest, the cradle of my research. To the communities and conservation practitioners who have sacrificed much for the biodiversity of these landscapes, I say *Murakoze* cyane (Thank you very much), and to the rich and beautiful biodiversity *(not just birds, the highly venomous snakes too*), I sincerely say*: "Murakarama iteka"* (may you thrive forever).

Preface

The idea of studying the effects of land-use change on birds originated from my passion for birding and my experience in the conservation of the African Great Lakes region, which exposed me to the increasing degradation of wild habitats in the name of "development". The high modification of natural landscapes has outpaced scientific studies, not only in my region of work, but across the tropics. To contribute to filling this gap, I designed a study that would assess the spatial and temporal effects of anthropogenic activities in the Nyungwe National Park, a tropical montane rainforest in the south west of Rwanda. Collaboration with the Wildlife Conservation Society-Rwanda (WCS), the main institution in charge of research and monitoring of the Nyungwe forest, was organized, however, in the process of preparing formal agreements, the dataset of interest was given to another doctoral student. Although there was no substantial overlap between our studies, the best ways to prevent any future competing claims were: i) to leave out the temporal assessment aspects, ii) collect my own data and iii) exclude in my thesis shared points of analysis, mainly edge and road effects.

The thesis by paper route was thus more appropriate for my case. Three empirical papers submitted to peer-reviewed journals, an introduction, literature review and conclusion mark the departmental requirement. This route offers a high flexibility and room for creativity. I have presented the literature review in the form of perspective and review articles to facilitate subsequent developments into publishable materials. Initially, I planned to have a separate paper on the effects of habitat degradation on avian seed dispersal in the study area, however, there were very few observations to support a solid scholarly publication. The results are incorporated in a review paper (Chapter 5).

Three manuscripts have been prepared based on newly collected avian occurrences data. The core assessment dimension is the functional diversity, however, the taxonomic diversity proved indispensable, being the unit most conservation practitioners are familiar with. The phylogenetic diversity facet was added to make the thesis more comprehensive following suggestions from the thesis assessors at earlier stages of the DPhil. Instead of writing papers assessing the taxonomic, functional and phylogenetic diversity components separately, I compiled at least two facets of the avian diversity in each empirical paper, for the reader to have an in-depth view of the study without necessarily waiting for the publication of a different facet. In addition to the three papers, a dataset collected using mist-netting will be submitted as a data paper. The papers have different lengths and reference styles due to the varying formatting preferences of journals.

Contents

Abstract 2
Dedication 3
Acknowledgments 3
Preface 6
Contents 8
Chapter 1 | Introduction 14
1.1 Background and Rationale 14
1.2 Aims 15
1.3 Study significance and contribution 16
1.4 Research themes 17
1.4.1 Land-use change 17
1.4.2 Land-use Management 18
1.4.3 Seed dispersal 20
1.4.4 Ecological restoration 22
1.5 Thesis structure 24
1.6 References 27
Chapters 2 and 3 | Literature Review 35
Chapter 2 | Functional diversity: advances, challenges and the way forward 35
2.1 Introduction 35
2.2 Functional diversity indices 37
2.2.1 Functional group richness 39
2.2.2 Functional attribute diversity (FAD) 39
2.2.3 Modified FAD (MFAD) 40
2.2.4 Functional Diversity (FD) 42
2.2.5 Generalized-FD 43
2.2.6 Functional Richness 44
2.2.7 Functional evenness 45
2.2.8 Functional Divergence (FDiv) 46
2.2.9 Quadratic entropy (Rao's *Q*) 46
2.2.10 Functional dispersion 47
2.3 Functional Diversity Applicability 49
2.3.1 Ecosystem functioning 49
2.3.2 Community assembly rules 51

2.3.3 Impact of environmental disturbances 52
2 .4 Challenges and way forward 54
2.4.1 Trait type and number dilemma 55
2.4.2 Ecological knowledge shortfall 55
2.4.3 Integrated comparative methodology 56
2.4.4 Long-term multi-level experiments with natural communities 58
2.5 Conclusion 60
2.6 References 61
Chapter 3 | Vertebrate-mediated seed dispersal in disturbed tropical forests 73
3.1 Abstract 73
3.2 Introduction 73
3.3 Seed dispersal by vertebrates 74
3.4 Seed dispersal effectiveness 77
3.5 Anthropogenic disturbances of seed dispersal processes 78
3.5.1 Fragmentation 78
3.5.2 Hunting 79
3.5.3 Fires 80
3.6 Gaps in the literature and the study contribution **81**
3.7 References **82**
Chapter 4 | Methods 88
4.1 Bird survey techniques 88
4.2 Sampling approach 92
4.3 Study area 92
4.3.1 Nyungwe landscape description 92
4.3.2 The vegetation and fauna of the Nyungwe National Park 93
4.3.4 Anthropogenic disturbances 95
4.4 Data collection 98
4.5 Fieldwork preparation, design, and execution 103
4.6 References 106
4.7 Further references 109
4.8 Appendix 1 113
Chapter 5 | Effects of habitat degradation on avian seed dispersal in an Afro-tropical rainforest: The case of Nyungwe montane rainforest, Rwanda 115
5.1 Abstract 115

5.2 Introduction 116
5.2.1 Research aims 116
5.3 Frugivores and plants sampling 117
5.4 Results and Discussion 118
5.4.1 Important frugivores in the network 118
5.4.2 Potential seed dispersal 125
5.4.3 Forest restoration: the last resort for the maintenance of seed dispersal functions in degraded tropical forests 127
5.5 References 129
Chapter 6 | Effects of land-use change on the avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest 132
6.1 Abstract 133
6.2 Introduction 135
6.3 Methods 138
6.3.1 Study area 138
6.3.2 Study design 140
6.3.4 Functional traits collection 142
6.3.5 Habitat assessment 143
6.3.6 Statistical analysis 143
6.4.1 Species composition 148
6.4.2 Species diversity 151
6.4.3 Functional diversity 151
6.4.4 Phylogenetic diversity 153
6.4.5 Habitat attributes 153
6.5 Discussion 156
6.5.1 Altered patterns of species composition and diversity 156
6.5.2 Differential response of functional diversity to land-use change 157
6.5.3 Loss of community phylogenetic structure with agriculture 158
6.5.4 Habitat attributes effects on taxonomic, functional and phylogenetic diversity 159
6.5.5 Conservation implications 160
6.6 Acknowledgements 163
6.7 References 164
6.8 Appendix 2 174
Chapter 7 | Functional and phylogenetic diversity of a tropical agricultural matrix avifauna: an assessment of farmland heterogeneity 187

7.1 Abstract 188
7.2 Introduction 189
7.3 Materials and Methods 192
7.3.1 Study area 192
7.3.2 Bird surveys 194
7.3.3 Avian functional traits collection 194
7.3.4 Farm assessment 195
7.3.5 Statistical analysis 195
7.4 Results 198
7.4.1 Community structure 198
7.4.2 Phylogenetic and functional diversity between farm types 202
7.4.3 Effects of habitat descriptors on phylogenetic and functional diversity 204
7.5 Discussion 206
7.5.1 Avian diversity varies with farming practice 206
7.5.2 Similar habitat attributes drive phylogenetic and functional diversity 208
7.5.3 Landscape management implications 210
7.6 Acknowledgements 210
7.7 Authors' contributions 211
7.8 References 212
7.9 Appendix 3. 220
Chapter 8 | Assessing forest restoration success using bird habitat use as a potential indicator: an Afrotropical case study 226
8.1 Abstract 227
8.2. Introduction 228
8.3 Methods 231
8.3.1 Study site description 231
8.3.2 Avian and vegetation survey 231
8.3.3 Functional traits collection 235
8.3.4 Data analysis 235
8.4 Results 238
8.4.1 Species composition 238
8.4.2 Beta diversity 240
8.4.3 Avian richness and diversity estimates across habitat types and dietary guilds 241
8.4.4 The relationship between avian taxonomic diversity and vegetation attributes 243

8.4.5 The relationship between avian traits and vegetation attributes 244
8.5 Discussion 246
8.5.1 Dynamism of avian taxonomic diversity with forest regeneration 246
8.5.2 Mixed responses of avian diversity features linked to ecosystem functions 247
8.5.3 Efficacy of the restoration project actions in benefiting birds 248
8.5.4 Study contribution to global restoration frameworks 250
8.6 Authors' contributions 251
8.7 Acknowledgement 251
8.8 References 252
8.9 Appendix 4 259
Chapter 9 | Synthesis of major findings, implications, and conclusion 270
9.1 Avian diversity declines with land-use change 270
9.2 Avian response to farmland heterogeneity 270
9.3 Effectiveness of assisted-natural regeneration approach 271
9.4 Implications for conservation in Rwanda and the Afrotropical countries 272
9.5 Study limitation 274
9.6 Further research 275
9.7 Conclusion 276
9.8 References 277
Appendix 5 278
Making space for birds: sourcing solutions from the mountain gorilla conservation model in Rwanda 278
1 Abstract 280
2 Introduction 281
3 Avian diversity 284
4 Bird conservation challenges 284
4.1 Human population pressure 284
4.2 Institutional reformation 285
4.3 The protected area framework 287
5 The Mountain gorilla conservation case 289
5.1 Initiating the conservation of the mountain gorilla 289
5.2 The setting up of a gorilla-based tourism 290
5.3 Transboundary collaboration 293
6 Adapting the mountain gorilla conservation approaches to avian conservation 296

6.1 Enhancing avian research and monitoring 296
6.2 Protecting complementary bird habitats 297
6.3 National and transboundary institutional collaboration 299
6.4 Avitourism for efficient conservation 300
6.5 Increasing public awareness and engagement 304
7 Multi-stakeholder partnerships as the way forward 306
8 Conclusion 307
9 Acknowledgements 307
3.10 References 308
Appendix 6 317
Publication status 317
Main conferences and workshops attended 318
Co-authorship statements 319

Chapter 1 | Introduction

1.1 Background and Rationale

Land-use change, commonly defined as the conversion of natural landscapes to anthropogenic activities that in many instances degrade the environment, has been unanimously positioned among the main drivers of biodiversity loss (Haines-Young, 2009, Malhi et al., 2014, IPBES, 2019). Such activities include deforestation, land drainage, intensive and extensive agriculture, and urbanisation (Foley et al., 2005, FAO, 2019).

In Rwanda, approximately 80% of the population carry out agriculture and being one of the most densely populated country in Africa, recourse has been sought in the conversion of natural landscapes for agriculture and settlement (Karamage et al., 2016, Musana and Mutuyeyezu, 2011). Consequently, 90% of the populations of the 700 birds species found in Rwanda are now confined within reserves surrounded by agriculture landscapes (Vande weghe & Vande weghe 2011). It has been argued that the long-term survival of such populations depends on the permeability of the agricultural matrix enhanced by eco-friendly agricultural practices, such as agroforestry, and the prohibition or minimum application of chemical pesticides and fertilizers (Bhagwat et al., 2008, Şekercioğlu, 2012). On the other hand, proponents of intensive agriculture regard it as the best approach to prevent the clearance of natural habitats (MEA, 2005, Lal et al., 2015). Little evidence exists to back these arguments in Sub-Saharan Africa, and there is scant research addressing this knowledge gap in Rwanda.

Aside from agriculture-based habitat modification, human induced fires have also ravaged natural habitats (Fig. 4.1, Fig. A1.1). For instance, at least 12% of the Nyungwe National Park (Nyungwe NP) has been degraded by fires (Masozera and Mulindahabi, 2007). Assisted

natural regeneration was started in 2003 by the park management and the Wildlife Conservation Society, and has been carried out through systematic cutting of opportunistic ferns that colonized burnt areas. Although the vegetation has recovered visibly and is being monitored, little is known of the associated fauna. Birds can serve as effective bio-indicators (Morelli et al., 2017), thus assessing their habitat use aids in evaluating whether restoration activities are concretely contributing to the recovery of biodiversity and ecosystem services. Additionally, birds perform a range of "biodiversity service" and fill various ecological functions (Seddon et al., 2016). Their high mobility and ability to occupy a broad range of climates and habitats (Vande weghe and Vande weghe, 2011), alongside their sensitivity to environmental changes (Patthey et al., 2012, Morelli et al., 2017) and their tractability as a study group in terms of taxonomic data availability, identification, and field methods, make them an ideal group for assessing the impact of land-use changes.

1.2 Aims

The overall aim of this study was to quantify how land-use change has affected bird communities in and around the Nyungwe National Park (hereinafter, Nyungwe landscape).

Specific objectives:

1) To determine how different degrees and forms of habitat transformation affect species composition, taxonomic, functional and phylogenetic diversity within the Nyungwe landscape.
2) To assess the influence of agricultural wildlife-friendly practices, such as agroforestry, and heterogenous croplands on avian diversity.
3) To evaluate the efficacy of restoration efforts in terms of bird habitat use.

1.3 Study significance and contribution

Although, the approach of studying avian functional traits to understand and predict bird response to land-use changes in the tropics has been gaining momentum (Bregman et al., 2016, Pigot et al., 2020), very few studies have focused on Africa, despite past and on-going forest conversions in high biodiversity areas, such as Nyungwe NP, a key landscape in the Albertine Rift and a region of high conservation significance (Olson and Dinerstein, 2002, Brooks et al., 2006, Plumptre et al., 2006).

This study aims to fill that gap and to contribute to trait-based research, which not only remain key research priorities (Pigot et al., 2016), but also have potential to contribute to improved ecosystem service management and the mitigation of further disturbances (de Bello et al., 2010, Luck et al., 2015).

This study took an integrated approach by incorporating existing data on bird functional traits, with novel data collected on bird occurrences, vegetation structure, disturbances, and land management practices, in order to assess how birds respond to habitat degradation and current ecological restoration efforts. Analyses focused on avian diversity, as well as the functional role of birds in relation to seed dispersal, an aspect that is still poorly understood in respect of tropical montane forest systems (Chapman et al., 2016).—Through these components, it is hoped that the findings will inform conservation programmes in the Nyungwe landscape.

1.4 Research themes

1.4.1 Land-use change

"Land-use" as applied herein, relates to past and present "economic and social functions" supported by a land area, and is distinguished from "land-cover" which describes the physical attributes of a land surface (Haines-Young, 2009). Positive results of land-use change can include the accretion of species diversity, particularly of farmland birds, water-birds and in cases, exotic species of birds (Flather et al., 1999, Hansen et al., 2001). Furthermore, land-use change undeniably contributes to the economic development of a given area. Roads remove the isolation of remote areas, granting people living in these areas access to markets, hence cutting down costs associated with migration and clearing for subsistence farming (Chomitz and Gray, 1996).

Despite the apparent benefits, land-use transformations have far-reaching consequences for the structure and functioning of ecosystems. Transformation of natural vegetation alters the magnitude and frequency regimes of disturbance agents such as bushfire, flooding, and landslides (Hansen et al., 2001, Foster et al., 2003). In addition to which, large-scale deforestation increases soil erosion and nutrient leaching, alters the surface water balance and leads to reduced transpiration, cloud formation and rainfall, thus aggravating drying and the transformation of forests into shrubland or grassland (Dickinson, 1991, Foley et al., 2005, Koellner et al., 2013).

Coupled with other factors, particularly climate change, land-use change has been found to favour dispersal of non-native species, facilitating the introduction of pests, and pathogens, whilst often impeding dispersal of those native species dependent on native habitat types, especially forest habitat (Hansen et al., 2001, Aguirre-Gutiérrez et al., 2020). Typically,

forest degradation leads to the loss of native species diversity, and increased biological homogenization for a variety of taxa (Dupouey et al., 2002, Newbold et al., 2014, de Castro Solar et al., 2015).

Within a population, land-use changes influence traits such as birth, growth, death and dispersal rates of individuals, which also determine the distribution and abundance of species (Hansen et al., 2001, Newbold et al., 2013). Luck et al. (2012) define functional traits as: "morphological, physiological and life-history features measured at the individual level". The notion of functional traits is commonly used in community and ecosystem ecology to refer to species ecological roles as depicted by the way they interact with the environment and other species (Lavorel and Garnier, 2002, Newbold et al., 2014). Studying bird community responses in Nyungwe National Park (Nyungwe NP), particularly how these responses translate in terms of functional traits, will give a clear image of forest conversion and land-use consequences on ecosystem functions and it is hoped that the results will inform better strategic conservation plans.

1.4.2 Land-use Management

Similar to forest conversion, management choices are strong determinants of the degree of impacts on the ecosystem (Kim et al., 2014, Jakovac et al., 2015). Minor practices such as firewood collection and grazing inside the forests interfere with biomass production and species structure despite the fact that the forest area remains unaltered (Schulze et al., 2004, Foley et al., 2005). Intensive land-use is known to be detrimental to biological, chemical and physical constituents of the soil (Morugán-Coronado et al., 2015) by for instance, increasing the salinization of irrigated lands, accentuating soil erosion, polluting and interfering with ground water (Foley et al., 2005, Koellner and Scholz, 2008). Even after afforestation or

reforestation, land-use practice impacts can still be observed. Dupouey et al. (2002), in a study in France, reported that the pH and soil phosphorus content increased with land-use intensity in forested areas that had been once converted to agriculture, settlement and latter re-afforested. The understory vegetation had also changed.

Intensive land-use can also affect biodiversity and ecosystem services as evidenced by the bee decline and low pollination services frequently caused by pesticide applications (Fell, 2013). At a community level, Bregman et al. (2016) noticed that in Amazonia it is not forest logging, but rather the land-use intensification that followed it which destabilised frugivore and insectivore assemblages by impairing their functional diversity and altering trait dispersion. Moreover, the toxicity associated with intensive farming chemicals, such as those containing chlorinated hydrocarbons, accumulate up the food chain, and cause bird population collapse in the long run by, for example, increasing eggshell thinning and embryo mortality (Prinzinger and Prinzinger, 1979, Strazds et al., 2015).

Abundant evidence shows that agricultural management remains a major driver of biodiversity change worldwide (MEA, 2005, IPBES, 2019). Although preference for agricultural areas is exhibited by less than 1% of the world's birds, at least 1/3 of all birds happen to use these landscapes (Şekercioğlu et al., 2007). Many agricultural systems favour less specialized species (Şekercioğlu, 2012), and the challenge has thus been how to render agricultural landscapes more suitable for a wide range of birds. To address this challenge, practices like agroforestry are being promoted on grounds that they provide habitat for a broad spectrum of species ranging from canopy species, omnivores, granivores, to small-bodied frugivores (Bhagwat et al., 2008, Şekercioğlu et al., 2019).

Other farming practices that have been endorsed for their high biodiversity include: (i) integrated farming, which aims at minimizing the applications of inorganic fertilizers and protective substances; and (ii) organic farming, which prohibits all use of synthetic substances and encourages techniques such as crop rotation, mixed cropping, and hence maintains the integrity and sustainability of the farm and the whole environment at large (Freemark and Kirk, 2001, Nemecek et al., 2011, Stefanova and Salek, 2014). On the other hand, conventional farming gives a higher yield and profit and it has been argued that it should be promoted in high biodiversity areas, particularly in Sub-Saharan Africa, on the basis that extensive agriculture is a far greater threat than intensive agriculture (MEA, 2005, Lal et al., 2015). This implies that promoting intensive agriculture would offset the consequences of natural habitat conversions through land-sparing. In fact, some studies affirm that land-sparing best conserves the avian diversity, particularly of endemic species (Edwards et al., 2015, Perrings and Halkos, 2015, Cannon et al., 2019).

This study evaluated the avian diversity of different farming practices in the Nyungwe agricultural landscape, with a view to contributing to ecological land-use science and management practices in Rwanda.

1.4.3 Seed dispersal

The persistence, and spatial distribution of a wide range of fleshy-fruited plants and the regeneration of forests, especially in the tropics and sub-tropics, rely largely on frugivores through dispersal processes (Herrera, 2002, Stoner et al., 2007). Seed dispersal is a mutualistic process in which the frugivores gain energy and nutrients, and plants are able to both colonize new areas and maintain genetic diversity within their areas of distribution, as

they escape from natural enemies and intense competition near their conspecifics (Howe and Smallwood, 1982, Farwig and Berens, 2012).

The tropical region is heavily dependent on animal seed-dispersers, which account for 90% of all seed dispersal processes (Howe and Smallwood, 1982, Terborgh et al., 2002). Birds in particular are key dispersers, and their high mobility ensures dispersal services that span local to transcontinental scales (Whittaker and Jones, 1994, Farwig et al., 2017). In terms of elevational gradients, Chapman et al. (2016) found that avian disperser had higher proportions at higher elevations than did mammalian dispersers.

Not all frugivorous birds take part in seed dispersal. Effective seed dispersal rests on the "quantitative and qualitative" contribution of frugivores (Schupp et al., 2010). The quantitative aspect is usually measured from the frugivore visitation rate, or more precisely from the rate of fruit removal from plants, whilst the qualitative contribution hinges on the fruit handling manoeuvres (Vázquez et al., 2005, Schupp et al., 2010). The fruit-handling behaviour is what distinguishes legitimate dispersers (frugivores that swallow the fruit and discard the seed) from seed predators (frugivores that damage the pulp or the seed (Jordano, 2000)). Assuming they are correctly identified, "frugivorous" functional traits uphold the persistence of seed dispersal processes, for they influence bird response to habitat modification and underpin the quantity and quality of seed dispersal services they perform (Farwig and Berens, 2012, Dehling et al., 2016).

Seed dispersal is a broad process that encompasses not only the horizontal movement of seeds but also the whole process that leads to adults emerging from the dispersed fruit (Schupp et al., 2010). Although, frugivore–plant interactions do not necessary imply seed-dispersal events, it is the best proxy where there is not enough information on dispersal

effectiveness (Pigot et al., 2016). Therefore, this study assessed the potential seed dispersal processes in a bid to provide baseline information for future studies exploring seed dispersal efficiency and effectiveness.

1.4.4 Ecological restoration

Disturbances in forest ecosystems are normal, if not necessary, and have always been part of ecosystem dynamism (Thom et al., 2017)**.** What is referred to today as pristine forests have generally been modified by humans to various degrees at some point in the past (Willis and Birks, 2006). Nonetheless, anthropogenic disturbances such as fire have increased in their frequency and destructiveness, consequently changing the vegetation and degrading habitat conditions for the associated avifauna (Albanesi et al., 2014). High vegetation diversity and heterogeneity influence avian species diversity and composition (MacArthur and MacArthur, 1961, Fahrig et al., 2011), hence, simplified environmental systems support fewer species and lower functional diversity (Patthey et al., 2012, Albanesi et al., 2014, Lee and Martin, 2017).

In the face of ongoing habitat loss and degradation, forest restoration offers a solution in regaining biodiversity and ecosystem functions (Rey Benayas et al., 2009, Jacobs et al., 2015). The UN declared 2021 – 2030, as the "UN Decade on Ecosystem restoration", and national and various international frameworks, such as the Convention on Biodiversity, REDD+[1]and Bonn challenge[2], have promoted and initiated restoration targets of varying scales across the world. Many projects, however, have resulted in forests supporting low levels of biodiversity and ecosystem services (Li et al., 2014, Jacobs et al., 2015). This failure

[1] Reduced Emission from deforestation and forest degradation and sustainable management of forests, conservation of forest carbon stocks and enhancement of forest carbon stocks constituting (http://www.un-redd.org/)

[2] "The Bonn Challenge is a global effort initiated in 2011 to restore 150 million hectares of the world's degraded and deforested lands by 2020 and 350 million hectares by 2030" (http://www.bonnchallenge.org).

can be attributed to the fact that there is still a lack of sound scientific knowledge, and practice of what constitutes a successful restoration program (Li et al., 2014). Landscape restoration actions are dominated by the plantation of trees (Fig. 1.1), and afforestation targets have even included non-forest ecosystems such as African Savanna landscapes (Bond et al., 2019). Moreover, the restoration baseline and feasibility of full recovery of biodiversity and ecosystem functions is at times impractical, if not inconceivable (de Nascimento et al., 2009, Bullock et al., 2011).

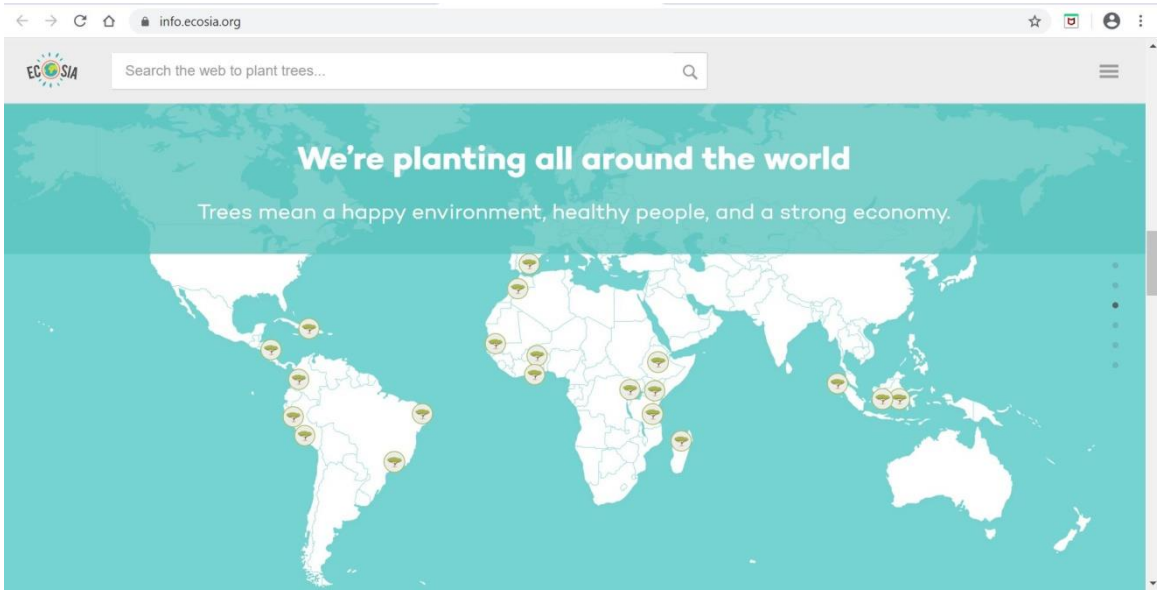

Figure 1.1 Tree planting sites supported by Ecosia, a search engine that claims to use 80% of profits generated from running advertisement, in restoring degraded habitats (www.ecosia.org accessed on 10/06/20). The sites are concentrated within the southern hemisphere, where the company deems trees are needed most.

Within the Bonn challenge commitment, Rwanda has pledged to restore 2,000,000 ha of degraded forests and lands under the so-called "Border to border" restoration program (http://www.bonnchallenge.org/content/rwanda last accessed 03/03/2019). One of the

ongoing projects is happening in Nyungwe NP. After visible failure in self-regeneration of many anthropogenic fire-degraded areas inside the park, in 2003, the park management implemented the assisted natural regeneration method. As reported by Masozera and Mulindahabi (2007) in 2007, different sites amounting to 495 000 m^2 were prepared for restoration. This approach has yielded promising results, as ferns were eliminated, and seeds sprouted in the restored sites.

The present study assessed the restoration success of the Nyungwe restoration project in terms of bird habitat use, given that no single study has been conducted in that line so far. In Europe, birds have been studied to infer the effectiveness of restoration program from the quality of restored sites (Patthey et al., 2012, Morelli et al., 2017). Recommendations from such studies can help to cut out costs associated with ineffective restoration practices, and inform future restoration schemes in similar landscapes (Patthey et al., 2012, Steen et al., 2013).

1.5 Thesis structure

The first chapter of the thesis is the Introduction. It contains background information of the research project, including the research aims and the study contribution to the ecology and conservation disciplines. The main themes of the study are introduced, and the chapter ends with a description of the structure of the thesis.

The literature review is divided into sections. The first section forms chapter two and reviews the challenges and progress of the application of the traits-based approaches in ecological studies. The focus is put on the functional diversity dimension since it is the core unit of assessment I wished to employ. The third chapter constitutes a review of seed-dispersal in tropical forests, with an emphasis on studies in the Afrotropics. An additional perspective

article is presented in Appendix 5. The article explores the threats to birds in Rwanda and proposes policy and practical actions to address the challenges using the mountain gorilla conservation model. The article sets the context of the processes that have led to the transformation of the natural landscapes in Rwanda and develops for the reader a broader view of the significance of this thesis to the conservation of birds and their habitats in Rwanda.

The Methodology constitutes the fourth chapter. It elaborates the methods applied in the research, the rationale behind their usage in comparison to other existing methods, and provides reflections from the fieldwork experience, which may help to improve the design of future work in these landscapes. It also includes the compositional properties of mist-netting data, and other descriptive work that could not be presented in the empirical papers.

Chapter 5 is a report of the results from the frugivore survey. The study was an attempt to go a step further and quantify seed dispersal as a key ecosystem function performed by birds. The section marks the beginning of the empirical chapters.

Chapter 6-8 are three academic articles submitted to scholarly journals. Chapter 6 explores how species composition, taxonomic, functional, and phylogenetic diversity vary across major land-use types within Nyungwe landscape, and the relationship between habitat characteristics and avian diversity. Chapter 7 compares species composition, phylogenetic and functional diversity between two major farming types around Nyungwe NP (tea monocultures and mixed crops farms) and determines the relationships between farm attributes and avian diversity. Chapter 8 assesses the restoration success of fire-degraded habitats within the Nyungwe forest using bird habitat use as an indicator.

Chapter 9 synthesizes the major findings under the elected themes and discusses their implications. The study limitations are stated, and future research directions are proposed. The chapter ends with a conclusion that highlights key findings and the contribution of the study to tropical forest ecology and conservation.

The last section is an appendix that contains the published perspective article, the status of submitted manuscripts, conferences attended, and co-authorship statements.

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Chapters 2 and 3 | Literature Review

Chapter 2 | Functional diversity: advances, challenges and the way forward

2.1 Introduction

Functional diversity has emerged as an alternative method to measure biodiversity given the limitations of classical measures such as taxonomic diversity, often equated to species richness, in capturing differences in species ecological roles and contribution to ecosystem functions and services (Walker et al., 1999, Loreau et al., 2001, Matthews et al., 2014, Gagic et al., 2015). The concept of functional diversity rests on the capacity to identify the traits that determine the ability of species to adapt to the environment and the kind of functions they will perform (Walker et al., 1999, Lavorel and Garnier, 2002, Webb et al., 2010). Functional diversity is widely defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). This definition has been often modified to either make it more specific (Petchey and Gaston, 2006), analogous to Hutchison's niche concept (Rosenfeld, 2002), or to reflect components of biodiversity such as richness, evenness and divergence (Mason and De Bello, 2013).

Before the establishment of current measures of functional diversity, it was perceived that either all species are functionally unique, or that certain species share the same functional identity, permitting them to be grouped under a particular functional group (Root, 1967, Petchey and Gaston, 2002a, Magurran, 2004). In the functional group perspective, such functional redundancy makes the notions of species richness lose importance, for what matters most is the biomass contributed by all species within those functional groups (Petchey and Gaston, 2002a). In this line of thinking, the most significant species to

ecosystem functioning is assumed to be the most abundant species, i.e. that which contributes the greatest biomass to the community (Grime, 1998). Even though this mass-ratio hypothesis can be validated, especially for autotrophs, it loses credibility when applied to heterotrophs, when considering for instance the role of parasites, and keystone species (Grime, 1998). Moreover, some studies, at particular scales of analysis, have found the most productive ecosystems to be less species diverse (Huston, 1994, Grime, 2001).

A classic paper by Petchey and Gaston (2002a) analysed data for a mixture of plant and animal assemblages from different places, comparing the magnitude of species loss according to two functional diversity measures: functional group diversity and Functional Diversity (FD). FD was measured quantitatively from species functional traits such as eco-physiological properties in plants and foraging and feeding behaviour in animals. They noted that species extinction lead to higher losses in FD than in functional group diversity. They also showed the order in which extinction occurred mattered, the losses in FD being high when extinction involved species with greater contribution to functional diversity. This contrasts with the view that extinction has the greatest impact on functional diversity when it involves the most abundant species (Sala et al., 1996). This study also demonstrated that a range of methods do not quantify functional diversity consistently.

The need to reduce discrepancy and inaccuracy in measures of functional diversity coupled with the need to incorporate more information relevant to ecosystem functioning, such as abundance of species, has led to a range of indices being devised. This review discusses major indices, core applications of the functional diversity concept, presents challenges and suggests future orientation.

2.2 Functional diversity indices

A panoply of indices have been devised to quantify this facet of biodiversity, and they principally take into account species functional traits and have later started considering species cover, abundance, or biomass.

Functional traits include particular behavioural and ecological attributes that encompass the species niche, such as diet, foraging strata and time, as well as morphological features such as body mass, beak width, beak depth, gape width, tarsus length, tail length, wing length and Kipp's distance, which are associated with energy requirements, foraging behaviour, feeding preferences, as well as locomotory and dispersal abilities (Wheelwright, 1985, Dehling et al., 2016, Pigot et al., 2020)

Classic multivariate indices and commonly used indices will be described here and their limitations explained (Table 2.1).

Table 2.1 Classic and widely applied functional diversity metrics. The computation method and integration of species abundances are provided for each metric.

Index		**Description**	**Method**	**Incorporates Abundance**
Functional group richness	FGR	Number of functional groups present in a species assemblage	Hierarchical classification	No
Functional attribute Diversity (Walker et al., 1999)	FAD	Sum of pair-wise distances between species	Distance Matrix	No
Modified Functional Attribute Diversity (Schmera et al., 2009)	MFAD	Sum of pair-wise distances between functional units	Distance Matrix	No
Functional Diversity (Petchey & Gaston, 2002)	FD	Sum of branch length of a functional classification	Hierarchical classification	No
Generalized Functional Diversity (Mouchet et al., 2008)	GFD	Sum of branch length of a functional classification	Hierarchical classification	No
Functional Richness (Cornwell et al. 2006, Villéger et al., 2008)	FRic	Convex Hull Volume	Trait values	No
Rao's quadratic c entropy (Rao, 1982)	Rao's *Q*	Sum of pairwise distances between species weighted by relative abundance	Distance Matrix	Yes
Functional Divergence (Villéger et al., 2008)	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	Trait values	Yes
Functional Evenness (Villéger et al., 2008)	FEve	Sum of Minimum Spanning Tree branch length weighted by relative abundance	Trait values	Yes
Rao's quadratic c entropy (Rao, 1982)	Rao's *Q*	Sum of pairwise distances between species weighted by relative abundance	Distance Matrix	Yes
Functional dispersion (Laliberté & Legendre., 2010)	FDis	Abundance weighted mean of species distance to the abundance weighted centroid	Distance Matrix	Yes

2.2.1 Functional group richness

One of the earliest ways of measuring functional diversity, particularly species resource use complementarity, was to categorize species with the same trait profiles into the same groups following an *a priori* classification (Root, 1967, Hector et al., 1999, Petchey, 2004). Functional groups are often termed plant functional type in plant sciences and guilds in animal sciences (Pla et al., 2011).

This measure has been heavily criticised for being subjective due to a number of reasons: i) the classification method is neither mathematical nor statistical, ii) the significance of the parametric test undertaken to test differences between species is arbitrarily concluded by the researcher, iii) it does not incorporate species abundance, and iv) the formation of groups inevitably results in information loss (Petchey and Gaston, 2002a, Wright et al., 2006, Mouchet et al., 2010). These limitations drove calls for developing and applying functional diversity metrics that are continuous and objective (Petchey et al., 2004).

To improve the efficacy of functional group richness, Gitay and Noble (1997) called for the use of multivariate techniques when forming groups and Petchey (2004) noted that randomising (bootstrap) the critical significance value rendered the formation of groups more correct.

2.2.2 Functional attribute diversity (FAD)

In the quest to quantify functional diversity in a continuous way, Walker et al. (1999) proposed the functional attribute diversity index (FAD), which is expressed as FAD1 and FAD2. FAD1 is defined as the number of different combinations of functional traits present in a community. FAD1 has to be less than or equal to the total number of species considered. FAD2 is measured as the sum of the standardized pairwise distances between species within a

trait space. The strength of FAD lies in its capacity to determine the contribution of individual species to the whole functional diversity of the community (Ricotta, 2005, Mouchet et al., 2010).

The FAD2 index is calculated as follows:

$$\mathrm{FAD2} = \sum_{i=1}^{S} \sum_{j=1}^{S} ED_{ij}$$

where S is the total number of species, and ED_{ij} is the dissimilarity between species i and j computed by measuring the ecological distance (E.g. expressed by an Euclidean distance measure) between functional attributes of species i and j.

When dealing with categorical traits, FAD1 can quantify functional richness reasonably well, but it is less efficient in the face of continuous traits (Pla et al., 2011). Other flaws of FAD include: changing systematically with the number of species, and the number of functional attributes studied, not incorporating abundances, and assigning a different functional diversity value when one species is split into two different species with identical functions and abundances, for instance when correcting taxonomic identification. (Mason et al., 2005, Pla et al., 2011). Species splitting is particularly relevant in plant species, where lack of proper species identification can lead to confusing species with similar functions and abundance, and thus giving different values in FAD2 than if proper identification was done (Mason et al., 2005).

2.2.3 Modified FAD (MFAD)

To rectify the problem that FAD changes with the number of species, regardless of their functions, Schmera et al. (2009) proposed an improved version termed ″modified FAD″, which works on functional units rather than species. MFAD is calculated by first merging

species with identical trait profiles into the same functional units (also termed functional species (Ricotta, 2005)). Hence, the total number of species S is reduced to N, the number of functional units (where $N \leq S$). The N x N distance matrix is then calculated. For this purpose, Schmera et al. (2009) suggested applying a dissimilarity metric confined between 0 and 1.

The advantage of FAD as opposed to dendrogram-based indices, is that computing it does not necessitate having information on the whole species pool (Schmera et al., 2009). In contrast to FAD, MFAD was built to meet criteria of "set monotonicity" where functional diversity increases when a new, functionally different species is added to the community (Ricotta, 2005), and "twinning" (Weitzman, 1992, Ricotta, 2005), meaning that functional diversity remains unaffected with the addition of a species because it is functionally identical to another species in the community.

$$\mathrm{MFAD} = \frac{\sum_{h=1}^{N}\sum_{k=1}^{N} d_{hk}}{N}$$

where N is the number of functional units, and d_{hk} is the distance/dissimilarity between functional units h and k.

Schmera et al. (2009) affirmed that MFAD could measure the dispersion of species functional traits, hence rendering possible comparison of MFAD across different communities. Colas et al. (2013) concluded that MFAD could measure functional divergence (see Chap.2.2.8). However, Mouchet et al. (2010) and Pavoine and Bonsall (2011) have down-played MFAD effectiveness on the basis of its high correlation with species richness.

2.2.4 Functional Diversity (FD)

One of the most widely applied dendrogram-based metrics in functional ecology is "functional diversity (FD)", an index proposed by Petchey and Gaston (2002b), which is analogous to the Phylogenetic Diversity (PD) index (Faith, 1992)**.** FD quantifies functional diversity from the total branch length of a dendrogram built from functional traits of species within the same community (Petchey and Gaston, 2002b). Steps to calculate FD entail: i) forming a matrix based on species traits, ii) transforming the traits matrix into a distance matrix, iii) building a dendrogram from clustering the distance matrix, and iv) summing the dendrogram branch lengths.

According to Petchey and Gaston (2002b), FD quantifies species dispersion in the functional space, and thus stresses the complementarity of species trait values. It meets the “set monotonicity criterion”, and compared to functional group richness, it quantifies functional diversity on a broader scale, since it is continuous and does not lose information by summarizing species into groups, however, FD does not take into account abundance, which is an important aspect in functional diversity (Mason et al., 2003). Podani and Schmera (2006) reported that the value of FD tends to change with the type of distance metric and clustering algorithm used. For example, using Gower and Euclidean distances gave different FD values. Moreover, FD of single-species samples had a value of 1, with 0 being assigned when there is no species found. This was criticized for not being consistent with other diversity measures, e.g. Shannon entropy, which considers communities with one species not to be diverse and hence returns a 0 value (Podani and Schmera, 2006).

Following the concerns expressed by Podani and Schmera (2006), Petchey and Gaston (2007) proposed another way a dendrogram could be calculated, and recommended considering only

the total branch length linking species to each other, thus omitting branches connecting to the root, which is termed “the regional species pool” (Fig. 2.1). They also defined FD of zero for single species assemblages instead of empty assemblages.

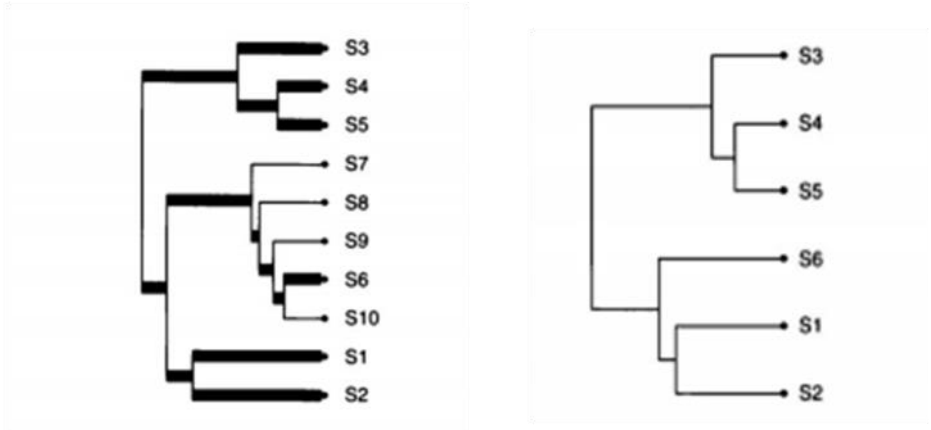

Figure 2.1. Two ways of quantifying functional diversity for a community comprising species 1-6 (Modified from Petchey and Gaston 2007). On the left, FD is calculated from the total branch length of the species found (thick lines) across the regional dendrogram connecting species 1-6, as per Petchey and Gaston (2006). On the right the FD calculation excludes the root, i.e., the dendrogram is built from functional traits of only species 1-6 as per Podani and Schmera (2006).

2.2.5 Generalized-FD

To address the flaws of FD values varying with the distance and clustering methods applied, Mouchet et al. (2008) proposed another index called Generalized-FD (GFD). The new approach was recommended after further investigation of the performance of different method of building dendrograms in procuring a more correct depiction of the functional distribution of species in a community. They concluded that there was no combination of distance and clustering method that performed best in all cases, as performance was influenced by a range of factors, such as correlations of traits and species richness. They

proposed testing out different combinations of distances and clustering methods and also testing consensus trees constructed from the combinations of various clustering algorithms, and opting for a tree that gives more accurate values of FD. A consensus tree captures aspects that are common to many trees whilst minimising the dissimilarities from the original distance matrix (Darlu and Tassy, 1993, Mouchet et al., 2008).

It has been argued that proper estimation of Functional diversity should take into consideration different components of Biodiversity related to richness, evenness and divergence of traits (Mason et al., 2005, Petchey and Gaston, 2006, Villéger et al., 2008). For multiple traits, Villéger et al. (2008) proposed three independent indices, namely: functional richness, functional evenness and functional divergence, and argued that although individually the indices did not meet all the required properties, the ensemble did. Laliberte and Legendre (2010) further developed an improved distance-based framework that permits computation of the three indices regardless of the type and number of traits, and the type of distance measure used.

2.2.6 Functional Richness

For multiple traits, the Functional Richness (FRic) index measures the amount a species assemblage occupies within a trait space (Mason et al., 2005, Villéger et al., 2008). It is similar to the convex-hull hyper-volume approach of estimating functional space (Cornwell et al., 2006). The convex hull volume algorithm identifies and connects the most extreme species, thereby enabling all species with less extreme values to be considered in the convex hull volume (Cornwell et al., 2006, Villéger et al., 2008). For FRic to be calculated, the number of species has to be higher than the number of traits, and species distribution in the functional space should not be linear, as this would give the hull volume of 0 (Villéger et al.,

2008). For cases where the number of species is less than that of traits, FRic can be calculated using Principal Components Analysis for quantitative traits, and Principal Coordinates Analysis for categorical or nominal traits (Villéger et al., 2008, Pla et al., 2011). Although a useful index, analogous to the range, FRic provides an estimate of functional dispersion, but, it does so crudely. In addition, since it does not incorporate abundance, it will thus be highly sensitive to rare species with extreme trait values (Laliberte and Legendre, 2010, Pla et al., 2011).

2.2.7 Functional evenness

Functional evenness (FEve) measures the regularity of spaces between species and the evenness of the distribution of their relative abundance in the functional space (Mason et al., 2005). A similar univariate index, Functional Regularity (FRO), was also proposed as a measure of functional evenness, specifically for single traits (Mouillot et al., 2005). However, FRO was found to be less robust when extended to multiple traits as it relied on ordination methods that do not perform well when there are only weak correlations among traits (Villéger et al., 2008).

The calculation of FEve proceeds with the conversion of species distribution in a multidimensional functional space to a single axis using the minimum spanning tree, which essentially connects species in the multidimensional space through the minimum sum of branch lengths of the tree (Villéger et al., 2008). FEve is independent from the species richness and functional richness, and ranges between 0 and 1. It is high when species abundances are evenly distributed or when functional distances among species are regular. FEve requires at least three species in the dataset since this is the minimum number to form minimum spanning trees. FEve is given as:

$$\text{FEve} = \frac{\sum_{l=1}^{S-1} \min\left(\text{PEW}_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

Where PEW_l is partially abundance-weighted evenness of a branch, l, of the minimum spanning tree.

2.2.8 Functional Divergence (FDiv)

Functional Divergence (FDiv) quantifies the distribution of abundance of trait values within the volume of functional space filled by a species assemblage (Villéger et al., 2008). Computing FDiv entails first calculating the centre of gravity of species making the vertices of the convex hull, and then computing abundance-weighted deviance (Δd) and absolute abundance-weighted deviances ($|\Delta d|$) based on the mean distances of individual species to the centre of gravity ($\overline{dG}$). Lastly, the index is bounded between 0 and 1. FDiv is then given as:

$$\text{FDiv} = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}$$

FDiv is low when the most abundant species are near the centre of gravity and is high when the most abundant species are far from the centre of gravity.

2.2.9 Quadratic entropy (Rao's *Q*)

The Quadratic entropy (Rao's *Q*) measures abundance-weighted pairwise functional distances between species (Rao, 1982). This index is based on the entropy theory (Rao, 1982), and behaves like a weighted Simpson Diversity index (Botta-Dukát, 2005). Mason et al. (2005) asserted this index also calculates functional divergence. Rao's quadratic entropy is one of the most widely used measures of functional diversity as it was one of the first indices to incorporate dissimilarities between species traits and abundances, to handle both single and multiple traits, and to remain unchanged by a species splitting into two functionally identical

species for example after taxonomic revision (Botta-Dukát, 2005, Pavoine and Dolédec, 2005, Schmera et al., 2017).

On the other hand, Rao's *Q* is criticized for decreasing when species richness increases, which can be explained by the fact that the index considers both abundance and dissimilarity between species (Botta-Dukát, 2005). As much as a new species contributes to increased abundance, it might also lower the average dissimilarity between species (Botta-Dukát, 2005). Modifications to improve the index have been put forward, for example, to permit quantification of a mixture of categorical and continuous trait variables (Lepš et al., 2006). Rao's *Q* is similar to FAD, the major difference being the method used to calculate the distance matrix (Schleuter et al., 2010). Rao's *Q* is given as:

$$\sum_{i-1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j$$

Where *S* is all of the species in the community, and d_{ij} is the dissimilarity between species *i* and *j*, P_i and P_j denote the relative abundances of species *i* and *j*, respectively.

2.2.10 Functional dispersion

Functional dispersion (FDis) measures the spread of the deviation of individual species trait values from the functional centroid of all species in the community (Laliberte and Legendre, 2010). FDis is a modification of the multivariate dispersion index (Anderson et al., 2006) and is analogous to measures of spread in univariate statistics such as the mean absolute deviation, the variance, standard deviation, etc (Laliberte and Legendre, 2010). It incorporates abundance by weighting the centroid by the relative abundances of all species, which ultimately relocates the centroid towards the most abundant species (Laliberte and Legendre, 2010).

