

**Effects of landscape and forest structural characteristics on the
avian communities in Southern Mistbelt Forests, Midlands of
KwaZulu-Natal, South Africa**

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ABSTRACT

Globally forest ecosystems are under threat from land-use changes threatening biodiversity. Biodiversity conservation in forest systems has become a major concern as these impacts affect ecosystem functioning. Habitat destruction results in highly fragmented forest patches with reduced habitat quality. Therefore, it is essential to assess species' responses to these changes for conservation. Like other parts of the world, South African forests are threatened by destruction, mainly habitat conversion to exotic commercial tree plantations. Forest bird species within this system have been reported to be declining. Considering these impacts, it is important to understand the main drivers at different spatial scales. This study aimed to assess local and landscape drivers of avian communities in the Southern Mistbelt Forests in the Midlands of KwaZulu-Natal, South Africa. The objectives were to assess (1) the local scale drivers and influences on bird species richness, use and functional diversity, (2) microhabitat requirements and occupancy of understorey forest specialist bird species using camera traps, and (3) landscape attributes influencing bird species richness, habitat use and functional groups.

Firstly, the influence of forest structure and composition on bird species richness, habitat use and functional diversity in 14 selected Southern Mistbelt Forest patches of KwaZulu-Natal were assessed. The bird species were surveyed using point count surveys. Functional diversity for each surveyed patch was quantified using three indices: functional richness, functional evenness and functional divergence. Species-specific responses were assessed by focusing on three forest specialists, orange ground-thrush *Geokichla gurneyi*, forest canary *Crithagra scotops*, and Cape parrot *Poicephalus robustus*. Bird community and forest bird specialists' responses to forest structure and tree species diversity varied. Forest structural complexity, canopy cover, and tree species richness were the main structural characteristics

influencing bird functional diversity. Also, forest composition and structure are important for bird species and functional richness.

Secondly, the microhabitat requirements of forest specialist bird species using camera surveys in the selected 14 Southern Mistbelt Forests were assessed. The results showed that the microhabitat requirements of the understorey forest specialist species are specific. Occupancy models showed that forest specialist understorey birds are mainly influenced by tree species richness, understorey cover of leaf litter and water.

Lastly, the bird species richness, habitat use and functional groups' responses to selective logging history, livestock grazing and adjacent matrix type were assessed. The bird communities were surveyed using point-counts. Functional diversity was quantified using functional richness, functional divergence and functional evenness estimated using bird functional traits. The disturbance did not affect bird species richness. Forest specialists' responses to disturbance were species-specific depending on the type of disturbance and intensity. The orange ground-thrush and forest canary were affected by livestock grazing, while the Cape parrot was influenced by forest logging history. Functional richness for all functional groups was high in disturbed forests, while functional evenness for forest specialists and insectivores was low in disturbed sites.

The results of this study provide insight into the local and landscape drivers of avian species richness and diversity. Forest patches with high tree species diversity and structural complexity should be maintained to conserve forest specialists, bird species richness and functional richness. Also, to maintain the persistence of the understorey forest specialists, forest structures within 5 m of the forest floor should be maintained. It is recommended to use functional diversity indices with taxonomic indices to understand bird species responses to disturbance better.

PREFACE

The data described in this thesis were collected in the Southern Mistbelt Forests in the midlands of KwaZulu-Natal Province, Republic of South Africa, from October 2020 to September 2021. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs, Dr David A. Ehlers Smith and Dr Yvette C. Ehlers Smith.

This thesis, submitted for the degree of Doctorate of Philosophy in Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



.....
Nasiphi Bitani

July 2023

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.



.....
Prof Colleen T. Downs

Supervisor

July 2023

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DECLARATION 1 - PLAGIARISM

I, Nasiphi Bitani, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
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DECLARATION 2 - PUBLICATIONS**

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

PUBLICATION 1 (Formatted for *Journal of Ornithology*- not submitted)

Anthropogenic effects on avian communities in African forests: a systematic review

N Bitani, DA Ehlers Smith & CT Downs

Author contributions:

NB conceived paper with DAES and CTD. CTD sought funding. NB collected the data. NB analysed data, and wrote the paper. CTD and DAES contributed valuable comments to the manuscript.

PUBLICATION 2 (Formatted for *Ecology and Evolution* -published)

Avian species functional diversity and habitat use: the role of forest structural attributes and tree diversity in the Midlands Mistbelt Forests of KwaZulu-Natal, South Africa

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Author contributions:

NB conceived paper with DAES, YCES and CTD. CTD sought funding. NB AND CP collected the data. NB analysed data, and wrote the paper. CTD and DAES contributed valuable comments to the manuscript.

PUBLICATION 3 (Formatted for *Forest Ecology and Management*- published)

Microhabitat requirements and occupancy of understorey bird forest specialists in Southern Mistbelt Forests of KwaZulu-Natal, South Africa

N Bitani, CP Cordier, DA Ehlers Smith, YC Ehlers Smith & CT Downs

Author contributions:

NB conceived paper with DAES, YCES and CTD. CTD sought funding. NB AND CP collected the data. NB analysed data, and wrote the paper. CTD and DAES contributed valuable comments to the manuscript.

PUBLICATION 4 (Formatted for XXXX- in review)

Responses of bird functional communities to anthropogenic disturbances in fragmented Southern Mistbelt Forests in the Midlands of KwaZulu-Natal, South Africa

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Author contributions:

NB conceived paper with DAES, YCES and CTD. CTD sought funding. NB AND CP collected the data. NB analysed data, and wrote the paper. CTD and DAES contributed valuable comments to the manuscript.

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July 2023

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“Before I formed you in your mother’s womb, I knew you; before you were born, I set you apart” Jeremiah 1:5

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CHAPTER 1

INTRODUCTION

1.1 Background

Land-use change is the most dominant threat to forests globally, driving species distribution and composition shifts (Watt et al., 2002; Martínez et al., 2009; de Castro Solar et al., 2016). The increased human population has increased the demand for natural habitat modification for various activities, including agriculture, grazing and selective logging (Flynn et al., 2009; Cosset et al., 2020; Lindenmayer et al., 2020). Biodiversity loss driven by anthropogenic activities is a global threat associated with irreversible changes, economic loss and human well-being impacts (Balmford et al., 2005; Díaz et al., 2006; Pecl et al., 2017; Benedetti et al., 2020). In forest systems, structural damage leads to habitat loss or fragmentation of remaining vegetation cover (Bueno et al., 2018; Lindenmayer et al., 2020). Habitat loss and fragmentation change the vegetation cover's composition, amount, and configuration (Fahrig, 2003; Cadavid-Florez et al., 2020). Such changes in habitat type and distribution lead to changes in species richness, structure, composition and functional diversity (Neuschulz et al., 2011; Bregman et al., 2016; Bovo et al., 2018; Leaver et al., 2019). Consequently, monitoring biodiversity has become crucial to respond to the changes in species structure and assemblages (Kremen et al., 1993; Bradfer-Lawrence et al., 2020).

Considering spatial scale is vital in biodiversity monitoring and understanding species' habitat preferences (Wiens, 1989; Lecours et al., 2015). Different habitat characteristics influence biodiversity patterns and habitat selection at different spatial scales (Pennington & Blair, 2011; De Knegt et al., 2011; Bosco et al., 2021; Hingee et al., 2022). For example, in forests, species habitat selection is influenced by landscape attributes (i.e. patch size, landscape matrix) (Wethered & Lawes, 2003; Kennedy et al., 2010, Ehlers Smith et al., 2018; Ngcobo et al., 2022) to local characteristics (habitat heterogeneity) (Gillespie & Walter 2001, Gumede et

al., 2022). At different spatial scales (i.e. landscape, local), species habitat selection is an ecological process often linked to habitat quality and resource availability (Krausma, 1999; Bjørneraas et al., 2012; Beerens et al., 2015; Nisi et al., 2023). Despite acknowledging this, multiscale studies are relatively rare (Spake et al., 2019). Therefore, understanding the drivers of biodiversity at multiple scales is essential for biodiversity conservation and management, especially for declining species.