Computing FDis necessitates at least 2 species, and there is no upper boundary (Laliberte and Legendre, 2010). The authors also recommended that a community bearing only one species will have a FDis value of 0. FDis is easily computed from quantitative traits, but can also work with semi-quantitative as well as qualitative traits through the use of principal coordinates analysis (Fig. 2.2, Pla et al., 2011).

FDis is computed as follows:

$$\mathbf{c} = [c_j] = \frac{\sum a_i x_{ij}}{\sum a_j}$$

$$\text{FDis} = \frac{\sum a_i z_j}{\sum a_j}$$

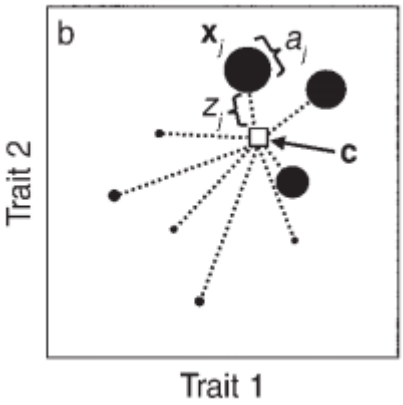

Figure 2.2. The calculation of FDis, after Laliberte and Legendre (2010)
Black circles denote individual species, and size corresponds to the species abundance. **C** is a vector with coordinates of the weighted centroid of all species, X_j is a vector indicating the position of species *j*, a_j indicates the abundance of species *j*, z_j is the distance of species j to the centroid. In this case species have varying abundances, hence to obtain FDis, Z is weighted by species relative abundances.

According to Laliberte and Legendre (2010), FDis is not affected by species richness, and correlates with Rao's *Q*, but is better in computing presence/absence data, where it permits further functional diversity analysis through the use of multivariate statistics. FDis is not confined within the 0–1 range proposed by Mason et al. (2003), and does not meet the "set monotonicity property" (Ricotta, 2005), a property which the authors argue is more of an ecological question than a mathematical flaw.

2.3 Functional Diversity Applicability

2.3.1 Ecosystem functioning

Ecosystem functioning encompasses multi-scale and multi-level interactions of biological, physical, and biogeochemical processes and components occurring within and across ecosystems. The challenging task has been to show a link explicitly between species functional traits and ecosystem functioning (Díaz and Cabido, 2001, Hatfield et al., 2018).

Studies have demonstrated the link between plant functional traits and both higher N fixation and retention in the soil as well as to enhanced water and sediment retention (Díaz and Cabido, 2001, Hooper et al., 2005). Ecosystem functioning was also found to be driven by species resource use strategies (Tilman, 2001, Mason et al., 2005), for instance high niche complementarity can considerably boost ecosystem productivity and resilience (Dukes, 2001, Hooper et al., 2005, Mason et al., 2005). Experiments with plant species in temperate grasslands of Europe and US have shown a positive relationship between primary production and functional group diversity (Loreau et al., 2001). Using remote-sensing techniques to measure functional diversity along the Amazon-Andean elevation gradient, Durán et al., (2019) revealed that foliar traits were strong predictors of both Gross and Net Primary Productivity. An earlier study in the same region had also demonstrated that plant functional

traits (and solar radiation) explained more variation in forest primary productivity than climate (Fyllas et al., 2019).

In contrast to plants, whose role in ecosystem functioning, particularly regulating functions, can be relatively straightforward to determine and has been increasingly quantified, for animals little has been done to uncover this relationship (Bello et al., 2015, Seddon et al., 2016) and it is only recently that animal functional trait studies have begun to pay sufficient attention to this question (Bregman et al., 2014, Dehling et al., 2016). Bird morphological traits have been found to mark the difference between effective pollinators in agro-ecosystems (Larsen et al., 2005), and behavioural as well as physiological traits such as the manner a seed is handled and treated in the gut determines seed dispersal effectiveness (Gross-Camp and Kaplin, 2011, Dehling et al., 2016).

Some authors have argued that functional diversity of particular groups, guilds or taxa, does not solely explain ecosystem functioning, especially when considering other parameters such as climate, large-scale ecosystem disturbances, and multi-trophic processes (Wardle, 1999, Loreau, 2000, Raffaelli et al., 2002, Griffiths et al., 2016). Further, experiments on the relationship between biodiversity and ecosystem function have been criticized for potential sampling effects, where the ecosystem functions could not be attributed to the diversity of the ensemble, but more probably attributed to a dominant species, or other factors co-varying with diversity (i.e. “hidden treatment” effects) (Huston, 1997, Wardle, 1999). A review by Hatfield et al. (2018), based on studies recently conducted in the tropics, concluded that the linkage between measures of functional diversity with ecosystem functioning was not fully explored, as few studies had explicitly investigated the topic and their findings did not give strong support for such linkages.

2.3.2 Community assembly rules

Deciphering mechanisms behind the structure and composition of biological communities and the relationship with ecosystem functioning remains a divisive ecological challenge (Mason and De Bello, 2013). Recourse to functional diversity is claimed by advocates to promise elucidation of these mechanisms through the links between species functional traits and their distribution and abundance (Mouillot et al., 2007). In the context of functional diversity, these mechanisms are often hypothesized under three major assembly rules. (1) The niche-limitation or limiting-similarity hypothesis postulates high competition among species, with similar functional traits leading to their low abundance (MacArthur and Levins, 1967). (2) Niche/Environmental-filtering predicts that environmental conditions exclude species with less optimal traits, resulting in the coexistence of species with similar functional traits (Van der Valk, 1981, Keddy, 1992, Zobel, 1997). (3) The neutrality rule assumes organisms are equivalent and thus their functional traits are irrelevant to their coexistence and persistence (Hubbell, 2001).

Accumulating evidence, particularly from plant studies, has shed light on the role of species functional traits in determining community assembly processes (Díaz and Cabido, 2001) (Mason and De Bello, 2013, Mouchet et al., 2013), thus rendering functional diversity metrics an effective means of discerning these mechanisms/patterns with real species assemblages at different scales (Chalmandrier et al., 2013). For example, when functional diversity is greater than expected by chance it implies niche complementarity, and when it is lower than expected by chance, it evinces environmental filtering, whereas, intermediate values could imply neutral assembly (Cornwell et al., 2006, Mason and De Bello, 2013, Mason et al., 2013).

In their study on fish assemblages in a Brazilian lagoon estuary, Mouchet et al. (2013) found that environmental filtering shaped fish community structure rather than competitive exclusion, whereas Mason et al. (2008) found that it was niche complementarity that governed the structure of French lacustrine fish communities. These differences show that other factors, such as the type of ecosystem, and associated disturbance, may be at play**.** Furthermore, scale matters when applying functional diversity measures to discern community assembly processes (Herben et al., 2013, Laliberté et al., 2013, Münkemüller et al., 2020). Chalmandrier et al.'s (2013) study on French alpine plant communities found evidence that environmental filtering exerted greater influence at larger spatial and evolutionary scales, while neutral processes characterised smaller scales of analysis.

Assembly mechanisms may also occur successively along environmental gradients (Mason et al., 2007), or concurrently, resulting in a more complex pattern (Helmus et al., 2007). On the other hand, environmental change can greatly impede, minimize, or otherwise alter the extent to which resource-use complementarity regulates species assembly and ecosystem functioning (Hooper et al., 2005, Laliberté et al., 2013). Therefore, there is need to use a mixed-method approach that integrates functional diversity as well as other diversity measures, such as investigating phylogenetic relationships, to properly disentangle drivers of species assembly mechanisms (Webb et al., 2002, Pavoine and Bonsall, 2011).

2.3.3 Impact of environmental disturbances

Accumulating evidence shows that the functional diversity approach is more effective in assessing the effect of disturbances and how species respond than other popular approaches, such as the use of species diversity metrics, since the latter may conceal slow losses, particularly in terms of traits and abundances (Petchey and Gaston, 2002a, Haddad et al.,

2008, Mouillot et al., 2013). For example, Flynn et al. (2009) noted that FD was a better predictor of the effects of agricultural disturbances on bird and mammal communities in temperate and tropical regions of South America. Disturbances can, in cases, be associated with an increase in species richness, however, functional analysis usually highlights an increase in functional redundancy at the expense of functionally specialization, as evidenced through analysis of morphology, foraging, breeding traits or habitat affinities (O'Dea and Whittaker, 2007, Villéger et al., 2010, Coetzee and Chown, 2016)**.** A study on the impact of urbanisation and agriculture in a south African savanna biome found a local turnover of species, but, fewer functionally unique species, such as large-bodied ground nesters (Coetzee and Chown, 2016).

A trait-based approach can also be effective in assessing and predicting the impact of biotic invasions on invaded communities (Mouillot et al., 2013). Biotic invasions are quite challenging for not all exotic species become invasive, and not all invasive species are exotic. Notorious invasive species such as *Lantana camara* are endowed with morphological and eco-physiological traits that render them competitive and hostile to native species (Goulson and Derwent, 2004). Trait differences between invasive non-native and native species might result in overall fitness differences, leading to the displacement of the less fit (Gross et al., 2015). On the other hand, the existence of overlapping traits between invaders and natives is also common, whereby competitive advantage, due for example to establishment away from natural enemies, influences the success of the invasive species (Olden et al., 2006, Haddad et al., 2008).

We live in a period of great human influence, dubbed by some the Anthropocene, marked by multiple disturbances acting in concert. The factors involved include defaunation,

urbanization, agricultural extension and intensity, and climate change, to mention but a few (Ehlers and Krafft, 2006, Jetz et al., 2007, Perrings and Halkos, 2015). The trait-based approach has potential to provide a rapid warning system for species and ecosystems vulnerable to a combination of disturbance, thus facilitating better-coordinated conservation intervention (Mouillot et al., 2013, Aguirre-Gutiérrez, 2020). My study system, Nyungwe National Park (NNP), a tropical montane rainforest in Rwanda, exemplifies these issues as it faces increased anthropogenic fires, high population pressure, warming in the region, and the extirpation of megafaunas (Gross-Camp et al., 2009, Seimon, 2012). The loss of megafauna seed dispersers may potentially cause long-lasting disruption of nutrient transfer processes (Doughty, et al., 2016). Prioritizing functionally important species, such as large-bodied frugivores, could shed light on biodiversity responses to disturbances and the effect they might have on associated ecosystem processes such as seed dispersal process and forest regeneration in NNP.

2 .4 Challenges and way forward

The extensive application of the functional diversity concept has been aided by advances ranging from the development of computational and statistical tools, large trait databases and protocols identifying traits relevant ecosystem functioning (Kleyer et al., 2008, Kattge et al., 2011, Moretti et al., 2017), and the formulation and refinement of cross-discipline indices and models quantifying functional diversity at different scales (Villéger et al., 2008, Chalmandrier et al., 2013, Chao et al., 2014). Nonetheless, there are still some gaps and challenges, which when remedied, will enhance the usefulness of the functional diversity approach in answering both ecological and conservation questions (Fig. 2.3).

2.4.1 Trait type and number dilemma

Biodiversity is multidimensional (Purvis and Hector, 2000), thus, identifying which traits are more representational, and how relevant they are to ecosystem functions is still a challenge (Webb et al., 2010, Moretti et al., 2017). Little is known on how transferable traits can be across different organisms, ecosystems, temporal and spatial scale, as different choices yield different interpretations (Petchey and Gaston, 2006, Gagic et al., 2015, Münkemüller et al., 2020).

Addressing this problem requires ample specification of the ecosystem function of interest, and having profound understanding of how that function operates, and also interaction of organisms of interest across different scales and along environmental gradients (Lavorel et al., 2013, Seddon et al., 2016). The required ecological knowledge might be obtained and cross-checked from direct observation, the literature, and expert knowledge. There are currently different datasets with important traits for a range of ecosystem functions (Kleyer et al., 2008, Kattge et al., 2011, Moretti et al., 2017). These can be further developed and extended to other taxa.

2.4.2 Ecological knowledge shortfall

The significance of *a priori* ecological knowledge in choosing the type and number of traits to study is indisputable, however, this knowledge is scant for some taxa and ecosystems (Petchey and Gaston, 2002b, Riddle et al. 2011, Gagic et al., 2015). Sound empirical research linking animal functional diversity and ecosystem functioning has only recently emerged (Seddon et al., 2016), and most such research is focused on temperate ecosystems (Schmera et al., 2017).

Future research should equally explore other regions, such as the Afro-tropics, which are rich in biodiversity, but facing significant threats due to climate change and land-use changes (Newbold et al., 2014, Aguirre-Gutiérrez, 2020). Funding resource constraints can be overcome through multi-institution collaboration with, for instance, museums, botanic gardens, and universities across the world. Herben et al. (2013) noted a range of useful forms of data, linking demography and plant traits, could be retrieved from botanic garden records. Moreover, many significant insights have been made from studies based on avian morphological traits retrieved from museums (Bregman et al., 2016, Pigot et al., 2020). Biodiversity data-sharing platforms such as the Global Biodiversity Information Facility (GBIF) can also extend beyond species occurrence data to include functional traits. This step has already been taken in vegetation science, as exemplified by the TRY plant trait database[3] (Kattge et al., 2011).

2.4.3 Integrated comparative methodology

Although, new indices continue to be produced for quantifying functional diversity, some supposedly complementary indices are not mathematically very different (Pavoine and Bonsall, 2011), some are inaccurate in their calculations (Petchey and Gaston, 2007, Podani and Schmera, 2007), and others are influenced by methodological choices, or species richness, rather than functional trait information (Poos et al., 2009).

To address these problems, guides on how to identify and apply the right indices are emerging through reviews on the performance and classification of different indices (Schleuter et al., 2010, Mouchet et al., 2013, Boersma et al., 2016). The set of desirable properties an index should meet has also been advanced (Ricotta, 2005, Mason and De Bello,

[3] TRY is a multi-institution initiative that provides a platform for the collection and sharing of a wide range of curated plant traits https://www.try-db.org/TryWeb/Home.php

2013), and recent indices have attempted to abide by these requirements (Villéger et al., 2008, Laliberte and Legendre, 2010). Some of those properties include: confinement within the range of 0.0–1.0 for intuitive interpretation; depicting correctly the range of functional characters selected; quantifying each species contribution in relation to its abundance; not varying systematically with species richness; being unaffected by units used to measure abundance; and not changing when a species splits into two species with identical functional characters and abundances (Ricotta, 2005, Mason and De Bello, 2013).

There is also wide support for the notion of decomposing indices based on the functional diversity components of functional richness, functional evenness and functional divergence, so that when one index does not match desirable criteria, the combination of the chosen indices does (Villéger et al., 2008, Pavoine and Bonsall, 2011). Additionally, multivariate indices have been found to be less subjective to trait choice, and indices incorporating abundances add more information relevant to ecosystem functioning (Schleuter et al., 2010, Gagic et al., 2015).

Several authors have called for the adoption of integrated comparative methods, particularly the incorporation of phylogenetic diversity, as this may disclose trait information not captured by functional diversity metrics (e.g. co-evolutionary relatedness, tolerance to pathogens), and because comparing the information content of phylogenetic and functional diversity indices may also reveal which traits are consistently important in predicting functional processes (Cadotte et al., 2011, Flynn et al., 2011, Pavoine and Bonsall, 2011, Si et al., 2017). However, many diversity metrics in taxonomic, functional and phylogenetic diversity fields have been developed independently, and there is still confusion in the metrics nomenclature (Pavoine and Bonsall, 2011, Tucker et al., 2017). Unifying frameworks for

taxonomic, functional and phylogenetic diversity metrics are emerging (see Chao et al., 2014, Pavoine and Ricotta, 2019), and deeper interdisciplinary collaboration between ecologists and mathematicians and statisticians promises further advancements.

Further, the adoption of phylogeny and traits-based approaches in grass-root conservation may conflict with existing conservation frameworks, since the intrinsic and instrumental values afforded to species vary from local to global scales and across cultures (Bhagwat et al., 2014; Maier, 2018, Rapaccioulo et al., 2019)

2.4.4 Long-term multi-level experiments with natural communities

Functional diversity studies have been dominated by theoretical work (Hooper et al., 2005, Mason and De Bello, 2013). There is still a lack of integrated studies involving large datasets that examine the pattern of assembly processes, responses and effects on ecosystems along ecological gradients (Chalmandrier et al., 2015). Additionally, very little is known on the extent to which intraspecific variability drives functional diversity (Albert et al., 2012, Schmera et al., 2017). Moreover, critics have pointed out that in real communities links between diversity and ecosystem functioning are clouded with confounding factors such as abiotic and biotic interactions (Huston, 1997, Hooper et al., 2005, Pool et al., 2016).

Hence, there is need to carry out more long-term, large-scale research involving multiple tropic levels, conducted with mixed methods. This will enrich our understanding of biodiveristy, and will significantly clarify the role of functional diversity in ecosystem dynamism from that of climate and disturbance regimes (Pool et al., 2016, Si et al., 2017).

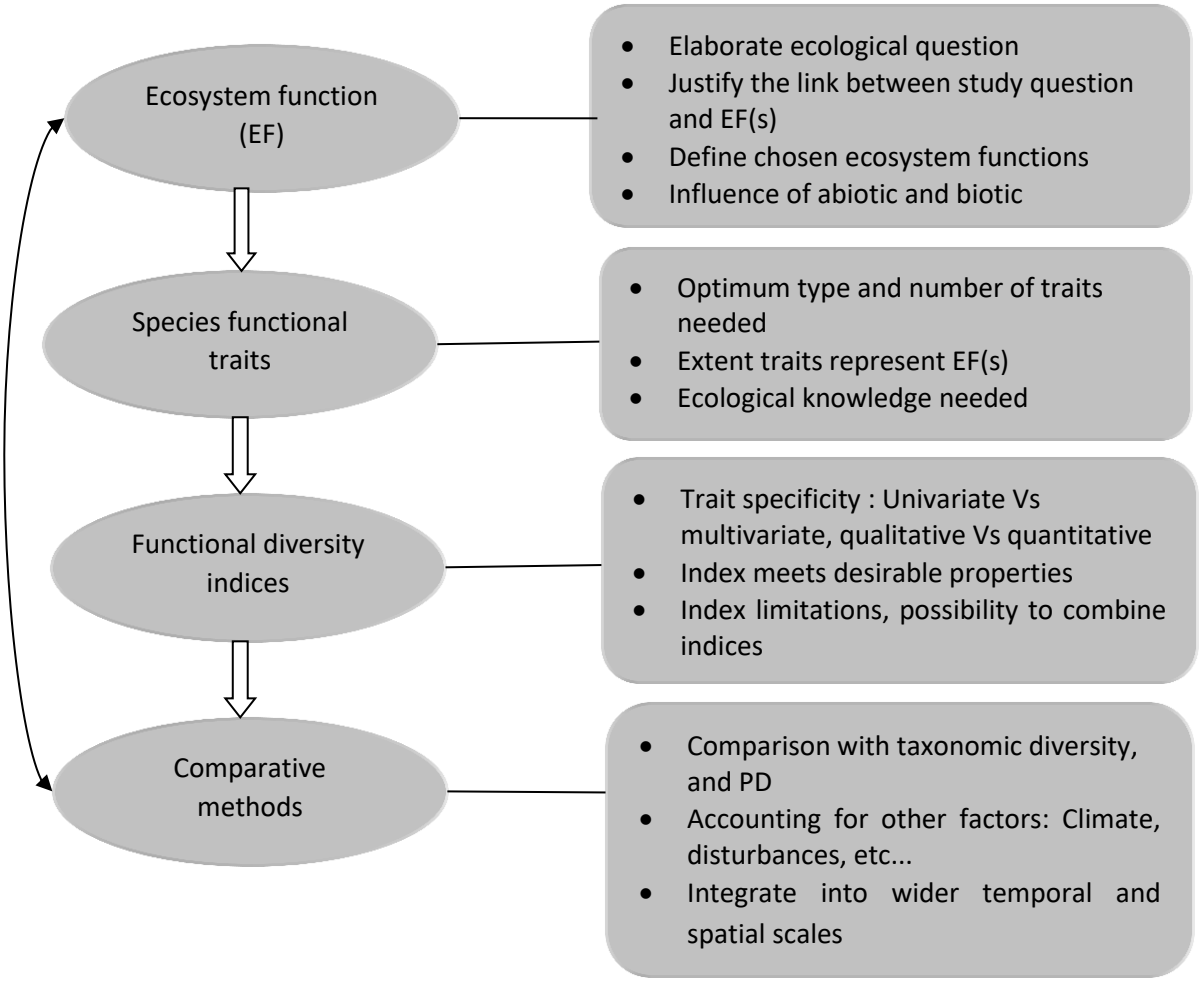

Figure 2.3. The process of using the functional diversity approach to quantify and predict ecosystem functioning. Major steps entail: i) choosing the ecosystem function of interest as determined by the research questions, ii) selecting the functional traits pertinent to the ecosystem function, iii) using metrics that meet a range of recommended properties (Mason et al., 2003, Ricotta, 2005), iv) comparing findings with other complementary methods, whilst taking into account large scale processes influencing the ecosystem function of interest.

2.5 Conclusion

Considerable progress has been made in the functional ecology field: from the realization that functional traits matter, to the development of functional diversity indices, and their extensive use to answer ecological questions. The use of functional diversity measures is not intended to undermine other biodiversity measures, but rather to complement them by providing another lens to quantify and predict the contribution of organisms to ecosystem processes. The plethora of indices available should not be regarded as a weakness, but rather a sign of the dynamism of the field. Addressing existing challenges will require interdisciplinary and multi-institution collaboration, championing data- and knowledge-sharing as well as more efforts directed at less well explored taxa and ecosystems.

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Chapter 3 | Vertebrate-mediated seed dispersal in disturbed tropical forests

3.1 Abstract

The mutualistic associations of plant species and vertebrate seed dispersers are crucial to the maintenance of the biodiversity and ecosystem functions provided by tropical forests. With an emphasis on the Afrotropics, we review the roles of vertebrates as seed dispersal agents and show how they are impaired by anthropogenic activities, particularly habitat fragmentation, hunting and forest fires. We conclude by highlighting the need for more integrative studies in terms of the forms of disturbances and the range of seed dispersers that are assessed.

3.2 Introduction

Seed dispersal, the processes by which seeds are released or moved from parent trees, deposited in favourable sites, and mature to adult plants strongly underpin the maintenance of plant structure, diversity, spread and dynamism (Bawa and Hadley, 1990, Vander Wall et al., 2005a, Schupp et al., 2010). This process entails advantages to plants, including escape from competition and diseases, and presents opportunities for gene flow and migration as a response to environmental changes (Janzen, 1970, Connell, 1971, Jordano et al., 2007, Corlett, 2009).

Morphological traits of the diaspore, such as the size, structure and weight are determinant of the dispersal mode (e.g. wind versus animals) and the distance travelled (Gautier-Hion et al., 1985, Corlett, 2009, Howe, 2016). In contrast to temperate forest ecosystems where wind dispersal prevails, in the tropics, seed dispersal is largely ensured by animals. One way which occurs to a small extent is the epizoochorous dispersal of seeds, where seeds are attached to

the fur (or feathers) of animals by adhesive mucus, and different forms of hooks and barbs, as sometimes observed in herbaceous members of the plant families Asteraceae and Apiaceae (Howe and Smallwood, 1982, Sorensen, 1986). The major dispersal mode for woody plants in tropical forests is endozoochory, the dispersal of seed via ingestions by animals. With endozoochory, plants produce fleshy fruits consumed by animals, and the passage through the gut often enhances germination and growth for both large and small seeded-species (Traveset et al., 2007, Fuzessy et al., 2016).

3.3 Seed dispersal by vertebrates

In tropical forest, more than 80% of woody species are dispersed by vertebrates, particularly mammals and birds (Howe and Smallwood, 1982, Jordano, 2000). A study by Blake et al. (2009) concluded that elephants were the most important dispersal agents of large-seeded trees among large vertebrates of the Ndoki forest of Congo, based principally on the amount of seeds defecated and the range of distance travelled (up to 2,226km^2). A single elephant dung pile was found to contain an average of 30.8 intact large seeds (≥ 1 cm), the maximum recorded being 1,102 intact large seeds. The average number of large seeds dispersed by an elephant community with a density of 0.66 individuals/km^2 was estimated as 345.6 seeds/km^2/day. Elephants were also found to travel the longest distance of 57 km during a typical gut retention time, dwarfing the 7 km distance travelled by hornbills (Holbrook and Smith, 2000, Blake et al., 2009).

Primates, especially great apes also form an important group of dispersers of tropical forests. Gorillas were documented to disperse 464.7 seeds/km^2/day in the Dja forest, in Cameroon, making them the most important seed dispersers among the primate community of the forest (Poulsen et al., 2001). In the Gishwati forest, a 14 km^2 fragment forest in north-western

Rwanda, Chancellor et al. (2017) counted seeds of at least 18 fruit species belonging to 14 families in the dung of chimpanzees. 95% of the dung encountered contained fruits (total fecal samples = 1,381), and 93% of the seeds were intact (total seeds identified =71,206). The most abundant seeds were of *Ficus* spp., *Myrianthus holstii*, a large-seeded tree, and *Maesa lanceolata*, a small seeded tree. The latter two species were the most abundant species of trees in the sample sites. 11 of the 12 tree species dispersed were large-seeded species. Based on the density of the chimpanzee community in Gishwati (1.7 individuals/km^2) the apes dispersed on average 592 (> 2mm) seeds /km^2/day. As demonstrated by other studies based in this region, apart from seed defecation, seed spitting constitutes another seed handling mode for primates that may also involve some degree of dispersal, and its frequency varies across primate species and depends on the type of seed size and the seasons (Kaplin and Moermond, 1998, Gross-Camp and Kaplin, 2011). Gross-Camp and Kaplin (2011) found that in comparison to seeds defecated or discarded in wadges, seeds that were spat out had the highest rate of germination and establishment.

Although seed dispersal services by carnivorous species had been previously overlooked, reports of significant levels of frugivory in carnivorous species are emerging (Mudappa et al., 2010, Timóteo et al., 2018). The African civet (*Civettictis civetta)* has been placed among the main seed dispersers in the Ngorongosa National Park, contributing significantly to the restoration of the forest (Timóteo et al., 2018).

Rodents constitute another category of seed dispersers overlooked principally on the grounds that they are involved in seed predation. Studies have revealed how caching and scatter-hoarding rodents are crucial as primary or secondary seed dispersers of a range of tropical forest plants (Sidhu and Datta, 2015, Chapman et al., 2016). Unused seeds by caching and

scatter-hoarding rodents benefit from the alleviation of desiccation, favourable temperatures, and safety from other seed predators (Vander Wall, 2001, Forget and Cuijpers, 2008). In forests deprived of large vertebrates, large-seeded trees rely on rodents for their dispersal, as documented in Nyungwe NP, where the large-seeded *Carapa grandiflora* (African crabwood, a large tree in the Meliaceae) in the absence of elephants is dispersed by the Kivu Giant Pouched Rat (*Cricetomys kivuensis*) (Nyiramana et al., 2011).

Volant seed dispersers – frugivorous bats and birds – play a particular role of dispersing seeds at larger scales, at times initiating plant colonization, as documented for the Krakatau Islands, whose vegetation had been completely destroyed by volcanic activities in the 1900s (Whittaker and Jones, 1994, Shilton and Whittaker, 2009). The high mobility of bats and birds enable penetration in areas hostile to other dispersers, hence facilitating vegetation succession (Ingle, 2003; Seltzer, Ndangalasi, & Cordeiro, 2013). Mobility in birds increases with body size in migrating and non-migrating species (Jetz et al., 2004, Şekercioğlu and Hakki, 2006). Large birds such as pigeons, turaco, and hornbills traverse some of the longest distances (Whittaker and Jones, 1994, Sun and Moermond, 1997). For instance, *Ceratogymna* hornbills in the Dja forest have a home range of 4,472 ha and traverse distances of 290 km (Holbrook and Smith, 2000), although the distance travelled by such species can dependent on the characterisics of the landscapes encountered and especially, for forest-dependent species, can be adversely affected by the conversion of forest to open landscapes. The high mobility of volant dispersers may have adverse consequences, including introductions of invasive species at large scales, as documented for *Maesopsis eminii* (umbrella tree, a West and Central African tree in the Rhamnaceae), which is an introduced and seriously invasive species in the Usambara mountains of Tanzania, dispersed by hornbills in both invaded and native ranges (Şekercioğlu and Hakki, 2006).

3.4 Seed dispersal effectiveness

Frugivores are often subdivided into biters, mashers and swallowers. These different ways of handling fruits can determine dispersal success, whereby biters and mashers tend to deposit the seeds under the parent tree, thus limiting dispersal success, while swallowers often carry the seeds away from the parent tree where the chances of germination, and survival and growth are high (Terborgh et al., 2002). However, not all seed removal results in dispersal success. A range of frugivorous birds and mammals are known to destroy seeds as a result of their mouth and gut handling (Traveset et al., 2007), and frugivores can switch between seed destruction and dispersal depending on fruit resource availability (Kaplin and Moermond, 1998). There is a thin line between seed predators and dispersers, as both can be done by the same individual. An example is the *Cricetomys* species of giant pouched rats. Although they are known as seed predators, an experimental study in Nyungwe NP provided evidence of the scatter-hoarding behaviour of the Kivu Giant Pouched Rat (*C. kivuensis*) and that it thus provides dispersal services, as seedlings were found to have emerged from cached seeds (Nyiramana et al., 2011).

Different phases of the seed dispersal process facilitated by more than one agent may reinforce seed dispersal effectiveness (Vander Wall et al., 2005b, Schupp et al., 2010). For instance, when seeds are removed from the tree, but due to their large sizes remain on the surface, burial by scatter-hoarding rodents may tangibly increase their dispersal and establishment success (Vander Wall, 2001, Vander Wall et al., 2005b, Schupp et al., 2010). Plant dispersal modes also are not mutually exclusive and the described main dispersal syndrome may often not predict the actual mode of dispersal in particular cases (Vander Wall, 1992, Higgins et al., 2003). In Nyungwe NP, primates were recorded feeding on wind-dispersed tree species, including *Albizia gummifera*, *Entandophragma excelsum*, and

Newtonia buchananii, which increases their chances of spreading at larger scales (Sun et al., 1996).

3.5 Anthropogenic disturbances of seed dispersal processes

3.5.1 Fragmentation

The vast majority of tropical forest have been fragmented due to clearance for agriculture, and settlements, and have been dissected by road networks often introduced for resource extractive purposes (Laurance et al., 2006, Turubanova et al., 2018, Hansen et al., 2020). The lower vegetation complexity coupled with the scarcity of fruit resources in agricultural sites often represents the most hostile environments for large-sized dispersers, and forest specialists in particular, hence limiting the dispersal of plants relying on these animals (Morante-Filho et al., 2018, Emer et al., 2020). In the events of successful deposit of the seeds in degraded areas by habitat generalists, seeds and seedlings face increased predation by vertebrates and insects, impeding germination and establishment stages (Hammond, 1995, Notman and Gorchov, 2001, Ssali et al., 2017).

Further consequences from edge effects were reported by Melo et al. (2007) in the Coimbra forest in Brazil. The authors assessed the seedling of large-seeded woody in forest edges (0–200m) and forest interior (>250m) and noted no difference in the average seedling density at plot level, but the species richness levels and the proportion of large-seeded species were lower at edges than in forest interiors. In the same vein, for bird communities, a study by Watson et al. (2004) on the guild composition of bird communities in forest interiors, forest edges and the matrix of Madagascan littoral forests found frugivores to be sensitive to forest edges.

Fragmentation is also known to affect flocking species (Whittaker and Fernández-Palacios, 2007). A study in the Usambara mountains of Tanzania, which investigated small fragments of <31ha and six continuous forests, found that smaller fragments had smaller flocking sizes, less species richness and a higher proportion of generalists and non-forest species (Cordeiro et al., 2015). In contrast, neutral effects of fragmentation as well as positive ones on dispersal services have been documented (Farwig et al., 2006, Markl et al., 2012). Differences in the responses of frugivores and plants can be species specific, scale dependent and factors linked to landscape structure may be at play (Melo et al., 2007, Whittaker and Fernández-Palacios, 2007, Menke et al., 2012, Martino, 2015)

3.5.2 Hunting

Hunting of forest animals for leisure is an old tradition embedded in many cultures across the world. However, improved hunting technologies, coupled with an increased reliance on meat-based diets underpin the unsustainable harvest of forest animal resources, impacting adversely on plant–animal interactions, and in the worst scenario have led to descriptions of "empty" defaunated forests (Redford, 1992, Chapman and Onderdonk, 1998, Duda et al., 2017, El Bizri et al., 2020). A review by Kurten (2013) showed that defaunation leads to declines in primary seed-dispersal for large-seeded trees, resulting in higher recruitment near conspecific trees. Changes in the plant community structure are argued to be characterized by lower species richness and diversity, and higher dominance of certain species. Defaunation may have long-lasting effects on biogeochemical cycles, as exemplified by the present Phosphorous limitation in Eastern Amazonia caused by substantial reductions in large-scale lateral translocation of nutrients following Pleistocene megafauna extinctions (Doughty et al., 2013).

Poulsen et al. (2011) compared forests in northern areas of the Republic of Congo that experienced logging, and hunting, to intact forest where no logging and hunting took place. They found that large mammals were greatly affected by logging and hunting as shown by a considerable reduction in the relative abundances. The frugivore community registered a shift towards small bodied-animals, such as squirrels and small birds**.** In another paper from the same area, Poulsen et al. (2013) found that partial defaunation was sufficient enough to change the connectivity of plant–animal interactions in hunted forests in the Republic of Congo. They noted a 22% decrease in the distance at which tree species were dispersed by nine mammals. The mean dispersal distance was considerably shorter in hunted than in intact forest. Significant lower aboveground biomass was noticed in hunted forest than in logged or intact forest.

3.5.3 Fires

Anthropogenic activities have increased the frequency and severity of human-induced fires, particularly in moist tropical forests. Barlow and Peres (2006) investigated the effects of fires in the terra firme forest of central Amazonia and found that the first burning led to 42% mortality of stems ≥ 10 cm, and a 29% decline in the basal area of fruiting trees, while the second fires led to a 74% mortality of stems and doubled the loss of basal area in fruiting trees to 62%. The effects were more severe for woody lianas, which experienced more than 89% and 97% loss of the crown cover for the first and second fires, respectively. Vertebrates declined after the first fire, and the majority of forest specialists disappeared with the second fire, leading to an increase of secondary forest species. An earlier study by Cochrane and Schulze (1999) had found similar drastic effects of fires in the Eastern Amazon, where fire lead to reduction of the canopy cover, biomass, and adult stem densities at 10–30 % levels of unburnt forest. Saplings and lianas were most impacted, even at low intensity fires, with

destruction of more than 70% of their populations. A rise in pioneer species with fire intensity was also noticed, and fire events increased the flammability of the forest, since more than 70% of the area has been burned more than once. Fires may also lead to the dominance of opportunistic plant species, particularly bracken ferns (*Pteridium aquilinum*), which can impede regeneration for decades (Masozera and Mulindahabi, 2007, Ssali et al., 2017).

3.6 Gaps in the literature and the study contribution

Different forms of disturbances of tropical forest processes often act in concert (IPBES, 2019). For instance, climate change-linked droughts increase the flammability of forests, and the construction of roads in forests is often followed by higher levels of hunting, and slush-and-burn activities (Laurance et al., 2006, Poulsen et al., 2009, Malhi et al., 2014). A study by Emer et al. (2020) also found that defaunation was strongly negatively correlated with fragment area (r= -0.89). Nonetheless, few studies have attempted to evaluate the combined effects of different disturbances on a range of seed dispersers. In order to devise effective conservation measures, a broader understanding of the combined effects of anthropogenic disturbances on seed dispersal processes is indispensable. To contribute to filling this gap, in Chapter 5, we present the case of Nyungwe National Park, an Afrotropical montane forest that has undergone varying degrees of habitat degradation.

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Chapter 4 | Methods

4.1 Bird survey techniques

A broad range of techniques have been used to survey bird communities in modified habitats, including line and point transects (Ornelas et al., 1993), capture-mark-recapture (Dulle et al., 2016, Ulrich et al., 2016), camera traps (Gregory et al., 2014), acoustic recording (Waltert et al., 2004) and tape playback (Boscolo et al., 2006). Although each of these methods provides distinct avenues to investigate birds' response under land-use changes, they each have inherent strengths and limitations that might render them more or less effective depending on the nature of the study (Table 4.1). As a result, some authors have recommended the use of a combination of alternative methods (Whitman et al., 1997, Gregory et al., 2004).

Table 4.1. A comparison of preferred methods of surveying bird communities compiled from the published and unpublished literature. See note for sources.

Point-counts	**Mist-netting**	**Acoustic-recording**	**Camera trap**	**Play-back**
Suits a range of species, particularly populations with high species richness and density.	Better suited for cryptic species, skulking, and understorey birds.	Suits rare, endangered species, and hard-to-see birds in dense vegetation.	Suits elusive, large, nocturnal and ground-dwelling species.	Suits shy, territorial species during the breeding season. Response can also be induced outside peak and breeding period.
Less effective with furtive species, or outside a given species' peak time.	Fails to trap larger species, agile aerial foragers and canopy dwellers.	Less effective for birds with complex, or infrequent vocalization.	Less effective with camera-avoiding species, and those in which individuals are not easily identifiable.	Less effective when targeting many species.
Suits a range of habitats, especially dense habitats such as forest and scrub.	Suits habitats with dense undergrowth.	Suits habitats with dense vegetation and those with less extraneous noise.	Suits a range of habitats	Suits a range of habitats
Enables high species detectability. The ground is covered quickly, and minimum movements within stations increases birds spotted and identified.	There is less bird detectability, unless more sampling efforts and time are expended.	There is overall same detection probability or slightly higher than point counts.	Detection is only high within the camera detection zone. A high proportion of photos are typically of non-target stimuli like leaves.	Increases detectability of targeted species, however, response probabilities are not always constant, differing between species and varying seasonally.

Point-counts	Mist-netting	Acoustic-recording	Camera trap	Play-back
Less intrusive. Little disturbance to birds may be incurred when the surveyor approaches the point.	Very intrusive, and when improperly done stress, injuries, cuts and predation might occur.	The least intrusive. Little disturbance might occur when installing and collecting recorders.	Moderately intrusive, camera flashes and sounds can cause birds'flee.	Very intrusive and sometimes considered unethical. Lured birds might get exposed to predators, or cause unnatural stress on the bird, which might result in abandonment of the territory.
Effective for estimating birds relative abundance, and enables the estimation of bird density per habitat, as it is easy to describe vegetation structure and composition associated with each point.	Less effective in determining species relative abundance, as it does not capture birds in direct proportion to their presence in the habitat. It can be useful in estimating population size or to obtain a population index, particularly when individuals are marked.	Effective for estimating bird relative abundance, density and associated habitat conditions.	Less effective for relative abundance estimation, but it captures activity patterns, distribution and habitat use, hence good for occupancy analysis.	Best for bird occurrence studies, but not recommended for abundance studies.
Enables the surveyor to collect additional visual data, such as foraging and feeding behaviour, and habitat use.	Most effective at procuring data on phenotypic traits, movements, and a range of population demographics.	Gives limited information other than presence/absence data, especially for breeding males.	Documents a high amount of data, ranging from phenotypic traits, health condition, behavioural activities like frugivory, and predation.	Captures little information on species status other than presence/absence data, and habitat use.

Point-counts	Mist-netting	Acoustic-recording	Camera trap	Play-back
Influenced by observer skills, sample size and station placements.	The net quantity, quality, and dimensions can limit likelihood of recording birds.	Performance relies on the technical specifications of the recording equipment E.g.: detection radius of the microphone and noise filtering capacity.	Influenced by the camera model, positioning and detection system.	Influenced by the tape model, as well as bird habituation and response frequency.
Time is lost while moving between stations and information captured when moving does not contribute to final analysis.	Trapping and processing can be time consuming, especially when there are cases of mist-net avoidance.	The recording is time-saving, however, listening to the audio-files and examining spectrograms can be time-intensive, unless the analysis is automated reliably.	The actual trapping is time saving, and does not need high qualified personnel, however, viewing photos/videos taken can be time-intensive unless appropriate automated programs are used.	It is relatively time-saving in comparison to the other methods, but only for one species at a time.
Constrained by physical barriers such as steep slopes.	Effective deployment limited by external environmental factors, such as strong winds and rain.	Recorders may be damaged by exposure to extreme environmental conditions.	High risk of camera damage by wind and sun exposure, as well as wildlife and people.	Dense vegetation can attenuate high pitched songs (higher than 2 kHz), thus only capturing calls nearby.

Note: For the literature consulted, the reader is referred to the section: “Further references”.

4.2 Sampling approach

Ideally, a random sampling approach, where all survey units have an equal chance of being selected, would ensure an unbiased coverage of the study area, given that all habitat features are surveyed in proportion to their abundance (Fowler et al., 1998, Gregory et al., 2004). However, such an approach is impractical since this research focuses on the influence of specific habitat variations in terms of land cover and management on bird communities and some habitat types are of rather limited extent. The cost and access could also be a hindrance in random sampling, particularly in dense and steep forests, such as Nyungwe NP. Therefore, a stratified sampling method was chosen, as it not only proved to be cost effective, but also permitted more coverage of habitats of interest that were less abundant.

Sites in the Nyungwe landscape which fell in the study categories that reflect major forest cover changes due to past and present land-uses were identified with a team of three Wildlife Conservation Society staff with long term experience in research and monitoring of Nyungwe NP.

4.3 Study area

4.3.1 Nyungwe landscape description

The Nyungwe forest (1,019 km^2; Fig. 4.1) is Rwanda's largest rainforest and is situated in the southwestern part of the country spanning an elevational range from 1600 to 2950 m. The chain of mountains, which form part of the Congo-Nile divide, dissect the forest from north to South. The Nyungwe forest contains the farthest source of the White Nile, and its wetlands are Rwanda's largest water reservoirs. The forest experiences average minimum and

maximum temperatures of 10.9^0 C and 19.6^0C, respectively and a mean annual rainfall of 1,744 mm (Sun et al., 1996).

In 2004, the Nyungwe forest, along with the adjacent Cyamudongo forest (300 ha) were gazetted as the Nyungwe National Park (Nyungwe NP). Cyamudongo forest is currently isolated from Nyungwe forest by 19 km distance due to past deforestation. The Nyungwe forest adjoins Kibira National Park, Burundi and together form the largest landscape of lower montane rainforest in Africa (Weber, 1989, Vedder, et al., 1992). This landscape is also part of the Albertine Rift, a 313 000 km^2 region encompassing the western branch of the East African Rift, stretching from the northern end of lake Edward to the southern tip of lake Tanganyika (Plumptre et al., 2003, 2007). The region harbours the highest number of vertebrate species in Africa, and of endemic vertebrate species in mainland Africa (Plumptre et al., 2003, 2007). The rich biodiversity of the Albertine Rift, coupled with increasing threats, has attracted recognition in conservation priority schemes, including Conservation International biodiversity hotspots (Brooks et al., 2006), WWF-200 Global ecoregions (Olson & Dinerstein, 2002), and BirdLife International endemic bird areas (Pomeroy, 1999).

4.3.2 The vegetation and fauna of the Nyungwe National Park

Nyungwe NP harbours a mosaic vegetation comprising the afro-montane vegetation, swamps and moorlands, and montane savannas. The forest counts at least 260 species of trees and shrubs, and 280 plant species are Albertine Rift endemics (ARE) (Dowsett, 1990, Fischer and Killmann, 2008). The known ranges of 47 out of the 56 flowering plants that are endemic to Rwanda are restricted to Nyungwe NP. As described by Fischer and Killman (2008), the vegetation of the Nyungwe forest is stratified along an elevation gradient as follows:

The low Montane forest (1600 – 2100 m) is dominated by *Parinari excelsa, Carapa grandiflora* and *Newtonia buchanani*. This type of forest is mostly found in the western part of the forest, which is more humid than the eastern part, principally due to climatic, geologic, and edaphic factors. The eastern part has been heavily affected by anthropogenic activities and is largely covered by a secondary forest (*sensu* Putz and Redford, 2010).

The middle montane forest (2100 – 2600 m) is characterized by *Ocotea mickelsoni, Syzygium guineense, Beilschmiedia rwandensis, Macaranga kilimandscharica* and *Melchiorea Schliebenii*. The secondary forest in the eastern part is dominated by *Macaranga kilimandscharica*, and *Neoboutonia macrocalyx.* The only extensive stands of bamboo (*Sinarundinaria alpina*) are found in the south-eastern part of the forest.

The upper montane forest (2600-2900 m) covers the mountain summits. The vegetation is dominated by Ericaceous thickets (*Erica bequaertii* and *E. johnstonii*). The trees on Mt.Bigugu, the highest mountain (2950 m) are principally *Podocarpus latifolius, Syzygium guinnese, Psychotria mahoni.* Shrubs are dominated by *Mimulopsos solmsii*. An epiphytic layer is well developed and contains bryophytes and lichens, particularly *Usnea* species.

It is within the middle elevation range that extensive moorlands and swamps are found. The two major swamps, the Kamiranzovu, and Uwasenkoko, are located at 2300 m and 2400 m, respectively. The Kamiranzovu swamp (1300 ha) ranks among the largest peat bogs in Africa. Its centre is characterized by *Cyperus* and *Lobelia* spp*, Crassocephalum paludum* and orchids, mainly *Eulophia horsfallii, Satyrium crassicaule* and *Disa eminii,* while the riparian forest is largely composed of small-sized *Antocleisha grandiflora, Podocarpus latifolius,* and *Syzygium guineense* (Hughes, 1992, Ewango, 2001, Fischer and Killmann, 2008,). Kamiranzovu is classified as a Ramsar site (a wetland of international importance). This site

is one of the remaining habitats of the endangered and ARE bird species, *Bradypterus graueri*, in Rwanda.

The fauna of Nyungwe NP is equally rich, with 13 species of primates including the endangered eastern chimpanzee (*Pan troglodytes schweinfurthii*), the vulnerable owl-faced monkey (*Cercopithecus hamlyni*), and the largest group of black-and white Angolan colobus monkeys (*Colobus angolensis*) in the world, numbering 450 individuals (https://rwanda.wcs.org/Wildlife/Angolan-B-W-Colobus.aspx Accessed on 02/06/2020).The high hunting pressure of large mammals before the upgrade of the park's protection status led to the extirpation of the buffalos in the late 1980s, and the last elephant in 1999 (Plumptre et al., 1999). The avifauna counts at least 322 species, of which 27 are endemic to the Albertine rift, 3 are endangered, 5 are vulnerable and 6 are near threatened, according to the IUCN conservation status categorization. 42 species have not been observed in any other protected area in Rwanda (Vande weghe and Vande weghe, 2011), including *Dendropicos elliotii* and *Bycanistes subsylindricus* recorded by this study.

Subsequent reference to Nyungwe NP excludes Cyamudongo forest. For more information on the avian diversity of Rwanda, its threats, and conservation arrangements, the reader is referred to Appendix 5.

4.3.4 Anthropogenic disturbances

Major disturbances in the Nyungwe landscape have often had anthropogenic origins such as deforestation linked to agriculture and mining. Consequently, the vegetation composition has been altered through the replacement of late successional tree species by pioneer tree species, particularly, *Macaranga kilimandscharica* in the East, and *Musanga leo-errerae*, and Myriantus hostii in the western parts of the forest (Fischer and Killman, 2008). Agricultural

encroachment by surrounding communities between 1958 and 1979 led to the reduction of the forest size from 1,141km^2 to 971 km^2 (Weber, 1989), representing a loss of 15% in about two decades.

The mining of gold in Nyungwe began in 1935 under Belgian colonial rule and often took place near rivers and streams, and commenced with the deforestation of the surrounding areas (Plumptre et al., 1999, Roca and Carillo, 2016). The peak of mining activities was documented between 1970s and 1985, when 12,000 miners were reported to operate in the forest, and in 1993, the number fell to 2,528 workers living and operating in areas covering approximately 16,000 ha (Fimbel and Kristensen 1994; Plumptre et al., 1999; Roca and Carillo, 2016). Currently, mining in the Nyungwe forest is illegal, although isolated cases at subsistence levels still take place (Pers. Obs). Regrowth in most mining sites are dominated by early successional species, such as *Hagenia abyssinica* and *Dichaetanthera corymbosa* (Roca and Carillo, 2016). In addition to the mining of gold and sand, other human forest uses have included bee-keeping activities, wood cutting, and hunting of animals, particularly ungulates (Plumptre et al., 1999).

To minimize the encroachment of the Nyungwe forest by surrounding communities, the government of Rwanda, in partnership with the Swiss Technical Agency, transformed parts of the periphery forest into a buffer zone largely composed of non-native tree species of *Pinus* and *Eucalyptus* (Plumptre et al., 1999). By the early 1990s, the buffer zone plantations were occupying more than 10, 000 ha (Gross-Camp et al., 2015). Commercial exploitation of the plantations was privatized in 2011 for 8,500 ha (Gross-Camp et al., 2015). Beyond the buffer zone, the landscape is dominated by tea and mixed crop farms. For more information on agricultural practices surrounding the Nyungwe forest, the reader is referred to Chapter 8.

In the last twenty-three years, anthropogenic fires in the Nyungwe forest ravaged more than 12% of the forest (Weber et al., 2005). 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, mainly *Syzygium guineense*, have been replaced by dense thickets of opportunistic ferns, typically *Pteridium aquilinum*, leading to arrested succession (Masozera and Mulindahi, 2007).

In early 2000, the park management and conservation partners initiated trials to establish 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 and 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. The recruitment of shade-tolerant primary forest species follows later after the canopy starts to close (Protais Niyigaba. pers. obs.).

4.4 Data collection

We used the point count sampling method to record birds within six major land-use types: primary forest (PR: sites were classified as primary forest if they contained old growth forest, i.e. late stages of stand development, with little recent human-induced degradation (Putz and Redford, 2010). In Nyungwe NP, such sites are characterized by tree species such as *Syzygium guineense*, *Strombosia schefflera*, and *Entandophragma excelsum*), secondary forest (SC: this term is herein restricted to secondary regrowth after non-fire disturbances), fire-degraded areas undergoing self-regeneration (FD; Fig.A1.2), restored areas by assisted-natural regeneration method (RS), non-native plantations forming the buffer zone (PT), and cultivated areas constituted of tea and mixed-crops systems (CT) (Fig. 4.1, Fig. A1.1). Birds were recorded in 1200 points of 100 m radius, replicated over two seasons in 2017-2018. In addition to birds, all frugivores in fruiting trees were recorded. A focal individual was chosen and observed for a fixed period of one minute. Its time of arrival and departure, the tree species, the number and manner of fruits handled and the total amount of time spent foraging were also noted. In each point count site, a smaller circular plot of 20 m radius was established to assess habitat and vegetation attributes. In the case of farms, informal interviews were administered to farmers and agronomists on the usage of agrochemical

inputs. Habitat data were initially collected along with bird recordings, however, it was perceived to encroach much on the optimum time for surveying birds. To correct this, bird data were collected one to two stations ahead, and observers marked the stations for easy recognition by the habitat surveyor.

The first round of data collection started in Early November 2017 and was completed in Mid-February 2018. The second sampling phase started in Early June and was completed in End August. The first phase covered the short rainy season. This season was important because it is the breeding season for many birds and the migrants are present (Vande weghe and Vande weghe, 2011). The second phase covered the long dry season, and it was relevant to this study because it corresponds to a tree fruiting peak (Sun et al., 1996).

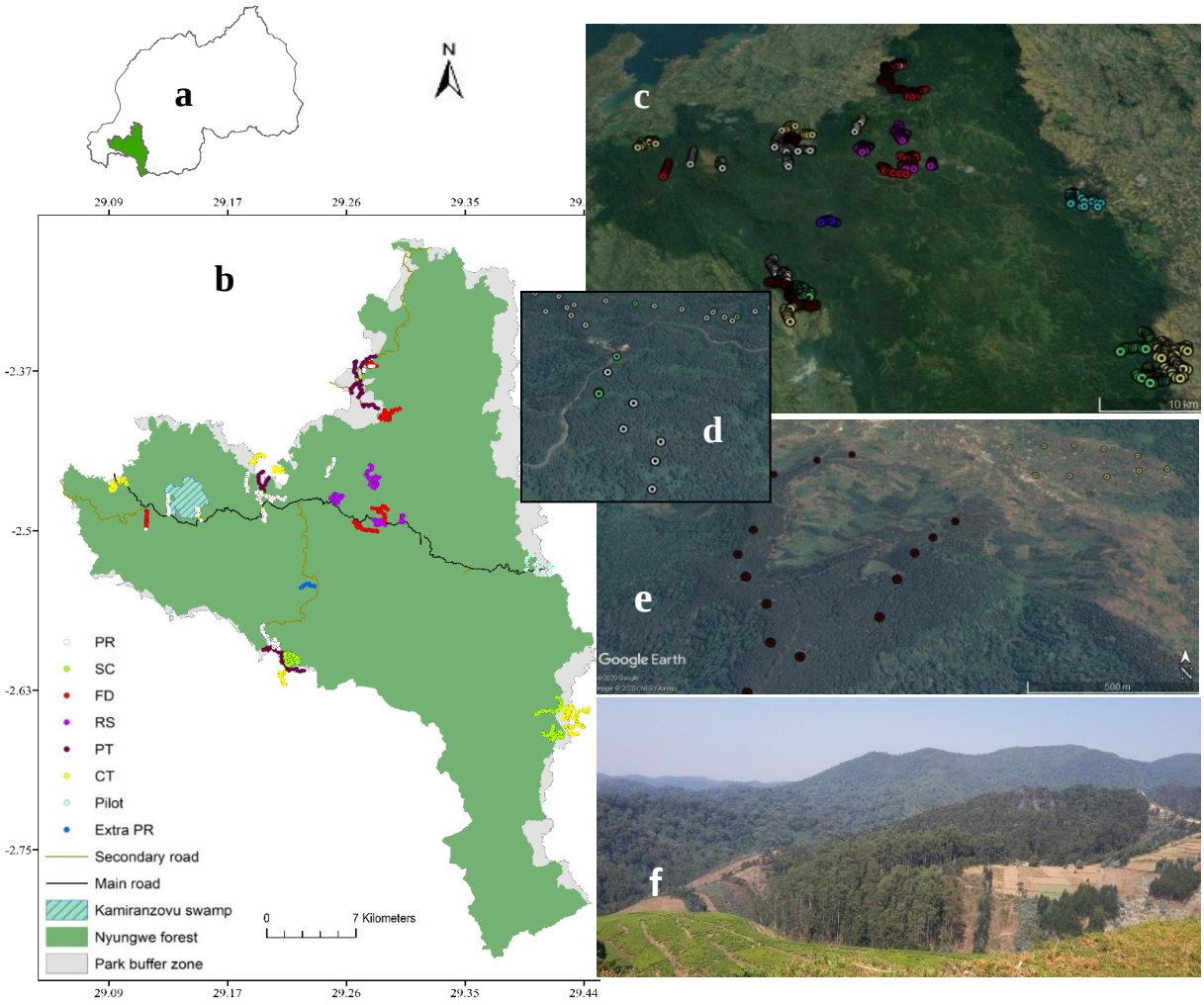

Figure 4.1 Study area in Nyungwe landscape. Map of Rwanda showing the location of Nyungwe National Park (**a**). Location of point counts stations in the Nyungwe landscape **(b)**. PR: Primary forest; SC: Secondary forest; FD: Fire-degraded areas; RS: Restored areas; PT: Plantation of non-native trees; CT: Cultivated areas; Extra PR: additional 10 points sampled in the primary forest during the second season. Satellite images displaying all the study stations **(c)**, the position of stations in relation to the main road **(d)**, the forest edge, with the buffer zone in the foreground **(e)**. The view of the Nyungwe landscape from the East (Kitabi) showing farms in the foreground, and the secondary forest in the background **(f)**. Base map sources: WCS 2018, Google Earth, 2020.

To increase the chances of recording cryptic understorey birds, four 2.5 m x 20 m 36mm mesh nets were set up across dense habitats in primary, and secondary forests, and once in a fire-degraded area (Fig. 4.2), 4 hours before sunset (Trnka et al., 2006). The number of nets was increased to eight in the second season in order to boost sample efforts. Trap sites were marked with a GPS, and were spaced at least 20 m from each other. Nets were checked every 30 minutes, and captured birds were carefully placed in appropriate cotton bags to keep them calm. They were then weighed, and morphological traits— the bill, wing, tail and tarsus were measured with wing rules and callipers. Birds were then marked and released in the habitats where they were caught, but in a distance from the nets to prevent recaptures (Owiunji et al., 2005). Bird capture techniques, when hastily done, can harm birds by reducing their feeding time, exposing them to predators and harsh weather conditions (Gosler, 2001), thus extra care was taken to prioritize each bird's welfare by ensuring quick extraction, proper handling, and placing nets in shade and at different locations to avoid predator habituation, and direct sun light. Mist-netting was conducted over 20 and 18 days in the first and second seasons, respectively.

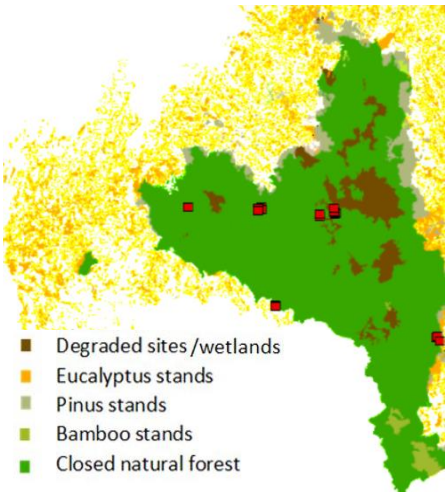

Figure 4.2 Location of mist-net sites in Nyungwe NP indicated by red rectangles. At each site, four and eight nets were established in the first and second season, respectively.

Although mist-netting was weather-dependent, demanded more sampling time, and is known to be less effective for recording canopy birds, it remains ideal for sampling rare and less vocal birds (Table 4.2 and Table 4.3). For instance, a new species record for Nyungwe forest was discovered by the project team. The bird (an immature individual) was photographed and sent to experts (Fig. A1.1). It is thought to be either a Grey Longbill (new for Rwanda), or an Olive-green Camaroptera (new for Nyungwe NP). A second record of an adult will help to resolve the identification mystery.

Since traits we collected using mist-netting only covered a small representation of species found in the study area, to compute functional diversity metrics, we used eco-morphological traits data measured on specimens collected in British museums. Twenty five out of the 60 species were recorded once, and only 9 species were recorded more than 5 times (Table 4.2).

Table 4.2 A comparison of birds recording performance of the point count and mist-netting methods in the Nyungwe landscape. 8 658 individuals of 170 bird species were recorded using point counts, while 262 individuals of 60 species were recorded by mist netting. More individuals and species were recorded in season 1 than season 2 using point counts and the reverse is true for mist-netting.

	Point counts			**Mist-netting**		
	Season 1	Season 2	All	Season 1	Season 2	All
Individuals	4467	4191	8658	110	152	262
Species	153	145	170	43	47	60
AR* endemics	20	19	20	10	8	13
Unique species per season	14	15	29	10	11	21
New record					1	1
unique Species per method	112	104	127	2	2	4
Time (min)	6 000	6 000	12 000	3 600	3 240	6 840

*Albertine Rift. There are 27 Albertine Rift endemic birds in Nyungwe NP.

4.5 Fieldwork preparation, design, and execution

I took a bird ringing course organized by the Slapton Ley, Field Studies Council. In addition to ringing birds, I was introduced to setting up mist-nets, extracting birds, and assessing bird condition and taking body measurements. Negotiations were undertaken for this research to be hosted by the Wildlife Conservation Society (WCS), one of the major stakeholders of Conservation and Research in the study area. WCS has been implementing research and conservation programs in Nyungwe NP for three decades. Collaborating with WCS allowed me to work with experienced field assistants and to easily access information relevant to this project such as the safety, accessibility, degradation, or restoration history of different parts of Nyungwe NP.

Three field assistants were employed by this project: one botanist who conducted the vegetation sampling, and two ornithologists who assisted with the point-count method, and the frugivore sampling. The first two weeks of fieldwork were used to sort out fieldwork permits, camping sites, to train field assistants, and to conduct a pilot study. Acoustic recording was attempted for two weeks, and was later abandoned due to the poor quality of the recording.

We realized that the point count sampling technique was equally effective in recording understorey birds as mist-netting (Table 4.2, Fig. 4.3), and did not require as much site preparation, thus we resorted to using point counts as the study primary sampling method. It was conducted in the morning, while mist-netting was done in the evenings. Furthermore, mist netting was considerably affected by rainfall events particularly in the first season. We also noticed site preparation activities, such as vegetation cutting and erecting poles scared away birds, so we decided to install nets one day after preparing the sites. As a compensation for the loss of trapping days, nets were doubled to eight in the second season.

Table 4.3 The most recorded bird species (N > 5) using mist-nets in the Nyungwe NP during two sampling seasons (2017/2018). The number of individuals recorded by point-counts is given for comparison.

Species	Family	Mist-net	Point-count
EURI.LATI	Pycnonotidae	38	374
CINN.REGI	Nectariniidae	26	242
ZOST.SENE	Zosteropidae	24	579
POGO.STEL	Muscicapidae	22	98
OREO.RUWE	Cisticolidae	8	112
CRYP.JACK	Estrildidae	8	6
ILLA.PYRR	Pellorneidae	6	102
PLAT.CYAN	Platysteiridae	6	0
CRIT.STRI	Fringillidae	6	67

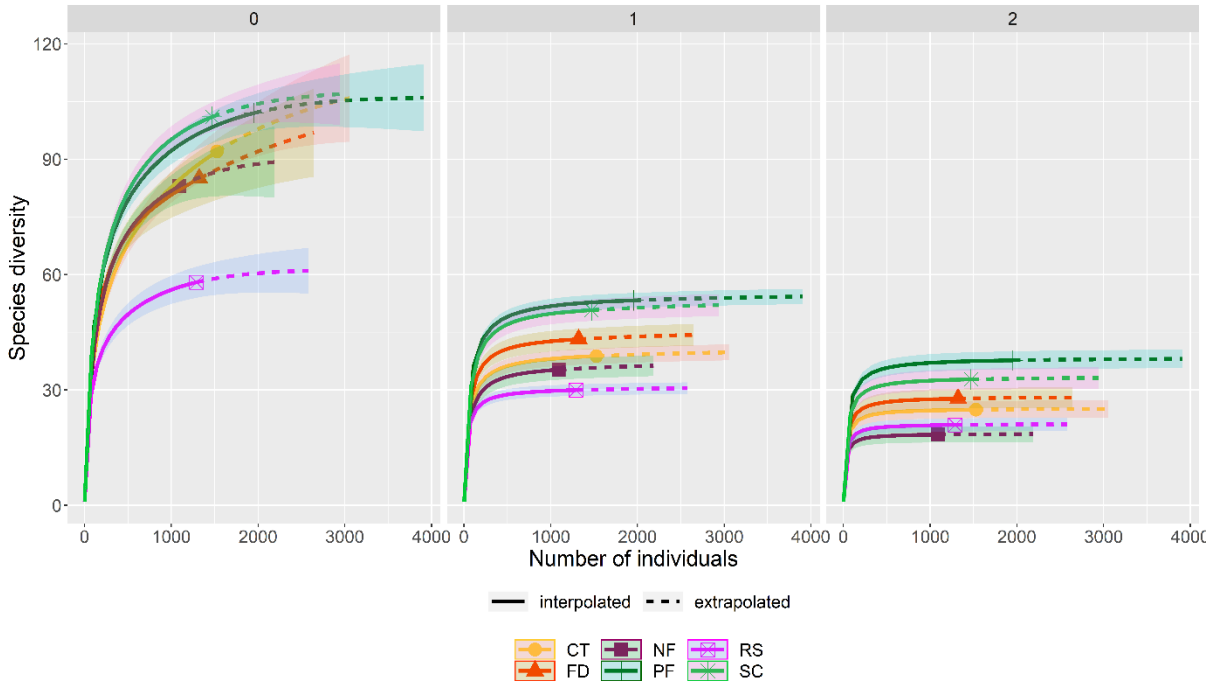

Figure 4.3 Individual-based rarefaction and extrapolation curves for major land-use types within Nyungwe NP, Rwanda, showing 95% Confidence intervals. The calculations are based on Hill numbers: with q = 0 representing species richness, q = 1: Shannon entropy index, and q=2 the inverse of the Simpson diversity index. The graph and diversity estimates were generated by the R package "iNext" (Hsieh et al., 2016).

During the second season, a new site was chosen to increase representation of primary forest areas that are distant from the forest edge, and at lower elevation (Fig. 4.1). However, only 10 points were established due to the travel cost and lack of considerable difference in species recorded from other primary forest sites. The additional points were not included in the final analysis. Overall, point-count sampling efforts were adequate as shown by the rarefaction curves for species diversity that levelled off in each land-use type (Fig. 4.3).

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4.8 Appendix 1



FIGURE A1.1 From top left: Primary forest, Field team in a secondary forest, Fire degraded area. Middle left: Restored area, Field assistant Vénérand Ngirababyeyi extracting a Cinnamon-bracken warbler (*Bradypterus cinnamomeus*) from the net, a non-native stand of pine trees forming the buffer zone. Lower left: A new non-identified bird for Nyungwe NP, a mixed crop farm, a tea plantation.

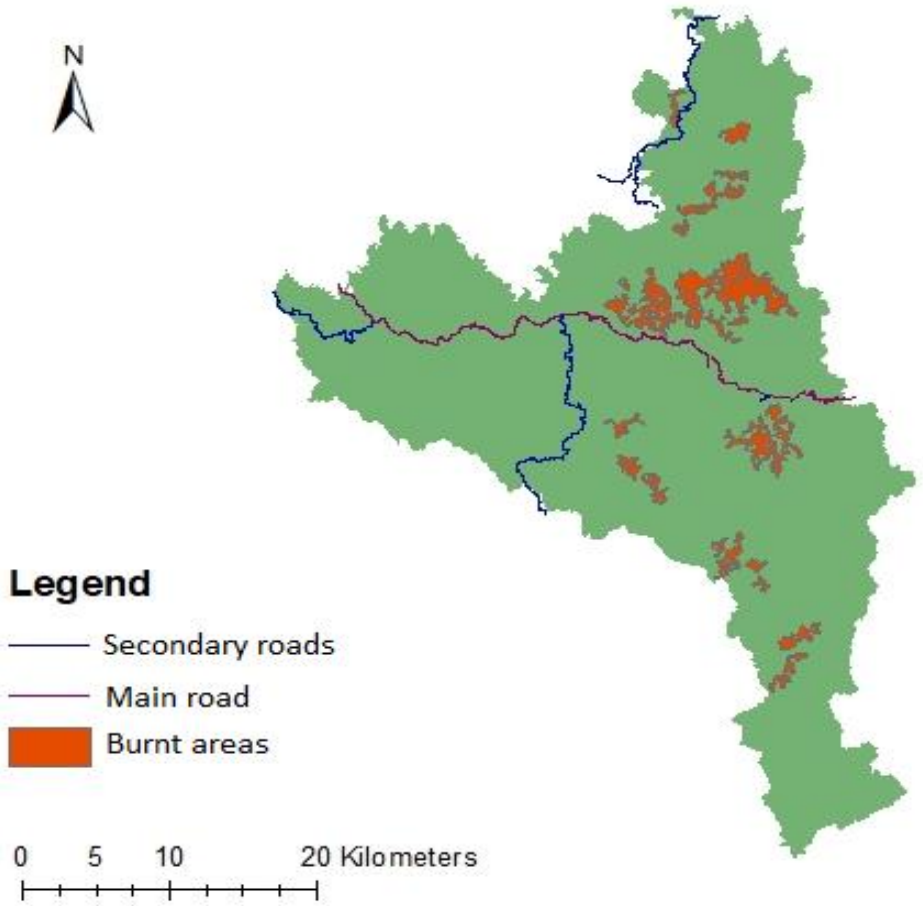

FIGURE A1.2. Extreme fire-degraded areas within Nyungwe National Park, Rwanda. Most fires had anthropogenic origins, particularly honey collection, hunting, and mining practices. Extensive fires took place during the El Niño period of 1997–1998. Map source: WCS-Rwanda.

Chapter 5 | Effects of habitat degradation on avian seed dispersal in an Afro-tropical rainforest: The case of Nyungwe montane rainforest, Rwanda

5.1 Abstract

Although habitat loss and degradation feature among the leading drivers of biodiversity loss in tropical rainforest, there is scarce information on their effects on key ecosystem functions, such as seed dispersal. To contribute to addressing this gap in knowledge, we report a small-scale study based on 12000 minutes of recording fruit handling by vertebrate frugivores during field surveys in 2017–2018 in the Nyungwe National Park, Rwanda. We found that small-bodied birds, in particular, *Eurillas latirostris* (the yellow-whiskered greenbul), dominated the plant–frugivore interactions. The potential number of seeds dispersed depended on the habitat and frugivore functional group. Large birds dispersed more seeds in undisturbed habitats than in disturbed habitats, and the reverse was true for primates. Although our findings are consistent with previous studies, they were based on few observations. Extensive surveys of the wider network of plant – frugivore of the forest will be needed to yield conclusive results. Alleviating the disruptions of seed dispersal processes in tropical forests necessitates ecological restoration approaches that take into consideration the disturbance history of the landscape and the differential responses of frugivorous assemblages.

Key words: Anthropogenic disturbances, birds, ecological restoration, Nyungwe National Park, seed dispersal, tropical forests, vertebrates.

5.2 Introduction

Nyungwe National Park (Nyungwe NP) is a 1,019 km^2 high-elevation montane forest situated in South-western Rwanda ($2^0$15'-$2^0$55'S, $29^0$00'-$29^0$30' E). The forest receives a mean annual rainfall of 1,744 mm, and the daily temperature ranges from 10.9^{0}C to 19.6^{0}C (Sun et al., 1996). Before being gazetted as a National Park, parts of the Nyungwe forest were massively degraded by agricultural activities, anthropogenic fires, mining and hunting of the megafauna, which led to the extirpation of elephants (*Loxodonta africana*) and buffalos (*Syncerus cafer*) (Masozera and Alavalapati, 2004). Despite these disturbances, the forest harbours 13 species of primates including the Chimpanzee (*Pan troglodytes schweinfurthii*), the mountain monkey (*Cercopithecus lhoesti*), which is an Albertine Rift endemic species (ARE), and a group of 450 Colobus monkeys (*Colobus angolensis*). Nyungwe NP is an important bird area harbouring more than 275 bird species (Plumptre et al., 2006), of which 21 are endemic to the Albertine Rift. The vegetation is typical of montane forests, and comprises about 50 local endemics and 280 ARE (Fischer and Killmann, 2008). Although a number of studies have investigated seed dispersal processes in Nyungwe NP, they have focused either on a small number of trees (Gross-Camp et al., 2009b), or a small selection of frugivores (Sun et al., 1997, Sun and Moermond, 1997, Kaplin and Moermond, 1998).

5.2.1 Research aims

Our study aimed to explore the plant–frugivore network of the Nyungwe NP and to assess the effects of anthropogenic disturbances on seed dispersal processes. The network comprised birds, primates, and squirrels, and the fruiting plants they feed on.

We asked: i) which species play important roles in terms of plant–frugivore interaction frequency and the potential number of seeds dispersed (PSD), ii) How does PSD change with frugivore functional group and across the habitat types?

5.3 Frugivores and plants sampling

We used the point count sampling method to record frugivores within disturbed and undisturbed habitats of the Nyungwe NP. We conducted 100 points in undisturbed forest and 500 in disturbed forest habitats. Each point had a radius of 100m and was replicated over two seasons in 2017–2018. A focal individual was chosen and observed for a fixed period of one minute during a feeding event. Its time of arrival and departure, the tree species, the number of fruits and the total amount of time spent foraging were also noted. The duration of observations per point was 10 minutes, amounting to 12,000 minutes over the whole study. The frugivore survey was conducted by one field technician with over 20 years of experience of surveying plants and vertebrates in the study area.

To assess the topological positions of frugivores in the network, we calculated (i) the normalized degree, which measures the number of interactions involving a species, normalized between 0 and 1 (Martín González et al., 2010), and (ii) the species strength, which measures how much plant species depend on the frugivores (Bascompte et al., 2006). The metrics were computed using the bipartite package (Dormann et al., 2009). Due to the low number of observations and to avoid potentially misleading interpretations, advanced network-level analyses were not carried out.

Following Gross-Camp et al. (2009b), the potential number of seeds dispersed by a species was obtained by multiplying the seed dispersal rate for each species (the number of seeds

processed per minute) by the number of individuals belonging to that species, and by the time (total feeding duration of the species) per count. A 2-way ANOVA was performed to determine how PSD varied with the functional group type (small-sized birds, large-sized birds, primates and squirrels) and habitat type (disturbed and undisturbed). PSD values were then averaged per species. We transformed PSD values to meet normality assumptions using the log transformation. We checked homogeneity of variance and found it to be non-significant. Due to the unbalanced nature of our observations, we computed ANOVA using the Type-III sums of squares. Statistical analyses were performed using the R program (R CoreTeam, 2019).

5.4 Results and Discussion

5.4.1 Important frugivores in the network

We observed 45 interaction events involving 15 frugivores and 14 plant species. Of these, 21 interactions took place in undisturbed forest, and 24 in disturbed habitats. The frugivores recorded included eight small-bodied birds, one medium-sized bird, two large-bodied birds, two cercopithecine primates and one squirrel (Fig. 5.1). Most of the recorded frugivores consumed fruits at moderate to high levels (Table 5.1). Only *Crithagra burtoni*, *C. striolata* and *Zestorops senegalensis* were facultative frugivores. The best-represented family among frugivores was Pycnonotidae (bulbuls), which was represented by three species. *Eurillas latirostris* (the yellow-whiskered greenbul), a species of this family, had the highest interactions as demonstrated by a normalized degree of 0.21 and a species strength of 1.85

(Table 5.1). It was followed by *C. cristata*, of the family Musophagidae (Turacos), with a normalized degree and species strength of 0.14 and 1.75, respectively.

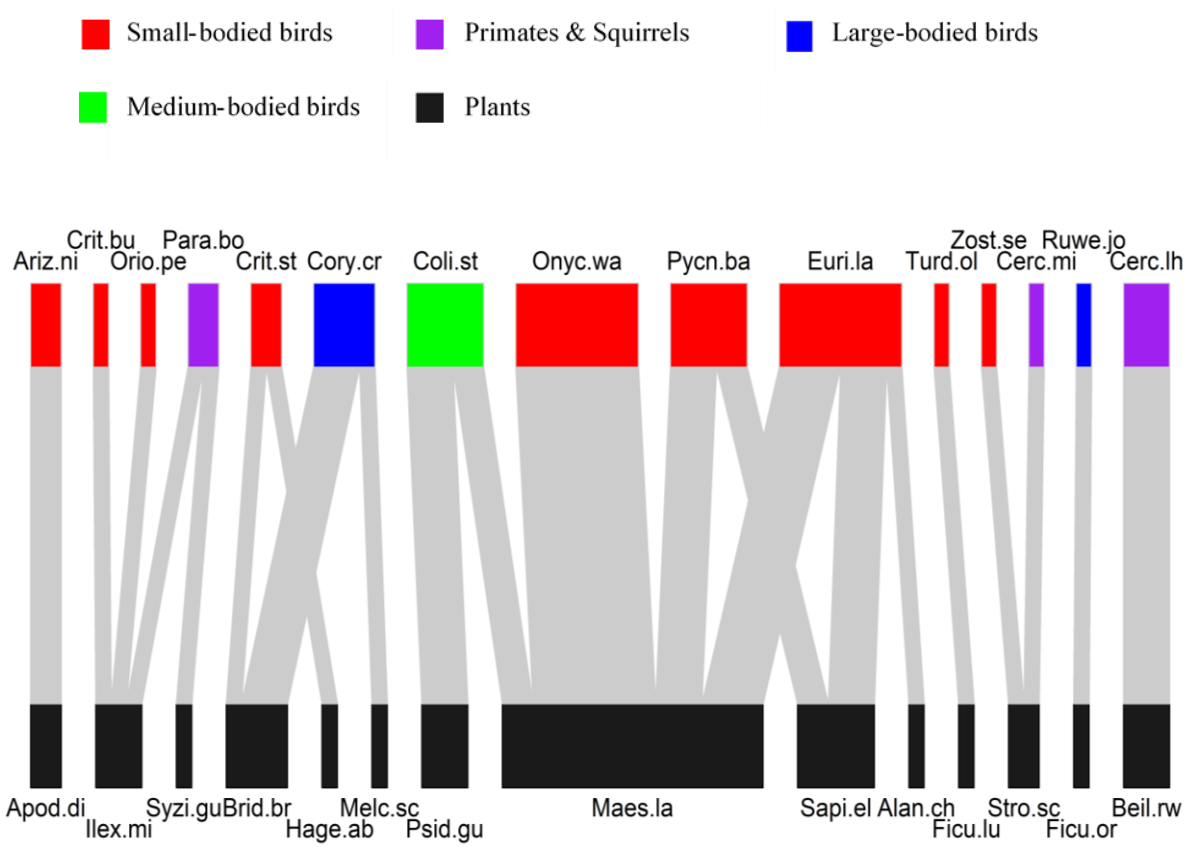

Figure 5.1 Plant–Frugivore network of the Nyungwe NP, Rwanda. Upper and lower boxes represent frugivores, and plants, respectively. The grey bars depict pairwise interactions, and their width indicate the frequency of the interaction for the whole study (N = 1200 minutes). Full names of the species are provided in Tables 5.1 and 5. 2.

The highest potential number of seeds dispersed (PSD) was attained by *Onychognatus walleri* (Waller's starling), with a score of 80, followed by *Pycnonotus barbatus*, a bulbul widespread across the country, and the guenon *C. lhoesti* with a score of 54. *O. walleri*, a flocking

species, was observed in a group of five at two different interactions. In each case they were feeding on the fruits of *Maesa lanceolata.* The main module in the network was formed by three small-bodied frugivores: *E. latirostris, O. walleri, P. barbatus* and three small-seed plants: *Alangium chinense*, *M. lanceolata*, and *Sapium ellipticum* (Fig. 5.1). The recorded plants were all indigenous trees, except *Psidium guajava*, a fruiting tree native to Central and South America and the Caribbean, which is grown in farms adjacent to the park. *Ficus lutea* begins as an epiphytic strangler fig, which becomes terrestrial as it develops and ages (Table 5.2; Fischer and Killmann, 2008).

Table 5.1 Species-level network analysis of 15 frugivorous species observed in Nyungwe NP, Rwanda in a survey conducted in 2017–2018. The percentage of fruits in the diet of each species is put in parentheses, where available. All are birds except: *Cercopithecus lhoesti*, *Cercopithecus mitis*, and *Paraxerus boehmi*. Source of the dietary information for *R. johnstoni* and *C. cristata*: Sun et al., 1997, *C. lhoesti*: Kaplin and Moermond (2000), *C. mitis* and *P. boehmi*: Kingdon et al. (2013), all other species: Wilman et al. (2014). PSD stands for Potential seed dispersal. The potential seed dispersal (PSD) of each species is averaged across all plants consumed during the study period.

Species	Family	Frugivory level	Normalised degree	Species strength	PSD
Arizelocichla nigriceps	Pycnonotidae	High (60)	0.07	1	6
*Cercopithecus lhoesti**	Cercopithecidae	Moderate (42)	0.07	1	54
Cercopithecus mitis	Cercopithecidae	Moderate (40)	0.07	0.5	18
Colius striatus	Coliidae	High (70)	0.14	1.12	15
Corythaeola cristata	Musophagidae	High (73.3)	0.14	1.75	52
Crithagra burtoni	Fringillidae	Low (30)	0.07	0.33	50
Crithagra striolata	Fringillidae	Low (30)	0.14	1.25	11
Eurillas latirostris	Pycnonotidae	Moderate (50)	0.21	1.84	20
Onychognathus walleri	Sturnidae	Moderate (50)	0.07	0.47	81
Oriolus percivali	Oriolidae	Moderate (50)	0.07	0.33	2
Paraxerus boehmi	Sciuridae	High	0.14	1.33	8
Pycnonotus barbatus	Pycnonotidae	Moderate (50)	0.14	0.58	70
*Ruwenzorornis johnstoni**	Musophagidae	High (91)	0.07	1	1
Turdus olivaceus	Turdidae	Moderate (40)	0.07	1	30
Zosterops senegalensis	Zosteropidae	Low (30)	0.07	0.5	4

* Albertine Rift endemic birds and mammals

Contrary to our expectations, *Ruwenzorornis johnstoni*, a turaco endemic to the Albertine Rift, scored the lowest PSD despite having the highest proportion of its diet constituted of fruits (Sun and Moermond, 1997). The low record of *R. johnstoni* in comparison its sympatric *C. cristata* may be explained by the different foraging and ranging behaviour exhibited by the two species. While *R. johnstoni* is territorial, and often forages in pairs, *C. cristata* has a

larger home range, which is 50 times greater than the territory of *R. johnstoni,* and a flocking size of 6–20 (Sun and Moermond, 1997). Sun et al. (1997) concluded *C. cristata* dispersed seeds the furthest distance from a parent tree, largely due to its long flight distances and higher gut retention time, while *R. johnstoni* dispersed the highest number of seeds from a parent tree, owing to its shorter feeding duration per tree and quick departures after feeding events.

Although, the number of frugivores encountered was low in relation to the duration of observations (12,000 minutes), this is not unusual for the Nyungwe forest. A study by Martino (2015) conducted from November 2011 to September 2012, focusing on fruiting individuals of two large seeded tree species, *Chrysophyllum gorungosanum* (N = 24), and *Syzygium guineense* (N=24), recorded only seven species of birds. Observations spanned 6 am – 7 pm and a focal tree was observed for a fixed period of 2 hours. The specimens of *Chrysophyllum gorungosanum* received attention from only one bird and six primate individuals for the whole duration of the study. Species recorded by Martino (2015), but missed by our study include: two large frugivores: *Tauraco schuetti*, *Bycanistes subcylindricus*, one small-bodied bird, *Treron calvus*, three primates: *Cercopithecus mona, Colobus angolensis Ruwenzori*, and *Lophocebus albigena*. These species, along with *Paraxeus* sp., were recorded feeding on the fruits of individuals of the large-seeded tree *Syzygium guineense.*

In our study the fruits of *S. guineense* were observed to be consumed by *P. boehmi. S. guineense* is the most common tree species in the Nyungwe forest, with a relative density of 12.8/ha (Kaplin et al., 1998), and constitutes a high proportion of the diet of *Cercopithecus*

mitis doggeti, *Cercopithecus lhoesti* and *Pan troglodytes* (chimpanzee) (Kaplin et al., 1998, Gross-Camp et al., 2009a, Gross-Camp and Kaplin, 2011). *Beilschmiedia rwandensis,* another large-seeded tree observed in our study, was the most dispersed tree (mean of 54) by *Cercopithecus lhoesti.* The small-seed trees *F. oreodryadum* and *Melchiora schliebenii,* both dispersed by *R. johnstoni* and *C. cristata*, were also highly dispersed by Cercopithecines in a study conducted by Kaplin and Moermond (1998). The authors found seeds of the two trees in 70% of dung samples of *Cercopithecus lhoesti*, 66 % and 84% of the dung of *Cercopithecus mitis doggetti*, respectively.

Table 5.2 Plant species consumed by frugivores in Nyungwe NP, Rwanda recorded in our survey conducted in 2017–2918. The source of information on fruit size were, for *Hagenia* abyssinica: https://uses.plantnet-project.org/en/Hagenia_abyssinica_(PROTA), for *Psidium guajava*: https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/psidium, for *Ficus oreodryadum*: measured from the field, and for the rest: Fischer and Killmann (2008). The internet resources were last accessed on 28/05/2020.

Full name	**Family**	**Fruit size**
Alangium chinense	Alangiaceae	0.6–0.8 cm L, 0.4 x 0.8 cm W
Apodytes dimidiata	Icacinaceae	0.5–1.1 cm L, 0.3–0.4 W, 0.5–0.9 H
Beilschmiedia rwandensis	Lauraceae	4–6cm L
Bridelia brideliifolia	Euphorbiaceae	0.7–1.2 L x 0.4–0.7 cm W
Ficus lutea	Moraceae	1–2.5 up to 3.5 cm D
Ficus oreodryadum	Moraceae	1.5 cm D
Hagenia abyssinica	Rosaceae	2.5 mm D (Achene)
Ilex mitis	Aquifoliaceae	0.4–0.7 cm D
Maesa lanceolata	Myrsinaceae	0.3–0.5cm D
Melchiora schliebenii	Theaceae	2–3cm L | 1 cm D
*Psidium guajava**	Myrthaceae	5–10 cm D
Sapium ellipticum	Euphorbiaceae	0.8–1cm D
Strombosia scheffleri	Olacaceae	2–5cm L
Syzygium guineense	Myrtaceae	0.8–1.2cm D

Note: *B. rwandensis* is endemic to Rwanda. D and L, W, H stand for diameter, length/long, width, and height, respectively. *P. guajava* is a non-native fruit tree grown in farms and home gardens.

5.4.2 Potential seed dispersal

We found a statistically significant interaction between the effects of habitat and functional group (small-sized birds, large-sized birds, primates and squirrels) on PSD ($F_{2, 21} = 4.144$, $p = 0.03$). Primates dispersed more seeds in disturbed habitats than in undisturbed habitats and the reverse was true for large birds (Fig. 5.2). Although, the observations were too few to generalize to the whole study area, a similar pattern was observed by Martino (2015)**,** who noted that visits by large birds to fruiting trees, their foraging time and the number of fruits removed, were considerably lower at forest edges adjacent to tea farms than in forest interiors, while primates had more visits, foraged longer and removed more seeds at forest interior sites. Gross-Camp and Kaplin (2011) noticed that *Cercopithecus lhoesti* dispersed seeds in open habitats, including in fire-degraded areas and near roads. In a separate study within Nyungwe NP, Gross-Camp et al. (2009b) found that frugivores differed in their PSD depending on the tree species. Large-bodied birds and cercopithecines had the highest PSD for the large-seeded tree species *Ekebergia capensis*, while Chimpanzees had higher PSD for *S. guineense*. The differences in the responses functional groups to disturbances might depend on the types of plant species available, which in turn depends on the type and degree of disturbance.

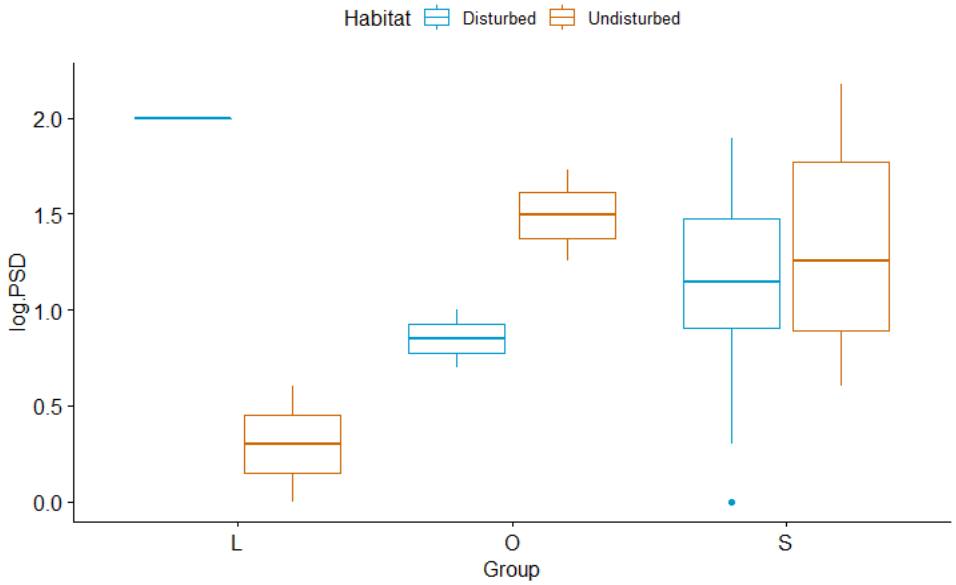

Figure 5.2 The potential number of seeds dispersed by large-bodied birds (L; N = 5, Species =2), primates and squirrels (O; N = 7, Species = 3), small-bodied birds (S; N = 34, Species = 10) recorded during 45 feeding events in Nyungwe NP, Rwanda. *Colius striatus*, the only medium-sized bird recorded, is classed among small birds in this analysis. PSD values were transformed (log_{10}) to meet ANOVA assumptions.

There was no significant difference between the PSD values of small-bodied birds between disturbed and undisturbed habitats. Gross-Camp et al. (2009b) showed that the potential number of seed dispersed by small-bodied birds was greatly influenced by the fruiting neighbourhood. The study noted as many squirrel visits to some of the focal trees as cercopithecines, however, their PSD was penalized if the seed was dropped. Although, seed handling manoeuvres are strong determinants of seed dispersal effectiveness (Schupp et al., 2010), they were not considered in our study due to the difficulties of making accurate observations in the field, and the uncertainty of the fate of the seed after removal from the trees. Gross-Camp et al.'s (2009a) study on Chimpanzee showed that seeds that had been spit

out had higher rates of germination than those defecated, despite close proximity to the parent tree. Similar observations were made by Lambert (2002) in Kibale forest for seeds spat out by the red-tailed monkey (*Cercopithecus ascanius*, a species also found in Nyungwe NP. In contrast, Wrangham et al. (1994) noted that seeds of *Chrysophyllum gorungosanum* defecated by chimpanzee and elephants had a higher rate of germination than those collected underneath parent trees. These contradictions underline the need for further studies on differential seed handling of frugivores and implications on seed establishment and recruitment.

5.4.3 Forest restoration: the last resort for the maintenance of seed dispersal functions in degraded tropical forests

The multitude of human disturbances in tropical forests have culminated in frugivore communities that are dominated by small-bodied frugivores, and such alterations shift the vegetation structure and composition towards poorly dispersed plants (Kurten, 2013, Poulsen et al., 2013). Ecological restoration is thus imperative for the reversal of the impairment of dispersal functions, where it is possible. Passive restoration methods, where the cause of the degradation is halted to permit natural regeneration processes to resume, have enabled the recovery of the vegetation structure across the tropics (Chazdon, 2017, Chazdon and Guariguata, 2018). However, the success of this approach in some forests is limited by the low input of forest seeds, predation of the seeds and seedlings and the presence of certain plants such as bracken or grasses that inhibit any succession (Ingle, 2003, Holl, 2017, Ssali et al., 2017).

Although regeneration by tree plantings might be costly for tropical countries already facing financial constraints, the planting of a few indigenous trees, particularly in agricultural areas, may sustain resilient dispersers by acting as stepping stones, improving connectivity of the landscape (Gillies and St. Clair, 2010, Cottee-Jones et al., 2015). Other low-cost, and effective approaches have included the combination of clearing of the inhibiting plants and the supply of artificial perches (Schubert et al., 2020). Nonetheless, such low-cost restoration presents no silver bullet for all disturbed forests since frugivore assemblages respond differently to disturbances. Factors such as disturbance history of the landscape, and habitat affinities of members of the frugivore networks should be taken into account when devising restoration approaches. Accumulating such information will necessitate extensive research of all demographic stages of the seed dispersal process. As advancements are made in surveying technologies and the application of artificial intelligence, such monumental tasks will become more manageable.

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Chapter 6 | Effects of land-use change on the avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest

Published in *Diversity and Distributions*

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6.1 Abstract

Aim: Although land-use change figures among the leading causes of biodiversity loss worldwide, there is scant information on the extent to which it has affected bird community properties in the Afrotropical region. This study aimed to quantify how different degrees and forms of habitat transformation affect avian species composition, taxonomic diversity, functional trait structure and phylogenetic diversity.

Location: Nyungwe landscape, an Afrotropical montane rainforest and adjoining farmlands in South west Rwanda.

Methods: Data on occurrence, abundance, and functional traits indicative of habitat type and use were collected using point counts, and habitat assessment conducted in major land-use types in 2017/2018. Data on morphological traits of study birds were collected from museum specimens. To quantify avian diversity, metrics including the Inverse Simpson index, functional dispersion and standardized effect size of mean nearest taxon distance were used.

Results: In comparison to the primary forest, land-use change altered species composition, and reduced species diversity. Loss of functional diversity was accentuated in restored areas and cultivated areas. In contrast, the phylogenetic structure was similar across the land-use types, but declined in cultivated areas. Soil moisture, elevation, and lower vegetation height were major attributes influencing avian diversity, however, they exerted varying effects on the three facets studied.

Main conclusions: The sensitivity of forest species to low levels of disturbances highlighted the indispensability of primary vegetation. Extreme habitat transformation such as agriculture

filtered certain avian clades, and subsets of traits linked to key ecological functions. Long-term conservation of bird communities in the Afrotropics necessitates halting wide-scale destruction of the natural vegetation and extending ecological restoration of degraded habitats. As different components of avian diversity respond to differing land use and micro-climatic drivers, the study highlights the challenges of developing comprehensive conservation prioritizing approaches at the landscape scale.

Key words: Birds, functional diversity, land-use change, Nyungwe forest, phylogenetic diversity, taxonomic diversity, tropical forest

6.2 Introduction

Tropical forests harbour about 50% of the world's terrestrial species, including 91% of terrestrial avian species, and provide essential ecosystem services ranging from carbon sequestration, to climate and water regulation **(**Barlow et al., 2018; Dirzo & Raven, 2003; Phillips, Newbold, & Purvis, 2017). Of greatest interest are the tropical montane ecosystems whose exposure to high fluctuation of abiotic factors, mainly climatic ones has contributed to their rich and distinct taxonomic and phylogenetic assemblages (Quintero & Jetz, 2018; Rahbek et al., 2019). Despite the multitude of services provided by tropical forests, they are facing increasing biodiversity loss due to land-use change, mainly in the form of conversion of natural habitats for agriculture (IPBES, 2019; Turubanova, Potapov, Tyukavina, & Hansen, 2018).

Using a low environmental degradation scenario incorporating the combined effects of climate change and land-use change for 8,750 bird species, global projections by Jetz, Wilcove, and Dobson (2007) showed that 900 land bird species will experience range contractions of at least 50 % by the end of this century. The study indicated a particularly bleak future for tropical montane endemic species, due to accelerated anthropogenic habitat conversions. In a similar vein, Ayebare, Plumptre, Kujirakwinja, and Segan (2018) predicted up to 75% loss of suitable habitat by 2080 for 162 endemic vertebrate and plant species under future climate change using climate-based niche models within the Albertine Rift. The Albertine Rift, (313 000 km^2) is part of the East African Rift and supports the highest number of Africa's vertebrate species, and the highest number of endemic vertebrate species in mainland Africa (Plumptre et al., 2003, 2007).

Although birds have been the focus of many land-use change studies, research coverage in the Afrotropics remains poor, and is dominated by the species richness as the response variable of interest. Analysis of species diversity patterns remain very relevant, mainly due to the wide utility of the species concept from local to global conservation schemes, however, it has been proven insufficient in capturing species' links to ecosystem processes, and responses to environmental disturbances (Cadotte, Carscadden, & Mirotchnick, 2011; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Petchey & Gaston, 2002; Walker, Kinzig, & Langridge, 1999). To fill this gap, functional trait-based approaches are gaining prominence. A functional trait is defined herein as a quantifiable aspect of an organism that influences its interaction with the environment (Flynn et al., 2009). The complexity of avian interactions with their environment prohibits exhaustive quantification, however the use of measurable morphological traits, for instance beak measurements allows the assessment of aspects of the trophic niche, and thus enable inferences to be made on the magnitude of perturbances on ecosystem functions such as seed dispersal, and pest control (Pigot et al., 2016).