Birds are facing significant effects of habitat destruction and loss (Andren, 1994; Mortelliti et al., 2010; Maseko et al., 2020). Therefore, birds are an important taxon to study the effects of landscape and local scale drivers. Birds are essential ecosystem players as they perform vital ecosystem services, have well-described traits linked to ecological functions and are good indicators of environmental change (Boesing et al., 2018; Janousek et al., 2019; Cosset et al., 2020). For example, birds provide pollination (Chain-Guadarrama et al., 2019) and seed dispersal services (Whelan et al., 2008; Garcia et al., 2010) essential for maintaining plant communities. Bird species declines have been shown to affect ecosystem functioning and ecosystem services (Anderson et al., 2011; Edwards et al., 2017; Benedetti et al., 2020; Ali et al., 2023). For example, habitat disturbance reduces bird species' functional trait variability, which has implications for ecological functions (Flynn 2009).

In South Africa, the forest biome is the smallest (~0.41%; Deng et al., 2020) and is regarded as one of the highly vulnerable vegetation types (von Maltitz et al., 2003). As a result of the rich fauna and flora, these forests are of high conservation value (Geldenhuys & MacDevette, 1989; Lawes et al., 2000; Symes et al., 2002). These forests are highly fragmented and dominated by small (< 100 ha) and a few large patches (> 1000 ha) (Cooper 1985; Geldenhuys, 2004). About 6.5% (n = 41) of bird species in South African forests are forest-dependent (Oatley, 1989). About 50% of forest-dependent species are declining, and the losses are more prevalent in the Eastern Cape and KwaZulu-Natal Provinces (Cooper et al., 2017).

These declines have been attributed to habitat loss, fragmentation, and habitat quality in relation to human disturbance. South African forests are threatened by anthropogenic disturbance, mainly forest conversion of the matrix for agriculture and exotic tree plantations (Freeman et al., 2018). Previous studies have shown the significant impacts of forest fragmentation and degradation on avian communities in South Africa (Wethered & Lawes, 2003; Ehlers Smith et al., 2018; Leaver et al., 2019).

1.2 Study area

This study was conducted in fourteen selected indigenous Southern Mistbelt Forest patches in four regions within the Midlands of KwaZulu-Natal, South Africa (Fig 1.1). The Southern Mistbelt Forest patches were selected from four regions: Karkloof (n = 4), Balgowan (n = 2), Dargle (n = 4) and Bulwer (n = 4). The Southern Mistbelt Forests are one of the eight forest types in South Africa. Southern Mistbelt Forests of the Midlands of KwaZulu-Natal were naturally fragmented (Eeley et al., 1999) but have also experienced human induced disturbances since formation. The average mean annual precipitation is about 1600 mm and falls mainly during the South African summer (Nov-January) (Wirminghaus & Perrin, 1993; Lawes et al., 2004). Temperatures vary seasonally from -4 to 37 °C, with a mean annual temperature of 25°C (Low & Rebello, 1996). These forests are tall, multilayered patches on southeast-facing slopes dominated by *Afrocarpus/Podocarpus* spp. (Mucina et al., 2006), and occurring between 1000 to 1500 m asl (von Maltitz, 2003). The Southern Mistbelt Forest patches of KwaZulu-Natal are dominated by small (0.1-10 ha) forest patches and a few large patches > 300 ha. The studied forest patches varied in size (2.23 – 1685) (Table 1.1). In the past, the Southern Mistbelt Forests of KwaZulu-Natal were extensively logged for approximately 150 years (Adie et al., 2013), affecting their ecology (Downs and Symes, 2004). They have been left to naturally recover from the habitat alteration (Adie et al., 2013). Some forest patches are now managed,

but uncontrolled exploitation by local residents continues (Kotze and Samways, 1999; Lawes et al., 2007; Downs and Grieve, 2015). Present threats include the conversion of the surrounding grasslands to exotic tree plantations, fire mismanagement and alien plant invasion (Mucina et al., 2006; Grieve & Downs, 2015).

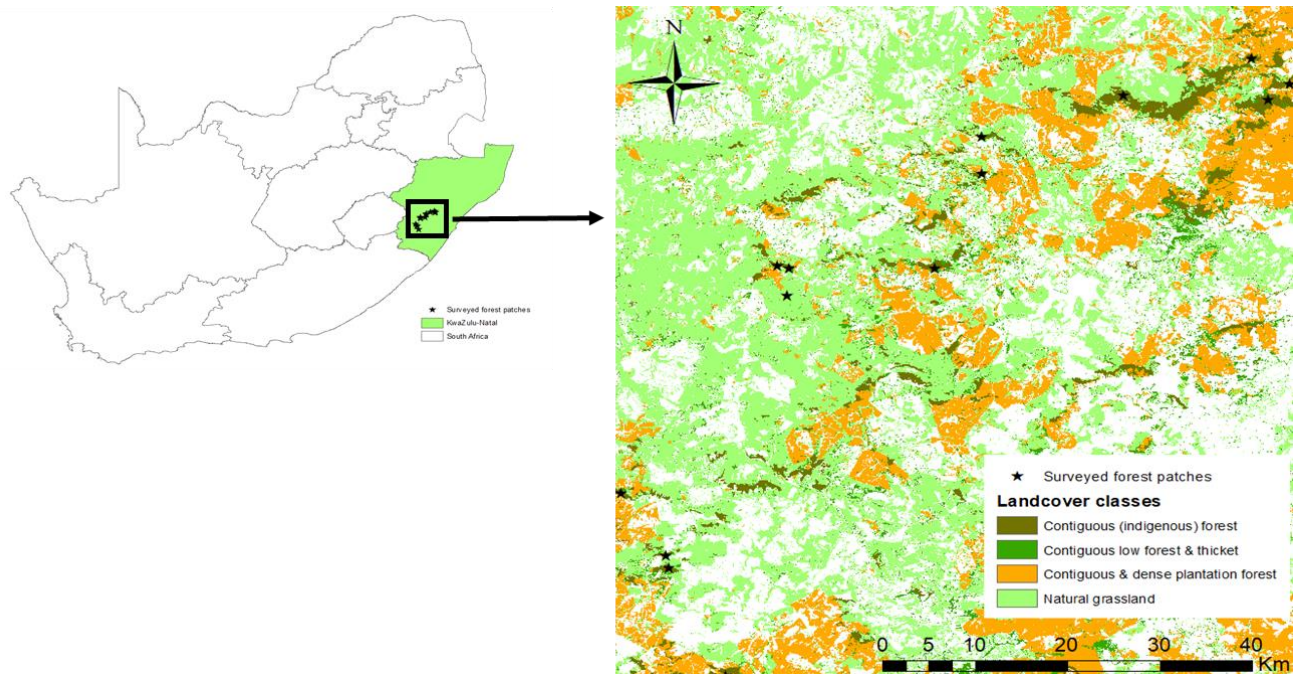


Figure 1.1 Location and distribution of the 14 Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Table 1.1 Location and patch size of the studied fourteen indigenous Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal. (Landownership is indicated by the superscripts with private (^a) and state-owned (^b) forest patches).