Studies on functional diversity in the tropics have found declines with increasing land-use change, mainly agriculture (Flynn et al., 2009; Şekercioğlu, 2012). Despite this previous work, other land-use types remain poorly assessed, and there is still little known on the exact functions being affected by anthropogenic disturbances since a range of traits representing different trophic processes are often pooled together in studies assessing multiple functional traits (but see Bregman et al., 2016; Trisos et al., 2014).

Additionally, measures of evolutionary history, often termed phylogenetic diversity (PD) are increasingly used to determine community responses to environmental disturbances for a range of taxa (Rolland et al., 2012, Aguirre-Gutiérrez, 2020). For example Helmus et al.'s (2010) experimental study of zooplankton communities in 18 North American lakes, made up of both undisturbed lakes and those subjected to a range of abiotic and biotic disturbances, reported that disturbance events always culminated in community assemblages of phylogenetically related species regardless of the nature of the disturbance. Comprehensive assessment of land-use change effects on avian communities, thus necessitates the consideration of different facets of biodiversity in order to guide conservation strategies effectively (Chapman, Tobias, Edwards, & Davies, 2018; Devictor et al., 2010).

In this study, we assessed how land-use change (i.e modification from relatively undisturbed primary forest to other land-use types) has affected bird communities within Nyungwe forest— a key landscape in the Albertine Rift, and adjoining agricultural farms located in south west Rwanda, a region that is underrepresented in ecological and biogeographical research. In particular, we asked how avian species composition, and taxonomic, functional, and phylogenetic diversity vary across different land uses. Since land-use change often entails the modification of the physical and vegetation structures of a habitat, we also examined the important habitat attributes driving the different components of avian diversity in this system. In accordance with the Environmental-filtering hypothesis, we predict that new habitat conditions induced by land-use change will exclude species on the basis of their traits, resulting in: i) lower species diversity, ii) species with similar functional traits (Keddy, 1992, Mouillot et al., 2013), and iii) species with closer phylogenetic relationships (Webb et al., 2002, Tucker et al., 2017). Since the vegetation structural complexity is known to drive

avian diversity (MacArthur & MacArthur, 1961; Evans, Reitsma, Hurlbert, & Marra, 2018), we also predict that iv) habitat attributes representing vegetation structure, such as lower vegetation height and tree cover will drive positively the three components of avian diversity.

The study focused on birds due to the extent of information available on their taxonomy, distribution, eco-morphometric traits, dated species-level phylogeny, and their sensitivity to environmental change (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Seymour, 2015). In addition to the exploration of different facets of the avian diversity, the study uses a range of diversity metrics, and two levels of functional diversity analyses, that is, combining multiple traits, and partitioning them in key ecological niche axes to gain broader insights into avian community changes across different land uses.

6.3 Methods

6.3.1 Study area

The study area comprised Nyungwe National park (Nyungwe NP) and surrounding agricultural areas, hereinafter Nyungwe landscape (Fig. 6.1). Nyungwe NP is a tropical montane rainforest covering an area of 1,019km^2 and is situated in south-western Rwanda at an elevation range of 1,600 – 2,950 m. The mean annual rainfall is 1500 – 2500 mm, and the average minimum and maximum temperature are 10.9^{0}C and 19.6^0 C, respectively (Seimon, 2012; Sun et al., 1996). Nyungwe NP was initially gazetted as a forest reserve in 1933, and gained the status of National Park in 2004. The forest is considered among the six key landscapes of the Albertine Rift in terms of endemic species and imminent threats (Plumptre et al., 2007).

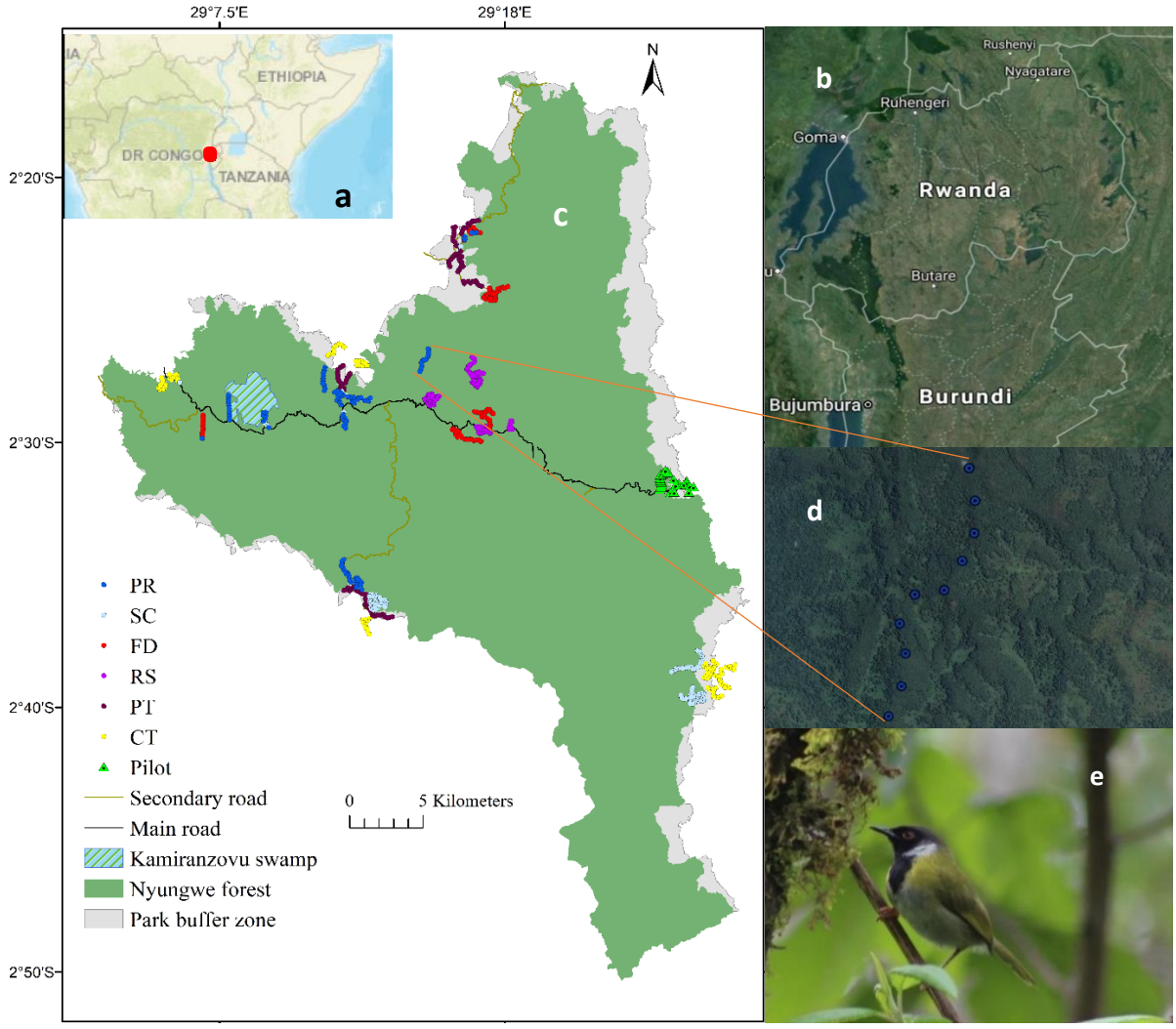


FIGURE 6.1 Location of the Nyungwe-Kibira landscape within Central and Eastern Africa (**a, b**). The extent of 600 point plots sampled in six different land-use types in the Nyungwe landscape, Rwanda (**c**). Each plot was sampled twice. The plots were mostly contiguous within the same sites and hence, due to overplotting, only a fraction of the 600 points can be seen on the map. Plots sampled in the primary forest at Mt. Bigugu (**d**). A high number of points in restored areas are close to the main road because one of the criteria considered by the restoration project was visibility from the road for tourism and aesthetic purposes (Masozera and Mulindahabi, 2007). *Apalis personata*, an Albertine Rift endemic bird that is commonly encountered in the Nyungwe forest (**e**). Base map source: WCS-Rwanda and Google Earth.

Changes to the Nyungwe landscape within the past 50 years have largely occurred in the form of forest clearing for agriculture, settlements and roads; gold and sand mining; and the harvesting of trees, and non-timber products, such as medicinal herbs and honey (Masozera & Alavalapati, 2004). To delineate the forest from community land holds, a buffer zone of non-indigenous trees was established in the 1980s, creating a distinct vegetation. According to Masozera and Mulindahabi (2007) fires largely resulting from honey collection and hunting practices have contributed to the degradation of at least 12% of the forest, in some areas impeding tree growth for decades due to the colonisation of opportunistic ferns. Assisted-natural regeneration activities were initiated in 2003 by the Nyungwe NP management and key conservation stakeholders to restore extreme fire degraded areas.

6.3.2 Study design

Based on the land-use history of the study area, six major land-use categories were identified. 1) Primary forest (PR): mature and old-growth forest whose vegetation structure and composition have not been substantially disturbed and appear relatively intact; 2) Secondary forest (SC): forest regrowth after non-fire disturbances, such as mining, and cultivation; 3) Fire-disturbed areas (FD): parts of the forest affected by fires, but undergoing natural regeneration; 4) Restored areas (RS): forest regrowth after human assisted natural regeneration of burnt areas; 5) non-native tree plantation (PT): non-indigenous plantations of pine and *Eucalyptus* trees serving as a buffer zone; and 6) Cultivated areas (CT): tea estates and mixed-crop farms adjacent to the park. A series of meetings with key people involved in the park management and monitoring was organized to identify sampling sites within each land-use type taking into consideration accessibility, and safety factors. A four-day pilot study was conducted to test the study methods and to train three field assistants. Sampling

was conducted in two phases: 14 November 2017 to 09 February 2018, and 06 June to 25 August 2018, corresponding to a long wet and and a long dry season, respectively.

6.3.3 Avifaunal sampling

A point-count transect method was used to collect data on the occurrence and abundance of birds in the Nyungwe Landscape. The method comprised selecting randomly the starting point in a predefined site and setting up 10 circular stations (plots) of 100 m radius. The distance between plots was at least 200 m to minimize the risk of double counts and to maintain a degree of randomness and statistical independence (Ralph, Sauer, & Droege, 1995). 100 plots (points) per land-use type were established, collectively surpassing the 300 points recommended when sampling rainforests (Ralph et al., 1995). At sites where trails were present, they were followed for practical reasons due to the rough and steep relief of the sites. Establishing plots along reconnaissance trails gives maximum attention to bird observation, whilst inducing little disturbance to habitats (Bibby, Jones, & Marsden, 2000). Where possible plots were positioned at right angles to the path and 30 m into the habitat (Gregory, Gibbons, & Donald, 2004). Sampling of the same plots was replicated in the second season, amounting altogether to 1,200 point counts. At each point, 1 minute was allowed to elapse, in a bid to let birds settle before taking records of birds seen or heard. Their distance from the centre of the plot was measured using a laser range finder. The count period was of 10 minutes duration (Buskirk & McDonald, 1995). All bird recordings were conducted by one observer with 30 years' experience of avifauna monitoring in the Nyungwe landscape. Sampling usually started at 5:45 and finished at 10:30 am.

6.3.4 Functional traits collection

Considered biometric data for species encountered in the Nyungwe landscape were culmen length, bill length, width, and depth, wing length, tarsus length, Kipp's distance (the length from the tip of the longest primary and the first secondary, on a folded wing) and tail length. The form and size of the bill are strongly associated with the trophic niche, whilst wing, tail and tarsus are indicative of locomotory, flight and foraging strategies (Grant & Grant, 2006; Hutchinson, 1957; Pigot et al. 2020; Schoener, 1965). Kipp's distance provides additional information on the wing morphology relevant to flight and dispersal abilities (Baldwin, Winkler, Organ, & Helm, 2010; Sheard et al. 2020).

Morphological traits were measured from museum specimens using a standardized protocol described in Pigot et al. (2020), and normally constituted two adult male and two adult female specimens per species. Attributes indicative of foraging strata were collected from the field, and were double checked in the *Handbook and Atlas of Birds of Rwanda* (Vande weghe & Vande weghe, 2011). The foraging stratum was classified into lower stratum: 3 metres and below, middle stratum: 4–7 metres, Upper stratum: >7 m. Data on diet for all study birds was extracted from Wilman et al. (2014), a global dataset containing literature-based estimates of dietary proportions for ten different food categories, which we combine to form the following five dietary categories: Invertivores (consuming terrestrial and aquatic invertebrates), Herbivores (consuming plant matter and seeds), Frugivores/Nectarivores, Carnivores/Scavengers (consuming vertebrates, fish and carrion) and Omnivores.

6.3.5 Habitat assessment

For each plot included in the point-count sampling, a smaller plot of 20 m radius was demarcated to record aspects related to the vegetation structure and composition, soil and weather in order to capture fine-scale habitat conditions. The ground cover (the extent of the ground covered with vegetation) was visually estimated and recorded in percentages. The depth of the litter was measured with a thin metallic ruler, and samples were taken and averaged from 4 different random points. The height of undergrowth < 3m (lower vegetation height) was measured with a 3 m folding rule. Tree species (for individuals with diameter at breast height (DBH, 1.3 m >5 cm) were identified, counted and their DBH was recorded in classes of 5-14, 15-50, 51-100, 101-200, and > 200 cm. Tree height was measured with a laser range finder. Canopy cover was estimated from the average of 4 readings, all taken with a spherical densitometer from the four cardinal directions (Cook, Stutzman, Bowers, Brenner, & Irwin, 1995; Jennings, Brown, & Sheil, 1999; Strickler, 1959). A portable data logger was used to record temperature, while soil moisture was measured with a portable soil moisture probe at 5 cm deep.

6.3.6 Statistical analysis

All analyses were conducted at a sample level, which comprised 10 point counts that were mostly contiguous within the same site. To explore differences in species composition across land-use types, a Detrended Correspondence Analysis (DCA) (Hill, 1979) was conducted (Fig. 6.2). To test whether samples within each land-use category exhibited greater compositional similarity than expected by chance, an analysis of similarity (ANOSIM) was performed in the CAP program (Seaby, Henderson, & Somes, 2014) (Table 6.1).

To determine how land-use change affected taxonomic, functional and phylogenetic diversity, the inverse Simpson diversity index, functional dispersion index (Laliberte & Legendre, 2010), and standardized effect size mean nearest taxon distance (ses.MNTD) were computed using the vegan, FD and Picante R packages respectively (Kembel et al., 2010; Laliberté, Legendre, & Shipley, 2014; Oksanen et al., 2010). These three metrics were chosen on the basis of a low correlation between them, and because they allowed the incorporation of abundances. Additional metrics were used for comparison purposes (discussed below).

The inverse Simpson index is a derivative of the Simpson's index that measures the probability that two individuals drawn randomly from a large community belong to the same species. It is weighted by the abundances of the most common species, and it is thus less sensitive to rare species, which abound in rainforest systems. The inverse Simpson index is more robust, intuitive and mathematically correct in comparison to many other species diversity indices (Chao, Chiu, & Jost, 2014; Magurran, 2004).

Functional dispersion measures the overall spread of species trait values in a multi-dimension space (Laliberté & Legendre, 2010). The functional dispersion index (FDis) is less sensitive to species richness than many other functional diversity metrics, and allows the comparison of samples with less than three observations which is not unusual for avian point-counts (Laliberté & Legendre, 2010). To circumvent the problem of considerable intra-specific trait variations, and correlation among avian morphological traits influenced largely by body size, a two-step Principal Components Analysis (PCA) was performed (Trisos et al., 2014). The first PCA was conducted on bill variables, and its second component was retained as an index of trophic processes. The second PCA was performed on tarsus, wing and tail variables, and

its second component was retained as an index of locomotive abilities. To obtain an index of body size, a third PCA was performed on the first axes obtained from the previous PCA analyses. The hand-wing index, an additional index associated with flight and dispersal abilities, was computed from the Kipp's distance and wing variables (Sheard et al., 2020). The obtained indices were then processed as inputs for the computation of the functional diversity metrics in the R package "FD" (Laliberté et al., 2014). Functional diversity was assessed on a pool of all study traits, and at individual subsets of traits indicative of the trophic, dispersal, locomotory and size niche axes.

To perform phylogenetic analyses, a set of 1000 avian phylogenies based on the Ericson backbone (Ericson et al., 2006, Jetz et al., 2012) were extracted from birdtree.org on December 2018. The phylogenetic trees were pruned to match the study species. A consensus tree was then built and converted into a distance matrix from which phylogenetic diversity measures were calculated using the "ape" and "picante" R packages (Kembel et al., 2010; Paradis, Claude, & Strimmer, 2004)**.** We calculated the standardized effect size of mean nearest taxon distance (MNTD) which quantifies the average phylogenetic distance separating individuals from their closest relatives, corrected for species richness using a null model that randomises the tip labels of the phylogeny (999 iterations) (Webb, Ackerly, McPeek, & Donoghue, 2002).

For comparison purposes, additional metrics were computed, including: (i) the functional richness metric (FRic), which measures the volume of functional trait space occupied by a species assemblage (Villéger et al., 2008); (ii) Faith's (1992) phylogenetic diversity metric (PD), which is the sum of branch lengths of a phylogenetic tree encompassing a given

sample, and; (iii) the standardized effect size of mean pairwise distance (ses.MPD), which is the average pairwise phylogenetic distance among individuals in an assemblage corrected for species richness (Webb et al., 2002).

Statistical significance of differences in diversity between the primary forest and other land-use types were tested with the Analysis of Variance (ANOVA) where the metrics fulfilled the test assumptions, otherwise the Kruskal-Wallis test was performed. The tests were followed by a Tukey's post hoc test and Dunn's tests, respectively. Due to the repeated measure nature of the study (temporal replication) and the randomness of sample placements, three linear mixed effects models were first conducted to determine the influence of habitat attributes on the diversity metrics. Sample identity was held as the random variable. A likelihood ratio test showed no significant contribution of the random variable (Kuznetsova, Brockhoff, & Christensen, 2017). Additionally, spatial autocorrelation of the model residuals tested using Moran's *I* coefficient was non-significant for the metrics considered, thus the standard linear regression analysis was performed instead. Canopy height, litter and temperature were not included in the analysis due to their high correlation with other habitat attributes (Pearson's r > 0.7) (Fig. A2.1). Model selection was carried out based on BIC using the "Mumin" package due to the high number of predictors (Barton, 2019). Models within ΔBIC < 2 of the most parsimonious model were then averaged. All analysis, except where otherwise mentioned, weas performed in the R 3.6.1 environment (R CoreTeam, 2019).

6.4 Results

The study recorded a total of 8,656 individuals belonging to 170 species of birds across 1,200 plots sampled in six different land-uses (Fig. 6.1). Per land-use type, the number of

individuals encountered was: Primary forest: 1,954, Secondary forest: 1,471, Fire-disturbed areas: 1,322, Restored areas: 1,289; Non-native tree plantation: 1,093, and Cultivated areas: 1,527. Among the most encountered species was *Zosterops senegalensis*, a small flocking invertivorous species that was mostly recorded in forested sites, *Bradypterus cinnamomeus*, a small understorey invertivore mostly associated with forest edges and clearings, *Apalis personata* and *Phylloscopus laetus*, small Albertine rift endemic (ARE) invertivores exclusively recorded inside the forest, *Onychognathus walleri*, a small flocking frugivorous species which was mostly recorded in the primary forest, *Crithagra citrinelloides* which had about 90% of its abundances in open areas, and *Cinnyris regius*, an ARE sunbird which mostly used forested land-use types (Fig. A2.2). The top 10 abundant species occupied 40 % of all raw abundances.

Albertine Rift endemic species constituted 17.6% of all encountered individuals (N = 8656). The primary forest had the highest number of species (n = 20) and individuals (n = 406), followed by the secondary forest (species: n = 18, individuals: n = 304), while the smallest number of species was recorded in cultivated areas (species: n = 4, individuals: n = 13). Most of the species were recorded in the primary forest, except *Caprimulgus ruwenzorii*, which was recorded in the secondary forest and in fire-disturbed forest, and *Geokichla tanganjicae*, which was only recorded in the fire-disturbed forest. Two individuals of the rare species *Apalis argentea* were only recorded in the primary forest. For one third of ARE, their abundances in the primary forest was double the number recorded in other land-use types.

Phylloscopus laetus was mostly found in the restored forest (n=107), and its abundance was at least double that found in other land-uses.

We recorded 16 migrating species, including seven Palearctic migrants, namely: *Merops apiaster* (N = 68), *Anthus trivialis* (16), *Apus apus* (4), *Buteo buteo* (4), *Hirundo rustica* (4), *Phylloscopus trochilus (2), Falco subbuteo* (1)*;* one Intra-African migrant that breeds in Sub-Saharan Africa (*Clamator jacobinus*); and 8 partial migrant species, part of whose population resides and breeds in Rwanda, while part is involved in intra-African migration, including *Apaloderma narina* (58), *Cuculus clamasus* (29), which were the only migrating species found in the primary forest (Table A2.3). Cultivated areas had the highest number of migrating species (9), and encountered individuals (106), while the primary forest had the smallest number of species (2), and individuals (13). 84% of Palearctic migrant individuals were recorded in cultivated areas (N = 106).

Most of the study species are classified as of 'least concern' according to the IUCN red list of threatened species. Two species are classified as endangered: *Balearica regulorum* (n = 4), an emblematic crane only recorded in cultivated areas, and *Bradypterus graueri* (n = 13), a warbler inhabiting montane swamps. *Cercococcyx montanus* (49) is classed as 'vulnerable', while *Kupeornis rufocinctus* (n = 13) and *Stephanoaetus coronatus* (n = 8) are classified as 'near threatened'. The primary forest harboured 38 % of the abundances of the above-mentioned classified species (N = 104).

6.4.1 Species composition

The DCA (Hill, 1979) estimated the first ordination axis as 3.7 SD units long (Fig. 6.2), implying a considerable species turnover among the land-use types (4 units indicates approximately complete replacement, Jongman, 1995). A forest-to-open area gradient is evident on the first axis, with the primary forest samples on the leftmost side and the

cultivated areas dominating the right side. Secondary forest and fire-disturbed areas showed the highest overlap with other land-use types, but overall segregation of the land-use type was clearly visible. The second axis relates to the elevational gradient, with FD and RS occupying higher elevations and PR at the lower extreme. Sample positions shift with seasons, however, the clustering pattern per land-use type persists, indicating little variation in species composition across sampling seasons (Fig. 6.2).

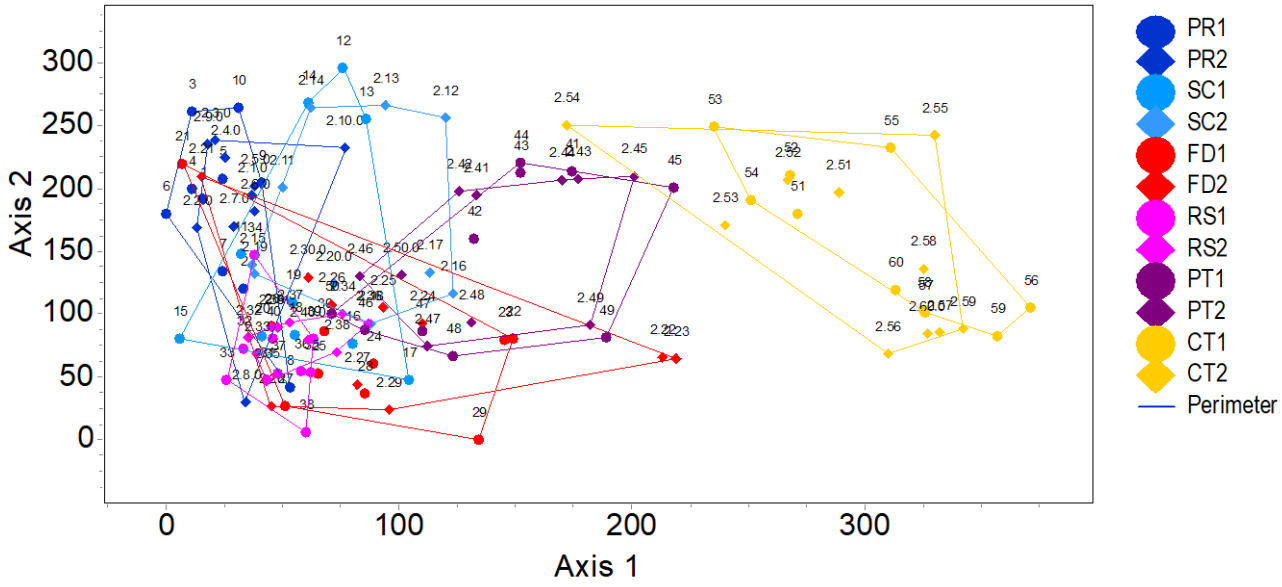


FIGURE 6.2 Detrended Correspondence Analysis (DCA) of bird community composition showing the distribution of samples (N = 120) belonging to the six land-use types within the Nyungwe Landscape, Rwanda, along the first and second ordination axes. The categories constituted of relatively undisturbed primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), restored areas (RS), non-native tree plantation (PT), and cultivated areas (CT). The first sampling was conducted over the wet season and a replication was done over the dry seasons. Circles and diamonds denote the first (wet) and second (dry) seasons, respectively. Each sample has a unique name, and the prefix 2 indicates the replication. The plot was generated using the CAP 5 program (Seaby et al., 2014). The units are standard deviations of species turnover x 100.

The ANOSIM comparing samples (n = 20) within each land-use generated a Sample Statistic (R) of 0.49, (p = 0.01), indicating that samples were significantly similar in composition than expected. Pairwise comparisons among the land-use types were also statistically significant (p = 0.01), indicating separation of the defined land-use types. The least similarity was observed between primary forest habitats versus restored areas and cultivated areas (Table 6.1).

TABLE 6.1 Pairwise comparisons of similarity of bird communities among study land-use types in the Nyungwe landscape, Rwanda. Sample size is 20 per land use. Raw shared species numbers are below the diagonal, and ANOSIM sample R above. Theoretically, R values range from +1 to -1. Values close to +1 indicate that the most similar samples belong to the same group, reflecting higher difference between the compared pair.

	PR	**SC**	**FD**	**RS**	**NF**	**CT**
PR	–	0.21	0.47	0.65	0.63	0.92
SC	81	–	0.18	0.33	0.27	0.83
FD	67	69	–	0.14	0.35	0.80
RS	53	51	50	–	0.53	0.92
PT	63	67	58	44	–	0.63
CT	43	49	40	29	51	–

Note. PR: Primary forest (number of species (N) = 102); SC: Secondary forest (N =101); FD: Fire-disturbed area (N = 83); RS: Restored area (N = 58); PT: Non-native tree plantation (N = 83); CT: Cultivated area (N = 92).

6.4.2 Species diversity

Species diversity, as measured by the Inverse Simpson diversity index, decreased along the disturbance gradient. Species diversity in primary forest was statistically different from those in other categories ($F(5, 114) = 14.11$, $p = 9.788e\text{-}11$), as revealed by ANOVA followed by Tukey's post hoc test. Sharp diversity falls were registered in fire-disturbed areas, restored areas, and monocultures of tree plantation and cultivated areas (Fig. 6.3). The decline in diversity with land-use change intensity was equally observed when other metrics were applied, such as species richness (Kruskal-Wallis ($H(5) = 23.21$, $p < 0.001$), and rarefied species richness (Kruskal-Wallis ($H(5) = 27.60$, $p < 0.001$; Fig. A2.3).

6.4.3 Functional diversity

Functional diversity, measured by functional dispersion (FDis), remained stable across the land-use types (Fig. 6.3), whilst functional richness (FRic) declined in restored and cultivated areas relative to primary forest (Kruskal-Wallis ($H(5) = 19.48$, $p = 0.002$; Dunn's test, $p = 0.006$ and $p = 0.016$, respectively). Separate analyses of niche axes revealed statistically significant differences in FDis levels for the trophic axis only in restored areas (Kruskal-Wallis ($H(5) = 21.85$, $p = 0.0006$; Dunn's test, $p = 0.006$; Table A2.1), and a similar pattern was observed with FRic (Kruskal-Wallis ($H(5) = 16.37$, $p = 0.006$; Dunn's test, $p = 0.002$). There were no evident differences in FDis among land-uses for the dispersal and body size axes, but FRic of body size was significantly lower in restored areas compared to primary forest, and the decline was close to significant in cultivated areas and non-native tree plantation (Kruskal-Wallis ($H(5) = 15.21$, $p = 0.009$; Dunn's test, $p = 0.01$, $p = 0.063$, and $p = 0.072$, respectively). Changes in FDis values across the land-uses for the locomotion axis were only discerned in cultivated areas and non-native tree plantation, where the changes

were both negative relative to levels in the primary forest (Kruskal-Wallis (H(5) = 12.32, p = 0.03; Dunn's test, p = 0.029, and p = 0.067, respectively), and the pattern persisted for FRic (Kruskal-Wallis (H(5) = 16.22, p = 0.006; Dunn's test, p = 0.02, and p = 0.013, respectively).

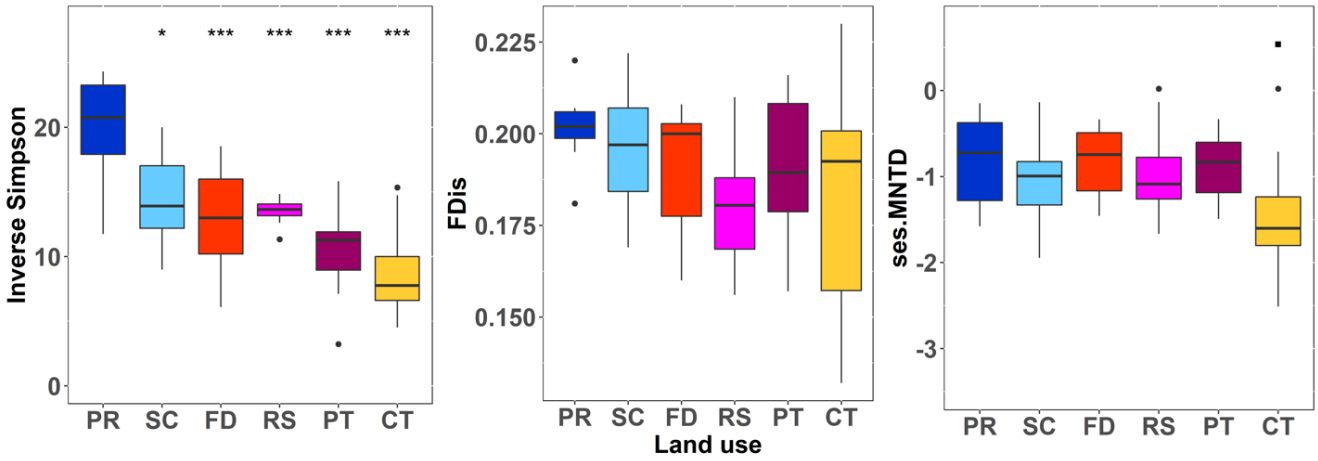


FIGURE 6.3 Effects of land-use change on the Inverse Simpson diversity index (Inverse Simpson), functional dispersion index (FDis), and phylogenetic diversity,(ses.MNTD) for bird communities in the Nyungwe landscape across six land-use types: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), restored areas (RS), non-native tree plantation (PT), and cultivated areas (CT). Sample sizes (n = 10) are equal among categories, and each sample is a pool of 10 point counts within the same land-use type. Each point count was replicated, however, averaged values are used for statistical independence purposes. Asterisks indicate statistically significant differences in comparison to diversity in primary forest: '*' 0.05, '**' 0.01, '***' 0.001. Statistical significance was tested using an ANOVA followed by a Tukey's post hoc test.

6.4.4 Phylogenetic diversity

Differences in phylogenetic diversity measured using ses.MNTD were close to significance across the land-uses, ($F(5, 54) = 2.16$, $p = 0.072$), with lower levels uncovered in cultivated areas (Fig. 6.3; Tukey's post hoc test: $p = 0.068$). ses.MPD remained stable across the land-use types, while Faith's (1992) Phylogenetic diversity metric (PD), which does not incorporate abundances, showed declines in restored areas, and non-native tree plantation, and steeper loss in cultivated areas compared to primary forest habitats (Table A2.2).

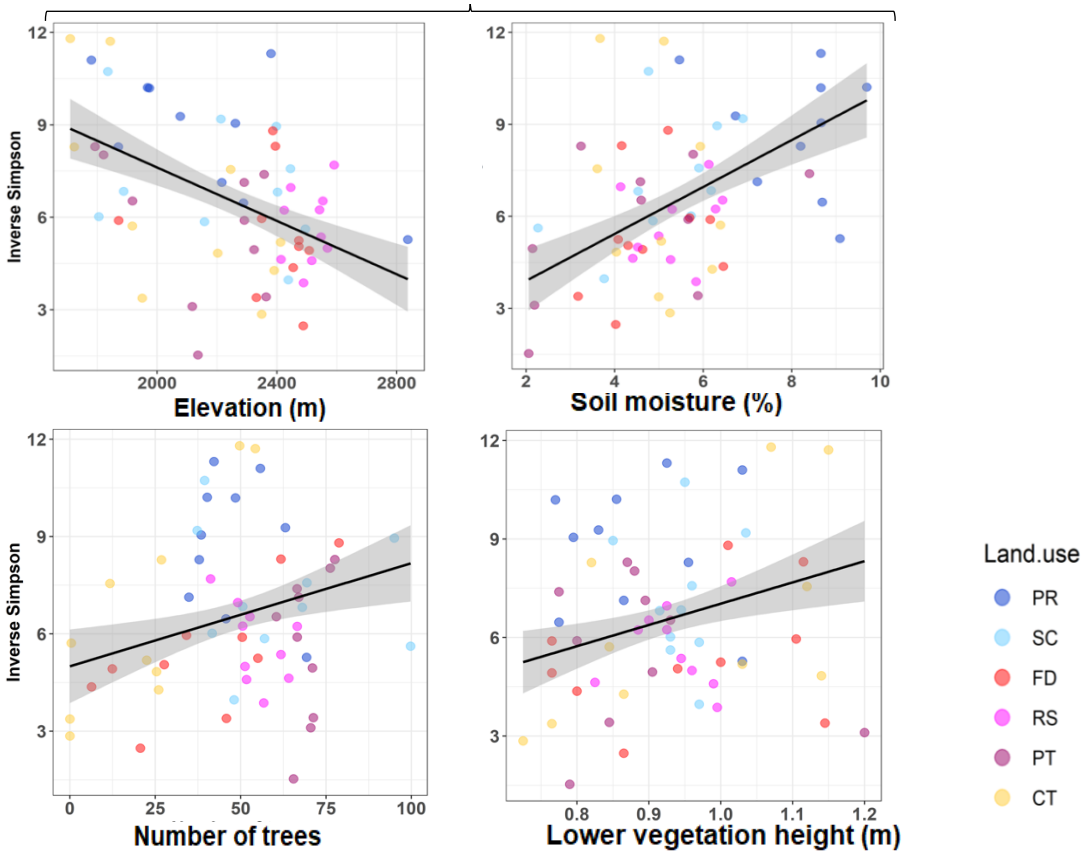
6.4.5 Habitat attributes

The regression model selection analyses revealed elevation as a primary negative influence on species diversity, and functional diversity (Table 6.2, Fig. 6.4a-b). Soil moisture and the lower vegetation height had contrasting effects, in that they influenced species diversity positively, and phylogenetic diversity negatively (Table 6.2). The number of trees was only important for species diversity. Canopy cover and ground cover had weak positive influences on phylogenetic and taxonomic diversity respectively, whilst DBH did not exert much effect (Table 6.2). The models explained a reasonable amount of variation, except for FDis.

TABLE 6.2 Relationship between avian diversity and habitat parameters across sample plots (n= 60). Only models within Δ BIC < 2 are presented. The average of the models and the relative importance of predictors are indicated for each diversity metric. The relative importance is computed by summing Akaike weights over all models containing a given predictor, and ranges from 0 to 1. Values close to 1 represent a strong importance, while those close to 0 represent a weak importance.

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

(a) Taxonomic diversity



(b) Phylogenetic

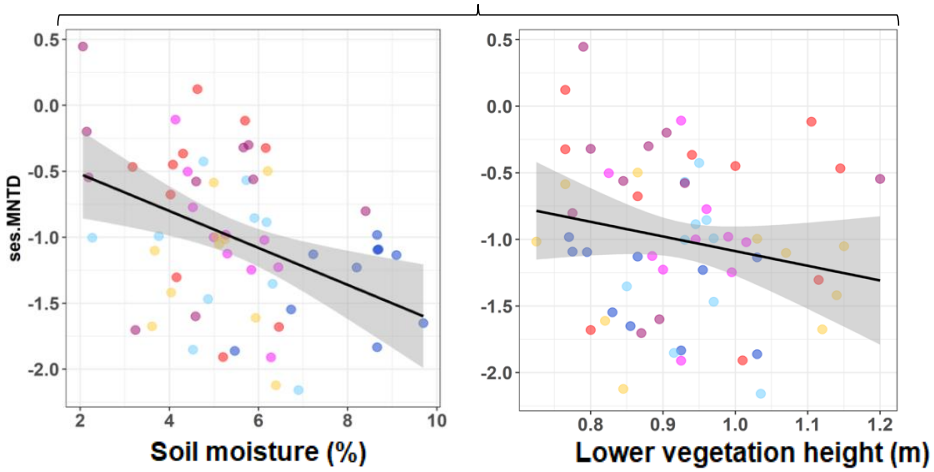


FIGURE 6.4 a-b Relationships between avian species diversity (a), and phylogenetic diversity (b) and habitat parameters of study samples (N=10 per land-use) in the Nyungwe landscape. Species diversity, and phylogenetic diversity are quantified using Inverse Simpson diversity index (Inverse Simpson index), and standardized effect size of mean nearest taxon distance (ses.MNTD) respectively. Results were obtained from a linear model fitted on unscaled raw data. Model estimates obtained from scaled data are given in Table 6.2. The grey band represents ± 95% confidence interval. Models for habitat attributes with lower relative importance values (<0.5) and low adj.R^2 are not displayed.

6.5 Discussion

6.5.1 Altered patterns of species composition and diversity

As predicted, increasing degrees of land-use change altered species composition, and reduced species diversity. The species diversity pattern noted here agrees with studies that concluded bird species diversity within tropical forested landscapes was reduced with intense human habitat transformations, particularly agricultural uses (Albanesi, Dardanelli, & Bellis, 2014; Bregman et al., 2016). Although primary forest and secondary forest had almost equal species richness, the composition of the bird communities was significantly different, highlighting the sensitivity of some forest species even to low levels of disturbances, and the crucial roles that primary vegetation plays in maintaining distinct communities (Barlow et al., 2007; Gibson et al., 2011; O'Dea & Whittaker, 2007). Although a higher species diversity is often reported in secondary forests, the gain usually originates from the influx of generalists and gap-tolerant species (Coetzee & Chown, 2016; Foord et al., 2018; Moura et al., 2013). For instance, in this study, *Platysteira concreta, and Ploceus insignis*, known closed-forest species, were only recorded in the primary forest, while open air and generalist species in the genera *Estrilda*, *Crithagra*, and *Ploceus* were mostly recorded in secondary forests. The degree of disturbance and the time lapsed since release from disturbance may also determine the species diversity supported by secondary forests. Areas restored from fire, which are 1 to 20 years in development had slightly more than half the taxonomic diversity found in the the primary forest, exemplying the long time needed for a full recovery of species diversity in tropical forests (Catterall, Freeman, Kanowski, & Freebody, 2012).

The detection of marked changes in taxonomic diversity across adjoining land-uses at fine-scale of analysis highlights the sensitivity of birds to small scale habitat changes, and evinces

the importance of local conservation interventions (Gonçalves, Cerqueira, Brasil & Santos, 2017).

6.5.2 Differential response of functional diversity to land-use change

Overall functional diversity (measured using the FDis index) was not considerably affected by land-use change, however, analysis at traits axes levels revealed effects of varying magnitude. Restored areas were the most affected land-use type. The registered falls in the trophic and size axes can be explained by the absence of large-bodied birds such as those in the Accipitridae family, typical forest raptors such as *Aquila africanus*, large invertivores (e.g. *Apaloderma vittatum),* large frugivores (e.g. *Bycanistes subcylindricus*). There was overall domination by small-sized insectivorous birds in the restored forests and poor representation of other guilds (Fig. A2.4). Granivores were the least-represented guild as exemplified by the absence of any of the eight forest and non-forest *Ploceus* species recorded by the study. The reduced niche in restored areas can be attributed to the high degradation of the sites by anthropogenic fires before the restoration activities commenced (Masozera and Mulindahabi, 2007). The degree of degradation also underlines the lack of a similar pattern of functional diversity loss in unrestored fire-disturbed habitats (FD). FD sites sampled in our study had experienced fires of varying severity, and some old sites supported a fully established continuous canopy cover.

Cultivated areas in particular, and non-native plantations to some degrees, experienced the contraction of the locomotory niche. This change can be attributed to the homogenous vegetation of these land-use types. The plantations constituted mainly of mature monoculture stands of *Eucalyptus* and *Pinus* species, whilst many cultivated areas contained monocultures of tea plantations (*Camellia sinensis*). The simplified vegetation of these land-uses limits the need for a higher locomotory manoeuvres. Contrary to what is often reported, there was no

decline in avian body size in cultivated areas. Species only encountered in cultivated areas included medium and large birds of prey, insectivorous birds, and large wading birds. Examples of large-sized wetland birds, particularly those in the Ciconiidae, Ardeidae and Threskiornitidae families that have unexpectedly adapted well to agricultural transformations in Rwanda, have been documented in previous work (Vande weghe & Vande weghe, 2011). The maintenance of functional diversity in secondary forests despite a species diversity loss in our study could be explained by the functional redundancy of natural ecosystems (Cooke, Bates, & Eigenbrod, 2019).

The differential filtering of functional traits with land-use change observed in this study agrees with the environmental-filtering theory (Keddy, 1992; Mouillot et al., 2013). The coexistence of species within a land-use type was mediated by particular optimum traits. A similar pattern of species coexistence mediated by their functional traits has also been observed in other human-modified tropical landscapes (Bregman et al., 2016; Coetzee & Chown, 2016; Hanz, Böhning-Gaese, Ferger, Fritz, Neuschulz,, 2018).

6.5.3 Loss of community phylogenetic structure with agriculture

Overall, the loss of species with land-use change culminated in lower phylogenetic diversity (Faith's PD). Additionally**,** bird communities across the land-use types were characterized by short~~er~~ phylogenetic distances, as shown by negative values of ses.MNTD, and ses.MPD, which imply high co-occurrence of closely related individuals. An explanation for the general phylogenetic clustering in the study area may be environmental filtering by historical disturbances. The Nyungwe landscape forms part of the Albertine Rift, which is theorized as a refugia for rainforest birds during the alternating extreme climatic cycles over the Pleistocene (Kahindo, Bates, & Bowie, 2017; Lyons et al., 2015; Prigogine, 1988). Historical anthropogenic disturbances of the Nyungwe landscape may also have had legacy effects on

the vegetation and associated fauna. In this study, further loss of phylogenetic diversity was accentuated by agriculture. Ecological filtering of certain clades by agriculture has been reported by other studies in an array of taxa (Egorov et al., 2014; Frishkoff et al., 2014; Prescott et al., 2016). Frishkoff et al. (2014) compared birds in forest reserves, and those in agricultural sites in Costa Rica, and found a wide spread of clades were using agricultural sites, however, closely related species tended to have similar habitat affinities.

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

6.5.4 Habitat attributes effects on taxonomic, functional and phylogenetic diversity

Fine-scale habitat heterogeneity in terms of the vegetation structure and landscape morphology have been reported to drive species, functional and phylogenetic diversity patterns in tropical birds and other taxa (Foord et al., 2018; Karp et al., 2012; Maseko, Zungu, Ehlers Smith, Ehlers Smith, & Downs, 2019; Prescott et al., 2016). As expected, attributes linked to vegetation heterogeneity were important determinants of avian diversity. Tree density positively drove taxonomic diversity, creating favourable conditions for forest specialists, canopy dwellers, and frugivores. The present study also noted varying effects of habitat attributes on the three avian diversity components. Lower vegetation height and soil

moisture positively affected Inverse Simpson index values, but adversely affected ses.MNTD values. These attributes may favour closely related understorey insectivorous and ground-nesting species, but cause detriment to canopy dwellers and clades with bare-ground affinities (Maseko et al,, 2019).

Functional diversity was rather largely influenced by elevation, demonstrating the resilience of this diversity dimension in the face of moderate modification of the vegetation structure which might affect some species depending on the functional traits they exhibit (Concepción et al., 2017). Elevation was also a strong negative driver of taxonomic diversity. This finding can be attributed to the fact that high elevation areas are often characterized by extreme climate conditions, which in turn inhibit complex vegetation stature and heterogeneity that might otherwise support a range of species with different varying functional traits (Jankowski et al., 2013, Quintero & Jetz, 2018).

6.5.5 Conservation implications

This study has shown how varying degrees of land-use change impact differentially the taxonomic, functional, and phylogenetic diversity components of avian communities in the Nyungwe landscape. It can thus be deduced that one particular diversity component cannot sufficiently perform a surrogate role when assessing responses of avian biodiversity to anthropogenic disturbances at a landscape level. Species-based approaches are well established in many conservation and monitoring schemes, and can potentially serve as early detection systems, however complementary approaches based on functional traits and phylogenies are imperative for the maintenance of key ecosystem functions and services and the conservation of a more complex biodiversity, with greater “evolutionary potential” (Pellens & Grandcolas, 2016).

In practice, implementing conservation interventions that integrate equally different facets of avian diversity at a landscape level may prove challenging due to the specificity of each land-use towards certain species or functional groups. Overall, the primary forest had the highest taxonomic, functional and phylogenetic diversity, harboured the highest number of Albertine Rift endemic species, and the highest number of threatened species. On the other extreme, cultivated areas ranked lowest in the three diversity facets, but had the highest number of migratory species, and contained the vulnerable Grey-crowned crane, an iconic species in Rwanda. This pattern was also observed in the North of Rwanda, where ARE endemic birds were abundant in the Volcanoes National Park, while migrating species were mostly found outside the park (Gatesire et al., 2014). Conservation measures would have to balance local and global priorities, and also take into consideration that promotion of phylogeny and trait-based approaches may overshadow other implementation frameworks, such as those based on normative importance, or prioritization of range-restricted species, or high cultural significance (Maier, 2018, Rapaccioulo et al., 2019).

This study also demonstrated the predicament of ecological restoration processes. The low species and functional diversity levels found in restored forests might be misinterpreted as failures in the eyes of stakeholders in need of fast results. Consequently, the plantations of fast-growing trees, particularly non-native species, might become a preferred option as observed outside Rwandan protected areas, and in different restoration schemes across the world (Ndayambaje, Mugiraneza, & Mohren, 2014; Fagan, Reid, Holland, Drew, & Zahawi, 2020). This study has shown the poor performance of such plantations in maintaining avian taxonomic and functional diversity. These findings may inform future restoration policies in Rwanda, and in similar tropical landscapes.

The conversion of natural habitats within the Nyungwe landscape mirrors what is happening in many parts of Africa. With the current rising population density, further adverse effects may persist. Although human modification of rainforest landscapes has happened for centuries both in Rwanda and elsewhere, with varying effects on the avian diversity, the recent increase in frequency and severity of anthropogenic disturbances have outpaced scientific coverage. The novelty of this study lies in the simultaneous documentation of such effects on taxonomic, functional and phylogenetic diversity of avian communities in a montane rainforest, an ecosystem that has not received as much research focus as lowland rainforests, despite its role as an epicentre of species richness and endemism. Montane forests continue to serve as refuges for both climatic and land-use change events. Several avian species that used to be widespread in Rwanda, are now confined within these forests, as suitable habitats mostly at lower elevations have been lost (Vande weghe & Vande weghe, 2011). Conservation efforts should be steered into preventing further degradation of existing natural ecosystems, specifically relatively intact forests, by working with local communities in finding alternative sources of livelihoods, and devising management plans that account for the dynamism of threats under present and future environments, such as the practicing of ecofriendly agriculture.