Region	Forest Patch	Coordinates	Patch size (ha)
Karkloof	Karkloof Nature Reserve ^a	29°17'50"S; 30°13'59" E	1685
	Mbona Private Nature Reserve ^a	29°15'27"S; 30°21'29" E	679
	L'Abri ^a	29°17'08"S; 30°23'40" E	199
	Benvie Farm ^a	29°18'08"S; 30°22'26" E	101
Balgowan	Rameron (Boshoek complex) ^a	29°20'34"S; 30°05'43" E	207
	Milestone Forest Walk ^a	29°22'57"S; 30°05'40" E	77
Dargle	Maritzdaal ^a	29°29'05"S; 30°02'57" E	558
	Sharedown (New Forest) ^a	29°28'57"S; 29°53'44" E	112
	Wakefield Forest ^a	29°29'06"S; 29°54'28" E	4.43
	Waterfall Forest ^a	29°30'54"S; 29°54'18" E	2.23
Bulwer	Ingelabantwana Nature Reserve ^b	29°43'43"S; 29°44'35"E	338
	Xotsheyake Nature Reserve ^b	29°47'46"S; 29°47'16"E	98
	Marutswa Nature Reserve ^b	29°48'36"S; 29°47'25"E	268
	Nxumeni (Nkwezela State Forest) ^b	29°55'38"S; 29°50'42"E	385

1.3 Problem statement

Forests are under severe threat from anthropogenic pressures resulting in forest degradation (Peres et al., 2006; Steel et al., 2023). Globally, managers struggle to maintain forests that provide multiple ecosystem services under anthropogenic disturbance (Dekeuleire et al., 2019). Therefore, it is crucial to monitor and assess biodiversity to respond to the shifts in the structure

and assemblage of species (Bradfer-Lawrence et al., 2020). Over the past two decades, in the indigenous Southern Mistbelt Forests in the midlands of KwaZulu-Natal previous studies have determined the effects of habitat disturbance on different taxa (Supplementary Information Table 1.1). These studies have focused on habitat fragmentation mainly on matrix quality (Supplementary Information Table 1.1). Also, these studies have been restricted to selected forest patches in the Karkloof area and some in Balgowan (Supplementary Information Table 1.1). Therefore, a broader spatial scale study may provide more insight into landscape drivers influencing avian communities in the Southern Mistbelt Forest patches in the midlands of KwaZulu-Natal. Beyond habitat fragmentation and loss, disturbance has major impacts on habitat quality because of structural changes (Lindernmayer & Fischer, 2006). At a local scale, habitat quality studies have focused on single species (e.g. Downs & Symes, 2004; Lawes et al., 2006) and specific forest structure characteristics (e.g., dead trees). Furthermore, to my knowledge, the effects of local-scale forest structure attributes (i.e., vegetation composition) contributing to the forest quality have not been explored for the whole bird community. One of the major issues of forest habitat fragmentation is that it is often compounded by the introduction and proliferation of alien invasions (Raghubhanshi & Tripathi, 2009; Hansen et al., 2018). In the Southern Mistbelt Forests in the Midlands of KwaZulu-Natal, habitat fragmentation has led to alien plant invasion, particularly of *Solanum mauritianum*, *Acacia mearnsii* and *Eucalyptus nitens* (Mucina et al., 2006; Scott-Shaw & Everson, 2019). In the Southern Mistbelt Forest patches, previous studies have focused on habitat fragmentation in isolation (Supplementary Information Table 1.1) despite acknowledging the alien invasive plants invading the forest patches. Therefore, there is still a lack of information on the influence of alien plant invasion in the Southern Mistbelt Forest patches on bird communities.

Approximately half of the forest specialist bird species have been reported to be declining in South African forests (Cooper et al., 2017), yet the habitat needs of these species

are not well understood. Therefore, knowledge of the habitat requirements of these species at multiple scales is vital for habitat protection. Furthermore, forests must be continually monitored using more accurate methods to prevent further declines in bird communities (Mulvaney & Cherry, 2020). In recent years camera traps have become one of the most important tools to monitor species. However, a recent systematic review on using camera traps for research in Africa showed that birds were amongst the least taxa surveyed in the continent (Cordier et al., 2022). To my knowledge, in the Karkloof-Bulwer area, no study has used camera traps to assess the habitat requirements of forest birds. Therefore, this will be one of the few studies in the African continent that use camera traps for biodiversity monitoring. This study will expand the understanding of landscape and microhabitat forest characteristics influencing forest bird communities. Also, this study will fill a significant gap needed for effectively conserving forest bird communities, especially those more vulnerable groups, to habitat destruction or alteration.

1.4 Aims and objectives

The overall aim of this study was to assess microhabitat and landscape characteristics influencing forest avian species' communities. The objectives of the study were to determine:

1. Threats to avian communities and bird community responses.
2. Microhabitat structural drivers and influences on bird species richness and functional diversity.
3. Microhabitat requirements and occupancy of understorey forest bird specialists using camera traps.
4. Landscape attributes influencing avian species functional communities.

1.5 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is a brief introduction which includes the problem statement and aims of the study. The second chapter (Chapter 2) is a systematic literature review on anthropogenic impacts on avian communities in African forests, and the next three chapters (Chapters 3, 4 and 5) are data chapters, each covering a specific objective. The hypotheses and / or predictions are presented in each. Each chapter is formatted according to the journal it is intended to be (or has been) submitted to. Because of this thesis format, a certain degree of repetition was unavoidable, especially in the methods section. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Chapter 2 investigated threats to avian communities and species responses in African forests. The main objective of this chapter was to synthesize existing knowledge in the African continent forests on the main anthropogenic impacts on avian communities. Chapter 3 investigated the influence of forest structure characteristics and composition on the bird species richness and functional diversity. The main objective of this chapter was to determine how forest structure and composition characteristics affect (1) bird species' community structure, richness, and functional diversity and (2) species specific responses of forest specialist's birds. Chapter 4 investigated the microhabitat requirements and occupancy of understorey forest specialists. The objective of this chapter was to determine (1) the community of bird specialists using the understorey of the southern Mistbelt Forest (2) microhabitat requirements influencing occupancy and detection probability of these birds (3) if the microhabitat requirements vary seasonally. Chapter 5 investigated the impact of forest selective logging history, livestock grazing, alien plant invasion, and landscape matrix type on avian assemblages. The objective of this chapter was to determine how logging history, livestock grazing, landscape matrix and alien plant invasion affect bird functional

groups. The final chapter (Chapter 6) provides an overview of the study's main findings and their implications.

1.6 References

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1.7 Supplementary Information

Supplementary Information Table 1.1: Studies assessing forest anthropogenic impacts in indigenous forest patches (Southern Mistbelt) in the Midlands of KwaZulu-Natal, South Africa (2000-2022).

Author/s	Taxa	Single species, multiple or community	Anthropogenic process	Scale	Aspect	Studied region
Lawes et al., 2000	Mammal	Multiple	Habitat fragmentation	Landscape	Patch size & isolation	Balgowan, Karkloof
Wethered & Lawes, 2003	Bird	Community	Habitat fragmentation	Landscape	Surrounding matrix	Karkloof
Downs & Symes, 2004	Bird	Multiple	Habitat disturbance	Local	Patch quality	Creighton & Dargle
Lawes et al., 2005	Invertebrates	Community	Habitat fragmentation	Local	Patch quality	Balgowan, Karkloof
Lawes et al., 2005	Plant	Community	Habitat fragmentation	Landscape	Edge effect	Balgowan, Karkloof
Wethered & Lawes, 2005	Bird	Community	Habitat fragmentation	Landscape	Matrix quality	Karkloof
Lawes et al., 2006	Bird	Single	Habitat fragmentation	Local & landscape	Patch quality, Matrix quality, patch size	Karkloof
Moir et al., 2021	Bats	Community (insectivorous bats)	Habitat fragmentation	Landscape	Edge effects	Bulwer (i.e., Nxumeni)
Saks, 2021	Mammal	Single	Habitat fragmentation	Landscape	Dispersal ability	Balgowan, Dargle
Mthimunye & Munyai 2022	Insect	Community (ants)	Habitat fragmentation	Landscape	Matrix quality	Dargle

References for Supplementary Information Table 1.1

- Downs, C.T. & Symes, C.T. (2004). Snag dynamics and forest structure in Afromontane forests in KwaZulu-Natal, South Africa: implications for conserving cavity-nesting avifauna. *South African Journal of Botany*, **70**(2), 265-276.
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CHAPTER 2

Anthropogenic effects on avian communities in African forests: A systematic review

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Running header: Forest bird communities in Africa

2.1 Abstract

Ecosystems are threatened globally by anthropogenic impacts. These changes have implications for ecosystems' functionality; therefore, they must be understood for forest management and conservation. Here, we systematically searched the literature to assess the anthropogenic impacts on avian communities in African forest systems. In our search, 67 papers were eligible. Our results showed geographical location and taxonomic diversity bias in these studies. Most studies were conducted in South Africa and Madagascar, and species responses were assessed using taxonomic diversity indicators. The main anthropogenic impacts on avian taxa in African forests were forest fragmentation and degradation because of forest conversion to exotic plantations or agricultural land, selective logging and alien invasive plants. Bird species' responses to degradation and fragmentation varied depending on the disturbance type and bird species or guild sensitivity. The community or guild assemblage approach was shown to conceal clear species responses when assessing species-specific responses. Research efforts to understand bird species' responses to anthropogenic impacts in Africa need to address the research gaps in the responses of avian functional diversity to forest disturbance.