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6.7 References

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6.8 Appendix 2

TABLE A2.1 Variation of Functional dispersion (FDis) and Functional richness (FRic) among land-use types in comparison to the primary forest (PR) within Nyungwe landscape, Rwanda: Secondary forest (SC), fire-disturbed areas (FD), Restored areas (RS), forest plantations (PT), and cultivated areas (CT). Differences are tested with a two-tailed Dunn's Test, and P-values are adjusted using the Benjamini-Hochberg method. Sample size is 10 per land-use type, and comprises 200 point counts averaged over two sampling seasons. Where differences are significantly different at alpha = 0.05, values are marked in bold.

		Trophic		**Dispersal**		**Locomotion**		**Size**	
		Z	*P*	Z	*P*	Z	*P*	Z	*P*
FDis	PR-SC	1.037	0.450	-0.077	0.939	1.076	0.423	1.152	0.748
	PR-FD	0.781	0.543	0.538	0.682	1.357	0.328	1.024	0.655
	PR-RS	3.342	**0.006**	0.819	0.563	1.690	0.273	2.266	0.352
	PR-PT	0.896	0.505	-1.216	0.480	2.612	0.068	1.613	0.800
	PR-CT	-1.140	0.424	-2.215	0.134	3.098	**0.029**	1.472	0.705
FRic	PR-SC	0.775	0.658	-0.346	0.782	0.749	0.524	0.794	0.534
	PR-FD	1.460	0.271	1.178	0.326	1.562	0.253	1.953	0.153
	PR-RS	3.726	**0.003**	1.549	0.202	2.170	0.090	3.399	**0.010**
	PR-PT	1.492	0.291	-0.627	0.663	3.111	**0.014**	2.497	0.063
	PR-CT	2.228	0.078	-2.446	0.072	3.163	**0.023**	2.343	0.072

TABLE A2.2 Comparisons of phylogenetic structure (ses.MNTD) and diversity (PD) for bird communities in the Nyungwe landscape across six land-use types: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), Restored areas (RS), non-native tree plantation (PT), and cultivated areas (CT). Sample size is 10 per land-use type, and each sample is a pool of raw abundances from 20 point counts averaged over two sampling seasons. Statistical significance for ses.MNTD was assessed using an ANOVA followed by a Tukey's post hoc test, whilst PD was tested using Kruskal-Wallis, and a two-tailed Dunn's tests. Diff is the difference between values of the compared pair as calculated by Tukey's post hoc test. P-values from Dunn's test are adjusted using the Benjamini-Hochberg method. Values in bold indicate statistically significant/ close to significant differences in comparison to diversity in the primary forest at alpha = 0.05.

	ses.MNTD		**Faith's PD**	
	Diff	*P*	Z	*P*
PR-SC	0.238	0.914	1.242	0.179
PR-FD	0.038	1.000	2.113	**0.052**
PR-RS	0.669	0.985	2.727	**0.016**
PR-PT	0.087	0.999	3.303	**0.004**
PR-CT	0.669	**0.068**	3.905	**0.001**

TABLE A2.3 Species list of bird species recorded in Nyungwe National Park, Rwanda. Nomenclature follows the IOC world bird list, version 8.2. Doi: 10.14344/IOC.ML.8.2. ARE: Albertine Rift endemic species. P: Palearctic migrant; I: Intra-African migrant; B/I: Partial intra-African migrant. Conservation status: E: Endangered; VU: Vulnerable; NT: Near threatened, where blank: Least concern.

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
ACCI MELA	Accipiter melanoleucus	Great Sparrowhawk			
ACCI RUFI	Accipiter rufiventris	Rufous-breasted Sparrowhawk			
ACCI TACH	Accipiter tachiro	African goshawk			
ANTH TRIV	Anthus trivialis	Tree Pipit		P	
APAL ARGE	Apalis argentea	Kungwe Apalis	ARE		
APAL CINE	Apalis cinerea	Grey Apalis			
APAL JACK	Apalis jacksoni	Black-throated Apalis			
APAL NARI	Apaloderma narina	Narina Trogon		B/I	
APAL PERS	Apalis personata	Black-faced Apalis	ARE		
APAL PORP	Apalis porphyrolaema	Chestnut-throated Apalis			
APAL VITT	Apaloderma vittatum	Bar-tailed Trogon			
APUS APUS	Apus apus	Common Swift		P	
APUS CAFF	Apus caffer	White-rumped Swift			
AQUI AFRI	Aquila africana	Cassin's Hawk-eagle			
ARDE MELA	Ardea melanocephala	Black-headed Heron			
ARIZ NIGR	Arizelocichla nigriceps	Eastern Mountain Greenbul			
BALE REGU	Balearica regulorum	Grey Crowned-crane			E
BATH RUFU	Bathmocercus rufus	Black-faced Rufous Warbler			
BATI DIOP	Batis diops	Ruwenzori Batis	ARE		
BATI MOLI	Batis molitor	Chinspot Batis			
BOST HAGE	Bostrychia hagedash	Hadada Ibis			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
BRAD CINN	Bradypterus cinnamomeus	Bracken Warbler			
BRAD GRAU	Bradypterus graueri	Grauer's Swamp-warbler	ARE		E
BRAD LOPE	Bradypterus lopezi	Evergreen Forest Warbler			
BUTE AUGU	Buteo augur	Augur buzzard			
BUTE BUTE	Buteo buteo	Common Buzzard		P	
BUTE OREO	Buteo oreophirus	Mountain Buzzard			NT
BYCA SUBC	Bycanistes subcylindricus	Black-and-white-casqued Hornbill			
CAMA BRAC	Camaroptera brachyura	Green-backed Camaroptera			
CAMP ABIN	Campethera abingoni	Golden-tailed Woodpecker			
CAMP FLAV	Campephaga flava	Black Cuckooshrike		B/I	
CAMP NIVO	Campethera nivosa	Buff-spotted Woodpecker			
CAPR POLI	Caprimulgus poliocephalus	Ruwenzori Nightjar	ARE		
CENT MONA	Centropus monachus	Blue-headed Coucal			
CERC MONT	Cercococcyx montanus	Barred Long-tailed Cuckoo			Vulnerable
CEUT AERE	Ceuthmochares aereus	Blue Malkoha			
CHAL SENE	Chalcomitra senegalensis	Scarlet-chested Sunbird			
CHAM POLI	Chamaetylas poliophrys	Red-throated Alethe	ARE		
CHRY CUPR	Chrysococcyx cupreus	African Emerald Cuckoo			
CHRY KLAA	Chrysococcyx klaas	Klaas's Cuckoo		B/I	
CINN REGI	Cinnyris regius	Regal Sunbird	ARE		
CINN STUH	Cinnyris stuhlmanni	Ruwenzori double-collared sunbird	ARE		
CINN VENU	Cinnyris venustus	Variable Sunbird			
CIST AYRE	Cisticola ayresii	Wing-snapping Cisticola			
CIST CHUB	Cisticola chubbi	Chubb's Cisticola			
CLAM JACO	Clamator jacobinus	Jacobin Cuckoo		I	
COCC QUAR	Coccopygia quartinia	Yellow-bellied Waxbill			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
COLI STRI	Colius striatus	Speckled Mousebird			
COLU ARQU	Columba arquatrix	African Olive-pigeon			
CORA CAES	Ceblepyris caesius	Grey Cuckooshrike			
CORV ALBI	Corvus albicollis	White-necked Raven			
CORV ALBU	Corvus albus	Pied Crow			
CORY CRIS	Corythaeola cristata	Great blue turaco			
COSS ARCH	Cossypha archeri	Archer's Robin-chat	ARE		
COSS CAFF	Cossypha caffra	Cape Robin-chat			
COSS HEUG	Cossypha heuglini	White-browed Robin-chat			
CRIT BURT	Crithagra burtoni	Thick-billed Seedeater			
CRIT CITR	Crithagra citrinelloides	African Citril			
CRIT STRI	Crithagra striolata	Streaky Seedeater			
CRYP JACK	Cryptospiza jacksoni	Dusky Crimson-wing	ARE		
CUCU CLAM	Cuculus clamosus	Black Cuckoo		B/I	
CUCU SOLI	Cuculus solitarius	Red-chested Cuckoo		B/I	
CYAN ALIN	Cyanomitra alinae	Blue-headed Sunbird	ARE		
CYAN OLIV	Cyanomitra olivacea	Olive Sunbird			
CYAN VERT	Cyanomitra verticalis	Green-headed Sunbird			
DEND GRIS	Dendropicos griseocephalus	Olive Woodpecker			
DRYO GAMB	Dryoscopus gambensis	Northern Puffback			
ELMI ALBI	Elminia albiventris	Elminia albiventris			
EMBE FLAV	Emberiza flaviventris	African Golden-breasted Bunting			
EMIN LEPI	Eminia lepida	Grey-capped Warbler			
ESTR KAND	Estrilda kandti	Kandt's Waxbill			
ESTR NONN	Estrilda nonnula	Black-crowned Waxbill			
ESTR PALU	Estrilda paludicola	Fawn-breasted Waxbill			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
EUPL CAPE	Euplectes capensis	Yellow Bishop		B/I	
EURI LATI	Eurillas latirostris	Yellow-whiskered Greenbul			
FALC BIAR	Falco biarmicus	Lanner Falcon			
FALC CUVI	Falco cuvierii	African Hobby			
FALC SUBU	Falco subbuteo	Eurasian Hobby		P	
FALC TINN	Falco tinnunculus	Common Kestrel			
FRAN SQUA	Francolinus squamatus	Scaly Francolin			
GEOK PIAG	Geokichla piaggiae	Kivu Ground-thrush	ARE		
GRAU VITT	Graueria vittata	Grauer's Warbler	ARE		
GYMN BONA	Gymnobucco bonapartei	Grey-throated Barbet			
HEDY COLL	Hedydipna collaris	Collared Sunbird			
HIRU ANGO	Hirundo angolensis	Angola Swallow			
HIRU RUST	Hirundo rustica	Barn Swallow		P	
IDUN SIMI	Iduna similis	Mountain Flycatcher-warbler			
ILLA PYRR	Illadopsis pyrrhoptera	Mountain Illadopsis			
INDI EXIL	Indicator exilis	Least Honeyguide			
INDI MIN	Indicator minor	Lesser Honeyguide			
KAKA POLI	Kakamega poliothorax	Grey-chested Babbler			
KUPE RUFO	Kupeornis rufocinctus	Red-collared Mountain-babbler	ARE		NT
LAGO SENE	Lagonosticta senegala	Red-billed Firefinch			
LANI AETH	Laniarius aethiopicus	Tropical boubou			
LANI COLL	Lanius collaris	Common Fisca			
LANI LUEH	Laniarius luehderi	Luehder's Bush-shrike			
LANI MACK	Lanius mackinnoni	Mackinnon's Shrike			
LANI POEN	Laniarius poensis	Mountain Boubou			
LONC CUCU	Lonchura cucullata	Bronze Munia			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
LOPH ALBO	Lophoceros alboterminatus	Crowned Hornbill			
LOPH OCCI	Lophaetus occipitalis	Long-crested Eagle			
MELA ARDE	Melaenornis ardesiacus	Yellow-eyed Black Flycatcher	ARE		
MELA FASC	Melaniparus fasciiventer	Stripe-breasted Tit	ARE		
MELA FISC	Melaenornis fischeri	White-eyed Slaty Flycatcher			
MELA LEUC	Melaniparus leucomelas	White-winged Tit			
MERO APIA	Merops apiaster	European Bee-eater		P	
MERO OREO	Merops oreobates	Cinnamon-chested Bee-eater			
MILV AEGY	Milvus aegyptius	Black Kite			
MOTA AGUI	Motacilla aguimp	African pied wagtail			
MOTA CAPE	Motacilla capensis	Cape Wagtail			
MUSC ADUS	Muscicapa adusta	African Dusky Flycatcher			
NECT FAMO	Nectarinia famosa	Malachite Sunbird			
NECT KILI	Nectarinia kilimensis	Bronze Sunbird			
NECT PURP	Nectarinia purpureiventris	Purple-breasted Sunbird	ARE		
NEOC POEN	Neocossyphus poensis	White-tailed Ant Thrush			
NIGR CANI	Nigrita canicapillus	Grey-headed Negrofinch			
ONYC TENU	Onychognathus tenuirostris	Slender-billed Starling			
ONYC WALL	Onychognathus walleri	Waller's Starling			
OREO RUWE	Oreolais ruwenzorii	Collared Apalis	ARE		
ORIO PERC	Oriolus percivali	Black-tailed Oriole			
PASS GRIS	Passer griseus	Northern Grey-headed Sparrow			
PHOE BOLL	Phoeniculus bollei	White-headed Woodhoopoe			
PHYL FLAV	Phyllastrephus flavostriatus	Yellow-streaked Greenbul			
PHYL LAET	Phylloscopus laetus	Red-faced Woodland-warbler	ARE		
PHYL PLAC	Phyllastrephus placidus	Placid Greenbul			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
PHYL TROC	Phylloscopus trocHIRUs	Willow Warbler		P	
PHYL UMBR	Phylloscopus umbrovirens	Brown Woodland-warbler			
PLAT CONC	Platysteira concreta	Yellow-bellied Wattle-eye			
PLAT PERT	Platysteira peltata	Black-throated Wattle-eye			
PLOC ALIE	Ploceus alienus	Strange Weaver	ARE		
PLOC BAGL	Ploceus baglafecht	Baglafecht Weaver			
PLOC BICO	Ploceus bicolor	Dark-backed Weaver			
PLOC CUCU	Ploceus cucullatus	Village Weaver			
PLOC INSI	Ploceus insignis	Brown-capped Weaver			
PLOC MELA	Ploceus melanogaster	Black-billed Weaver			
PLOC XANT	Ploceus xanthops	Holub's Golden Weaver			
POEO SHAR	Poeoptera sharpii	Sharpe's Starling		B/I	
POGO BILI	Pogoniulus bilineatus	Yellow-rumped Tinkerbird			
POGO CORY	Pogoniulus coryphaeus	Western Tinkerbird			
POGO STEL	Pogonocichla stellata	White-starred Robin			
POLY TYPU	Polyboroides typus	African harrier-hawk			
PRIN BAIR	Prinia bairdii	Banded Prinia			
PRIN SUBF	Prinia subflava	Tawny-flanked Prinia			
PSAL PRIS	Psalidoprocne pristoptera	Black Saw-wing			
PSEU ABYS	Pseudoalcippe abyssinica	African Hill Babbler			
PTER NOBI	Pternistis nobilis	Handsome Francolin	ARE		
PYCN BARB	Pycnonotus barbatus	Common Bulbul			
RALL CAER	Rallus caerulescens	African Water Rail			
RUWE JOHN	Ruwenzornis johnstoni	Ruwenzori Turaco	ARE		
SARO RUFA	Sarothrura rufa	White-spotted Flufftail			
SAXI TORQ	Saxicola torquatus	Common Stonechat			

Abbreviations	Scientific name	Common name	Endemism	Migration	Conservation Status
SCHI LEUC	Schistolais leucopogon	Tawny-flanked Prinia			
SHEP AEQU	Sheppardia aequatorialis	Equatorial Akalat			
SMIT CAPE	Smithornis capensis	African Broadbill			
STEL GRAC	Stelgidillas gracilirostris	Slender-billed Greenbul			
STEP CORO	Stephanoaetus coronatus	African Crowned eagle			NT
STRE LUGE	Streptopelia lugens	Dusky Turtle-dove			
STRE SEMI	Streptopelia semitorquata	Red-eyed Dove			
SYLV LEUC	Sylvietta leucophrys	White-browed Crombec			
TAUR SCHU	Tauraco schuetti	Black-billed turaco			
TCHA AUST	Tchagra australis	Brown-crowned Tchagra			
TELO DOHE	Telophorus dohertyi	Doherty's Bush-shrike			
TERP VIRI	Terpsiphone viridis	African Paradise-flycatcher			
TRER CALV	Treron calvus	African Green-pigeon			
TURD JARD	Turdoides jardineii	Arrow-marked Babbler			
TURD OLIV	Turdus olivaceus	Olive Thrush			
TURT TYMP	Turtur tympanistria	Tambourine Dove			
UROS NEUM	Urosphena neumanni	Neumann's Warbler	ARE		
VIDU MACR	Vidua macroura	Pin-tailed Whydah		B/I	
ZOST SENE	Zosterops senegalensis	African Yellow White-eye			

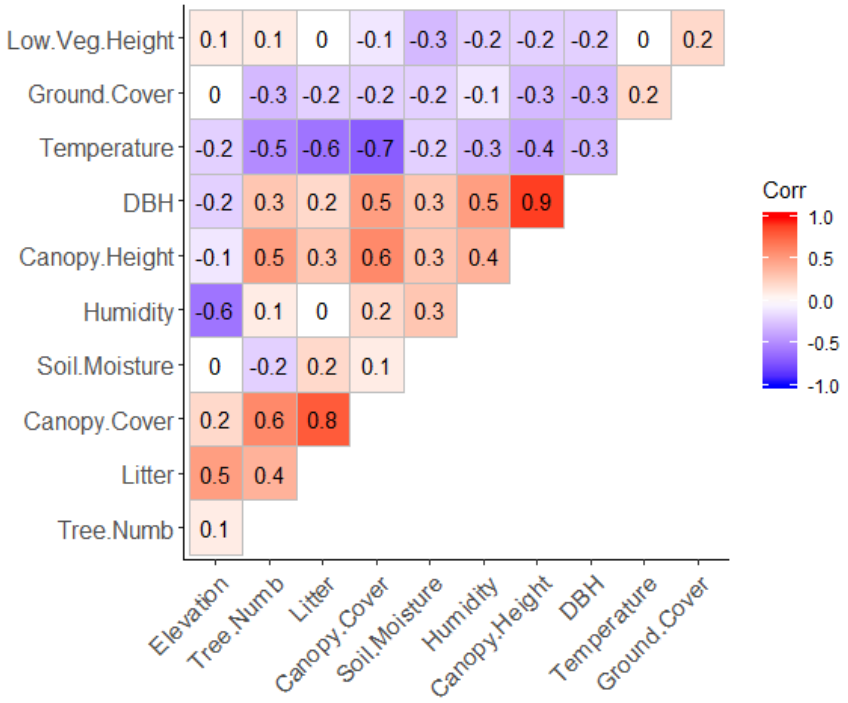

FIGURE A2.1 Correlation plot of habitat attributes showing correlation coefficient values. Each parameter was recorded in a plot of 20m radius. 100 plots were established per land-use, and a temperal replication was conducted in a different sampling season. Values were pooled at a sample level (10 plots) and were averaged over the two seasons. Litter, canopy height, temperature were omitted from further analysis due their high correlation with other habitat attributes. Low.Veg.Height stands for lower vegetation height.

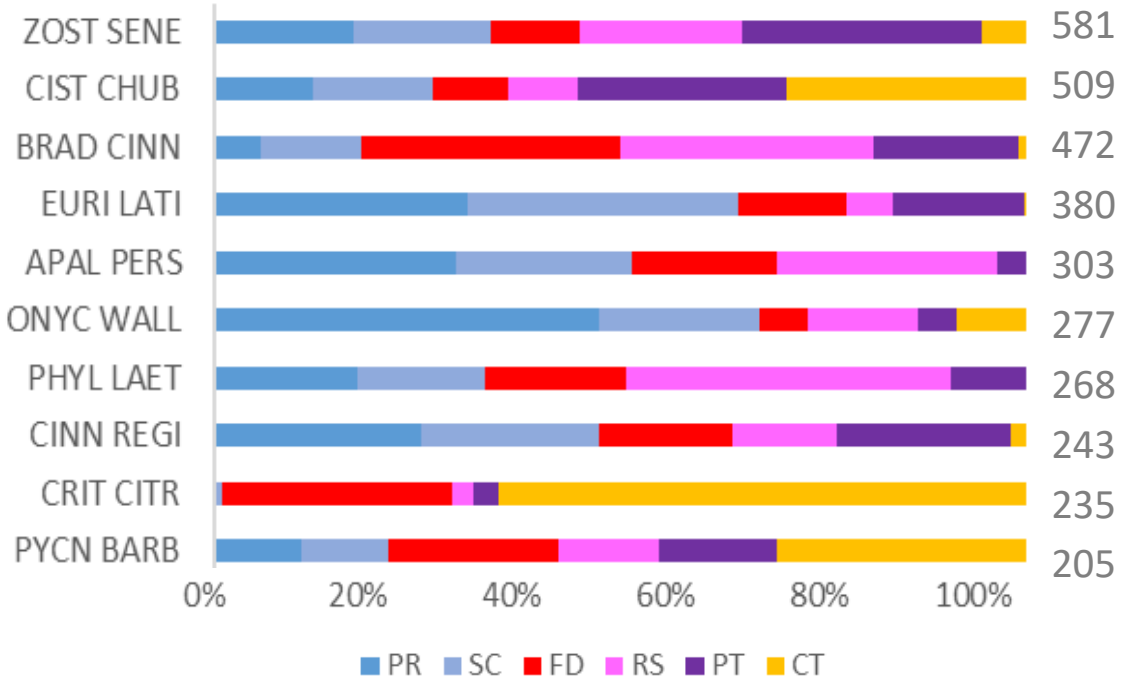

FIGURE A2.2 Percentage proportions of raw abundances of ten most abundant bird species across the land-use types in the Nyungwe landscape: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), Restored areas (RS), non-native tree plantations (PT), and cultivated areas (CT). Full names are given in the species list (Table A2.3).

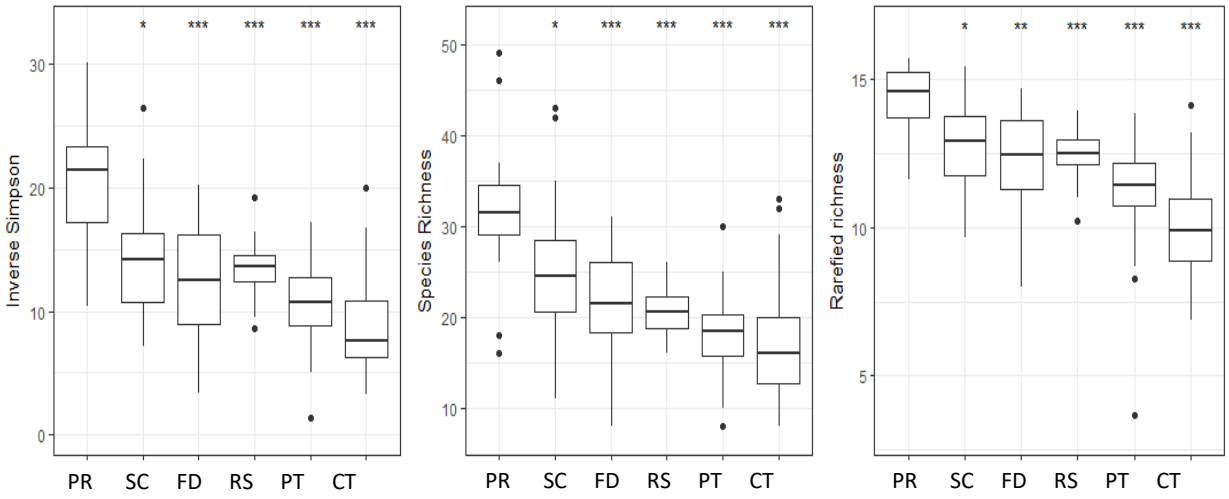

FIGURE A2.3 Effects of land-use change on Inverse Simpson diversity index (Inverse Simpson), Species richness, and Rarefied species richness (Rarefied richness) for bird communities in the Nyungwe landscape, Rwanda across six land-use types: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), Restored areas (RS), non-native tree plantation (PT), and cultivated areas (CT). Sample size (n = 20) is equal for all the categories, and each sample is a pool of raw abundances from 10 point counts. Rarefaction was performed using the smallest sample which had 20 individuals. Asterisks indicate statistically significant differences in comparison to diversity in primary forest: '*' 0.05, '**' 0.01, '***' 0.001. Statistical significance for the Inverse Simpson index was tested using an ANOVA followed by a Tukey's post hoc, while Kruskal-Wallis test and Dunn's tests were used for species richness and rarefied species richness.

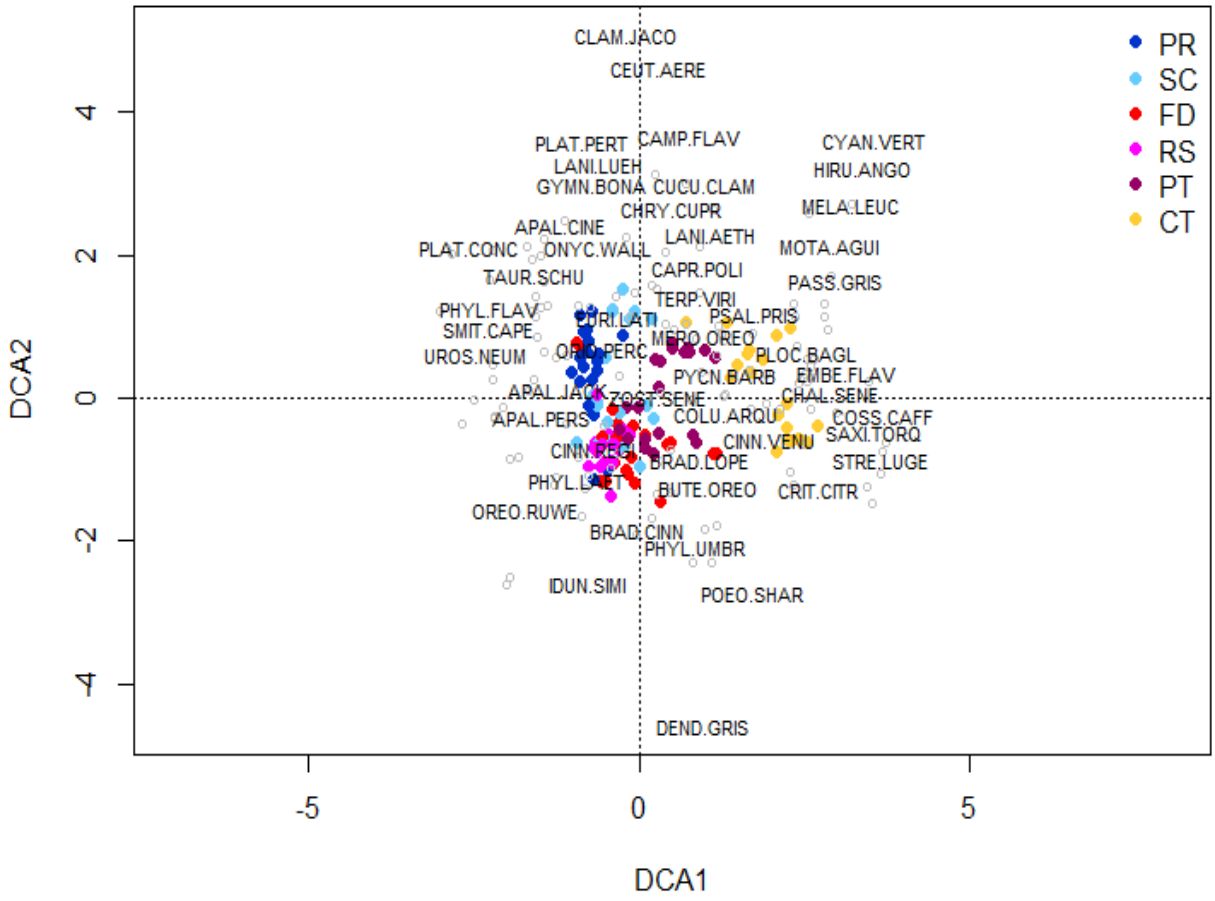

FIGURE A2.4 DCA showing the distribution of species (N =170) across six land-use types within the Nyungwe landscape: primary forest (PR), secondary forest (SC), fire-disturbed areas (FD), Restored areas (RS), non-native tree plantation (PT), and cultivated areas (CT). Birds at the extremes of the second axis are species that were rarely recorded by this study. Only two individuals of *Campethera nivosa* were encountered within Fire-disturbed areas and non-native tree plantation, while *Melaniparus leucomelas* was recorded twice in cultivated areas. For visual clarity species were weighted by abundances where display overlap occurred. The full names of species are given in Table A2.3. Figure produced using the "Vegan" package.

Chapter 7 | Functional and phylogenetic diversity of a tropical agricultural matrix avifauna: an assessment of farmland heterogeneity

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7.1 Abstract

1. Contemporary agricultural practices at household and industrial levels are the core drivers of biodiversity loss in the tropics. Although research on agricultural impacts has received extensive coverage in developed countries and in the Neotropics, there is still scant information in the Afrotropics, despite increasing threats.

2. We conducted 100 point counts in the dry season of 2017/18, all of which were repeated in the wet season in 2018, to compare different facets of avian diversity in monocultures of tea and mixed crop farming systems surrounding the Nyungwe rainforest in the south west of Rwanda. We also investigated the drivers of avian diversity at farm level.

3. Species composition was moderately different between farm types. Mixed crop farms supported higher phylogenetic diversity than tea plantations. There were no seasonal variations in species composition, functional and phylogenetic diversity.

4. Overall functional diversity did not differ between farm types, but the dispersion of trophic-related traits was significantly higher in mixed crops farms. Both functional and phylogenetic diversity were influenced by floristic diversity, vegetation height, tree number and elevation to varying degrees.

5. *Synthesis and applications.* The study contributes to evidence of the role of farmland heterogeneity with respect to roles for crop species composition, height, and tree cover extent in influencing avian diversity. While monoculture agriculture is often a favoured agricultural model, its impacts can be alleviated by extensive agroforestry, constituted largely of indigenous tree species.

Key words: Agrobiodiversity, agroforestry, birds, farmland heterogeneity, functional diversity, phylogenetic diversity, Rwanda

7.2 Introduction

Expansive agriculture, practiced at both subsistence and industrial levels, is responsible for the continued loss of biodiversity, particularly in the tropics and subtropics (IPBES, 2019, Malhi et al., 2014). Such unsustainable means of production are perpetuated by global trade interconnectivity and high consumerism in developed countries. Chaudhary et al. (2016) showed that 95% of "biodiversity damages" allocatable to Swiss food consumption in 2011 happened abroad, mostly in the tropics. These impacts were evaluated at a global level from estimates of species loss per unit area due to a given land-use, and were found to be up to 300 times greater than the damage resulting from domestic agriculture. Their analyses indicated that although crops, such as coffee, palm oil, rubber, tea, and soybean were grown on approximately a quarter of the global area on which cereals such as rice, maize and wheat were cultivated, the damage they inflicted on biodiversity was disproportionately higher because many of the areas affected supported substantial numbers of endemic and threatened species.

The production of cash crops contributes to the loss of diversity, largely through forest clearing, and reduction of crop diversity since they are often grown as extensive monocultures (Jiang et al., 2019; Lees et al., 2015; Perfecto et al., 2019). For example, Xu et al. (2018) reported that from 2010 to 2015, 9 335 ha of tea plantations were established in Menghai county, China, representing a 33.56% increase within five years. One third of the land converted was obtained by deforestation. A similar trend was observed in the Eastern Himalaya piedmont between 1874 and 2010, where a fall of 69.5% in forest cover was accompanied by an increase of 30.7% in tea plantations, independent of population growth (Prokop, 2018). Global tea production is rising, even in small countries, such as Rwanda,

which registered the highest global annual growth rate of 26.8% between 2007 and 2016 (IGT, 2018). Therefore, increased 'ecological footprints' associated with tea ought to be anticipated in the tropics, where the top producing countries are located.

The need to conserve farmland biodiversity has led to the development of conservation programs underpinned by the concept that heterogeneous landscapes— which comprise diverse habitats (compositional heterogeneity), varying in their spatial patterning (configurational heterogeneity), will provide greater and complimentary resources, facilitate dispersal processes and enable the coexistence of species of diverse functional strategies (Batáry et al., 2015; Fahrig et al., 2011). In Europe, agri-environment schemes of the EU's Common Agricultural Policy enable farmers within member states to access financial support to maintain or adopt measures that curb biodiversity loss (particularly of bird species) and which sustain ecosystem functions (Chamberlain, 2018; Kleijn and Sutherland, 2003). In the tropics, adoption of Agroforestry policies has gained prominence among governments and private stakeholders, with the aim of attaining biodiversity goals, and responding to socio-economic needs, such as fuelwood (Mukuralinda et al., 2016; Şekercioğlu, 2012). Although, a wide range of mechanisms to curb biodiversity loss have been trialled in different countries, there is still little evidence attesting to their effectiveness. Studies on agri-environment schemes have produced contrasting results (Batáry et al., 2015; Hiron et al., 2015; Lee and Goodale, 2018). The role of agroforestry systems in the maintenance of birds in tea plantations has been demonstrated (Chetana and Ganesh, 2012; Sidhu et al., 2010), however, the basis of assessment has largely been the taxonomic diversity. Studies in the tropics involving other components of the avian diversity, such as the functional traits structure and phylogenetic diversity have mainly focused on palm oil, and coffee. As a result,

research coverage, particularly in the Afrotropics, on the impact of tea agricultural practices and mitigation practices on different avian components remains scant.

The present study was conducted within Rwanda, a country whose vision to attain a 'green' economy is challenged by a high population density (477 people per km^2), with more than 80% of the population carrying out subsistence farming (NISR, 2018). We chose to work on birds due to their broad breadth of ecological niche, the range of farmland services they contribute to (e.g. pollination, pest control and seed dispersal), their role as ecosystem health indicators (Catterall et al., 2012; Şekercioğlu, 2012; Sinu, 2011) and the availability of data on their diversity in the study area. We hypothesized differences in bird species composition between mixed crops and tea plantations and owing to the greater structural and compositional complexity of mixed crops, hypothesised higher functional and phylogenetic diversity values for mixed crop farms compared to tea. We also expected functional and phylogenetic diversity to be driven by different habitat attributes, with crop heterogeneity and tree coverage being key factors.

7.3 Materials and Methods

7.3.1 Study area

The study was conducted in agricultural areas surrounding Nyungwe National Park, hereinafter Nyungwe NP, a tropical montane rainforest located in south west Rwanda (Fig. 7.1). Mean annual rainfall is 1500 – 2500 mm, and the average annual temperature is 15.25^{o}C. Two major farming types could be distinguished from the field. Monocultures of tea (*Camelia sinensis*) grown by tea companies and individual farmers, and farms containing mixed crops, mainly maize, beans (*Phaseolus vulgaris*), sweet potatoes and cassava. Outside the forest, farming was the predominant land-use, followed by settlements, which increased in density with distance from the forest. Tea estates were established after government-supported forest clearance in the 1980s. Due to the reinforced protection of the forest since 2004, and scarcity of land, the average household farm size around Nyungwe NP is around 1 ha (Masozera and Alavalapati, 2004).

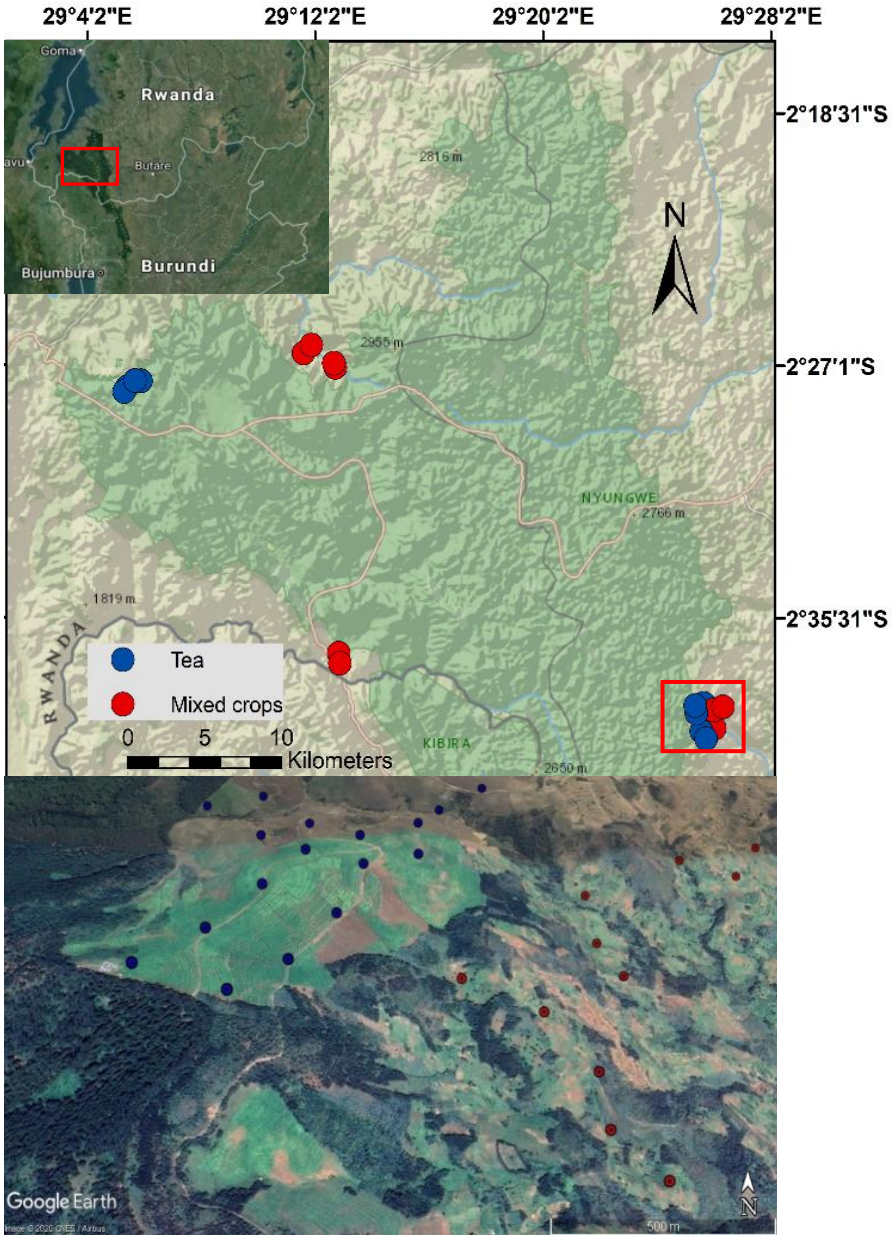

FIGURE 7.1 Geographic location of 100 point counts in tea and mixed crops farms around the Nyungwe National Park, Rwanda. The Nyungwe forest adjoins Kibira National Park, Burundi. Each point was sampled twice, once in the wet and once in the dry season between November 2017 and August 2018. Basemap and satellite image sources: National Geographic, and Google Earth.

7.3.2 Bird surveys

To record birds, the point count sampling was employed. 100 points of 20 m radius were established in tea plantations and mixed crops farms. The starting point was randomly allocated, and between each point, an interval of 200 m was left to ensure statistical independence and to prevent double counting (Ralph et al., 1995). At each point, birds seen or heard were recorded for 10 minutes. Observations were replicated in two seasons, totalling up to 200 points for the whole study. Sampling was done over the dry and wet seasons, from November 2017 to February 2018, and from June to August 2018. Bird recording typically began at 6 am and was completed by 10 am. No point counts were undertaken during rains. Bird recording was conducted by one surveyor with more than 20 years of experience.

7.3.3 Avian functional traits collection

Functional traits of birds in the study area relating to morphology, and habitat use were extracted from an existing dataset compiled from museum specimens (for the sampling protocol and grounds for choosing these traits see Pigot et al., 2020). Bill culmen, bill length, width, and depth were measured to represent the trophic niche; wing length, the Kipp's distance (the length between the longest primary and the first secondary measured on a folded wing), tarsus width and length represented locomotory and dispersal capabilities and foraging mechanism (Grant and Grant, 2006; Hutchinson, 1957; Schoener, 1965; Sheard et al. 2020). In most cases, biometric measures were taken from two adult male and two adult female specimens per species. The foraging strata were directly recorded from the field and supplementary information was obtained from Vande weghe and Vande weghe (2011). The foraging stratum was categorized as lower (3 m and below), middle (4 – 7 m), and upper (>7 m). Dietary data for each species were retrieved from Wilman et al. (2014), who compiled

proportions of the diet of each species in terms of major food categories, including: fruit, invertebrates, nectar, omnivores, plant matter, vertebrates, and seeds.

7.3.4 Farm assessment

For each point we sampled, we assessed aspects of ecological significance to birds (Sutherland and Green, 2004). We recorded the number and species identity of all plants within the radius of each pointcount, and the number of trees with a Diameter at Breast Height > 5 cm. The crop height (including non-crop species) was measured with a three-metre folding rule. We measured the temperature and humidity using a portable data logger, and soil moisture using a soil moisture probe. The application of agro-chemicals was not assessed due to the low-intensity farming methods practiced and the sporadic documentation of agro-chemicals when applied (Appendix 3). Measurements at each point were taken once per season by two field botanists with more than 15 years of experience.

7.3.5 Statistical analysis

We performed a Detrended Correspondence Analysis (Hill, 1979) to explore community composition within tea and mixed crops farming systems. We further conducted the analysis of similarity (ANOSIM) test using the CAP program (Seaby et al., 2014) to determine if samples within each farming type had a greater similarity than that occurring by chance. Statistical analyses were conducted at a sample level. Where seasonal effects were to be investigated, a sample comprised 5 contiguous points within the same area, sampled the same day in each season, amounting to 40 samples per study, otherwise, the values of the two seasons were averaged to avoid pseudo-replication, giving 20 samples.

We used the near tool from ArcGis 10.5.1 (ESRI, 2019) to calculate the nearest geodesic distance between the sample centroid and the Nyungwe forest. The sample centroid was

calculated using the Mean Center tool from ArcGIS, which averages the longitude and latitude coordinates of the five points. Measuring the proximity to the forest edge using linear distance tools may not represent accurately the spatial and structural complexity of the vegetation at a landscape scale. However, it was appropriate in our study due to the scarcity of large woodlots in the study farms.

To compare functional diversity and phylogenetic diversity between farm type, we used metrics that provided complimentary information and incorporated abundances.

Functional dispersion (FDis) – Measures the spread of species traits by quantifying the mean distance of each species to the centroid of all species weighted by abundance (Laliberte and Legendre, 2010). FDis retains a sample with less than three observations, which is often the case at a finer-scale of sampling.

Phylogenetic diversity (^{q}PD(T)) – The total diversity of branches of a phylogeny based on Hill numbers. q denotes the order of magnitude of abundance (q = 0 excludes abundance, and only species richness is considered, q = 1 considers common species, q = 2 includes only the most abundant species (Chao et al., 2010).

Standardized effect size of Mean Pairwise distance (ses.MPD)– The average pairwise phylogenetic distances among individuals in a community, adjusted for species richness. Higher values indicate that the community is composed of species which are evenly distributed across clades, while lower values indicate a community constituted of species that are phylogenetically clustered (Webb et al., 2002).

Standardized effect size of Mean nearest Taxon distance (ses.MNTD)– The average phylogenetic distance between an individual and its closest relative. The metric reveals phylogenetic structuring at the tips of the tree. A community that does not contain closely

related individuals will have higher sesMNTD values, and the opposite is true for lower sesMNTD values (Webb et al., 2002).

Due to the high correlation of avian morphological traits caused largely by body mass, and high intraspecific variations, a series of Principal Components Analyses (PCA) were performed, and resultant axes were used as indices of body size, trophic processes, locomotory abilities, and flight and dispersal capabilities, following Trisos et al. (2014). FDis was then computed from a matrix containing the obtained indices, diet, and foraging strata information using the R package FD (Laliberté et al., 2014). Quantitative traits were first rescaled (mean = 0, s.d. = 1) prior to the computation of FDis.

To analyse phylogenetic diversity, we downloaded 1000 trees from a global avian phylogeny based on the Erickson backbone (www.birdtree.org accessed 20 June 2019; Ericson et al., 2006, Jetz et al., 2012), and calculated PD(*T*) metrics using HillR packages (Li, 2018), and the sesMPD, and sesMNTD, using the picante package (Kembel et al., 2010).

Univariate type III repeated-measures ANOVA were used to compare diversity metrics across farm types and within seasons and t-tests were used to investigate variations in ses.MNTD, ses.MPD and differences in subsets of trophic related traits across farm types. To analyse the effects of farm attributes on PD and FD, two different multiple linear regression models were performed for ^{1}PD(T) and FDis containing floristic diversity, crop height, the number of trees, humidity, soil moisture, elevation and distance to the Nyungwe forest from the sample centroid as explanatory variables. Floristic diversity was computed as the exponential Shannon-Wiener index based on raw abundances of all crop and non-crop plant species found

in the point. Temperature and tree height were not included in the models due to their high correlation with humidity and vegetation height respectively (Pearson's R > = 0.7, Table A3.1).

We further employed a stepwise model selection procedure, based on the Akaike information criterion adjusted for sample size (AIC_c) using the MuMin package (Barton, 2019). The final model was obtained from averaging models within $\Delta AIC_c < 2$ of the model with the lowest AIC_c value. Spatial autocorrelation was evaluated on both model residuals using Moran's I test and it was found to be non-significant for both $^1PD(T)$ and FDis ($P = 0.082$ and 0.44 respectively). All analyses were conducted in R 3.5.3 (R CoreTeam, 2019).

7.4 Results

7.4.1 Community structure

We recorded 755 individuals belonging to 63 bird species, including three sunbirds endemic to the Albertine Rift region: *Nectarinia purpureiventris, Cinnyris Regius* and *C. stuhlmanii* (Table A3.2). 50 species were found in mixed crops, 33 in tea farms: 20 species were found in sites from both farm categories. The most abundant species were *Crithagra citrinelloides* and *Psalidoprocne pristoptera,* which constituted 11.7% and 9.4% of total abundances, respectively, across the two sampling periods. The dominant guild was the insectivores with 27 species out of 63. Within farm type, the pattern persists: small insectivores were the most commonly recorded guild, however, granivores were the most abundant type in mixed crop farms (Table 7.1). The Nyungwe NP provided the source for some forest species that strayed into the more open agricultural habitats, including the mentioned endemic birds. The majority

of these species were generalists. In total, 11 species were shared between the forest and tea farms, and 31 species between the forest and mixed crop farms.

TABLE 7.1. Feeding and size guilds of birds recorded in farms around Nyungwe NP, Rwanda. Sunbirds are classified as omnivores, due to the equal intake of invertebrates and nectar. The dietary classification used follows Wilman et al. (2014). Small: < 44 grams; Medium: 45-200g; Large: > 201 g. The percentage of abundances is computed within each farm type and given in brackets.

		Mixed crops			
	Invertebrates	**FruitNect**	**Omnivore**	**Plant/Seed**	**VertFishSc**
Small	20 (32.7)	4 (8.5)	5 (15.91)	10 (35.8)	
Medium		1 (1.27)	1 (1.63)	2 (0.36)	
Large	1 (0.72)	2 (1.27)	1 (0.36)		3 (1.45)
		Tea			
Small	12 (40.1)	2 (1.49)	8 (11.89)	4 (30.2)	
Medium	1 (0.5)		2 (4.46)	2 (1.49)	
Large		1 (6.93)			1 (2.97)

Note: FruitNect denotes birds feeding on fruits and/or nectar, while VertFishSc denotes birds feeding or scavemging on vertebrates, including fish.

The turnover of species among samples per season was high, as evidenced by the length of the DCA axes being above five standard deviation units (Jongman, 1995), with the first and second axes mostly reflecting elevation (Fig. 7.2; Fig. A3.1). The DCA shows a degree of overlap among the farm types. This was confirmed by the ANOSIM test, which revealed samples within the farm types were moderately distinct (ANOSIM sample statistic R = 0.299, Table A3.3), however, the differences were not statistically significant between seasons (Fig. 7.3, Table A3.3). Tea samples were more spread out, but the extremes were dominated by samples characterized by few species (in terms of encounter rate), particularly those normally affiliated to forest habitats including montane grasslands, such as *Columba arquatrix*, *Cisticola ayresi*, and *Cossypha caffra*.