Keywords: anthropogenic effects; Forest bird communities; forest persistence; functional diversity

2.2 Introduction

Globally, forest ecosystems are threatened by anthropogenic impacts (Morris et al., 2010; Prakash et al., 2022). Human activities are driving these changes causing major biodiversity losses (Clavero et al., 2009; Cardinale et al., 2012; Moi et al., 2022). The main threats to forests are land-use changes, logging, forest conversion to agricultural land and exotic plantation and biological invasions (Reynolds et al., 2011; Wilcove et al., 2013; Miranda et al., 2017; Copper et al., 2017; Gonzalez et al., 2023). Forest systems though resilient, are highly vulnerable to

these human-driven pressures that disrupt the structure and functioning of ecosystems (Gray et al., 2007; Gardner et al., 2009; Seidl et al., 2017) with long-lasting ecological impacts and potential impacts on the provision of ecosystem services (Hawkins et al., 2015). The ecological responses to these changes vary depending on the types of disturbance, taxa and geographic region (Williams et al., 2010; Lindenmayer et al., 2017; Andersen et al., 2019). Therefore, it is essential to understand these dynamics for biodiversity conservation.

Many bird species are forest-dependent and therefore are highly threatened because of habitat disturbance in forest systems (Simberloff, 1995; Lens et al., 1999; daSilva and Tabareli, 2000; Cooper et al., 2017). Birds are highly diverse among vertebrates and maintain many ecological functions (Sekercioglu, 2006). Birds provide many ecosystem services, such as seed dispersal, pollination and pest control agents (Clout et al., 1989; Gardner et al., 2019; Donoso et al., 2020). To inform conservation, it is essential to understand the main drivers of bird species populations in forest systems (Knowlton and Graham, 2011; Lepczyk et al., 2017).

Synthesizing existing knowledge contributed to advancing knowledge (Lim et al., 2022). A literature review allows for consolidating information to understand gaps in knowledge (Varjani et al., 2019; Krauss et al., 2022). Therefore, here we synthesized present knowledge on anthropogenic impacts on avian communities in African forests to determine (1) forest disturbance types dominant in African forests and (2) how bird communities respond to these impacts.

2.3 Methods

We conducted a systematic review following the PRISMA guidelines (Foo et al., 2021; O’Dea et al., 2021). Systematically searching for literature is important because it removes the subjectiveness of searching for specific literature (Pullin and Stewart, 2006). Published literature was searched from Google Scholar (<https://scholar.google.com/>), Web of Science,

Science Direct (<https://www.sciencedirect.com/>), Wiley Online Library (<https://onlinelibrary.wiley.com/>), accessed in May 2022. We used (forest AND disturb OR impact OR effect AND bird OR avian AND Africa AND country name) without year restrictions. We screened the article bibliographies for more literature.

2.4 Results and Discussion

We identified 317 studies, and then abstract and title level screening resulted in 215 papers being excluded. A total of 102 were full-text screened, and thereafter, 35 papers were excluded. The relevant literature for this review was 67 papers. The excluded papers included literature reviews, experimental papers, duplicates or research not done in Africa. From the 67 papers used here, studies assessing the effects of forest disturbance on avian communities in Africa have been increasing with a notable dramatic increase around 2014 (Figure 2.1).

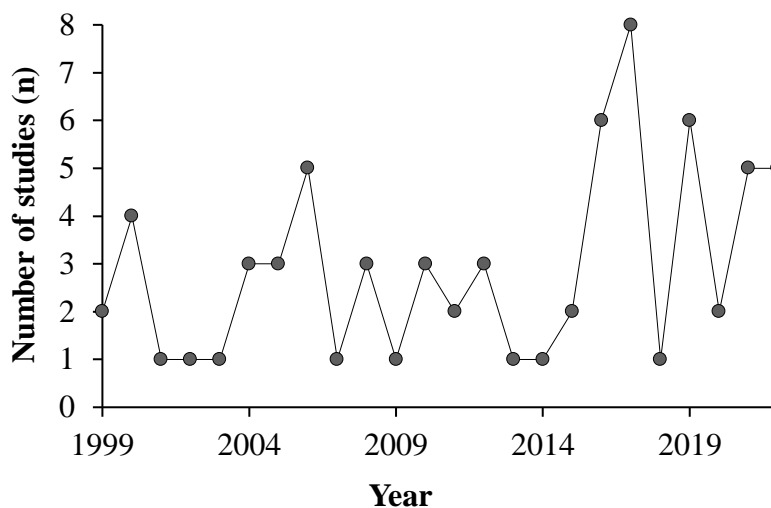


Figure 2.1 Total number of publications in Africa assessing the effects of forest fragmentation or degradation on bird species.

The collated data showed a geographic bias with more studies in southern African and Eastern African countries (Figure 2.2; Supplementary Information Table S2.1). Most studies

were conducted in South Africa (n = 18; 27%), Madagascar (n = 8; 12%), Kenya (n = 7; 10%) and Tanzania (n = 7; 10%). Also, our study showed that there was a strong bias in using taxonomic diversity indicators to assess bird species' responses to anthropogenic disturbances. Bird species richness, abundance, community and guild composition were the most used indicators to assess the effects of forest disturbance (Supplementary Information Table S2.1). There were a few exceptions in South Africa (Leaver et al., 2019; Maseko et al., 2020; Ngcobo et al., 2022) and in Rwanda (Rurangwa et al., 2021) that have used functional diversity to understand the effects of disturbance on avian forest communities. The main drivers affecting avian communities in African forests were fragmentation and degradation (Figure 2.3). Most studies assess the impacts of communities or assemblages with few species-specific responses (Supplementary Information Table S2.1). Most studies assessed disturbance at a local or landscape level with a few exceptions where both scales were considered (n = 7; Watson et al., 2004; Merson et al., 2006; Peters et al., 2008; Latja et al., 2016; Deikumah et al., 2017; Uwimbabazi et al., 2017; Gumede et al., 2022; Ngcobo et al., 2022).

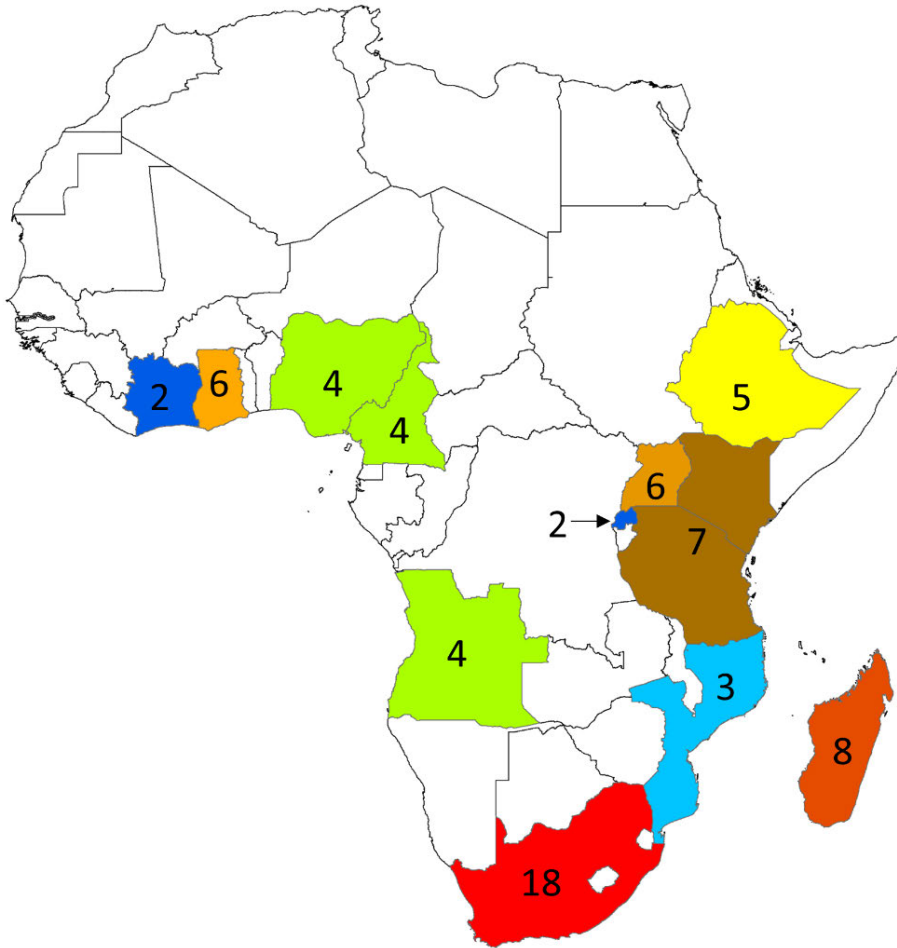


Figure 2.2 Map illustrating research efforts for the effects of forest fragmentation on bird species in Africa (n = 67). The represented numbers are the actual total number of studies in each country.

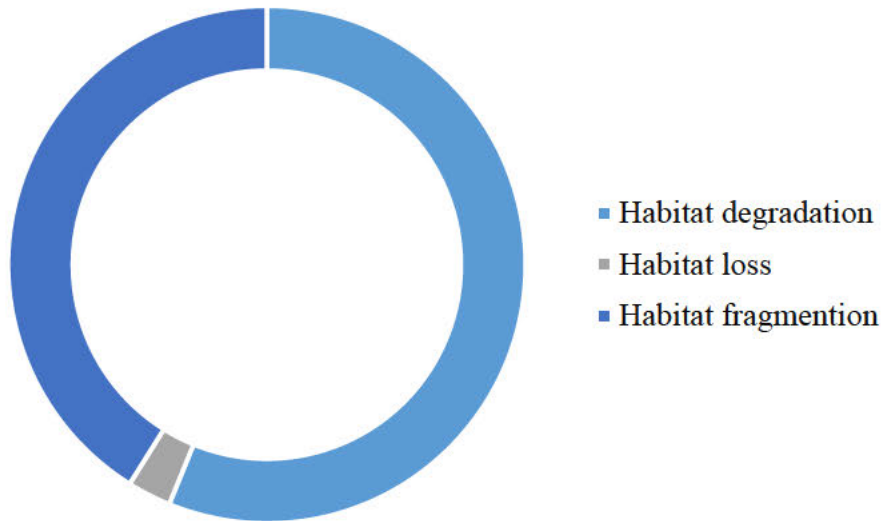


Figure 2.3 Forest disturbance types in African forest.

2.4.1 Habitat fragmentation

Forest fragmentation is a major threat in African forests. In these forests, fragmentation results mainly from the forest conversion and surrounding matrix to exotic plantations (Lawes and Wethered, 2003; Deikumah et al., 2017). Though species richness is often comparable in fragmented and undisturbed patches, the bird species composition differs (Latja et al., 2016; Bett et al., 2016 Asefa et al., 2019). Forest fragmentation has been shown to have a negative impact on forest-dependent bird species, with some species disappearing because of isolation and edge effects in Madagascar (Andrianarimisa et al., 2000; Watson et al., 2004) and exotic plantation matrix type (Lawes and Wethered, 2003) in South Africa. Therefore, species richness is maintained in fragmented patches by the increase in non-sensitive habitat generalist bird species. These highlight the importance of maintaining primary forests to maintain forest specialists. Contrary to other studies (e.g., Andrianarimisa et al., 2000; Lawes and Wethered, 2003; Watson et al., 2004, frugivores were also shown to be edge sensitive, while insectivores preferred disturbed edges in Madagascar (Watson et al., 2004). Similarly, in South Africa, Neuschulz et al. (2011) also showed that frugivores are sensitive to fragmentation. Research

assessing fragmentation effects has a strong focus on species-area relationships and isolation distance (>80%) (e.g. Andrianarimisa et al., 2000; Wethered and Lawes, 2003; Aerts et al., 2006; Merson et al., 2006; Olivier and Aarde, 2014; Maseko et al., 2020). In Nigeria, isolation distance and edge effects were a stronger predictor for bird species richness and composition changes than patch size (Manu et al., 2007). Dispersal ability influences species response to fragmentation, as in Mozambique, and forest bird species were not influenced by the patch area and isolation at a community level (Guldmond and Aarde, 2010); however, numbers of individual species decreased with increased isolation at the species level (Wilson et al., 2007).

Previous studies have focused on the effects of matrix quality to understand species' responses to fragmentation. For example, in South Africa (e.g., Wethered and Lawes, 2003, 2005; Neuschulz et al., 2011; Ngcobo et al., 2022), Ghana (e.g. Holbech, 2009), Kenya (e.g., Norfolk et al., 2017; Mahiga et al., 2019; Isaac et al., 2019) and Madagascar (Watson et al., 2004) have explored how bird species respond to land-use types surrounding natural forests. In South Africa, matrix quality has been shown to influence forest-dependent bird species (Ngcobo et al., 2022), forest bird assemblage composition and structure (Wethered and Lawes, 2005) and bird species density (Wethered and Lawes, 2003). Similarly, in Uganda, fragmented forest patches were associated with generalist bird species, and forest-dependent species preferred primary forests (Deikumah et al., 2017; Uwimbabazi et al., 2017). In Kenya, matrix quality affected specialised insectivores (Peters et al., 2008). Although matrix quality is essential for specialised species, monoculture plantations increase the dispersal ability of species between primary undisturbed patches in Kenya (Bett et al., 2016) and benefit frugivores in Uganda and Ghana (Deikumah et al., 2017; Uwimbabazi et al., 2017).

2.4.2 Habitat degradation

Forest degradation is driven by cultivation (Seddon et al., 1999) and selective logging (Aerts et al., 2006; Holbech, 2009; Latja et al., 2016). Bird species' response to habitat degradation varies linked to the bird habitat specificity (Leaver et al., 2019). At relatively lower spatial scales, the important determinants for variation in species responses were habitat structural characteristics, canopy cover and complexity (Lawes et al., 2000; Owiunji et al., 2000; Borghesio, 2008; Rurangwa et al., 2021) and hence the strong focus of studies on habitat quality characteristics (e.g., Caceres et al., 2017; Leaver et al., 2019; Gumede et al., 2022). In Madagascar, the bird species' responses to degradation at microhabitat scales were species-specific (Chouteau, 2004). Microhabitat variables explored in this study included tree stem density, litter depth and bare soil. In Ghana, the patch size influenced bird species' tolerance for degradation at the microhabitat level. For example, bird species recovered from forest degradation in relatively larger ($>50 \text{ km}^2$) patches (Holbech, 2005). However, in Uganda, changes in habitat quality because of logging showed that some species do not recover even after 40 years of natural regeneration of forests (Latja et al., 2016). Forest dependent specialists decreased with increased logging intensity while generalists remained constant (Holbech, 2005). Similarly, Latja (2016) showed that forest specialised species were higher in primary forests while generalists dominate clear cut or selectively logged forest patches.