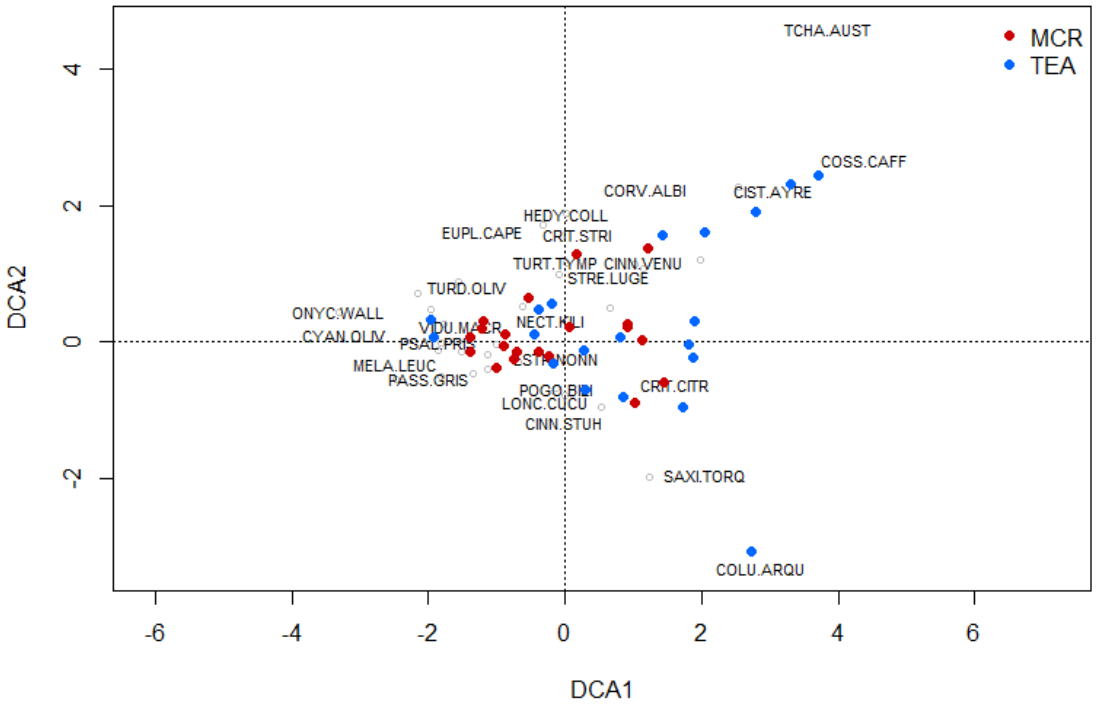

FIGURE 7.2 Biplot of Detrended Correspondence Analysis axes 1 and 2, showing bird species composition in 40 samples (each comprising 5 point counts sampled on the same day in close proximity) within tea and mixed crop farms around Nyungwe National Park, Rwanda in 2017-2018. The data comprise 20 such samples from November 2017 to February 2018, and the same sites resampled between June and August 2018. For readability, in cases of overlap, only the species with a higher occurrence value is displayed. For full species names, the reader is referred to Table S2. The outlying species *Columba arquatrix* was recorded at an unusually high number of 12, while *Tchagra australis* was the only species in its sample.

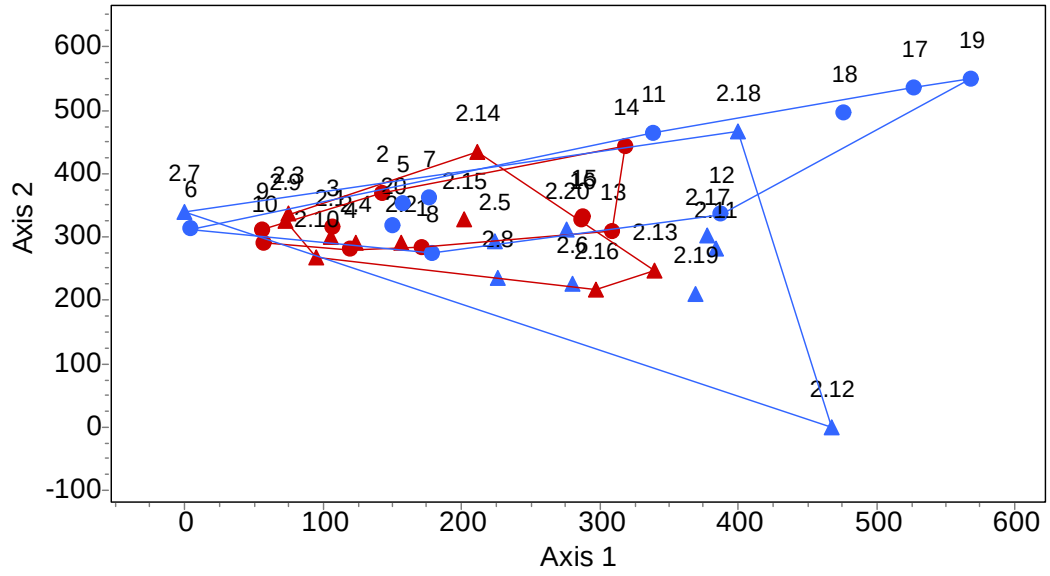

FIGURE 7.3 Detrended Correspondence Analysis plot showing sample site scores (N=40) along axis 1 and 2 based on raw abundances of birds surveyed in tea (blue) and mixed crop farms (red) around Nyungwe NP during the wet season (circles) and dry season (triangles). The outlying sample 2.12 comprised only 2 species, and one of them was *Columba arquatrix*, recorded in high numbers. Samples 17 and 18 had only two species: *Cisticola ayresi* and *Cossypha caffra.* Samples 18 had only 2 individuals, marking the lowest abundance value.

7.4.2 Phylogenetic and functional diversity between farm types

Phylogenetic diversity ^{1}PD(*T*) differed between farm types (Fig. 7.4). It was significantly higher in mixed crops than in tea farms ($F(1, 18) = 11.31$, $p = 0.003$). Varying the importance of abundances, the difference between farm types was more pronounced with ^{0}PD(*T*), which accounts only for species richness ($F(1, 18) = 15.56$, $p = 0.001$), and moderate for ^{2}PD(*T*), which places more emphasis on the most abundant species ($F(1,18) = 5.3410$, $p= 0.0329$).

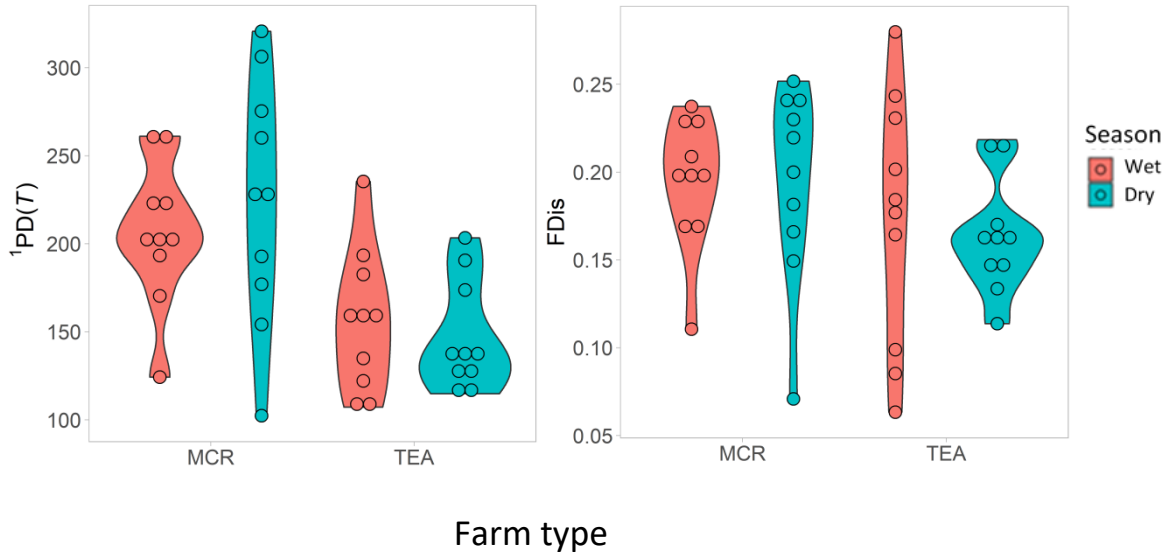

FIGURE 7.4 Comparison of avian phylogenetic diversity (^{1}PD(*T*)), and functional dispersion (FDis) values across two seasons in tea and mixed crop farming systems around Nyungwe NP , Rwanda. MCR denote mixed crops. Sample size (N = 40) was equal between the two farm ty pes. Each sample comprised 5 adjacent point counts. Statistical differences were tested using a univariate type III Repeated-Measure ANOVA and were found to be significant between far m types for ^{1}PD(*T*).

Overall FDis did not differ significantly between farm types. There was no effect of season, and the interaction with farm type on either PD(*T*) or FDis. A focus on a subset of traits revealed higher FDis values in trophic traits in mixed crops than in tea farms (Fig. 7.5, t(17.11) = 3.8854, p = 0.0012). Differences in ses.MNTD values between the farm types were not statistically significant (t (18) = 0.841, P = > 0.05), however, ses.MPD were close to significance with higher values exhibited by mixed crops than tea farms (t(18) = 2.08224, p = 0.0519).

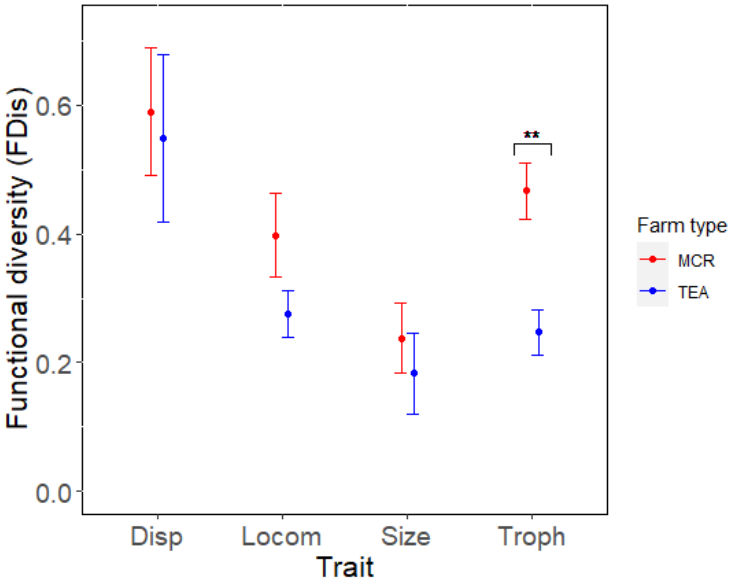

FIGURE 7.5 Effects of farming practice on morphological traits of birds found in the Nyungwe NP agricultural matrix, Rwanda (N=20). Functional diversity is calculated as functional dispersion (FDis). MCR: mixed crops, Disp: Dispersal, Locom: locomotory, Troph: Trophic. Error bars show the standard error of the mean. Statistical differences were tested using a Welch two sample t-test. Asterisks denote significant pairwise differences at *p < 0.1, **p < 0.05, and ***p < 0.01.

7.4.3 Effects of habitat descriptors on phylogenetic and functional diversity

The most parsimonious model showed crop height, and elevation to be important drivers of phylogenetic diversity, while floristic diversity was important for functional diversity. Averaging supporting models within delta $AIC_c < 2$ of the model with the lowest AIC_c revealed floristic diversity, crop height, elevation and tree number to be predictors with the most influence (Table 2a). The same predictors were also found to drive functional diversity, with tree number considered the most important factor (Table 2b). Relative humidity and soil moisture did not have a significant effect on either $^{1}PD(T)$ or FDis.

TABLE 7.2 a-b: Best supported models with $\Delta AIC_c < 2$ of the model with lowest AIC_c, analyzing the influence of farm attributes on $^1PD(T)$, and FDis of birds sampled in farmlands around Nyungwe NP, Rwanda (N=20 sites). Model average is calculated taking into consideration all initial predictors. The relative importance is obtained by summing the Akaike weights over all models in which the predictor variables appear. Only predictor variables retained in model selection are shown in the table. 95% Confidence Intervals (CI) are also given.

a) $^1PD(T)$

Model No.	Floristic diversity	Crop height	Elevation	Tree number	AIC_c	ΔAIC_c	weight
1		28.48	-22.43		205.31	0.00	0.089
2	27.67	17.86			205.45	0.14	0.083
3	39.29	0			205.52	0.21	0.080
4	35.01	0		14.02	205.56	0.25	0.079
5		22.68	-23.22	13.5	205.78	0.47	0.070
6	16.63	20.47	-13.89		207.03	1.72	0.038
7	26.94	13.91		10.78	207.14	1.83	0.036
8	25.44	0	-13.39	15.84	207.28	1.97	0.033
Average	**20.93**	**13.56**	**-9.07**	**5.83**			
CI-2.5%	5.54	-0.39	-40.65	-4.13			
CI-97.5%	55.49	43.99	0.71	31.33			
Importance	0.69	0.62	0.45	0.43			

b) FDis

Model No.	Tree number	Floristic diversity	Elevation	Crop height	AIC_c	ΔAIC_c	weight
1		0.02			-64.67	0.00	0.26
2	0.02		-0.02		-64.07	0.60	0.19
3	0.01	0.02			-63.82	0.84	0.17
4				0.021	-63.44	1.23	0.14
5	0.02				-63.15	1.52	0.12
6			-0.02		-63.11	1.56	0.12
Average	**0.01**	**0.01**	**-0.06**	**0.002**			
CI-2.5%	-0.01	-0.02	-0.03	-0.01			
CI-97.5%	0.03	0.03	0.01	0.02			
Importance	0.48	0.43	0.31	0.14			

7.5 Discussion

There was moderate support that bird species composition differed between tea plantations and mixed crops. Our prediction that avian diversity was higher in mixed crops than in tea plantations was strongly supported for phylogenetic diversity, but it was not statistically supported for functional diversity. Analysing subset of traits separately revealed less diversity of trophic related traits in tea plantations. Floristic diversity, crop height, elevation and the number of trees were found to be major attributes influencing both functional and phylogenetic diversity at varying degrees.

7.5.1 Avian diversity varies with farming practice

Although there was moderate overlap between bird species in tea and mixed crops farms, species in tea farms comprised a high number of rare species in terms of encounter rate, particularly those normally affiliated to forest and forest edges. These may have been attracted by the remnant trees and for the case of the afromontane endemic sunbirds, also by Eucalyptus woodlots whose flowers are increasingly important nectar sources, especially outside forests (Vande weghe and Vande weghe, 2011).

Mixed crops farms harboured twice the number of common bird species (those of ≥ 10 records) found in tea plantations. Since no significant changes were registered in the community phylogenetic structure as shown by ses.MPD and ses.MNTD values, the loss of phylogenetic diversity in tea farms compared to mixed crops can be explained by the reduction of species. Bird families filtered in tea plantations, but present in mixed crops included Threskiornithidae, Accipitridae, Laniidae, Bucerotidae, and Gruidae. Our findings concur with Frishkoff et al.'s (2014) study in Costa Rica, which found intensive monocultures

presented greater probability of species extirpation than more heterogenous agricultural systems.

The maintenance of overall functional diversity in tea plantations relative to mixed crop farms can be attributed on the one hand to the functional redundancy in the latter which mirrors that often found in natural ecosystems across a range of taxa (Cooke et al., 2019; Edwards et al., 2014; Prescott et al., 2016). For instance, both farm types were dominated by small-sized insectivorous birds. On the other hand, the absence of functional differences between the farming types can be explained by compensatory dynamics, where disturbance-tolerant species replace habitat specialists resulting in overall the maintenance of diversity at the community level (Morante-Filho et al., 2018; Supp and Ernest, 2014). For instance, some of the species only recorded in mixed crop farms had substitutes in tea farms with equivalent functional trait values, among them were: swallows, *Hirundo rustica*, substituted by *Psalidoprocne prisoptera*; pigeons, *Streptopelia semitorquata* by *Turtur tympanistra*; and shrikes, *Lanius mackinnoni* and *L. collaris* replaced by a cuckooshrike, *Coracina caesia* and a tchagra, *Tchagra australis*.

The main difference in functional diversity was found in trophic trait values. Tea harboured little niche breadth with very fewer sources of fruits and grains, which limited frugivores and granivores, including small mammals, consequently excluding raptors preying on them. Large-sized birds are often reported to be the first to disappear in agricultural systems, particularly in monocultures due to greater exposure to hunting (Frishkoff et al., 2014; Thiollay, 2006). The lack of difference in the size traits in our study could be explained by the

fact that the hunting of birds in Rwanda has not been a substantial tradition (Vande weghe and Vande weghe, 2011).

7.5.2 Similar habitat attributes drive phylogenetic and functional diversity

We found that avian diversity increased with floristic diversity and height on farmlands as more complex habitat structure and variability permits the coexistence of bird species of diverse lineages and functional traits (Karr and Roth, 1971; Huang et al., 2014). These findings concur with those of other studies conducted in tropical agricultural systems, which have described how the low niche-breadth of monocultures catalyse habitat filtering processes, particularly for understorey birds, affecting diet and foraging stratum traits (Almeida et al., 2016; Azhar et al., 2013; Flynn et al., 2009, Prescott et al., 2016). The proportion of non-crop vegetation in a farm also positively influences avian diversity and beneficial insects (Carvell et al., 2015; Grass et al., 2016; Lee and Goodale, 2018). In our study, the most diverse farms had the tallest species of non-crop plants, growing on uncultivated strips, resting land, as weeds or for farm demarcation and medicinal use. The non-crop plants were dominated by the Asteraceae, whose floral morphology attracts large numbers of insects and other invertebrates. Plants grown for farm demarcation also constituted different tree species and shrubs, particularly *Dracaena afromontana*, which provided variation of vertical layers for birds with different strata affinities.

The number of trees was particularly important for avian functional diversity. Some of the fruit-bearing trees were remnants of the cleared montane rainforest. Such forest remnants are crucial for the maintenance of frugivores and nectivores and thus enhance landscape connectivity and maintain seed dispersal and pollination processes in agricultural systems

(Şekercioğlu et al., 2019; Tscharntke et al., 2008). Trees also complement crops with upper storey habitats, which are used by canopy dwellers, perching birds and tree-nesting birds, hence permitting complimentary functional strategies (Kupsch et al., 2019; Şekercioğlu, 2012). The proximity of farms to forests in the tropics has been reported to contribute to the maintenance of avian diversity (Cannon et al., 2019; Raman, 2006), we thus expected to see a negative relationship between phylogenetic and functional diversity and distance from the adjacent 1000 km^2 Nyungwe forest. The lack of evidence for this effect could be attributed to the extreme loss of forest species in agrosystems and colonisation of lineages from a non-forest species pool.

Elevation negatively influences vegetation composition and structural configuration in natural ecosystems (Jankowski et al., 2013), hence, high correlation between elevaton and both floristic diversity and crop height should be expected. However, we suggest that human manipulation of agricultural systems, by for instance pruning tea plants at a certain height, or choosing the type and number of crops grown, may have limited this expected effect (Table S1). Furthermore, elevation is factored into the decision-making processes on the species and number of trees planted on a farm. A study by Mukuralinda et al. (2016) on tree-based systems in Rwanda found that farmers in high elevation areas preferred planting trees that could supply stakes for climbing beans, timber and help control soil erosion. As a result, trees planted in our study area were dominated by non-indigenous species of *Eucalyptus, Grevillea* and *Persea americana* (avocado). Non-native trees in Rwanda are known to support less avian diversity compared to indigenous species (Vande weghe and Vande weghe, 2011), thus their intentional displacement within high elevation areas could contribute further to elevation effects on the avian diversity.

7.5.3 Landscape management implications

The high frequency of crop-raiding events by forest animals makes commercially valuable monoculture crops, such as tea, ideal for growing around rainforests. However, the expansion of monoculture estates presents detrimental effects on avian diversity and threatens important ecosystem services such as predation, pollination, and seed dispersal, which directly influence farm productivity and cost, as evidenced by research in different parts of the tropics (Gurr et al., 2016; Sinu, 2011). The use of electrical fencing might help in deterring animals and minimise human-wildlife conflicts, and where tea monocultures are inevitable, practicing agroforestry guarantees maintenance of considerable levels of the avian diversity, and the meeting of restoration goals pledged by ministers of African countries and their representatives (2016) in the "Kigali declaration on forest landscape restoration in Africa".

The ongoing adoption of intensive agriculture in Afrotropical landscapes may prove counterproductive to restoration commitments, particularly those that align with the maintenance of forest biodiversity. The adoption of phylogeny or trait-based conservation approaches may not reveal the response of species of high conservation values, such as forest interior or endemic species, since these may be replaced by widespread open area species that have similar functional trait profiles as observed in the Nyungwe forest matrix. This is a topic that future studies should investigate for improved agricultural policy guidance.

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7.7 Authors' contributions

M.L.R. designed the study and analysed the data with inputs from R.J.W; M.R.L & P.N. coordinated and led data collection; J.A.T. provided the avian functional traits data; M.L.R led the manuscript write-up process with inputs from R.J.W. All authors edited the manuscript.

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7.9 Appendix 3.

Agricultural intensity

To determine the intensity and frequency of fertilizers and pesticides used, informal interviews were administered to two local agronomists, and 10 farmers in sites we sampled. We found out that there was generally low application of agro-chemicals in comparison to global standards, in part due to the prohibitive prices of industrial chemicals, and because of the traditional appreciation of organic fertilizers. The wide national donations of domestic animals, especially cows to farmers under the Gira inka munyarwanda program (translates as may each Rwandan have a cow) has also increased access to manure, thus curbing the need for industrial fertilizers.

Permission to conduct the study was sought from local authorities and farmers whose fields we sampled. The research proposal was evaluated and approved by the Central University Research Ethics committee and the Government of Rwanda.

TABLE A3.1 Correlation matrix of habitat descriptors recorded in 20 samples constituted of 100 points placed in tea monocultures and mixed crop farmlands around the Nyungwe NP, Rwanda. At each point measurements were taken twice over two seasons except for elevation (Elev) and distance to Nyungwe NP (D.S), which were recorded once.

	C.HT	Temp	Hum	S.M	T.H	T.N	C.eH	C.rich	Elev	D.S
C.HT	1.00	0.11	0.03	-0.29	0.84	0.41	0.65	0.68	-0.33	0.33
Temp	0.11	1.00	-0.77	0.16	0.08	0.14	-0.13	-0.12	0.01	0.14
Hum	0.03	-0.77	1.00	-0.24	-0.06	-0.08	0.43	0.42	-0.58	-0.32
S.M	-0.29	0.16	-0.24	1.00	-0.22	-0.35	-0.38	-0.37	0.23	-0.16
T.H	0.84	0.08	-0.06	-0.22	1.00	0.54	0.59	0.63	-0.28	0.49
T.N	0.41	0.14	-0.08	-0.35	0.54	1.00	0.31	0.33	-0.08	0.18
C.eH	0.65	-0.13	0.43	-0.38	0.59	0.31	1.00	0.99	-0.67	0.24
C.rich	0.68	-0.12	0.42	-0.37	0.63	0.33	0.99	1.00	-0.69	0.18
Elev	-0.33	0.01	-0.58	0.23	-0.28	-0.08	-0.67	-0.67	1.00	0.21
D.S	0.33	0.14	-0.32	-0.16	0.49	0.12	0.24	0.18	0.21	1.00

Note: C.HT: Crop height, Temp: Temperature, Hum: Humidity, S.M: Soil moisture, T.H: Tree height, T.N: Tree Number, C.eH: Exponential Shannon-Weiner index of plant species (floristic diversity), C.rich: Cropland plant species richness, Elev: Elevation, D.S: Distance from sample centroid to Nyungwe NP.

TABLE A3.2 List of bird species encountered in sampled farms around the Nyungwe National park, Rwanda, and the type of farm in which they were recorded. MCR denote mixed crops, and both implies that the species was recorded in both tea and mixed crops farms. The species nomenclature follows the IOC world bird list, version 8.2. Doi: 10.14344/IOC.ML.8.2.

Species name	Abbreviations	Farm type	Species name	Abbreviations	Farm type
Anthus trivialis	ANTH.TRIV	Both	Cisticola chubbi	CIST.CHUB	Both
Arizelocichla nigriceps	ARIZ.NIGR	MCR	Coccopygia quartinia	COCC.QUAR	Both
Balearica regulorum	BALE.REGU	MCR	Colius striatus	COLI.STRI	MCR
Bostrychia hagedash	BOST.HAGE	MCR	Columba arquatrix	COLU.ARQU	Both
Bradypterus cinnamomeus	BRAD.CINN	TEA	Coracina caesia	CORA.CAES	TEA
Buteo augur	BUTE.RUFO	MCR	Corvus albicollis	CORV.ALBI	Both
Bycanistes subcylindricus	BYCA.SUBC	MCR	Cossypha caffra	COSS.CAFF	TEA
Camaroptera brachyura	CAMA.BRAC	Both	Cossypha heuglini	COSS.HEUG	MCR
Chalcomitra senegalensis	CHAL.SENE	MCR	Crithagra citrinelloides	CRIT.CITR	Both
Cinnyris regius	CINN.REGI	TEA	Crithagra striolatus	CRIT.STRI	Both
Cinnyris stuhlmanni	CINN.STUH	TEA	Cyanomitra olivacea	CYAN.OLIV	TEA
Cinnyris venusta	CINN.VENU	Both	Melaenornis fischeri	MELA.FISC	MCR
Cisticola ayresii	CIST.AYRE	Both	Elminia albiventris	ELMI.ALBI	MCR

Species name	Abbreviations	Farm type
Emberiza flaviventris	EMBE.FLAV	MCR
Estrilda kandtii	ESTR.KAND	TEA
Estrilda nonnula	ESTR.NONN	Both
Estrilda paludicola	ESTR.PALU	Both
Estrilda quartinia	COCC.QUART	Both
Euplectes capensis	EUPL.CAPE	MCR
Hedydipna collaris	HEDY.COLL	TEA
Hirundo angolensis	HIRU.ANGO	Both
Hirundo rustica	HIRU.RUST	MCR
Lagonosticta senegala	LAGO.SENE	MCR
Lanius collaris	LANI.COLL	MCR
Lanius mackinnoni	LANI.MACK	MCR
Lonchura cucullata	LONC.CUCU	MCR
Milvus aegyptius	MILV.AEGY	MCR
Motacilla aguimp	MOTA.AGUI	MCR
Motacilla capensis	MOTA.CAPE	MCR
Muscicapa adusta	MUSC.ADUS	MCR
Nectarinia kilimensis	NECT.KILI	Both
Nectarinia purpureiventris	NECT.PURP	TEA
Nigrita canicapillus	NIGR.CANI	TEA
Onychognathus walleri	ONYC.WALL	TEA
Melaniparus leucomelas	MELA.LEUC	MCR
Passer griseus	PASS.GRIS	MCR
Ploceus baglafecht	PLOC.BAGL	MCR
Ploceus cucullatus	PLOC.CUCU	MCR
Pogoniulus bilineatus	POGO.BILI	MCR
Prinia subflava	PRIN.SUBF	MCR
Psalidoprocne pristoptera	PRIN.PRIS	Both
Pycnonotus barbatus	PYCN.BARB	Both
Saxicola torquatus	SAXI.TORQ	Both
Species name	Abbreviations	Farm type
Streptopelia lugens	STRE.LUGE	Both
Streptopelia semitorquata	STRE.SEMI	MCR
Tchagra australis	TCHA.AUST	TEA

Species name	Abbreviations	Farm type
Terpsiphone viridis	TERP.VIRI	MCR
Turdus olivaceus	TURD.OLIV	Both
Turtur tympanistria	TURT.TYMP	TEA
Vidua macroura	VIDU.MACR	MCR
Zosterops senegalensis	ZOST.SENE	Both

TABLE A3.3 ANOSIM pairwise tests for the study samples across seasons. The size of the sample is given in parentheses. Each sample constitutes 5 contiguous points within the same site. 1 and 2 denote the first and second sampling season, respectively. The overall sample statistic R was 0.241. R values close to 1 indicate greater similarity between samples of the same group, and lower similarity between the compared pair. The test was based on 1000 randomizations.

1st Group	2nd Group	P Value	R values
MCR1 (10)	MCR2 (10)	0.303	0.023
MCR1 (10)	TEA1 (10)	**0.001**	0.390
MCR1 (10)	TEA2 (10)	**0.003**	0.265
MCR2 (10)	TEA1 (10)	**0.001**	0.415
MCR2 (10)	TEA2 (10)	**0.007**	0.275
TEA1 (10)	TEA2 (10)	0.123	0.088

Note: MCR stands for mixed crop farm type

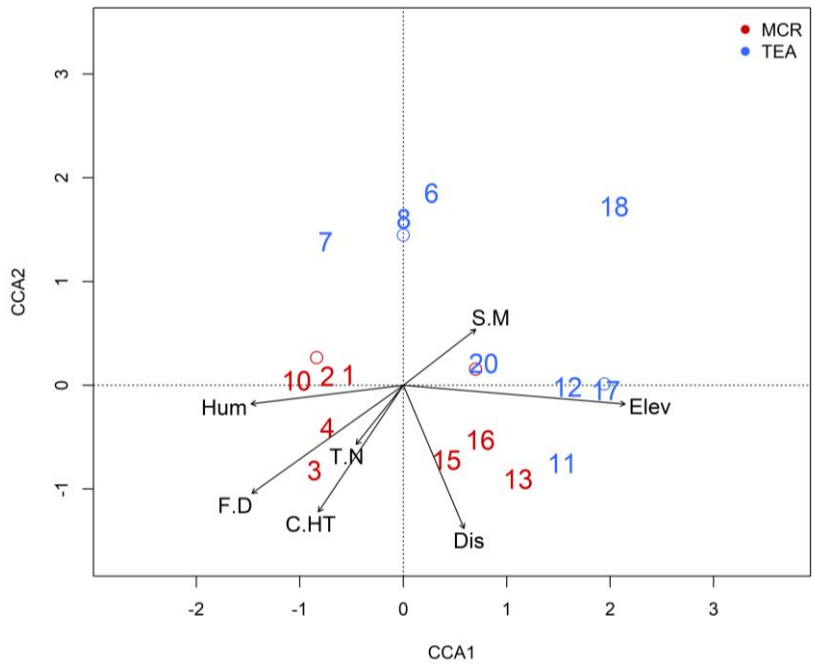

Figure A3.1 Constrained Correspondence Analysis plot axis 1 and 2, showing sample sites scores (N = 20), and habitat variables. Elev: Elevation, Dis: Distance from forest, C.H Crop height, T.N: Tree number, F.D: floristic diversity, Hum: Humidity, S.M: Soil moisture. The statistical significance of habitat variables were tested by a permutation test, which revealed that elevation was the sole significant environmental variable (P = 0.005) within the model.

Chapter 8 | Assessing forest restoration success using bird habitat use as a potential indicator: an Afrotropical case study

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8.1 Abstract

Although the necessity to restore rainforest habitats degraded by anthropogenic fires is widely recognized, research on restoration approaches has mainly centred on the recovery of forest structural complexity, and 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 avian taxonomic diversity, and functional trait structure of undisturbed primary forest and fire-affected habitats undergoing natural regeneration and assisted natural regeneration within the Nyungwe National Park in Rwanda. The point-count sampling method was employed to record bird occurrences, and avian morphological traits were obtained from museum specimens. We found marked differences in the species composition between primary forest habitats and regenerated forest, however, the similarity increased with recovery time. Taxonomic diversity was higher in primary forest, and similar between the two restoration pathways. Functional diversity declined in assisted naturally regenerated habitats, however, the functional traits profile was mostly stable across habitats. Among desired restoration outcomes, tree species diversity was the leading positive driver of avian species diversity, ferns 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 detriments on ecological processes are not easily reversed while restoration success is difficult to achieve given the complexity of forest 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.

8.2. Introduction

Fire has been part and parcel of African landscapes, contributing to the formation, and the maintenance of grasslands and savannas, and the high diversification rate of the associated biota (Cowling, 1987; He, Lamont, & Pausas, 2019; Sodhi, Şekercioğlu, Barlow, & Robinson, 2011). Nonetheless, its current frequency and intensity in less fire-adapted wet forests present detrimental effects that can hamper natural regeneration for a very long time (Cochrane, 2003; King, Moutsinga, & Doufoulon, 1997).

The most enticing option for restoration of degraded forest ecosystems involves the planting of seeds or seedlings (active restoration). Although in some cases, the recovery of forest above-ground biomass, flora and fauna species richness by means of active restoration has been attained (Latja, Valtonen, Malinga, & Roininen, 2016; Omeja et al., 2011; Trujillo-Miranda, Toledo-Aceves, López-Barrera, & Gerez-Fernández, 2018; Wheeler et al., 2016), in others, it has led to the destruction of naturally regenerating species (Sampaio, Holl, & Scariot, 2007), the planting of species which did not meet the resource demand for a range of frugivores (Brancalion et al., 2018), and less effective results in terms of targeted biodiversity goals than absence of intensive interventions (Morrison & Lindell, 2011). Moreover, the high labour and financial resources required by active restoration methods have restricted the scalability of such interventions over large areas, consistent with the view that active restoration is costly in comparison to "passive restoration" – where intervention is limited to stopping environmental disturbances, such as fire or agriculture (Crouzeilles et al., 2017; Shono, Cadaweng, & Durst, 2007), but for contrary views see Zahawi, Reid, & Holl (2014).

On the other hand, parameters such as the land-use history, topographic and edaphic factors, the forest type (e.g. dry vs moist forest), the surrounding matrix, and the presence of natural barriers such as ferns or grasses may impede any succession progress for decades if no human intervention is provided (Douterlungne, Levy-Tacher, Golicher, & Dañobeytia, 2010; Holl & Aide, 2011). In

such cases, the assisted regeneration approach— a less intensive management intervention which 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 (Chazdon, 2017; Elliott, 2016; Shono et al., 2007; Shoo & Catterall, 2013).

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, Wilson, & Shoo, 2017). A meta-analysis based on 20 studies across the tropics (but excluding the Afrotropics) concluded that the combination of herbaceous vegetation removal with enhanced propagule supply was the most effective method in restoring the forest structure (Shoo & Catterall, 2013). Even though assisted natural regeneration methods have long been practiced by various indigenous communities to regenerate forests (Dugan, Durst, Ganz, & McKenzie, 2003), aside from the vegetation assessment, there is scant information on its performance in the recovery of animal species diversity, and features linked to ecological functions. It is thus too early to generalize as to its efficiency, especially in the Afrotropics where it has received less research coverage (Reij & Garrity, 2016;Shoo & Catterall, 2013). This paucity of information also applies to the wider tropical restoration field since many existing studies are based on comparisons of projects with different timeframes or end-goals (Larkin, Buck, Fieberg, & Galatowitsch, 2019).

Our study aims to address this gap by comparing both naturally regenerated (passive restoration) and assisted naturally regenerated habitats to primary forest with 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 recovery of the fauna and associated ecosystem functions. Birds provide a well-

established indicator group of the vitality of ecosystems, 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 (Roels, Hannay, & Lindell, 2019; Şekercioğlu, 2012)**.**

We conducted our study in Nyungwe National Park (Fig. 8.1), 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 global initiative to restore 150 Mha of deforested and degraded landscapes by 2020 and 350 Mha by 2030 (www.bonnchallenge.org). 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 in Rwanda includes the restoration of burnt areas within the Nyungwe National Park, a project which was initiated in 2003. The project has used assisted-natural regeneration methods to increase tree cover and tree species diversity by combatting the opportunistic fern *Pteridium aquilinum* (L.) Kuhn, which inhibits forest regeneration processes (Masozera & Mulindahabi, 2007).

We asked 1) how avian species composition, diversity and functional trait structures vary across the habitat types; and predicted that: i) the three habitats (naturally regenerated, assisted naturally regenerated and primary forest) will have distinct species composition, taxonomic and functional diversity levels; ii) avian diversity levels will be higher in assisted-naturally regenerated than in naturally regenerated habitats, but will converge towards the composition and diversity of undisturbed primary forest habitats over time (Derhé, et al., 2016); and finally iii) that there will be a difference in the recovery of major guilds occupying naturally regenerated and restored sites, with frugivores being slow to recover due to their preference for a continuous forest cover (Farwig et al., 2017). We also asked 2) to what extent do changes in vegetation generated by the assisted restoration project influence avain 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 a reduced avifaunal community trait structure, particularly for the regenerated habitats (cf. Gould and Mackey, 2015, Ikin et al., 2019).

8.3 Methods

8.3.1 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 10.9^0C, whilst the maximum is 19.6^0 C (Seimon, 2012; Sun et al., 1996).

In the last two decades, anthropogenic fires in the Nyungwe forest ravaged more than 12% of the forest (Masozera and Mulindahabi, 2007). In some parts of the forest opportunistic ferns (mostly, *Pteridium aquilinum*) have occupied the cleared sites and induced arrested succession for decades. Assisted-natural regeneration activities were initiated in 2003 by the park management and conservation partners to allow the sprouting of tree seeds and involved the systematic cutting of ferns in areas visible from the main road that were void of tree cover (Masozera and Mulindahabi, 2007). Although regular monitoring of the vegetation cover in the restored plots has been conducted as part of the management of the park, no scientific study has been conducted to assess the recovery of the avifauna.

8.3.2 Avian and vegetation survey

Sampling was conducted in naturally regenerated habitats (NR), assisted naturally regenerated habitats (AR), and primary forest (PF), which is considered herein as the reference state. In Nyungwe NP, the primary forest is characterized by late successional tree species such as *Syzygium guineense*, *Strombosia schefflera*, and to a less extent *Entandophragma excelsum* which

was not recorded in regenerated habitats. 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 Nyungwe NP. 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 each habitat. 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.

100 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.

Point-count sampling was chosen due to its efficacy and frequency in surveying rainforest birds with little disturbance to the habitat and birds (Ralph et al., 1995). A minimum distance of 200 m was maintained between points to reduce the risk of double counting of birds and to maintain statistical independence.

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 (Cook, Stutzman, Bowers, Brenner, & Irwin, 1995; Jennings, Brown, & Sheil, 1999; Strickler, 1959). The percentage of ferns coverage was visually estimated, with 0% indicating absence of the ferns, 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, vegetation sampling was carried out in the wet season, and a replication was done in the dry season.

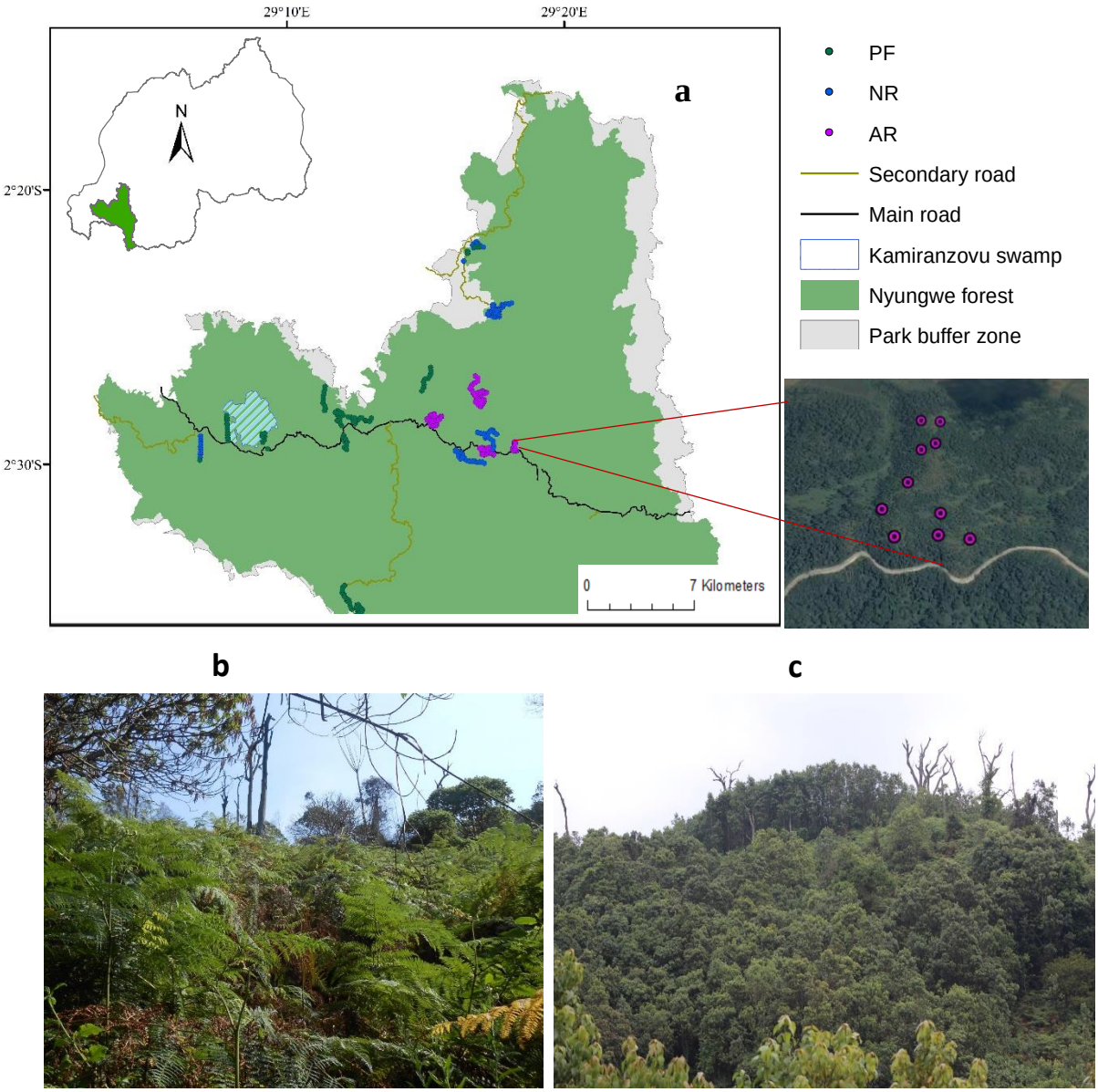

Figure 8.1 Geographic location of 300 point counts conducted in Nyungwe National Park, Rwanda (**a**), within primary forest (PF), naturally regenerated habitats dominated by *Pteridium aquilinum* (NR; **b**) and assisted naturally regenerated habitats dominated by *Macaranga kilimandscharica* (AR; **c**). 10 points counts were conducted within the same site per day. 5 adjacent points formed a sample. Each point was sampled once in the wet season, and a replicate sampling was done in the dry season. Base map sources: WCS, Rwanda, Google Earth.

8.3.3 Functional traits collection

Biometric data of study birds were measured on 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 (Grant & Grant, 2006; Hutchinson, 1959; 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).

8.3.4 Data analysis

Except where mentioned, the sampling unit of analysis for avian diversity and vegetation attributes was five adjacent points averaged over the two sampling seasons to avoid pseudo-replication. For analyses involving vegetation attributes, avian diversity metrics were calculated based on birds observed within 20 m radius of the point station instead of the 100 m radius, corresponding to the size of the vegetation assessment plots.

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 richness and diversity within each habitat, observed species richness, raw species abundances, estimated species richness, the exponential of Shannon entropy, pairwise and multi-site beta diversity (measured using Sørensen dissimilarity, and partitioned in spatial

turnover, and nestedness-resultant dissimilarity, based on a presence and absence matrix: Baselga (2012)) were computed using iNext, Vegan and Betapart packages (Baselga and Orme 2012; Hsieh, Ma, & Chao, 2016; Oksanen et al., 2010).

The "c0" algorithm and 999 simulations were used to test whether beta diversity observations deviated from random expectation. Beta diversity in this case was computed as multiple-site dissimilarities for all study samples. The variability of pairwise Beta diversity components across the three habitats was assessed using a nonparametric permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). To disentangle the contribution of differences arising from within-habitat variations, a permutation analysis of multivariate dispersions (PERMDISP; Anderson, Ellingsen, & McArdle, 2006) was also performed, followed by an ANOVA, and a Tukey's test. 999 iterations were used for each permutation method.

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 from Mantel tests (Aspin et al., 2018; Baselga, 2010).

To quantify functional diversity within each habitat type, functional dispersion (FDis), a distance-based multivariate metric which measures the spread of species in a trait space (Laliberté & Legendre, 2010), and the community-weighted mean (CWM) for the traits that are indicative of energy requirements, feeding, locomotion and dispersal functions were calculated for samples within each habitat based on Gower's distance using the FD package (Laliberté et al., 2014), and following analytical steps described in Bregman et al., 2016. We determined differences in

taxonomic and function diversity metrics across habitat types by bootstrapping the mean and confidence intervals (bias corrected) using 10 000 randomisations 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 their high correlation between the two and with tree diversity (Pearson's $R > 0.7$; Fig. A4.2). Vegetation attributes were standardized to mean of 0 and standard deviation of 1. Since the assumptions of linear regression models were met for the species diversity variable, we performed a multiple linear regression analysis for species diversity, and a generalised linear model (Quasi-Poisson) to account for overdispersion for the species abundance variable. We then performed model selection based on AIC_c (Akaike Information Criterion corrected for sample size), and $QAIC_c$, a modified AIC_c for models with overdispersion. The models were constructed using the Package "lme4", and "MuMin" (Barton, 2019; Bates, Maechler, Bolker, & Walker, 2014).

To explore the same relationship but with functional traits, a combination of the RLQ and Fourth-corner analyses (Dolédec, Chessel, Ter Braak, & Champely, 1996) was performed using the R package "ADE4" (Dray, Dufour, & Chessel, 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, L table from species abundance across samples, and the Q table from species traits. Although the two methods' inputs are similar, their output 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, Pettorelli, & Chessel, 2002), whereas the fourth-corner analysis focuses on the interaction between an individual trait and one environment attribute at a time (Dray & 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).

8.4 Results

8.4.1 Species composition

The study recorded 4,565 bird individual sightings belonging to 122 species across all samples over two sampling seasons. Twenty samples were collected per habitat. Each sample contained data for five adjacent points within the same habitat. The values are pooled for avian diversity, and averaged for vegetation attributes. The number of individuals per sample ranged from four individuals and three species in AR sites to 107 individuals and 34 species in 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). *Bradypterus cinnamomeus, Zosterops senegalensis,* and *Apalis personata* (an Albertine Rift endemic (ARE) were well represented across all habitat types and constituted 17% of all individuals. The dominant dietary guild in terms of species richness and individual sightings over the two seasons was invertivores, with 72 species and 2,675 individuals, followed by omnivores with 15 species and 681 abundances, and frugivores with 14 species and 578 individuals.. The top three recorded species among invertivores were: *B. cinnamomeus, A. personata,* and *Phylloscopus laetus* (ARE), frugivores: *Z. senegalensis*, *Ruwenzornis johnstonii*, *Arizerocicla nigriceps*, and omnivores: *Onychognathus walleri*, *Eurillas latirostris,* and *Cinnyris regius.* 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. A4.2).

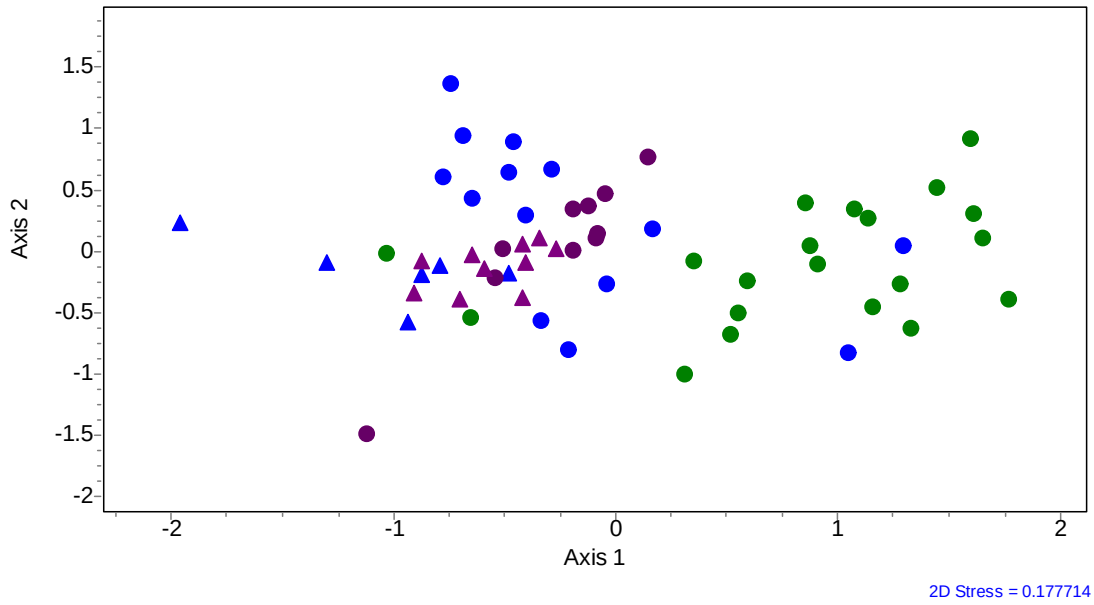

Figure 8.2 Two dimensional non-metric multidimensional scaling (NMDS) based on species raw abundances within primary forest (green; N = 20), young naturally regenerated (blue triangle; N= 6), mid-aged naturally regenerating (blue circles, N = 14), young assisted naturally regenerated (purple triangles; 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 lowest sample 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 averaged over the wet and dry seasons.