2.5 Conclusions

This study aimed to assess African forest research trends in anthropogenic impacts and avian species' responses. Over the years, the research effort to understand these dynamics has increased with geographic bias. Studies were primarily in South Africa and eastern African countries. Substantial evidence from the review literature showed that anthropogenic impacts that affect forest bird species in Africa are mainly habitat fragmentation and degradation

because of forest conversion to exotic tree plantations and agricultural land (Wethered and Lawes, 2003; Deikumah et al., 2017) and selective logging (Aerts et al., 2006; Holbech, 2009). This ongoing forest disturbance was shown to affect forest-dependent bird species negatively. The responses to habitat disturbance were shown to vary depending on the type of disturbance, ecological groups, and spatial scale and were species-specific. Therefore, habitat fragmentation responses cannot be generalised. Also, our understanding of anthropogenic impacts is limited to species composition, richness and abundance changes. Therefore, further African studies are needed to understand the impacts on bird functional diversity. Also, studies must assess species-specific and functional diversity at local and landscape levels.

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2.7 Supplementary Information

Supplementary Information Table S2.1 Summary of African studies on forest bird species.

Authors	Year	Country	Community/single	Taxonomic/ functional	Indicator	Broad disturbance type	Aspect	Spatial Scale
Fjeldsa et al., 1999	1999	Tanzania	Community	Taxonomic	Richness and composition	Habitat degradation	Habitat quality	Landscape
Seddon et al., 1999	1999	Tanzania	Species-specific	Taxonomic	Richness and abundance	Habitat fragmentation	Patch and isolation	Landscape
Lawes et al., 2000	2000	South Africa	Community	Taxonomic	Richness	Habitat degradation	Habitat quality	Local
Andrianarimisa et al., 2000	2000	Madagascar	Community	Taxonomic	Richness	Habitat fragmentation	Patch size and Isolation	Landscape
Owiunji	2000	Uganda	Community	Taxonomic	Richness and abundance	Habitat degradation	Habitat quality	Local
Ntiamoa-Baidu et al., 2000	2000	Ghana	Community	Taxonomic	Guild composition and abundance	Habitat degradation	Habitat quality	Local
Dale et al., 2001	2001	Uganda	Community	Taxonomic	Richness, abundance and guild composition	Habitat degradation	Habitat quality	Local
Sekercioglu, C.H., 2002	2002	Uganda	Community	Taxonomic	Richness, abundance, composition	Habitat degradation	Habitat quality	Local
Wethered & Lawes, 2003	2003	South Africa	Community	Taxonomic	Species richness	Habitat fragmentation	Matrix quality	Landscape
Downs & Symes, 2004	2004	South Africa	Species-specific	Taxonomic	Species richness and composition	Habitat degradation	Habitat quality	Local
Watson et al., 2004	2004	Madagascar	Community	Taxonomic	Richness and abundance	Habitat fragmentation	Matrix quality, edge effects	Both
Chouteau, 2004	2004	Madagascar	Species-specific	Taxonomic	-	Habitat degradation Habitat fragmentation and degradation	Habitat quality	Local
Wethered & Lawes, 2005	2005	South Africa	Community	Taxonomic	Species richness	Habitat fragmentation and degradation	Matrix quality	Landscape
Holbech 2005	2005	Ghana	Community	Taxonomic	Richness	Habitat degradation	Habitat quality	Landscape
Waltert et al., 2005	2005	Cameroon	Community	Taxonomic	Guild composition, richness	Habitat degradation	Habitat quality	Local
Lawes et al., 2006	2006	South Africa	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Sott et al., 2006	2006	Madagascar	Community	Taxonomic	Species composition and Sric	Habitat degradation	Habitat quality	Local
Chouteau, 2006	2006	Madagascar	Species-specific	Taxonomic	Composition and Sric	Habitat degradation	Habitat quality Habitat quality and Isolation	Local
Merson et al., 2006	2006	Madagascar	Species-specific	Taxonomic	Presence	Habitat degradation	Isolation	Both
Aerts et al., 2006	2006	Ethiopia	Community	Taxonomic	Richness, abundance, composition	Fragmentation	Patch size	Landscape

Manu et al., 2007	2007	Nigeria	Community	Taxonomic	Richness and composition	Habitat degradation & fragmentation	Patch size, isolation and edge effects and Habitat quality	Both
Borghesio 2008	2008	Kenya	Community	Taxonomic	Composition and Sric	Habitat degradation	Habitat quality	Local
Peters et al., 2008	2008	Kenya	Community	Taxonomic	Richness, abundance, composition	Habitat degradation and fragmentation	Patch size, matrix quality, Habitat quality	Both
Githiru & Dijene, 2008	2008	Uganda	Community	Taxonomic	Richness, abundance and guild composition	Habitat degradation	Habitat quality	Local
Holbech 2009	2009	Ghana	Community	Taxonomic	Guild composition	Habitat fragmentation	Matrix quality	Landscape
Newmark et al., 2010	2010	Tanzania	Community	Taxonomic	Richness and presence	Habitat degradation	Habitat quality	Local
Guldemond & Aarde, 2010	2010	Mozambique	Community	Taxonomic	Guild composition	Habitat fragmentation	Patch size and isolation, shape	Landscape
Waltert et al., 2010	2010	Côte d'Ivoire	Single	Taxonomic	Abundance	Habitat degradation	Habitat quality	Local scale
Neuschulz et al., 2011	2011	South Africa	Community	Taxonomic	Richness, composition and Beta diversity	Habitat fragmentation	Matrix quality	Landscape
Mengesha et al., 2011	2011	Ethopia	Community	Taxonomic	Richness, abundance, guild composition	Habitat degradation	Habitat quality	Landscape
Banks et al., 2012	2012	Kenya	Species-specific	Taxonomic	Richness, abundance	Habitat degradation	Habitat quality	Local
Dami et al., 2013	2013	Nigeria	Community	Taxonomic	Richness	Habitat fragmentation	Patch size and Isolation	Landscape
Wiafe & Nutsuwakor	2012	Ghana	Community	Taxonomic	Guild composition	Habitat degradation	Habitat quality	Landscape
Wilson et al., 2013	2013	Mozambique	Community	Taxonomic	Guild composition, richness, abundance	Habitat fragmentation	Patch size and isolation Isolation, Surrounding matrix	Landscape
Olivier & Aarde., 2014	2014	South Africa	Community	Taxonomic	Feeding guilds, Sric	Habitat fragmentation		Landscape
Arcilla et al., 2015	2015	Ghana	Community	Taxonomic	Richness, abundance, guild composition	Habitat degradation	Habitat quality	Local
Caceres et al., 2015	2015	Angola	Community	Taxonomic	Richness and composition	Habitat degradation	Habitat quality	Local scale
Langrand and Wilme 2007	2016	Madagascar	Community	Taxonomic	Presence, richness, abundance	Fragmentation	Patch size	Landscape
Hassan et al., 2013	2016	Tanzania	Community	Taxonomic	Richness, abundance, composition	Habitat degradation	Habitat quality	Local
Bett et al., et al.	2016	Kenya	Community	Taxonomic	Richness, abundance, composition	Habitat fragmentation	Matrix quality	Landscape
Latja et al., 2016	2016	Uganda	Community	Taxonomic	Richness, abundance and guild composition	Habitat loss, fragmentation and disturbance	Patch size and patch quality	Both
Okosodo et al., 2016	2016	Nigeria	Community	Taxonomic	Richness and abundance	Habitat degradation	Habitat quality	Local
Maseko et al., 2019	2017	South Africa	Species-specific	Taxonomic	Presence or absence	Habitat degradation	Habitat quality	Local

Chibesa & Downs, 2017	2017	South Africa	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Ehlers Smith et al., 2017	2017	South Africa	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Ehlers Smith et al., 2017b	2017	South Africa	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Uwimbabazi et al., 2017	2017	Uganda	Community	Taxonomic	Guild composition	Habitat fragmentation	Matrix quality, Patch size, Habitat quality	Both
Deikumah et al., 2017	2017	Ghana	Community	Taxonomic	Richness, assemblage composition	Habitat fragmentation	Matrix type and Habitat quality	Both
Asefa et al., 2017	2017	Ethiopia	Community	Taxonomic	Richness, abundance, guild composition	Habitat degradation	Habitat quality	Landscape
Caceres et al., 2017	2017	Angola	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local scale
Murphy et al., 2018	2018	Madagascar	Community	Taxonomic	Presence	Habitat degradation	Patch quality	Local
Leaver et al., 2019	2019	South Africa	Community	Both	Species and functional diversity	Habitat degradation	Habitat quality	Local
Mahiga et al., 2019	2019	Kenya	Community	Taxonomic	Composition and Sric	Habitat fragmentation	Matrix quality	Landscape
Norfolk et al., 2017	2019	Kenya	Community	Taxonomic	Composition and Sric	Habitat fragmentation	Matrix quality	Landscape
Isaac et al., 2019	2019	Kenya	Community	Taxonomic	Richness, abundance, composition	Habitat fragmentation	Matrix quality	Landscape
Asefa et al., 2019	2019	Ethiopia	Community	Taxonomic	Richness, abundance, guild composition	Habitat degradation	Habitat quality	Local
Maseko et al., 2020	2020	South Africa	Community	Both	Richness and guild composition	Habitat fragmentation and degradation	Patch size, isolation	Landscape
Tchombou et al., 2020	2020	Cameroon	Community	Taxonomic	Guild composition	Habitat degradation	Habitat quality	Local
Learver et al., 2021	2021	South Africa	Species-specific	Taxonomic	Abundance	Habitat degradation	Habitat quality	Local
Newmark et al., 2021	2021	Tanzania	Community	Taxonomic	Richness and abundance	Habitat fragmentation	Patch size and isolation	Landscape
Chaska et al.,	2021	Nigeria	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Rurangwa et al., 2021	2021	Rwanda	Community	Both	Functional diversity and richness	Habitat degradation	Habitat quality	Landscape
Gumede et al., 2022	2022	South Africa	Community	Both	Functional diversity Indices	Habitat fragmentation and degradation	Patch size, isolation, Habitat quality	Both
Gumede et al., 2022	2022	South Africa	Species-specific	Taxonomic	Presence	Habitat degradation	Habitat quality	Local
Ngcobo et al., 2022	2022	South Africa	Community	Both	Functional diversity indices, Sric	Habitat fragmentation and degradation	Isolation, Surrounding matrix, Habitat quality	Both
Asmera et al., 2022	2022	Ethiopia	Community	Taxonomic	Richness, abundance	Habitat degradation	Habitat quality	Landscape

CHAPTER 3

Avian species functional diversity and habitat use: the role of forest structural attributes and tree diversity in the Midlands Mistbelt Forests of KwaZulu-Natal, South Africa

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Running header: Forest avian species' functional diversity and habitat use

3.1 Abstract

Forest transformation has major impacts on biodiversity and ecosystem functioning. Identifying the influence of forest habitat structure and composition on avian functional communities is important for conserving and managing forest systems. This study investigated the effect of forest structure and composition characteristics on bird species community structure, habitat use and functional diversity in 14 Mistbelt forest patches of the Midlands of KwaZulu-Natal in South Africa. We surveyed bird communities using point counts. We quantified bird functional diversity for each forest patch using three diversity indices: functional richness, functional evenness and functional divergence. We further assessed species-specific responses by focusing on three avian forest specialists, orange ground-thrush *Geokichla gurneyi*, forest canary *Crithagra scotops*, and Cape parrot *Poicephalus robustus*. We found that bird community and forest-specialist species responses to forest structure and tree species diversity differed. Also, forest structural complexity, canopy cover, and tree species richness were the main forest characteristics better at explaining microhabitat influence on bird functional diversity. Forest patches with relatively high structural complexity and tree species richness had higher functional richness. Different structural characteristics influenced habitat use by the three forest specialists. Tree species diversity influenced *C. scotops* and *G. gurneyi* positively, while *P. robustus* responded negatively to forest patches with high tree species richness. Our study showed that site-scale forest structure and composition characteristics are important for bird species richness and functional richness. Forest patches with high tree species diversity and structural complexity should be maintained to conserve forest specialists, bird species richness and functional richness.

Keywords: bird species community structure; forest conservation; forest structure; Mistbelt Forests

3.2 Introduction

Land use change is the most prominent threat to forest systems impacting biodiversity and ecosystem functioning globally (Aquilué et al., 2020; Bregman et al., 2016; Morelli et al., 2020). The transformation of natural habitats leads to changes in forest structure, composition, and function, reducing native biodiversity and affecting different taxa's functional diversity, including birds (Ehlers Smith et al., 2017a; Foley et al., 2005; Newbold et al., 2019). These effects have driven a conservation issue and a lot of ecological questions relating to the impact of forest vegetation structural characteristics on species diversity. There is a strong link between forest structure and composition with habitat heterogeneity and ecosystem functioning (Rodrigues et al., 2017; Vanbergen et al., 2007). Diverse forest structures and composition provide many functions, including strengthening species community stability (Ehbrecht et al., 2017; Sanderson et al., 2002), microhabitat formation and supporting species with specialised niches (Brockerhoff et al., 2017; Dekeukeleire et al., 2019).

Avian communities are key in the ecosystems and contribute to ecosystem services and maintain ecosystem functioning (Bregman et al., 2015; Benedetti et al., 2020). Depending on their specialisation, bird species provide ecosystem services such as seed dispersal (Egerer et al., 2018), pollination (Clout & Hay, 1989) and pest control (Kellermann et al., 2008). Birds are an important taxon to study the influence of forest structure and composition because they are habitat quality indicators and respond relatively quickly to environmental change (Boesing et al., 2018; Cosset et al., 2020). In the last decade, most studies investigating the effects of either forest structure or composition on bird species diversity at a landscape level have mainly focused on the functional biodiversity aspect (Benedetti et al., 2020; Broms et al., 2016; Bueno et al., 2018; Burivalova et al., 2015; Ehlers Smith et al., 2017a, 2018; Gumede et al., 2022a; Ngcobo et al., 2022) This approach has been driven by conservation strategies increasingly targeting maintaining ecological functions (Mace, 2014). This is important because species'

functional groups indicate the resilience of ecosystems and maintain ecosystem functions and processes (Alexander et al., 2019; Bregman et al., 2016; Flynn et al., 2009). Also, this approach explains the potential effects of habitat change on the functioning of ecosystems (Coster et al., 2015; Morante-Filho et al., 2021). However, only focusing on certain functional groups or using only community measures can conceal species-specific responses to habitat variation (Lemaître et al., 2012). Different species use habitats differently, and bird species' responses to habitat structural changes are species-specific (Berl et al., 2015; Bouvet et al., 2016; Ehlers Smith et al., 2017b; Gumede et al., 2022b). For example, bird species with specialised niches that are functionally distinct are more vulnerable than others (Flynn et al., 2009). Therefore, exploring species-level responses to forest structure and composition is essential, especially for forest specialists more vulnerable to habitat changes.