NMDS revealed high segregation of PF from the other two habitat types, and considerable overlap between NR and AR samples (Fig. 8.2). The ANOSIM test (Table A4.1) concurred with the ordination graph, showing significant differences between most habitat types (r = 0.3, *P* = 0.001). As expected, mid-aged regenerated 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.

8.4.2 Beta diversity

We found the observed multi-site beta turnover (βsim) and nestedness (βsne) components for all study samples significantly different from random expectations (*p* = 0.001), however, the overall beta diversity was not significantly different. The variation of total beta diversity and its components was significantly different between habitats (PERMANOVA test, βsor: F = 3.74, P = 0.049; βsim: F = 4.7, *P* = 0.001, βsne: F= 4.69, p = 0.001). The within-habitat variation was only significant for 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 the regeneration time (time since a fire incidence) 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. 8.3a-c).

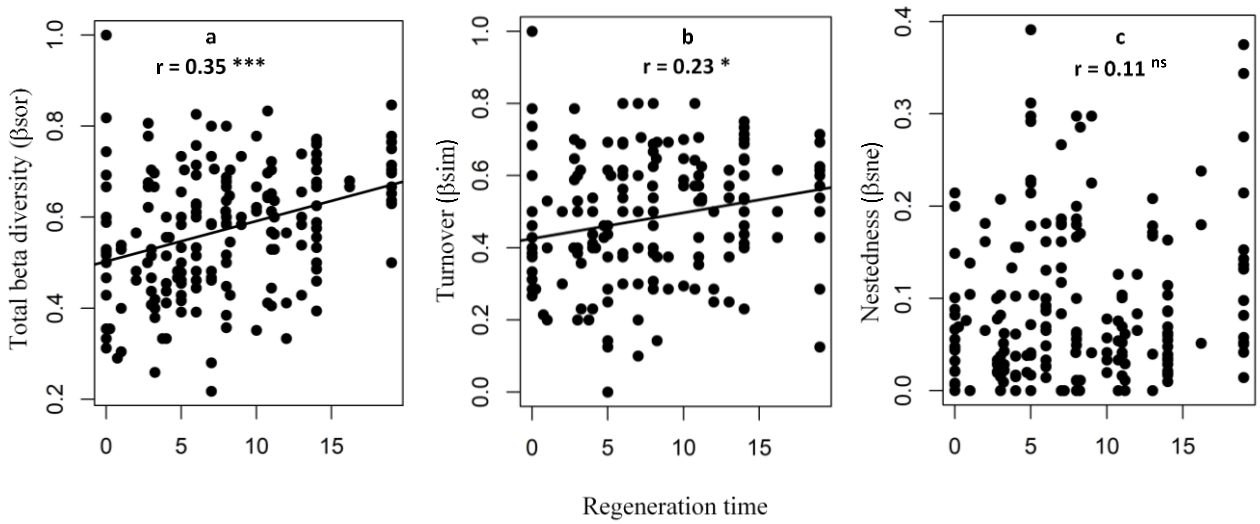

Figure 8.3. Correlation of pairwise dissimilarities in species composition of avian communities (species = 91) and habitat regeneration time (time since fire incidence or since restoration interventions) of naturally regenerated and assisted naturally regenerated habitats within Nyungwe National Park, Rwanda. **a**: Total beta diversity (bsor), **b**: turnover (bsim), and **c**: nestedness-resultant dissimilarity (bsne). 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 averaged over two sampling seasons.

8.4.3 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 8.1). 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, and they 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 8.1). 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 8.1. 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 for readability purposes.

	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.

8.4.4 The relationship between avian taxonomic diversity and vegetation attributes

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. Spatial autocorrelation was diagnosed on model residuals using Moran's I test and was not significant for both species diversity and abundance metrics ($P > 0.05$). Vegetation attributes were in most cases higher in PF, and mostly lowest in AR (Table A4.2).

An average of the most parsimonious model and a supporting model within $\Delta AIC_c < 2$ for PF, NR and AR habitats explained a reasonable amount of variation ($AdjR^2$: 0.38) and showed tree diversity as the leading driver of avian species diversity with a higher Beta coefficient and 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 8.2, Fig. A4.3). 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. 3).

Table 8.2 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 index.

8.4.5 The relationship between avian traits and vegetation attributes

The RLQ analysis showed on the first axis a gradient from primary forest sites with tall, large trees and a high diversity of trees, to sites with low values for each and with higher fern coverage (Fig. 8.4a). The second axis is largely structured by the naturally regenerated habitat (NR) and the assisted naturally regenerated habitat (AR). 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. 8.4b-c). Typical species include *Bycanistes subcylindricus, Lophoceros alboterminatus*, *Corythaeola cristata* (Fig. 8.4c, Fig. A4.4 and Table A4.4). 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 by birds with a plant-seed diet such as *Pternistis nobilis,* and *Turtur tympanistria*, and *Cryptospiza jacksoni* (ARE), while AR sites feature particularly invertivores and species that forage across multiple strata (Strat Gen).

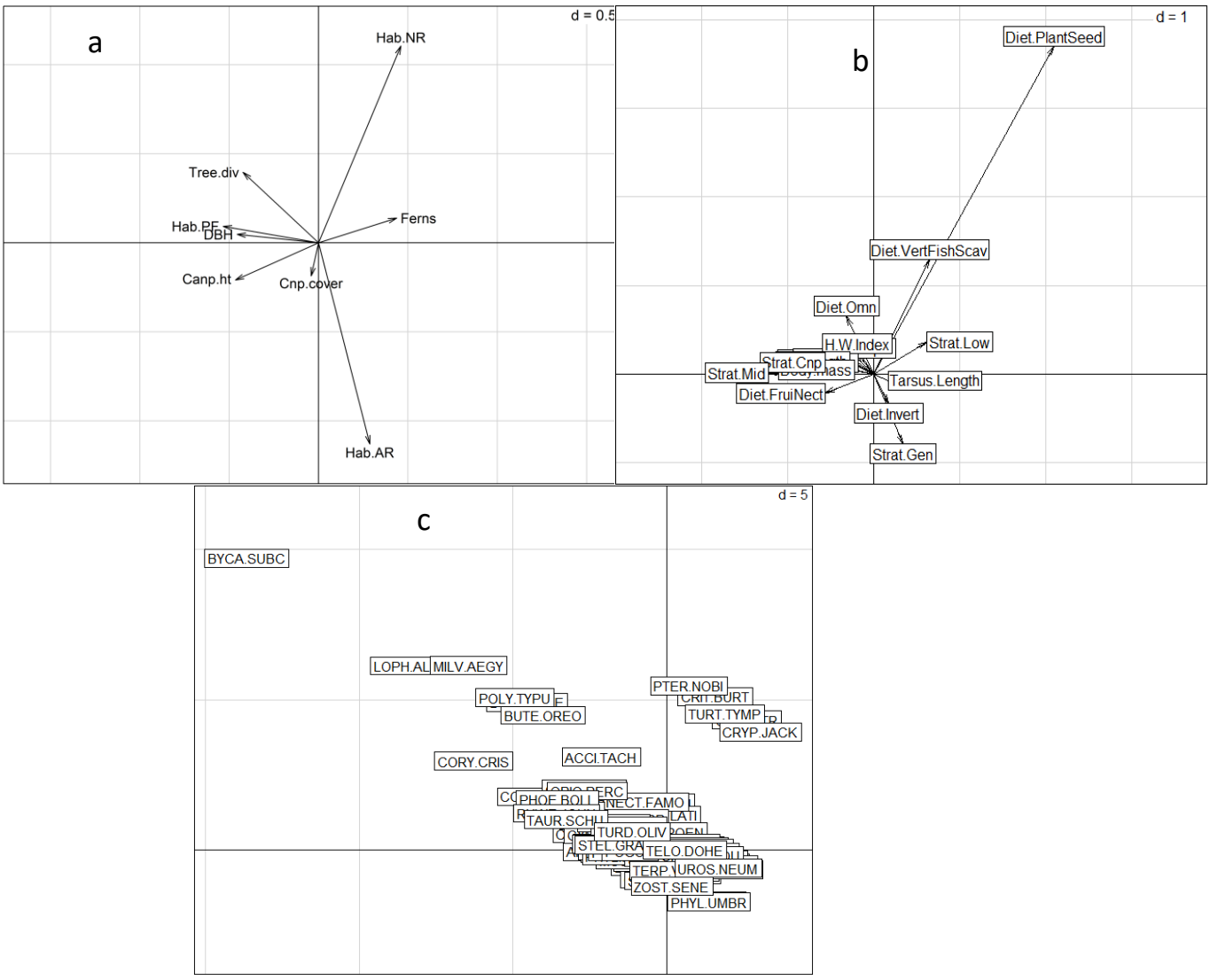

Figure 8.4 RLQ analysis showing relationships between avian traits and habitat variables related to restoration activities of fire-degraded sites within Nyungwe NP, Rwanda. **a**: Coefficients for the habitat variables, **b**: coefficients for the avian traits variables, **c**: scores of bird species. 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 A4.4.

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; Fig. A4.4). 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 ($P = 0.50$).

8.5 Discussion

8.5.1 Dynamism of avian taxonomic diversity with forest regeneration

As predicted, primary forest, naturally regenerated and assisted naturally regenerated habitats had distinct avian species assemblages. Although there was a degree of overlap between the regenerated habitats and across age classes, mid-aged habitat bird assemblages 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 & Peres, 2004; Barlow, Peres, Henriques, Stouffer, & Wunderle, 2006). Similarly, Gould and Mackey (2015), in their study in tropical northern Australia, noted different 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 beta diversity with 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 of two decades. Another explanation could be the high within-habitat avian diversity 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 by a study by Shoo, Freebody, Kanowski, and Catterall (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 less than half those found in the old-growth forest.

8.5.2 Mixed responses of avian diversity features linked to ecosystem functions

Taxonomi 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 $500m^2$ increased fragmentation effects, which may deter frugivores whose reliance on continuous forest cover has been noted (Farwig & Berens, 2012; Farwig, Schabo, Albrecht, & Rees, 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.* These species were only recorded in NR and PF, illustrated 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 undisturbed primary forests (Cooke, Bates, & Eigenbrod, 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.

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). The varying restoration interventions may 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).

8.5.3 Efficacy of the restoration project actions in benefiting birds

The present study found that in the course of 20 years of passive restoration and assisted natural regeneration, bird communities remained distinct and had lower diversity levels in comparison 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 superior effects of assisted naturally regenerated habitats over naturally regenerated habitats 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, Freeman, Kanowski, & Freebody, 2012). Further studies and experiments will be needed to address these questions.

An important factor that was not incorporated in this study is fire severity due to the unavailability of the data for the study period. 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 ferns coverage in hindering it. Although, tree cover can be indispensable for a high avian diversity (especially of insectivores and canopy foragers) in forested habitats (Ikin et al., 2019; Şekercioğlu et al., 2002), 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.

8.5.4 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.

8.6 Authors' contributions

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

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8.9 Appendix 4

TABLE A4.1 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 A4.2 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 A4.3 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 $DQAIC_c < 2$ 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.

TABLE A4.4 Species list of bird species recorded in 100 m radius points (N=600) in Nyungwe National Park, Rwanda. Dietary guild, foraging stratum and species loadings for Axes 1 and 2 of the RLQ ordination (Fig. 8.4c) are provided. The RLQ analysis involves on species recorded within 20 m radius plots. FruiNect: Fruit/Nect (Frugivore), Invert: Invertivore; VertFishScav: Vertebrate/Fish/Scavenger, Strat.Low: Lower stratum, Strat.Mid: Medium stratum, Strat.Gen: multiple strata, Omn: Omnivore. The guild Frugivore and 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	Diet	Stratum	AxcQ1	AxcQ2
ACCI.MELA	Accipiter melanoleucus	Great Sparrowhawk	VertFishScav	Cnp		
ACCI.TACH	Accipiter tachiro	African goshawk	VertFishScav	Cnp	-2.122	3.099
APAL.ARGE	Apalis argentea	Kungwe Apalis	Invertebrate	Cnp	0.209	-0.644
APAL.CINE	Apalis cinerea	Grey Apalis	Invertebrate	Cnp	0.302	-0.739
APAL.JACK	Apalis jacksoni	Black-throated Apalis	Invertebrate	Cnp	0.306	-0.688
APAL.NARI	Apaloderma narina	Narina Trogon	Invertebrate	Mid		
APAL.PERS	Apalis personata	Black-faced Apalis	Invertebrate	Cnp	0.407	-0.826
APAL.PORP	Apalis porphyrolaema	Chestnut-throated Apalis	Invertebrate	Cnp	0.347	-0.744
APAL.VITT	Apaloderma vittatum	Bar-tailed Trogon	Invertebrate	Mid		
APUS.APUS	Apus apus	Common Swift	Invertebrate	Mid		
APUS.CAFF	Apus caffer	White-rumped Swift	Invertebrate	Mid	-2.790	1.446
AQUI.AFRI	Aquila africana	Cassin's Hawk-eagle	VertFishScav	Cnp		
ARIZ.NIGR	Arizelocichla nigriceps	Eastern Mountain Greenbul	FruiNect	Mid	-2.223	-0.040
BATH.RUFU	Bathmocercus rufus	Black-faced Rufous Warbler	Invertebrate	Low	1.362	-0.416
BATI.DIOP	Batis diops	Ruwenzori Batis	Invertebrate	Mid	-0.666	-0.551
BATI.MOLI	Batis molitor	Chinspot Batis	Invertebrate	Cnp	-0.082	-0.378
BOST.HAGE	Bostrychia hagedash	Hadada Ibis	Invertebrate	Low		
BRAD.CINN	Bradypterus cinnamomeus	Bracken Warbler	Invertebrate	Low	1.284	-0.430
BRAD.GRAU	Bradypterus graueri	Grauer's Swamp-warbler	Invertebrate	Low	1.243	-0.366
BUTE.BUTE	Buteo buteo	Common Buzzard	VertFishScav	Cnp	-4.550	4.921
BUTE.OREO	Buteo oreophirus	Mountain Buzzard	VertFishScav	Cnp	-4.029	4.483
BYCA.SUBC	Bycanistes subcylindricus	Black-and-white-casqued Hornbill	FruiNect	Cnp	-13.683	9.710
CAMA.BRAC	Camaroptera brachyura	Green-backed Camaroptera	Invertebrate	Low	1.712	-0.645

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

Abbreviation	Scientific name	Common name	Diet	Stratum	AxcQ1	AxcQ2
GRAU.VITT	Graueria vittata	Grauer's Warbler	Invertebrate	Low	1.034	-0.221
GYMN.BONA	Gymnobucco bonapartei	Grey-throated Barbet	FruiNect	Cnp	-1.934	0.526
HEDY.COLL	Hedydipna collaris	Collared Sunbird	Invertebrate	Cnp	0.241	-0.570
IDUN.SIMI	Iduna similis	Mountain Flycatcher-warbler	Invertebrate	Low	1.190	-0.209
ILLA.PYRR	Illadopsis pyrrhoptera	Mountain Illadopsis	Invertebrate	Low	1.050	-0.252
INDI.EXIL	Indicator exilis	Least Honeyguide	FruiNect	Cnp		
KAKA.POLI	Kakamega poliothorax	Grey-chested Babbler	Invertebrate	Low	0.788	-0.101
KUPE.RUFO	Kupeornis rufocinctus	Red-collared Mountain-babbler	Invertebrate	Cnp	-0.635	-0.213
LANI.LUEH	Laniarius luehderi	Luehder's Bush-shrike	Invertebrate	Mid	-1.662	-0.037
LANI.MACK	Lanius mackinnoni	Mackinnon's Shrike	Invertebrate	Gen	-0.457	-0.406
LANI.POEN	Laniarius poensis	Mountain Boubou	Invertebrate	Mid	-1.471	-0.141
LOPH.ALBO	Lophoceros alboterminatus	Crowned Hornbill	Omnivore	Cnp	-8.286	6.130
LOPH.OCCI	Lophaetus occipitalis	Long-crested Eagle	VertFishScav	Low		
MELA.ARDE	Melaenornis ardesiacus	Yellow-eyed Black Flycatcher	Invertebrate	Low	0.483	0.147
MELA.FASC	Melaniparus fasciiventer	Stripe-breasted Tit	Invertebrate	Cnp	-0.284	-0.233
MELA.FISC	Melaenornis fischeri	White-eyed Slaty Flycatcher	Invertebrate	Cnp	-0.608	-0.135
MERO.OREO	Merops oreobates	Cinnamon-chested Bee-eater	Invertebrate	Cnp	-2.166	1.018
MILV.AEGY	Milvus aegyptius	Black Kite	VertFishScav	Cnp	-6.439	6.137
MUSC.ADUS	Muscicapa adusta	African Dusky Flycatcher	Invertebrate	Mid	-0.876	-0.337
NECT.FAMO	Nectarinia famosa	Malachite Sunbird	Omnivore	Low	-0.676	1.598
NECT.PURP	Nectarinia purpureiventris	Purple-breasted Sunbird	Omnivore	Cnp	-1.284	1.039
NEOC.POEN	Neocossyphus poensis	White-tailed Ant Thrush	Invertebrate	Low	-0.085	0.601
NIGR.CANI	Nigrita canicapillus	Grey-headed Negrofinch	Omnivore	Mid	-1.708	0.896
ONYC.TENU	Onychognathus tenuirostris	Slender-billed Starling	FruiNect	Cnp	-3.354	1.305
ONYC.WALL	Onychognathus walleri	Waller's Starling	Omnivore	Cnp	-2.678	2.033
OREO.RUWE	Oreolais ruwenzorii	Collared Apalis	Invertebrate	Low	1.523	-0.487
ORIO.PERC	Oriolus percivali	Black-tailed Oriole	Omnivore	Cnp	-2.580	1.971
PHOE.BOLL	Phoeniculus bollei	White-headed Woodhoopoe	Invertebrate	Cnp	-3.548	1.694
PHYL.FLAV	Phyllastrephus flavostriatus	Yellow-streaked Greenbul	Invertebrate	Mid	-1.464	-0.200
PHYL.LAET	Phylloscopus laetus	Red-faced Woodland-warbler	Invertebrate	Gen	1.329	-1.686

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

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

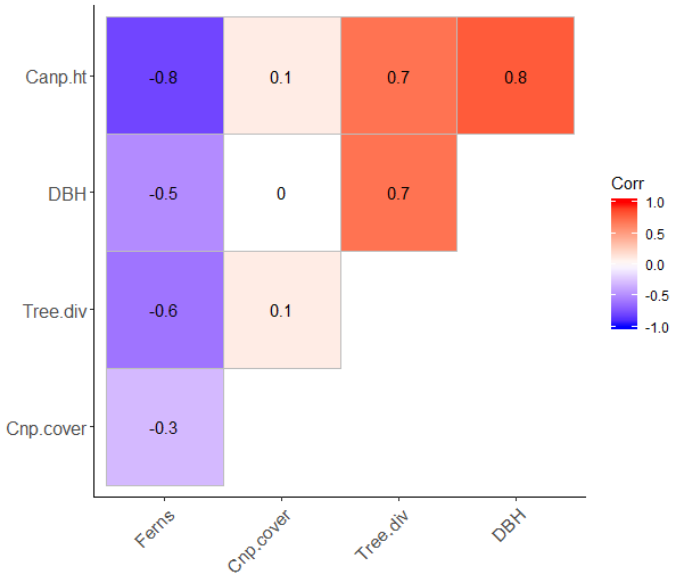

Figure A4.1 Correlation plot of vegetation attributes and corresponding Pearson R correlation coefficients for study samples (N= 60) within naturally regenerated, assisted-naturally regenerated and primary forest within Nyungwe NP, Rwanda. A sample comprised 5 adjacent plots. Each attribute was measured twice: in the wet season, and the dry season of 2017/2018. DBH and Canopy height (Cnp.ht) were excluded from further analysis.

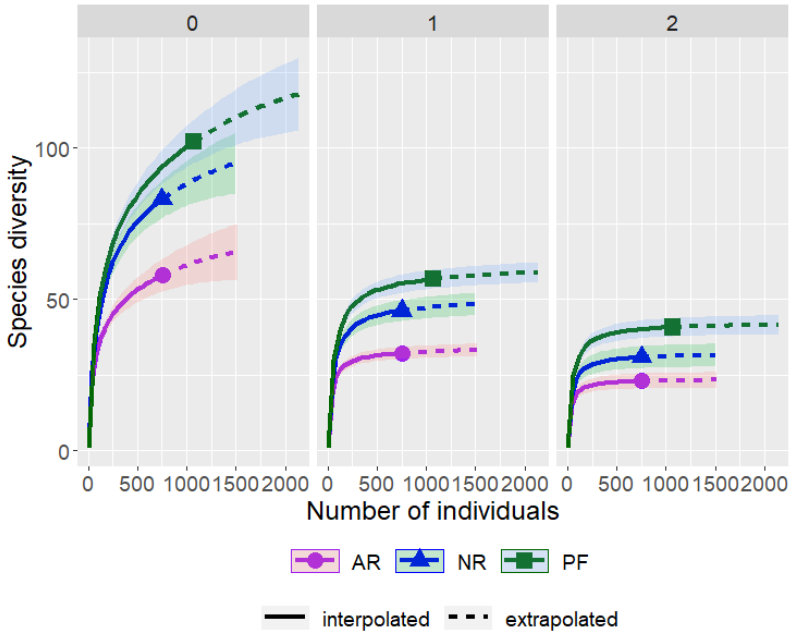

Figure A4.2 Species rarefaction curves computed for each habitat to evaluate the exhaustiveness of sampling efforts. The species diversity of birds is calculated for the Hill numbers, where q=0 is based on the Chao 1 species richness estimator, q=1: the Shannon entropy index, and q=2: the inverse of 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).

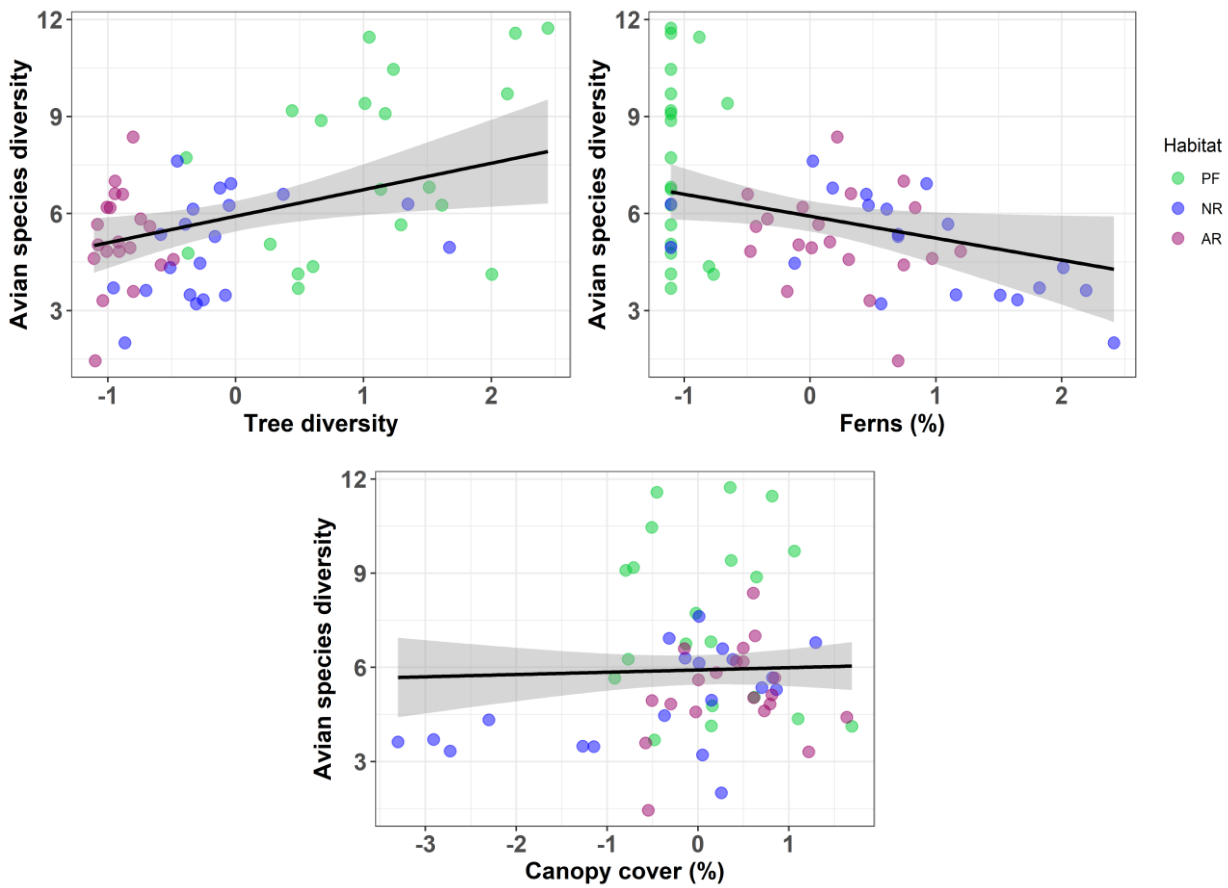

Figure A4.3 Relationships between avian species diversity (exponential of Shannon entropy), functional diversity, and vegetation attributes of study samples (N=20 per habitat) in the primary forest (PF), Naturally regenerated sites (NR), and assisted naturally regenerating sites within Nyungwe National 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.

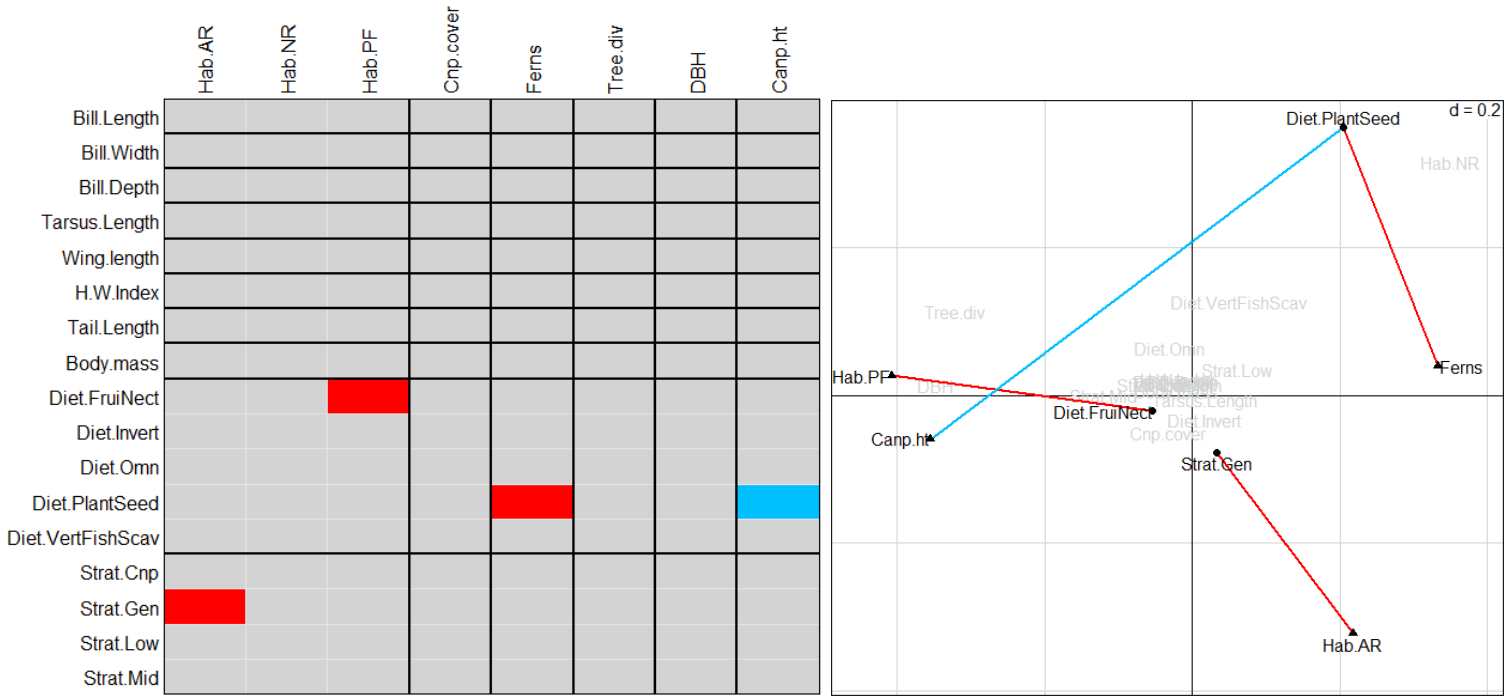

Figure A4.4 Left: Fourth corner analysis displaying relationships between traits variables and environmental variables for bird communities sampled in Nyungwe NP, Rwanda. Right: a biplot showing significant associations between variables tested by the Fourth-corner analyses and displayed using RLQ scores represent traits and habitat variables. RLQ scores are used to represent traits and environmental variables. Red and blue denote positive and negative significant relationships, respectively. Results obtained when using unadjusted p-values**.**

Chapter 9 | Synthesis of major findings, implications, and conclusion

9.1 Avian diversity declines with land-use change

The study showed how all degrees of land-use change led to changes in species composition and reductions in avian diversity levels. Marked declines were principally registered in taxonomic diversity, demonstrating the applicability of this facet of biodiversity as an early warning system. Functional redundancy buffered against losses in functional dispersion, especially when assessed based on the combination of various traits. This redundancy results from the presence of high species richness and reflects that multiple species occupy close positions in the eco-morphological space, a pattern considered typical of tropical forest (Oliveira et al., 2016, Cooke, Bates, & Eigenbrod, 2019). Unexpectedly, the same pattern was revealed in cultivated sites, which were dominated by non-forest species and generalists, reflecting the consistency of this pattern across different pools of species. Analysis of subsets of traits linked with key ecological functions uncovered the filtering of traits in restored areas and cultivated areas, implying the severity of the impact of anthropogenic fires and agricultural activities on habitat attributes ranging from soil properties to vegetation complexity. These drivers have resulted in anthropogenic habitats with less niche space and in the case of the agricultural landscapes, lead to the filtering of certain clades, and consequently occurrence of communities dominated by closely related species.

9.2 Avian response to farmland heterogeneity

At a landscape level (all land-uses combined), cultivated areas consistently ranked poorly in supporting avian diversity, but a focus on farmlands reconfirmed the explanatory power of

vegetation heterogeneity on patterns of avian diversity, reflecting previous extensive work on forest systems (MacArthur and MacArthur, 1961, Oliveira and Scheffers, 2019). Mixed crop farms, which were characterized by higher levels of crop species diversity, greater crop height and tree coverage, supported higher levels of phylogenetic diversity than the less complex monocultures of tea farms. Functional dispersion showed relatively little variance between farm types. This finding concurs with the patterns observed in a recent study conducted at a global level that found forest canopy height (which is often associated with complex vegetation structure), influenced avian and mammal species and functional richness, but not functional dispersion (Feng, Zhang, Girardello, Pellissier, & Svenning, 2020). The authors also attributed these results to the high functional richness of tropical systems.

The study findings have implications for the ongoing debate on the pertinence of land-sharing versus land-sparing in Africa with regards to meeting conservation goals and addressing livelihood needs (Koch, Schaldach, & Göpel, 2019). The study shows the indispensability of primary forests, and makes the case for their conservation, but also stresses the importance of tree cover in enhancing the permeability of agricultural areas. An example is the documented unexpected adaptation of certain clades to novel cultivated farmlands in Rwanda (Vande weghe and Vande weghe, 2011). The Grey-crowned crane, a national emblematic species whose conservation has become a national priority, is one of the species adapting to the farmlands (Nsengimana, Becker, Ruhagazi, & Niyomwungeri, 2019). A pragmatic question to pose would therefore be: “how to maximize both approaches (land-sparing and sharing)”? The long-term health and environmental consequences of intensive agriculture should be adequately weighed before agricultural intensification programs are widely adopted.

9.3 Effectiveness of assisted-natural regeneration approach

The low avian diversity levels in restored sites highlight the slow process of natural regeneration in tropical forest, which exceeded two decades in some of our sites. On the other

hand, the restoration methodology might not have maximized avian recovery. There was no attempt to lure frugivores at earlier stages of the restoration project, which holds potential to have diversified the tree species grown. Secondly, the application of the nucleation-centred restoration, although proven efficient for tree cover regeneration (Albornoz et al., 2013), might not necessarily aid forest specialists that need contiguous forested habitats. These factors shade light on the shortcomings of restoration projects, which often rely on vegetation surrogacy for the recovery of animals (Catterall, 2018). However, restoration with avian diversity as a central goal is not a light decision to take. This study demonstrated how certain habitat and/or vegetation attributes exert contrasting effects on the different facets of the avian diversity.

9.4 Implications for conservation in Rwanda and the Afrotropical countries

Previous land-use decisions culminated in substantial loss and degradation of the natural habitats of Rwanda, including reserves and National Parks. This study has shown how land-use-change has adversely affected avian diversity in the Nyungwe landscape. Although, Rwanda has shown high willingness to protect the remaining montane forests, and pledged to restore vast amounts of degraded areas across the country, policies and practices in the agriculture sector, mainly the adoption of policies of agricultural intensification, risks compromising the set conservation targets. The declines of avian diversity poses threats not only to the burgeoning avi-tourism industry, but also functional services provided by birds, such as pollination, and pest control, which are crucial for agricultural productivity.

The transformation of natural habitats within the Nyungwe landscape mirrors what is happening in many parts of Africa. The predicted upward shift of suitable habitats due to persistent habitat transformation and climate change pose further problems, particularly in mountainous landscapes that support rich avian diversity, but within narrow geographic ranges (Ayebare, Plumptre, Kujirakwinja, & Segan, 2018). Addressing these challenges in

Rwanda may have positive ripple effects as exemplified by some of the decisions pioneered by Rwanda that have spread to other countries. For instance, the ban of plastic bags was enforced in Kenya in 2017, and Tanzania in 2019, in both instances, the case of Rwanda was used as a proof of the feasibility of the policy within a developing country context. Emulations of *Umuganda*[4] have also been introduced in Burundi, Tanzania, and Ethiopia. More recently in Ivory Coast, a youth movement which had visited Kigali, the capital city of Rwanda, on their return mobilised other young people to clean up the city of Abidjan and plant trees under the slogan "Un jour Abidjan sera comme Kigali" [One day Abidjan will be like Kigali] (Douaye, 2019). Further, a Malagasy petition signed in 2019, calling upon the then elected president to prioritize the conservation of the country's biodiversity, cited Rwanda as an example:

"Indeed Malagasy companies looking for international investment often use biodiversity in their advertising, and the President's own election manifesto featured images of baobabs and ring-tailed lemurs. Following the examples of Costa Rica and Rwanda (which have both benefited greatly from tourism attracted by their biodiversity), Madagascar's wildlife could play a central role in sustainable development".

Conservation of Madagascar – Ivato petition

(https://www.atbc2019.org/petition-english accessed 05/06/2020).

It is therefore imperative that Rwanda makes the right environmental moves, since policies and practices it has championed are increasingly being adopted by other countries. The approaches undertaken in the conservation of the mountain gorilla has potential to serve as a model for a multi-stakeholder engagement in the conservation of birds and natural habitats.

[4] Umuganda —coming together, a mandatory monthly community service day.

9.5 Study limitation

Safe access to all parts of the park were the most constraining factor. The only bamboo habitat in Nyungwe lies in the southern sites of the park close to Burundi. These sites were removed from sampling due to security problems. The North-Eastern parts, which had been recently burnt, were also removed due to poor road conditions, especially in the wet seasons.

Although there are naturally regenerated habitats older than 20 years, the limited fieldwork time and small team meant we only prioritized sampling in young forests for easy comparison with the restored sites. Moreover, there was no secondary data to consult since no comprehensive study had been conducted in the regenerating habitats before.

Quantifying effective animal seed-dispersal is a monumental task that requires ample time to track the fate of the seed. Given the limited time, and the range of habitats and avian species covered by this study, we only quantified frugivore–plant interactions as a proxy for dispersal processes. The gaps uncovered by our research present a venue for future researches.

The reliability of Phylogenetic diversity (PD) metrics computed in chapter 6 and 7 depends on the quality of existing phylogenetic information. Although 137 out of 170 study species had genetic sequence data, the positions of the rest of the species on phylogenetic trees were inferred from the placements of closely related members with genetic information, such as congeners, reflecting a degree of uncertainty in the overall topology. Future molecular studies, and analysis of fossil evidences may potentially present different topological arrangements from the ones used in this study.

Further, the missing species genetic data may give rise to unfounded additional polytomies (multifurcations caused by incomplete taxonomic information) and these may be problematic when constructing consensus trees. A range of correction methods to resolve the polytomous nodes have been proposed in the literature, although with varying strength and shortcomings

(Kuhn et al, 2011; O'Reilly & Donoghue, 2018). This study used the majority-rule consensus tree (posterior probability = 0.5), a conservative method that prioritized the accuracy of the overall topology (O'Reilly & Donoghue, 2018). However, no comparison was done with other acclaimed correction methods to determine the best performing consensus tree. This may potentially affect the precision of derived PD metrics. Future publication revisions will take this into consideration.

9.6 Further research

Natural and human-induced processes underlying avian diversity are dynamic in nature, thus long-term studies that monitor changes at the landscape level that are influenced by land-use or climate change, will giver additional insights. Imminent changes of interest to this study are the current harvesting of the non-native buffer zone, which had been acting as a "soft edge" to the Nyungwe forest, and the adoption of the crop intensification program across the country.

Although, birds are considered as an effective indicator taxon for the overall impact of land-use change on the biodiversity and ecosystem functions of tropical forests, other groups such as mammals may exhibit divergent response patterns stemming from the influence of different underlying processes (Feng et al., 2020). Our assessment of seed dispersal in the study area showed contrasting response of primates and large birds to habitat disturbances with respect to the potential number of seeds dispersed. Future investigations in other taxa will be needed to provide a comprehensive view.

9.7 Conclusion

Land-use change, particularly in the form of agricultural conversion and anthropogenic fires, have led to declines in avian diversity in the Nyungwe landscape. Alleviating these adverse effects will necessitate the conservation of the intact forest, maintaining farmland heterogeneity in the forms of crop species composition, height, and tree cover and conducting restoration projects that include explicit animal diversity targets. This study has contributed to documenting information for a topic highly relevant, but poorly covered in the Afrotropics. The incorporation of taxonomic information, functional traits and phylogenies in the framework adopted herein provides a more comprehensive assessment of avian diversity than most previous studies. The study also cautions the complexity of implementing trait and phylogeny-based conservation approaches due to the differential conservation values of species, and their uneven distribution across various land-use types. The study provided evidence of the positive influence of farmland heterogeneity on avian diversity. It is my earnest hope that this information may be used to inform agrobiodiversity conservation strategies. Lastly, the study contributed to a global call to document the success and failures of restoration schemes at all stages. Such scientific documentation will enable policy makers and conservationists to devise future evidence-based restoration plans.

9.8 References

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Appendix 5

Making space for birds: sourcing solutions from the mountain gorilla conservation model in Rwanda

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Highlights

- Birds play vital roles in ecosystem functioning and human well-being, however, anthropogenic threats have led to alarming population declines and extinctions.
- Concerted efforts of international and local partners have attained tangible progress in the recovery of the mountain gorilla (*Gorilla beringei beringei*), demonstrated by a rise in numbers.
- The mountain gorilla conservation approach initiated in Rwanda has been scaled-up to include gorilla habitats in DRC and Uganda, and recently the Greater Virunga landscape, which comprises eight reserves.
- Adapting key steps from the mountain gorilla conservation model to birds presents multiple benefits, especially if conducted methodically within a Systematic Conservation Planning framework, notwithstanding obvious perceptual and geographical differences between the taxa.
- Birds provide an efficient conservation surrogate, therefore, management interventions targeting birds in Rwanda will simultaneously support other affected taxa and ecosystem services more broadly across the region.

1 Abstract

Rwanda being one of the most densely populated countries in Africa, a large proportion of its native vegetation has been converted into agriculture and settlements, leading to the extensive loss and degradation of natural habitats, with significance for birds as well as other taxa. Despite this, tangible success has been attained in the conservation of mountain gorillas thanks to the high priority afforded to this species and the vigorous protection of its habitats. This article reviews the current conservation approaches in Rwanda, and their effectiveness in addressing threats to the country's avifauna. Drawing lessons from the conservation of the mountain gorilla approach, and with reference to the principles of Systematic Conservation Planning, this paper argues that the creation of more reserves complementing existing protected areas, the development of bird-related tourism, and a multilevel collaboration of stakeholders at national and regional level, in which the public play a strong role, are crucial for the long-term conservation of birds. The aim of this analysis is both to provide policy options for Rwanda and to suggest an approach to conservation practice for wider application that is scalable and transferable within a developing country context.

Keywords

Avitourism, Bird conservation, Mountain gorilla, multi-stakeholder partnership, protected area, Rwanda, Systematic Conservation Planning.

2 Introduction

With roles ranging from food provisioning, pest and disease control, pollination, seed dispersal, top predators and environmental indicators, birds are vital to the functioning of ecosystems (Whelan et al., 2015). In addition to that, birds have always fascinated and inspired all human cultures and reinforced their social cohesion as evidenced by songs, poems, riddles and customs of which they form the basis. Bird watching and photography enterprises have substantially contributed to economic growth, particularly in developed countries. For example, a private company, Birding Ecotours, organizes regular three-weeks photo and birding tours in 11 reserves of Kenya for a cost of US$15,973 per person, including superior hotels where accessible (birdingecotours.com, accessed on 16/10/2019). Herget et al. (2016) reported that crane migration viewing at Vorpommersche Boddenlandschaft National Park in Germany generated 4.4 Million Euros, and in the UK, an estimation of over £750 000 was retrieved from seabird tourism in 2009 (RSPB, 2010). In 2016, wildlife watching expenditures in the USA amounted to US$ 75. 9 billion, and 88% of participants (N = 43.8 million) were observing birds (U.S. Fish and Wildlife Service, U.S. Census Bureau, 2018). An earlier survey in 2011 (Carver, 2013) had previously reported that US $41 billion was spent on bird-related annual trips and equipment, and consequently, 666 000 jobs were generated across the USA.

Despite their crucial ecological and socio-economical contribution, a significant number of bird populations have been declining globally (BirdLife International, 2018). A net loss close to 3 billion North American birds since 1970 has been reported (Rosenberg et al., 2019) and one third of bird species require urgent conservation intervention (NABCI, 2016). According to the PECBMS report (2019), 57% of European farm bird species populations registered population falls between 1980 and 2016. Africa's birds have not fared well. 10% of the 2 355 bird species are considered globally threatened, largely due to habitat loss and degradation

driven by agriculture and logging (BirdLife International, 2013). The situation is particularly severe for African vultures, whose populations have suffered declines of 80–97%, largely due to the consumption of poisoned carcasses of large carnivores (BirdLife International, 2018).

In Rwanda, the clearance of the natural vegetation, which covered half of the country 50 years ago, has led to plummeting bird populations outside reserves and ten bird species extinctions (Vande weghe and Vande weghe, 2011, Vande weghe, 2018). In contrast to the limited action towards the protection of birds, Rwanda has attained incredible success in the conservation of the mountain gorilla (*Gorilla beringei beringei*), which is the only great ape (excluding humans) that has been increasing in numbers in the last three decades (Gray et al., 2013, GVTC, 2018). Consequently, the IUCN conservation status of this gorilla subspecies was recently downlisted (Hickey et al., 2018). Investing similar efforts in the preservation of birds guarantees a broad array of advantages, particularly fulfilling Rwanda's quest to expand and diversify its tourism industry, which is heavily reliant on gorilla trekking activities **(**RDB, 2018a).

Parallels between mountain gorillas and birds can be hard to draw since the former are genetically closer to humans, hence their loss strikes a chord, hastening support and fund mobilization. Secondly, the conservation plan and management of one species (*Gorilla beringei*) confined in two sites that are in close geographic proximity is relatively easy compared to the management of hundreds of species of birds with different behaviour and habitat affinities. Nonetheless, there are shared elements crucial to the conservation of the two groups that make sensible the transfer of insights from the mountain gorilla conservation approach to birds. These commonalities lie in the forms and magnitude of their threats, the high charisma that garners quick support from the lay public and scientists, and the potential economic returns when effectively managed. Added advantages of planning for birds as a

whole taxon are their diverse functional traits, and ubiquitous dispersal patterns, which warrant wider conservation coverage of a diverse of species, ecosystems, and associated functions and services. This would be an important outcome, since focusing on mountain gorillas has not led to the cessation of threats to other animals within the same site, as shown by persisting antelope poaching incidences in Volcanoes NP (Sabuhoro, 2017).

The concept of prioritizing certain bird species, or the whole avian taxon as conservation surrogates has been extensively deliberated in the literature (Blair, 1999, Lambeck, 1997; Lindenmayer et al., 2002, Jones et al., 2016). Implementation on the ground of a global scheme was concretized in the late 1970s by BirdLife International's "Important Bird and Biodiversity Areas" (IBAs), which were identified based on the presence of species that are globally threatened, range or biome restricted, and congregatory (Fishpool and Evans, 2001). According to Birdlife International (2013, 2018), the majority of IBAs across the world lack legal protection, and investment funds. The leading threat in Africa has been habitat loss and degradation due to expansive and intensive agriculture, and a surge in infrastructure projects, particularly in the transport, and energy sectors. Effective and wider conservation coverage of avian biodiversity may gain from learning from successful conservation models, and adopting working methods using holistic planning tools.

The paper proceeds with an overview of the Rwandan avifauna, and discusses how current conservation approaches entail loopholes in protecting birds and their habitats. Through the lens of systematic conservation planning, the paper demonstrates how practical lessons learnt from the conservation of the mountain gorilla can be adapted and scaled-up to alleviate threats to birds, and subsequently benefit other associated taxa.

3 Avian diversity

Although Rwanda (26 338 km^2) has a small surface area, it is home to a large variety of vegetation types influenced largely by Eco-climatic zones comprising the Afro-alpine, humid, sub-humid and the sub-arid zones (Vande weghe and Vande weghe, 2011). The avifauna of some 703 species falls within the Afromontane, Guineo-Congolian, Lake Victoria, Zambesian, Soudan-Guinea savanna, Somali-Maasai, and Malagasy biogeographic regions (phytochoria), and 26% are vagrants, intra-African and Palearctic migrants (Kanyamibwa, 2001, Vande weghe and Vande weghe, 2011, Vande weghe, 2018). Although Rwanda has no strictly endemic bird species, eight of the nine Lake Victoria endemics and near endemics are present, and the Afro-montane habitats harbour 26 of the 37 Albertine Rift endemics (Kanyamibwa, 2001, Vande weghe and Vande weghe, 2011). 46% of 510 residents have adapted to the human-modified habitats, however, the persistence of the vast majority rests on continued conservation efforts (Vande weghe, 2018).

4 Bird conservation challenges

4.1 Human population pressure

With a projected human population of 12 089 720 in 2018 and a density of 477 people per sq.km, Rwanda is the most densely populated country in mainland Africa (NISR, 2018a). The Gross domestic product per capita has been increasing steadily from US$700 in 2012 to US$774 in 2017, however, 80% of the population are subsistence farmers, mostly residing in rural areas (NISR, 2018b). The burgeoning population over the last century exacerbated the quest for arable land and fuel woods, leading to massive degradation of all forests and wetlands outside reserves (Kanyamibwa, 2001, Masozera and Alavalapati, 2004, Weber, 1989). As a result, bird populations outside reserves have declined considerably, and five bird species without representation in National Parks are considered extirpated (Vande weghe and Vande weghe, 2011). Other environmental consequences have included increased flooding,

landslides, soil erosion, river siltation, and poor agricultural production (EPI, 2015, Hategekimana and Twarabamenya, 2007).

4.2 Institutional reformation

As commonly practiced in Africa, pre-colonial conservation in Rwanda was firmly rooted in a body of beliefs, such as the totemic system that extended the perception of the self to animal and plant species (Bigirumwami, 1974, Diawuo et al., 2017). Protected areas in Rwanda are largely a colonization legacy sustained predominantly by government institutions and international NGOs (Rutagarama and Martin, 2006). Established in 1973, the core conservation institution within Rwanda was the ORTPN (the Rwandan office of tourism and National Parks), which operated under the auspices of the Ministry of Agriculture. With an administrative and financial autonomy, the ORTPN had a final say in the allocation and use of tourism revenues, government subsidiaries, as well as bilateral and multilateral funding from international donors and organisations (Maekawa et al., 2013). The 1994 genocide against the Tutsi and the concurrent civil unrest hampered ORTPN management capacity, as it sustained loss of human life and infrastructure damage (Rutagarama and Martin, 2006). Further, ORTPN performance was affected by constant government restructuring. In late 1994, ORTPN was moved under the ministry of lands, Environment, Forestry, Water and Mines, and in 2011, it was transformed into a department of tourism and conservation of the Rwanda Development Board (RDB), a new institution that combined all major income-generating government agencies operating under the Ministry of Commerce.

Another key institution, The Rwanda Environment Management Authority (REMA), was established in 2005 under the Ministry of Environment and Natural resources, and has become the central regulating body for environmental management, particularly with emphasis on the formulation and enacting of laws, policies and regulations pertinent to the environment (ROR, 2011). In 2012, the Environment and Climate Change fund

(FONERWA) was established under the Ministry of Environment to finance activities that protect the environment and that mitigate effects of climate change. In the same year and under the same Ministry, the Natural Resource Management agency (RNRA) was formed by merging the National Forest Authority with other Environmental entities, including the Geology and Mines Authority. The RNRA had been pivotal to forest extension, in particular, the restoration of Gishwati forest. RNRA subsequently underwent further restructurings, culminating with it being split into three separate bodies (ROR, 2017).

Under the leadership of the above-mentioned institutions, important environmental legislation was passed, such as the Organic Law on the environment, the Biodiversity law, the wetland law, the well-known 2008 law banning the use and manufacturing and importation of polythene bags, and the forest policy, which won the 2011 UNEP future policy gold award for its contribution to forest cover increase despite a multitude of pressures (UN DESA, 2011, MINIFOM, 2010, ROR, 2005, 2011). Rwanda has also ratified a number of international conventions relating to bird conservation, such as the Convention on Biological Diversity, the African Convention on the Conservation of Nature and Natural Resources, the Convention on Migratory Species, and the African-Eurasian Migratory Waterbird Agreement.

Despite the increasing number of institutions and items of legislation, very little attention has been paid directly to birds. Recent forest policy interventions have been dominated by the expansion of monoculture plantations of non-indigenous trees, especially eucalypts (MINIFOM, 2010, Ndayambaje et al., 2014). Although such interventions respond to the cooking energy problem, they support significantly less biodiversity than native forests (Bizuru et al., 2015, Vande weghe and Vande weghe, 2011). There is no distinct national legislation on the protection of birds, nor a leading organization or department solely in charge of bird conservation. Moreover, constant restructuring of core government institutions creates redundancy and exacerbates the problem. Consequently, the only bird populations

that seem to be stable are those within protected areas, specifically National Parks, reflecting that the mandates of the institutions in charge – RDB and REMA are well stipulated in the law (Ministry of Trade and Industry, 2013, ROR, 2005). In other reserves and non-reserves, severe habitat degradation, roadkills, hunting largely for leisure, as well as indirect poisoning targeting large carnivores, have gone unpunished.

4.3 The protected area framework

Rwanda's contemporary biodiversity conservation strategy has principally centred on the protected area model. National Parks – the highest conservation status in Rwanda, cover 8.9 % of the land area (Fig. 1). The first National Park to be designated was Volcanoes National Park (Volcanoes NP). It was gazetted in 1925 to reinforce the protection of the mountain gorillas (*Gorilla beringeiberingei*) (Weber and Vedder, 1983). In 1934, the eastern savannas of Akagera and Umutara were designated as a National Park and reserved hunting area, respectively. In 2004, Nyungwe forest, the largest Afromontane rain forest in East Africa (Plumptre et al., 2007), and in 2015 the forest reserves of Gishwati and Mukura, were each upgraded to National Park status. In 2006, Rugezi marsh, a wetland located in the north of Rwanda was officially recognized as a wetland of international importance (Ramsar site) (Hategekimana and Twarabamenya, 2007).

One of the drawbacks of the protected area model is that it can indirectly confine the arena for conservation action within reserves, hence condemning outside landscapes to maximum exploitation, which eventually creates pockets of protected areas in extensive human-transformed habitats (Watson et al., 2011). The second and most fundamental problem of the protected area model is that the designation status, even when backed by laws, does not guarantee long term conservation, as it may be undermined by socio-political and economic changes (Watson et al., 2014). Since gazetting, most of the Rwandan reserves have lost at least half of their size, principally due to clearing for farming and human settlements

(Plumptre et al., 2005, Vande weghe and Vande weghe, 2011). The loss of habitat has been particularly severe for birds of prey, which often need large territories (Vande weghe and Vande weghe, 2011). On the other hand, tourism, particularly in national parks has been increasing (Fig. 2 and 3).

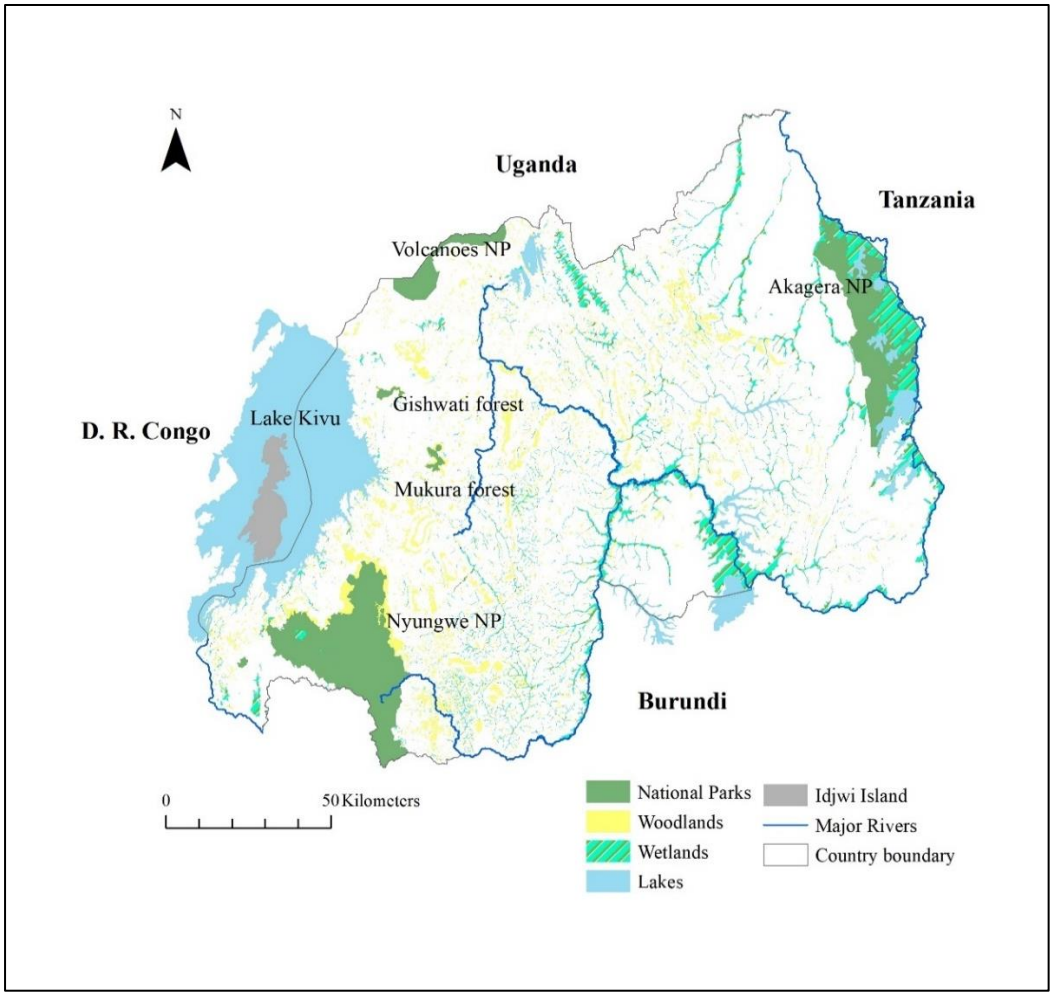

Figure 1. Map of Rwanda, showing location of National Parks. Volcanoes NP (160 km^2), and Nyungwe NP (1,010 km^2) are contiguous to national parks in neighbouring countries. The forests of Gishwati (15.7 km^2) and Mukura (19.88 km^2) are presently recognized as one protected landscape, the "Gishwati-Mukura National Park". Akagera NP (1,084 km^2) is a savanna ecosystem, whilst the rest are Afromontane forest ecosystems. All national parks with the exception of Gishwati-Mukura NP are recognized as Important Birds and Biodiversity Areas by Birdlife international. (Original figure).

5 The Mountain gorilla conservation case

The endangered mountain gorilla (*Gorilla beringei beringei*) is a sub-species of the eastern gorilla endemic to the high elevation montane forests (2500–4507m) of the Albertine rift region. One population of the mountain gorilla is found in the Virunga massif, a volcanic region encompassing the Volcanoes NP in Rwanda (160 km^2), Parc National de Virunga (PNVi) in DRC (250 km^2), and Mgahinga Gorilla National Park (MGNP) in Uganda (27km^2). The other population is found in Bwindi Impenetrable National Park (Bwindi INP) (321 km^2) in Uganda, and the contiguous réserve naturelle de Sarambwe (RN Sarambwe).

5.1 Initiating the conservation of the mountain gorilla

Research on mountain gorillas was initiated in the 1960s by George Schaller (Schaller, 1963) and then reinforced by the well-known primatologist Dian Fossey, through her establishment of Karisoke Research Center (KRC) in 1967, after relocating from Congo due to political insecurities. KRC has been a hub of long-term research on mountain gorillas, documenting a broad range of aspects related to gorilla ranging patterns, demography, behaviour and ecology (Harcourt, 1986, Robbins et al., 2001). The data collected are shared with park managers and scientists and form the basis of improved conservation measures (Robbins et al., 2001).

Mountain gorillas were facing a myriad of threats, among others are the degazetting of 55% of their habitat in Rwanda for the European-funded Pyrethrum farming project in the 1960s, fatal accidents from antelope-targeted snares, infant captures for zoos and the pet trade, trophy hunting, and intense livestock grazing in the park in the 1970s (Harcourt and Fossey, 1981, Weber and Vedder, 1983). Consequently, the number of gorillas in the Virunga massif plummeted from 450 to 225 between the 1960s and the late 1970s (Harcourt and Fossey, 1981).

Initially, the conservation of the mountain gorillas was spearheaded by ORTPN, and the Belgian government. KRC followed suit with active conservation, involving daily monitoring of gorillas and the removal of snares inside the park (Maekawa et al., 2013). The rise in the quest for gorilla trophies sparked the commencement of the Mountain Gorilla Project (MGP) in 1979. The MGP was a joint initiative of several leading international NGOs with the goals of instituting measures to curb poaching, developing a gorilla-based sustainable tourism, and raising public awareness (Vedder and Weber, 1990).

According to Harcourt (1986), the MGP's efforts lead to the prohibition of all cattle grazing in the forest in 1976, a threefold increase in the number of trained forest guards, and nationwide mass education on the conservation status, ecological role, and value of mountain gorillas, disseminated in the form of posters, seminars, broadcasting media and organised school and community visits to the park. Poaching levels declined significantly, the proportion of local farmers who wished to see the park converted declined from 50% in 1980 to 18% in 1984, and there was overall more support for gorilla conservation and prosecution of those who violated wildlife laws. A combination of strict law enforcement, and conservation education continues today, and has ensured increased public support and an almost total halt to habitat loss (Hickey et al., 2018, NISR, 2018a).

5.2 The setting up of a gorilla-based tourism

In 1978, Volcanoes NP had no proper tourism strategy and execution plan, and park costs exceeded tourism revenues, reflecting that generating profits was not perceived as a principal goal, but rather the maintenance of the park as a pristine area (Harcourt, 1986, Weber and Vedder, 2001). To bridge this gap the MGP implemented a tourism plan that entailed broader habituation of mountain gorillas, training guides, and installing appropriate tourist facilities and services (Maekawa et al., 2013, Vedder and Weber, 1990). As reported by Harcourt (1986), these efforts did not take long to yield results, for 5,790 people paid to visit

Volcanoes NP in 1984 compared to 1,352 people in 1978, and the gorilla trekking fee rose from US$5 to US$45. The number of Rwandan tourists remained low, at 2.3%, despite a lower trekking fee, equivalent to a 10th of the foreign tourist cost. The MGP phased out in 1991 and was succeeded by the International Gorilla Conservation Programme (IGCP), a coalition led by Fauna and Flora International (FFI), the World Wide Fund for Nature (WWF), and the African Wildlife Foundation (AWF), which pulled out of the coalition in 2015. In 2019, a new member, Conservation International joined.

Tourism management was then administered by the ORTPN, and the park financial resources continued to increase. A study by IGCP, conducted in 2001–2002, estimated regional gorilla-based tourism revenues at US$ 20.6 million per year, with 59% retrieved at national and local level, and 41% at international level (Hatfield, 2005). Maekawa et al. (2013) reported that in 2012 more than 180 people were employed in park operations, protection, research and tourism.

A revenue sharing scheme introduced in 2004 involved 5% of annual tourism revenue being allocated to the livelihood improvement of adjacent communities (Mugabukomeye, 2007). The revenue sharing scheme disburses 40% to community enterprises, such as: beekeeping modernization; cow and sheep rearing; agroforestry; seed production and storage; and rainwater harvest, whilst 60% is re-injected in public infrastructure, including schools, health centres, water tanks, and road repairs (Mugabukomeye, 2007, Munanura et al., 2016, Nielsen and Spenceley, 2011). Since the inception of the tourism revenue-sharing scheme, funds disbursed to communities have been increasing substantially, for example investiments in communities around VNP rose from US$25,003 in 2005 to US$235,171 in 2015 (Sabuhoro et al., 2017). More investiments are expected with the recent increase of the revenue-sharing quota from 5% to 10 %, which followed the adoption of the high-end tourism model

exemplified by Kenya and Mauritius and which involved doubling of the price of trekking gorillas for the second time from US$750 to US$1500 in 2017 (RDB, 2018a).

The bulk of national tourism revenues is contributed by Volcanoes NP, and the trekking of mountain gorillas remains the preferred tourist activity (Fig. 3.3). Tourist earnings in Volcanoes NP rose from US$ 430 542 in 1995 to US$ 17.1 million in 2017 (RDB, 2018a, Sabuhoro et al., 2017). Tourism has presented a public-private platform for the local community and the private sectors to fully engage with the mountain gorilla conservation cause. In June 2019, SafariBookings.com, an online marketplace for African safaris registered more than 1 165 national and international tour operators offering Volcanoes NP as a destination. In addition, public-private enterprises such as the Sabyinyo Silverback community lodge — a joint venture between local community, the government of Rwanda and a private company — are emerging and contributing considerably to the economic security of employees and their dependents (Nielsen and Spenceley, 2011, Rutagarama and Martin, 2006, Sabuhoro, 2017).

Tourism in Volcanoes NP has generally improved the quality of life of adjacent communities. The construction of schools, health centres, and water tanks around the park have considerably shortened travel distances used when seeking these amenities, thus saving time and resources (Ekise et al., 2013). A report by Black (2015) investigating the amelioration of community livelihood linked to the operation of the Sabyinyo Silverback community lodge, found that 16 out of 19 staff interviewed were satisfied by their job, and 14 affirmed that the lodge provided space for personal growth and empowerment. Sabuhoro (2017) noted similar positive perceptions on the socio-economic improvement of participants in tourism community enterprises around volcanoes NP, such as the Iby'Iwacu Cultural Village, formed in 2006 by the government of Rwanda, conservation partners, and a private tour operator to engage ex-poachers in culture-based tourism activities.

5.3 Transboundary collaboration

Since the initiation of the MGP to the present, the collaboration of Rwandan and international organizations to save mountain gorillas has been conducted in a manner that minimizes redundancy and promotes effective use of the available resources (Harcourt, 1986, Plumptre et al., 2007). The fact that mountain gorillas are not confined within the boundaries of Rwanda, made it imperative to garner cooperation of the whole Virunga massif authorities. The scale-up process to DRC and Uganda has been largely facilitated by the IGCP, the successor to the MGP. Transboundary collaboration started in the 1990s with the development of a communication system for regular information exchange and capacity building for park managers and field staff, as well as joint execution of standardized ranger-based monitoring, gorilla census, and law enforcement (Lanjouw et al., 2001, Plumptre et al., 2007).

Collaboration was later cemented by formal agreements between the three countries including: a 2001 declaration of park authorities endorsing the formation of a trans-frontier park between the Virunga massif and Bwindi INP; a 2004 Memorandum of Understanding between Protected Areas Authorities aiming at stepping up collaboration from park level to institutional level, expanding the geographical scope of this collaboration from the Virunga Massif, habitat of the Mountain gorilla, to the larger area currently known as the Greater Virunga Landscape encompassing eight parks; and a 2005 tripartite agreement between the ministries of the environment in the three countries, formalizing the collaborative conservation and management of the transboundary landscape. Another memorandum of understanding was signed by the three countries in 2006, agreeing on a 50% sharing of tourist trekking fees generated from a gorilla family that crossed the border.

Also in 2006, the Ten-year Transboundary Strategic Plan for the Central Albertine Rift was adopted, expanding the scope of cooperation from mountain gorilla conservation and tourism

to eight key areas entitled: “enabling environment, landscape management, effective management capacity, collaboration, law enforcement, education and awareness, economic development, and financial sustainability” (TCS, 2006). The expansion of the mandate necessitated a multi-level governing structure composed of representatives from the three countries who would ensure that activities of regional interest take precedence over national ones, and experts in the group are given a platform to share their insights (Refisch & Jenson, 2016). The core body was the Greater Virunga Transboundary Collaboration (GVTC), a secretariat constituted in 2008, and formalized in a 2015 treaty to oversee and coordinate transboundary activities across the Greater Virunga landscape.

Remarkably, regional conservation collaboration was maintained during extreme insecurity and even when the three countries were at political odds (Lanjouw et al., 2001, Maekawa et al., 2013). This helped considerably in curbing transfrontier threats ranging from trade in infant gorilla, ivory, illicit timber production, fire control, and an influx of 750 000 Rwandan refugees who resided at the boundary of Southern PNVi in 1994 to 1996 following the Rwandan civil war and genocide (Maekawa et al., 2013, Nielsen and Spenceley, 2011, Plumptre et al., 2007). From 2007 to 2009, a North-Kivu rebel group CNDP (Congrès National pour la Défense du Peuple), took control of the Mikeno sector, a part of the PNVi used by mountain gorillas. Although CNDP restricted access to ICCN, the Congolese wildlife conservation authority (Institut Congolais pour la Conservation de la Nature) and cross-border joint patrols were discontinued, rangers were allowed to pursue gorilla monitoring and anti-poaching patrols, and alternative arrangements were made for each park to be patrolled by its rangers, and bordering areas to be covered concurrently (Refisch & Jenson, 2016). Three years later, M23 – a rebel group composed of former members of CNDP who had been integrated in the Congolese army, resumed fighting and occupied a large portion of the mountain gorilla home range in PNVi. M23 allowed ICCN to conduct gorilla monitoring

activities, attesting to the trust afforded to conservation partners, and the latter's flexible communicative tactics, even with parties having unparallel mandates and goals (Milburn, 2016, Refisch & Jenson, 2016).

The concerted collaborative actions, along with quick veterinary intervention, and community involvement in development and conservation activities, such as the building of a stone buffer wall in exchange of payments, have facilitated the increase of the Virunga massif gorilla population from 380 individuals to 480 between 2003 and 2010, representing a 26.3% population increase and a 3.7% annual growth (Gray et al., 2013). The 2015–2016 census revealed a further increase from 480 to 604 (GVTC, 2018). Adding the 459 individuals (minimum count) recorded in Bwindi INP and RN Sarambwe (Hickey et al., 2019), the total number of mountain gorillas is currently estimated at 1,063 individuals. The increase in number and the mechanisms in place to curb major threats, recently prompted the downlisting of the conservation status of the mountain gorilla from critically endangered to endangered (Hickey et al., 2018).

Conservation measures taken to conserve the mountain gorillas in Rwanda are not entirely context-dependent, but at least in part may be transferable to other places and species. They have been emulated in the conservation of the most threatened ape in Africa, the Cross River gorilla (*Gorilla gorilla dielhi*) (except for tourism development), and efforts have come to fruition as evidenced by the creation of new protected areas that harbour gorilla populations, increased research, regular patrols which include joint patrols between Cameroonian-Nigerian rangers, involvement of the community as stewards of gorillas, a decrease in gorilla hunting, and the generation of alternative sources of livelihoods (Dunn et al., 2014, WCS, 2019).

6 Adapting the mountain gorilla conservation approaches to avian conservation

Effective conservation of any landscape or species necessitates conservation planning that goes beyond a prioritization framework and an associated execution plan (Jones et al., 2016, McIntosh et al., 2017). Systematic conservation planning methods aim to achieve this through a broad spectrum of quantitatively measured principles spanning representativeness, persistence, efficiency, flexibility, and accountability (Kukkala and Moilanen, 2013, Margules and Pressey, 2000, Margules and Sarkar, 2007). Grounded in these principles, key lessons learnt from the conservation of the mountain gorilla can be tailored to respond to the plight of birds and opportunities for their conservation in Rwanda (Fig. 4).

6.1 Enhancing avian research and monitoring

Although birds represent a globally well-studied taxon, for Rwanda relatively little is known beyond species prevalence. Regular surveys are mainly restricted within reserves, and the data are not readily accessible. With limited resources, research is often relegated to the lower end of priorities. However, such a sacrifice may prove counterproductive in the long-term. As noted in the case of the mountain gorilla, close monitoring and long-term research were crucial in devising appropriate interventions (Robbins et al., 2001). Further, research findings aid in the identification of priority sites, species or surrogates, and offer a baseline for measuring conservation impact, hence facilitating evaluations and accountability processes (McIntosh et al., 2017).

As often reported in avian conservation programs across the world, citizen science presents an ideal way to avert the cost of conducting research, and to keep engaged both enthusiastic birders and the general public, whilst building ecological knowledge. Platforms such as ebird[5], inaturalist[6], and xeno-canto[7] facilitate the ease of collecting and sharing avian data in a

[5] https://ebird.org/home
[6] https://www.inaturalist.org/

cost-effective manner. Institutions such as the University of Rwanda center of excellence in Biodiversity and natural resource management, and the IPRC-Kitabi (formerly, Kitabi College of Conservation and Environment Management) are well positioned to capitalize on citizen science tools to help build capacities of conservation practitioners and academics in Rwanda.

6.2 Protecting complementary bird habitats

In the face of increasing bird habitat transformation linked to anthropogenic pressures, it is imperative to confer and uphold legal status and protection of key bird habitats, particularly non-reserves as they still harbour a diversity of birds. Key habitats without a comprehensive protection status include: Akanyaru and Nyabarongo wetlands, which have been classified as IBAs (Kanyamibwa, 2001); lakes and associated wetlands in the Bugesera region; and remnants of afromontane forests such as Busaga, and gallery forests including Mashoza parike and Ibanda Makera. In addition to natural habitats, human-modified landscapes in urban or agricultural landscapes can still be inhabited by a high number of bird species. Gatesire et al. (2014) applied the point count sampling method to assess the bird species diversity in the city of Musanze, which is located 15 km away from Volcanoes NP and comprises built-up environments as well as agricultural and forested areas. In comparisons with checklists for Buhanga eco-park and Volcanoes NP, they found that the city had a higher bird diversity than Buhanga eco-park, and the same number as Volcanoes NP. Endemic birds were largely confined within the two protected areas, whereas migrating birds were mostly restricted within the city.

[3] https://www.xeno-canto.org/

Selecting which sites to conserve is not a trivial decision, and ought to be guided by the principle of "representativeness", whereby the conservation areas encompass samples of all or most biodiversity of a given area (Margules and Pressey, 2000). In the case of the mountain gorilla, this was achieved by gazetting as protected areas their habitats spread across the DRC, Rwanda and Uganda. However, given the high number of bird species, their broad distribution patterns, and constrained conservation resources, optimizing the number of birds conserved within Rwanda would therefore require the protection of complementary areas. "Complementarity" in this sense, would be achieved if a habitat added some desirable avian diversity features unrepresented by other selected habitats (Margules and Pressey, 2000). Existing compilations of important habitats which still harbour a wide range of birds (Bizuru et al., 2015, Kanyamibwa, 2001, Vande weghe, 2018, Vande weghe and Vande weghe, 2011) can serve as baselines for the site prioritization stage, and involvement of a range of stakeholders can be facilitated to minimize conflicts of interest.

As discussed above, the prominent form of protected areas in Rwanda is the "National Park", however, all important habitats need not acquire this status to be assigned rigorous biodiversity monitoring and management plans. Some habitats, particularly those in human-modified landscapes will require alternative conservation arrangements, for instance, extending protection to single plants and trees, and setting up a minimum size and form of green space. The idea of expanding important biodiversity habitats, as envisaged for Volcanoes NP, is attractive, however, its feasibility and support by communities may prove challenging due to the high population pressure, and lack of alternative "free" sites to establish expropriated homes and enterprises. It is thus crucial to secure protection of existing bird habitats, and to ensure, they are not mere paper parks, but recognised in development masterplans.

6.3 National and transboundary institutional collaboration

Given past downsizing of protected areas, the current degradation of natural landscapes outside reserves, uncertainties of climate change (Musana and Mutuyeyezu, 2011), and varying species trait-based adaptations, proper conservation planning should take into account biological and physical processes, as well as the dynamism of threats (Pressey et al., 2007, Botts et al., 2019). The question of persistence of bird populations, relating to how long conservation sites remain in good state and continue to contain viable populations (Margules and Sarkar, 2007, Kukkala and Moilanen, 2013), can only be thoroughly addressed with strong and stable institutions, clear laws and management plans, and cross-sectoral dialogues to prevent and mitigate conflicting policy agendas.

Within Rwanda, important bird habitats are almost always surrounded by a matrix of agricultural lands and settlements. Of great concern is the "Crop Intensification Program", a national policy initiated in 2008 with the aim to increase agricultural productivity of six economically valued crops: maize, wheat, rice, Irish potatoes, beans and cassava. The policy has centred on the consolidation of adjacent farmlands for the growth of one crop designated per region, and the use of improved seeds, and inorganic fertilizers, which are often subsidized by the government (Kathiresan, 2011). High national adoption of this policy will inevitably lead to the collapse of farmland bird populations due to the considerable reduction of crop diversity and the increased application of agrochemicals.

Landscape connectivity, and matrix permeability could be achieved with increasing indigenous tree cover on farms and homes, adopting widescale eco-friendly farming practices such as controlled use of harmful agro-chemicals and creating corridors between smaller and larger habitat fragments (Şekercioğlu et al., 2019). Restoration of sites and species populations offers an effective way to ensure long-term persistence of bird populations. Re-introduction of species has been done in Akagera NP, with the reintroduction of lions, and

rhinoceroses from South Africa, and the rehabilitation of Grey-crowned cranes previously held in captivity in Rwandan homes (Nsengimana et al., 2019, Sun et al., 2018).

Within the leadership of the ministry of the Environment, and the Bonn challenge commitment, a global initiative launched in 2011 to restore 150 million and 350 million ha of degraded and deforested lands by 2020 and 2030, respectively, Rwanda made a bold pledge to restore 2 million ha of degraded forests and lands under the so-called "Border to border" restoration program, representing the highest bid globally in proportion to the country's size (2.6 million ha) (Bonn Challenge, 2011, EPI, 2015). Nonetheless, the discrepancies in the perceptions of forest restoration, and divergent policy agendas in the agriculture and forestry sectors pose hindrances to the implementation of policies of forest restoration designed to optimise biodiversity and ecosystem functions (Chazdon et al., 2016, van Oosten, et al., 2018).

Aligning conflicting policies and agreements should also extend beyond national borders. As discussed above, a key aspect in the conservation of mountain gorilla is collaboration across borders. Three out of the four Rwandan National Parks and most of the major rivers and lakes are part of transboundary landscapes. Any efforts put in place by Rwanda, if not supported by neighbouring countries, will be in vain. Formal Institutions like the East African community provide ideal platforms for exchanging good Environmental practices. The transboundary collaboration in the Virunga landscape offers a model that can be adapted to maximise protection to the avian biodiversity even during episodes of political turmoil, such as many African states have experienced.

6.4 Avitourism for efficient conservation

Another theoretical strong point of systematic conservation planning is the efficiency in the management of conservation resources for the maintenance of biodiversity and functional

ecosystem services (Margules and Pressey, 2000, McIntosh et al., 2017). It has been argued that the cost of conservation, particularly in Africa, is not very high when accounting for both ecological and economic returns, such as water filtering, and ecotourism revenues (Naidoo and Adamowicz, 2005). Harcourt (1986) reported that in the 1980s the cost of mountain gorilla conservation in Rwanda was US$ 150 000 per year. Each gorilla was costing US$1250 per year, which was US$250 less than the cost of keeping them in zoos at that time, without accounting for the biodiversity and ecosystem services they were performing in their natural habitats. At present, the high gorilla-based tourism revenues not only contributes significantly to their conservation, but is also used to fund other national priorities (Nielsen and Spenceley, 2011, RDB, 2018a).

The tourism sector is generally growing in Rwanda, and has overtaken coffee and tea exports as the leading foreign exchange earner. Tourism revenues are predominantly retrieved from National parks, especially Volcanoes NP, which contributed 90% of the US$18.7 million generated from all National Parks visits in 2017 (RDB, 2018a). The number of tourists has doubled in the last 7 years (Fig. 2). The highest number of tourist visits is usually registered by Akagera NP, and more revenues are envisaged with the reintroduction of lions and rhinos in 2015 and 2017, respectively (NISR, 2018b, Sun et al., 2018). Avitourism on the other hand is still in its infancy (Fig. 3), although there is growing willingness on behalf of the government, as demonstrated by regular participation in international tourism exhibitions, such as the British Birdfair.

Naidoo and Adamowicz (2005) concluded that the reason why the costs of avian biodiversity conservation tend to outweigh their benefits in many places in Africa hinges on the undervaluation of tourism revenues. By modelling the costs associated with conserving the forest in comparison to other spatial land-uses, and surveying the actual prices tourists were willing to pay to watch birds in Mabira forest, Uganda, they estimated that up to 90% of all

bird species in the forest would be protected if tourist entrance fees were optimized from the US$5 charged to the US $47 tourists were willing to pay. In Nyungwe NP, birding packages are still few and undervalued compared to the range of birds and habitats found there (Lal et al., 2017, Banerjee et al., 2018). Improving eco-tourist facilities near these habitats, coupled with acute marketing strategies of Rwandan birds, would, we believe, guarantee substantial revenues, some of which could then be reinvested in the conservation of birds and their habitats. A few companies are already capitalizing on a high-end avitourism in Africa, including itineraries in Rwanda. Birding Africa, a South-African company offers a six-day guided tour in Rwanda for a group of six that costs US$ 3590 and typically covers Nyabarongo wetlands, Nyungwe NP and Akagera NP (birdingafrica.com, accessed on 09/10/2019). Birdwatchers are ideal tourists since they usually have a high education and income, are willing to spend more while pursuing their passion, and they are also supportive of conservation-related causes (Biggs et al., 2011, Steven et al., 2016).

A heightened tourism sector can underpin national economic growth, however, a diligent approach is needed, as tourism itself is known to add further stress to fragile ecosystems and can alienate local communities, undermining their sense of belonging and responsibility towards nature (Rutagarama and Martin, 2006, Sabuhoro et al., 2017).

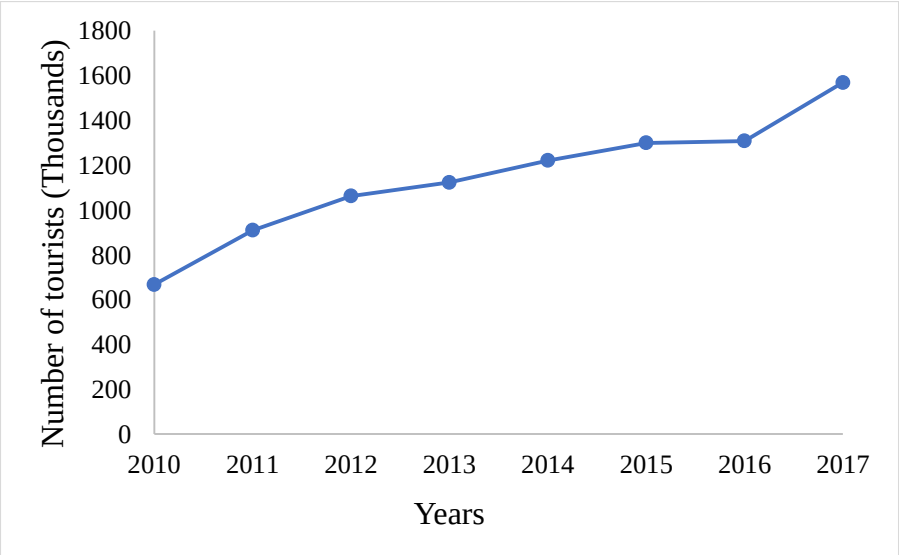

Figure 2. The growth of tourist arrivals in Rwanda from 2010 to 2017. Retrieved from NISR 2018b and RDB unpublished data. The numbers include foreign tourists visiting for a range of purposes including nature, culture and business.

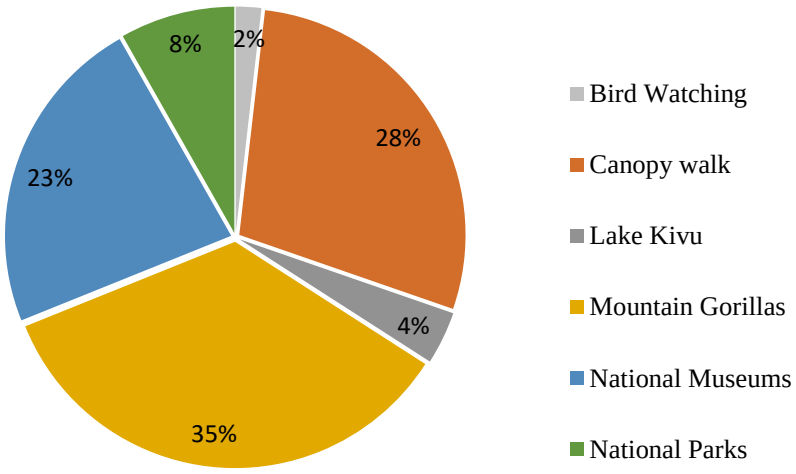

Figure 3 Preferred tourist attractions in Rwanda (N = 8088) according to the online poll by the Rwanda development Board-Tourism and Conservation department (RDB, 2018b). Although, there is overlap among the assessed attractions, bird watching per se stands out as the least preferred activity, while visiting Mountain gorillas ranks first. The Canopy walkway is a 90 m long bridge in the canopy of Nyungwe NP hanging at an elevation of 60 m. Lake Kivu is the largest lake in Rwanda, with the most diverse tourist facilities.

6.5 Increasing public awareness and engagement

It would be unusual to find a Rwandan who had never heard of a mountain gorilla, where it lives and its contribution to the country's development. This awareness can be attributed to mass education programs transmitted through formal and informal channels, as well as assisting communities to visit gorillas, and to engage in direct conservation activities (Vedder and Weber, 1990). Extending this to birds would be possible, through incorporating bird conservation information into the national curriculum, particularly at primary and secondary levels, and organizing community visits to nearest bird watching hotspots. Recurring public events such as *Umuganda*[8] could be used to sensitize the public, and also promote the planting of cultural significant indigenous trees such as fig trees, which are known to support high bird diversity (Kissling, 2007), instead of the most often planted non-native tree species. The promotion of indigenous trees would also be a way for Rwandans to reaffirm their cultural heritage. Cultural beliefs and practices have anchored the preservation of many sacred sites and species across the world (Bhagwat et al., 2014). Their annihilation may also have adverse effects as proven by the endangered status of the Grey-crowned crane (*Balearica regulorum*), which was once an emblematic totem of the Rwandan pre-colonial ruling monarch.

Although the loss of some traditions may not be reversed, there is always room to reinvent and adapt them to the present context. RDB has extended to mountain gorillas a traditional ceremony of naming a newborn baby, known as "kwita izina". During the event all infant gorillas born in the last 12 months are given names. The gorilla naming ceremony has become an annual conservation celebration event that gathers a multitude of people from environmentalists to Hollywood movie stars. Similar adaptation to birds would certainly be

[8] Umuganda —coming together, is a mandatory community service day that takes place on the last Saturday of every month all over the country. All residents gather for communal services ranging from building and repairing public infrastructures to planting trees.

positive. For instance, a citizen science style program to document and disseminate Kinyarwanda bird names and associated cultural stories would safeguard the language, and equally enable the passing on of traditional ornithological knowledge and reverence to the young generation.

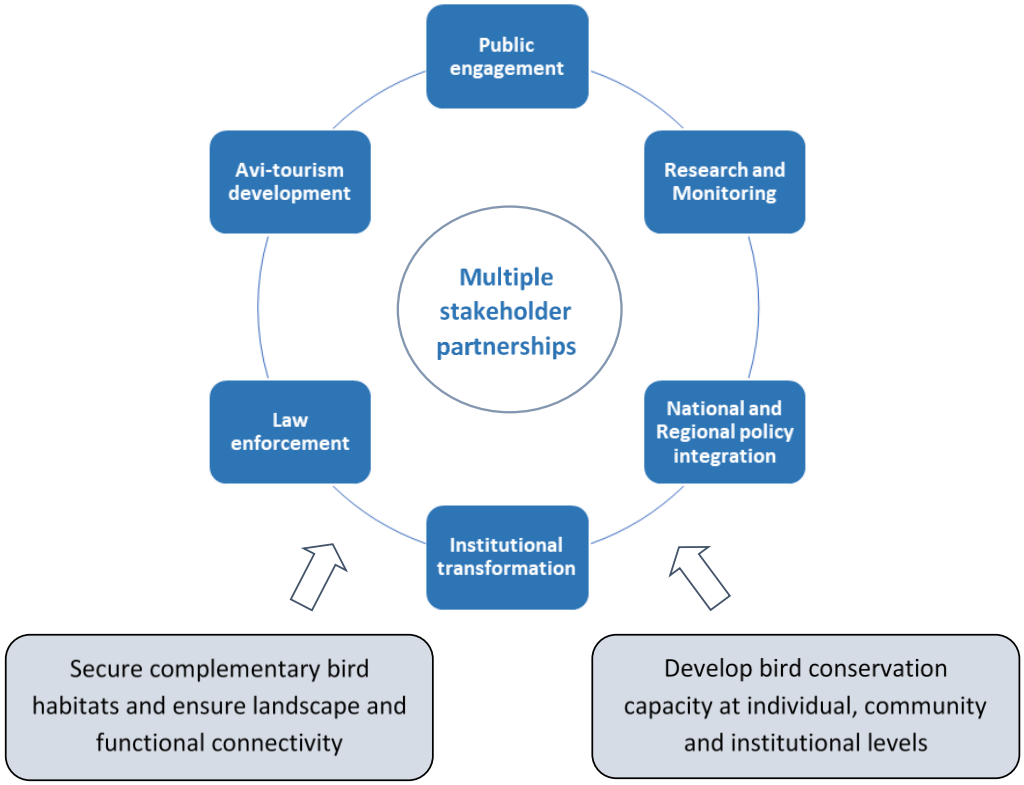

Figure 4 Framework for bird conservation that promotes partnerships between communities, governments, NGOs and the private sector in order to advance bird conservation, research and tourism. The stages of the framework are non-sequential and may happen concurrently. The legal protection of suitable bird landscapes, and the commitment of pro-conservation individuals and organisations are central to the effectiveness of the partnerships (Original figure).

7 Multi-stakeholder partnerships as the way forward

For any conservation plan to bear fruit, it should be flexible enough to garner maximum support from a range of stakeholders (Kukkala and Moilanen, 2013, Margules and Sarkar, 2007). The flexibility can be achieved by, for instance, prioritizing areas with high "irreplaceability" in terms of species and functional diversity, and devising alternative plans (Watson et al., 2014). For example, Nyabarongo wetland in Rwanda, has been designated as an Important Biodiversity and Bird area (Kanyamibwa, 2001), yet, its banks are extensively cultivated with sugarcane. Its long-term management will necessitate a transparent process engaging all major stakeholders (Fig. 4). A sensible trade-off would take into consideration economic returns, sugar-related health problems, flooding events, biodiversity support and ecosystem services. A hybrid arrangement could also be made to ensure an eco-friendly sugar cane production. Some cases would demand prudent dialogues. For instance, bushes and uncultivated wetlands are perceived as breeding sites for malaria-transmitting mosquitoes. Malaria being the leading cause of morbidity and mortality in Rwanda, the Ministry of health has launched campaigns of clearing or spraying bushes and wetlands with insecticides (The New Times, 2018). It is of utmost urgency that different parties engage in conversations before embarking on solutions that could have cascading effects on the environment.

8 Conclusion

The mountain gorilla is the only great ape that has been increasing in numbers owing to a high public awareness, cooperation between local and international stakeholders, a coordination of long-term research and monitoring of their status, and the development of a tourism that contributes substantially to national income. In contrast, the only relatively stable avian populations in Rwanda are currently restricted within four national parks. Past experiences have shown that the protection status of an area does not always buffer against detrimental changes. Emulating strategies that have successfully contributed to the wide support for the mountain gorilla conservation cause carry great potential in securing the protection of birds and associated ecosystem services, especially if conducted through a cooperative and transparent process, as provided by Systematic Conservation Planning tools. Conservation is often a continuous process. The fate of mountain gorilla remains conservation-dependent, and the threats to birds may seem insurmountable. However, there are rays of hope in human ingenuity, national and global willingness to restore degraded ecosystems, and gains from responsible nature-based enterprises.

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Appendix 6

Publication status

Paper 1: Effects of land-use change on avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest
Journal: Diversity and distributions
Status: Submitted on 05/06/2020.

Paper 2: Functional and phylogenetic diversity of a tropical agricultural matrix avifauna: an assessment of farmland heterogeneity

Journal: Applied Ecology
Status: Submitted on 15/06/2020

Paper 3: Assessing forest restoration success using bird habitat use as a potential indicator: an Afrotropical case study
Journal: Forest Ecology and Management
Status: Submitted on 08/06/2020

Perspective paper: Making space for birds: sourcing solutions from the mountain gorilla conservation model in Rwanda
Journal: Nature conservation
Status: Published

Main conferences and workshops attended

In July 2018, I gave a talk on my research in a seminar organized by the Centre of Excellence in Biodiversity and Natural resource management- University of Rwanda

In September 2018, I presented a poster in the Conversation on Conservation conference, which is the most important conservation event in Rwanda.

In August 2019, I presented a poster (Chapter 4) at the Association for Tropical Biology and Conservation (ATBC) conference in Madagascar.

In October, 2019, I presented a poster (Chapter 4) at the Student Conference on Conservation Science-New York.

Co-authorship statements

From:

Dr Thomas Matthews

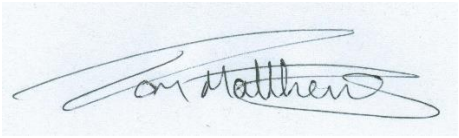
Research Fellow

University of Birmingham

Thesis submitted for the degree of Doctor of Philosophy by Laure Rurangwa

I declare that the manuscripts presented as Chapters 6 and 8 within this thesis, for which I am a co-author, is substantially the work of the first author, Laure Rurangwa. My role has been limited to statistical assistance and commenting on drafts. I therefore consent to the inclusion of this material in Laure's doctoral thesis.

Dr Thomas Matthews



22nd April 2020

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04/05/2020

To whom it may concern,

I write to confirm that I co-authored with Marie Laure Rurangwa the manuscript entitled: "Effects of land-use change on avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest". I give my consent to the inclusion of this material in Laure's thesis, since she carried out the vast majority of the work. My contribution was limited to statistical assistance, and commenting on drafts.

Kind regards,

Dr. Jesús Aguirre Gutiérrez

Environmental Change Institute
University of Oxford
Oxford, UK

Wildlife Conservation Society

Nyungwe Project

***Nyungwe** Office : Gisakura,Bushekeli, Nyamasheke, Western Province; Tel : 0788301641 ; Po Box : 1699 Kigali ; Email : mbana@wcs.org*

April 24, 2020

To**: The Director of Graduate Studies**

SOGE, University of Oxford

Dear Sir/Madam,

Re: **Co-authorship consent for my inclusion in the manuscripts of Rurangwa Laure's thesis**

My name is Niyigaba protais from the Wildlife conservation Society – Rwanda Programme.

I write to confirm that I co-authored with Marie Laure Rurangwa manuscripts presented as chapter 6, 7 and 8 of her thesis. My contribution was limited to the provision of data, fieldwork planning and coordination, and commenting on drafts. I give my consent to the inclusion of the manuscripts in Laure's thesis, since she carried out a substantial part of the work.

Concerned chapter names are:

6. Effects of land-use change on avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest
7. Functional and phylogenetic diversity of a tropical agricultural matrix avifauna: an assessment of farmland heterogeneity
8. Assessing forest restoration success using bird habitat use as a potential indicator: an Afrotropical case study

Should you need further clarification and more information, I can be reached through pniyigaba@wcs.org.

Sincerely.



Protais NIYIGABA

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12 May 2020

RE: Laure Rurangwa

To whom it may concern:

I am writing to confirm that I contributed to manuscripts presented by Marie Laure Rurangwa as chapter 6, 7 and 8 of her doctoral thesis.

Chapters:
6. Effects of land-use change on avian taxonomic, functional and phylogenetic diversity of a tropical montane rainforest
7. Functional and phylogenetic diversity of a tropical agricultural matrix avifauna: an assessment of farmland heterogeneity
8. Assessing forest restoration success using bird habitat use as a potential indicator: an Afrotropical case study

In these cases, my contribution was limited to the provision of data and making light textual comments on drafts. I give my consent to the inclusion of this material in Laure's thesis, and can confirm that to my knowledge she carried out almost all of the work.

Best wishes



Dr Joseph A. Tobias
Reader in Biodiversity & Ecosystems

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28 April 2020

I write to confirm that I was second author with Marie Laure Rurangwa on the article entitled "Making space for birds: Sourcing solutions from the mountain gorilla conservation model in Rwanda", and a co-author also on manuscripts constituting chapters 6, 7, 8 of her doctoral thesis. In each case Laure fully warranted the role of first author for her leading contribution in conceptualization of the problem, design and execution of the field work, collation and analysis of data and leading the write-up. My contribution was limited to supervisory guidance and commenting on drafts.

Yours sincerely

Robert J Whittaker

Supervisor