Forest ecosystems are three-dimensional, with different characteristics influencing bird species' habitat use (Thiollay, 1992). A recent study using camera traps to assess species habitat use showed bird species-specific vertical stratification patterns in temperate forests (Godoy-Güinao et al., 2023). Among others, bird habitat selection in forest systems is influenced by the structural features of forests like deadwood, canopy cover, canopy openness (Bradfer-Lawrence et al., 2020) and vertical foliage cover (grass, shrub, herbaceous, tree) and height (Gumede et al., 2022a; Maseko et al., 2019). Several studies have linked habitat selection and use to habitat quality and resource availability (Anderson et al., 1979; Böhm & Kalko, 2009; Thiel et al., 2021). For example, the availability of certain features and resources (nest sites, food availability) varies from the ground to the forest canopy. Considering the vertical stratification in bird species use in forests, it is important to understand habitat use in relation to habitat structural characteristics.

The indigenous forest biome is the smallest in South Africa, estimated to be 0.41 % (Deng et al., 2020), but of disproportionately high conservation and ecological value (Downs

& Symes, 2004; Lawes et al., 2000a). Mismanaged fires, timber harvesting and transformation for plantations are the main threats to the Southern Mistbelt forests (Mucina et al., 2006). These forests in KwaZulu-Natal were generally heavily logged for approximately 150 years, and the exploitation was dominant between the 1800s and early 1940s when illegal logging was prohibited (King, 1941; Wirminghaus et al., 1999). Selective logging affected the ecology of these forests, and the system has been left to recover naturally through successional processes (Adie et al., 2013). Government agencies or private owners have prioritised the forest biome for management. Despite being protected, the Mistbelt Forests remain illegally harvested (Grieve & Downs, 2015). Approximately 6.5 % of avian species in South Africa are classified as forest-depend (Oatley, 1989), and about half are experiencing range declines with > 16% average range decline since 1992 (Cooper et al., 2017). An understanding of forest features influencing habitat use to allow for the long-term persistence of birds, particularly forest specialists in these forests, is essential.

Understanding bird species' habitat use and selection allows for sustaining essential forest structural characteristics defining bird species microhabitats to prevent species loss (Díaz et al., 2005) and developing integrated habitat management plans (Hewson et al., 2011). The Southern Mistbelt Forests are multi-layered, naturally fragmented patches nested within a grassland mosaic landscape (Mucina, 2006). Human activities have further aggravated fragmentation with species' structure, configuration, and composition changes within the system (Adie et al., 2013; Leaver et al., 2019). Therefore, the Southern Mistbelt forest is a good system to study the influence of forest structure on forest bird specialists. In South African forests, the range of the selected bird species has declined substantially because of habitat destruction (Copper et al., 2017). As habitat specialists, the selected bird species are more vulnerable to habit disturbance, hence are valuable as focal species in assessing their habitat preference. In this study, we selected three forest-dependent bird species listed in Oatley (1989)

as focal species for species-specific responses. The orange ground-thrush (*Geokichla gurneyi*), forest canary (*Crithagra scotops*), and Cape parrot (*Poicephalus robustus*) are forest specialist species that differ in their vertical use of the forest strata (Hockey et al., 2005). The orange ground-thrush is a forest ground-dwelling bird and also feeds mostly on the ground; vegetation composition is essential for this species (Gumede et al., 2022b); the forest canary feeds mainly on seeds in the forest understory, while the Cape parrot is rather a forest canopy species hence the importance of vertical structural complexity to maintain the populations of this species. The average range decline of the Cape parrot, forest canary, and orange ground-thrush is 54%, 10% and 8%, respectively, in South African forests (Cooper et al., 2017). If habitat destruction continues, it will significantly impact the remaining bird species population. Consequently, their presence and habitat preference can be used to indicate the forest patch habitat quality (Gumede et al., 2022a, b).

Previous studies assessing avian communities in the KwaZulu-Natal Midlands Mistbelt Forest patches have either focused on certain landscape characteristics (e.g., Wethered & Lawes, 2003, 2005) or specific structural characteristics (snags) (Downs & Symes, 2004) or seasonality differences (Symes et al., 2002). The present study fills an important knowledge gap on the responses of bird communities and specific forest-dependent species on vegetation structure and composition characteristics. Our study examined the effects of the forest structure and composition on the avian community structure of the KwaZulu-Natal Midlands Mistbelt Forests in South Africa. Specifically, we asked how the forests' structural and compositional characteristics affect the bird species' community structure, richness, and functional diversity. We then selected three forest specialists (orange ground-thrush, forest canary and Cape parrot) occupying different vertical forest profile strata (i.e. ground-dwelling, mid-story, canopy) to assess the species-specific responses. Focusing on these forest specialists, we explored how forest structural and compositional characteristics influenced forest bird specialists' habitat use

and preference. We predicted that increased structural complexity would increase bird species richness and functional diversity. Forest specialist bird species have specific microhabitat requirements (Murphy et al., 2018) with a strong vertical stratification in habitat use (Godoy-Güinao et al., 2023). Also, the selected focal forest specialist species differ in their forest strata habitat use. Given these known differences in forest habitat selection (see Study species), we hypothesised that the forest structural characteristics would affect species-specific responses for the selected avian forest specialists differently. For example, we expected important forest structural characteristics for the ground-dwelling orange ground-thrush would be leaf litter, herbaceous cover, and grass. Also, we expected saplings and herbaceous cover to be an essential structural characteristic for the understory forest canary, while for the Cape parrot, canopy closure or openness would be important.

3.3 Methods

3.3.1 Study species

The orange ground-thrush is a near-threatened uncommon, ground-dwelling forest specialist bird species (Hockey et al., 2005). It is insectivorous, feeding mainly on earthworms and insects (Hockey et al., 2005). It nests in a bowl-shaped cup, avoiding dense foliage about 1-2 m above the forest floor (Tarboton 2001; Tarboton & Roberts, 2011). The forest canary is a small (15 g), granivorous forest understory bird (Hockey et al., 2005). This species is nearly endemic to South Africa, with a marginal distribution in Swaziland and Lesotho (Ward et al., 2003). The forest canary is sedentary and flocks during the non-breeding season (Hockey et al., 2005), and nests in a cup in a forest tree or sapling between 1-6 m (Tarboton, 2001; Tarboton & Roberts, 2011). The Cape parrot is a relatively large (300 g) endangered, rare forest specialist endemic to South Africa. The estimated population is less than 2000 birds (Downs et al., 2014). Some main threats to the Cape parrot are habit destruction, fragmentation and

specific feeding and nesting requirements (Downs et al., 2014; Leaver et al., 2023; Symes & Downs, 2002; Wirminghaus et al., 1999; 2001; 2002). It mainly feeds on the endocarp (kernels) of *Afrocarpus* or *Podocarpus* spp. fruits and then those of other indigenous forest fruits when these are unavailable, or they feed on exotics outside of forests (Hockey et al., 2005; Wimberger et al., 2023; Wirminghaus et al., 2002). It generally nests in a secondary cavity in a *Podocarpus* tree, often 15 m above the ground (Tarboton, 2001; Wirminghaus et al., 2001). Usually, the same cavity is used in successive years (Hockey et al., 2005; Tarboton, 2001; Wirminghaus et al., 2001).

3.3.2 Study area

Our study was conducted from October 2020 to September 2021 in fourteen selected patches of varying sizes (2.2 – 1685 ha) in four regions within the Midlands indigenous forests of KwaZulu-Natal Province, South Africa (Table 3.1, Figure 3.1). The four different regions studied were: Karkloof (n = 4), Dargle (n = 4), Balgowan (n = 2) and Bulwer (n = 4), all categorised as Natal Midlands Mistbelt Forests (Table 3.1, Figure 3.1). The studied regions receive summer rainfall with frequent summer mist and have similar altitudes, average rainfall and temperature (Downs & Symes, 2004; Kotze & Samways, 1999). The Mistbelt mixed *Afrocarpus/Podocarpus* forests in the midlands of KwaZulu-Natal occur on steep south-facing slopes comprised of a few large patches (>1650 ha) surrounded by small patches (Lawes et al., 2004). The landscape surrounding the Mistbelt forest patches is mainly grassland and exotic forestry plantations (Leaver et al., 2022).

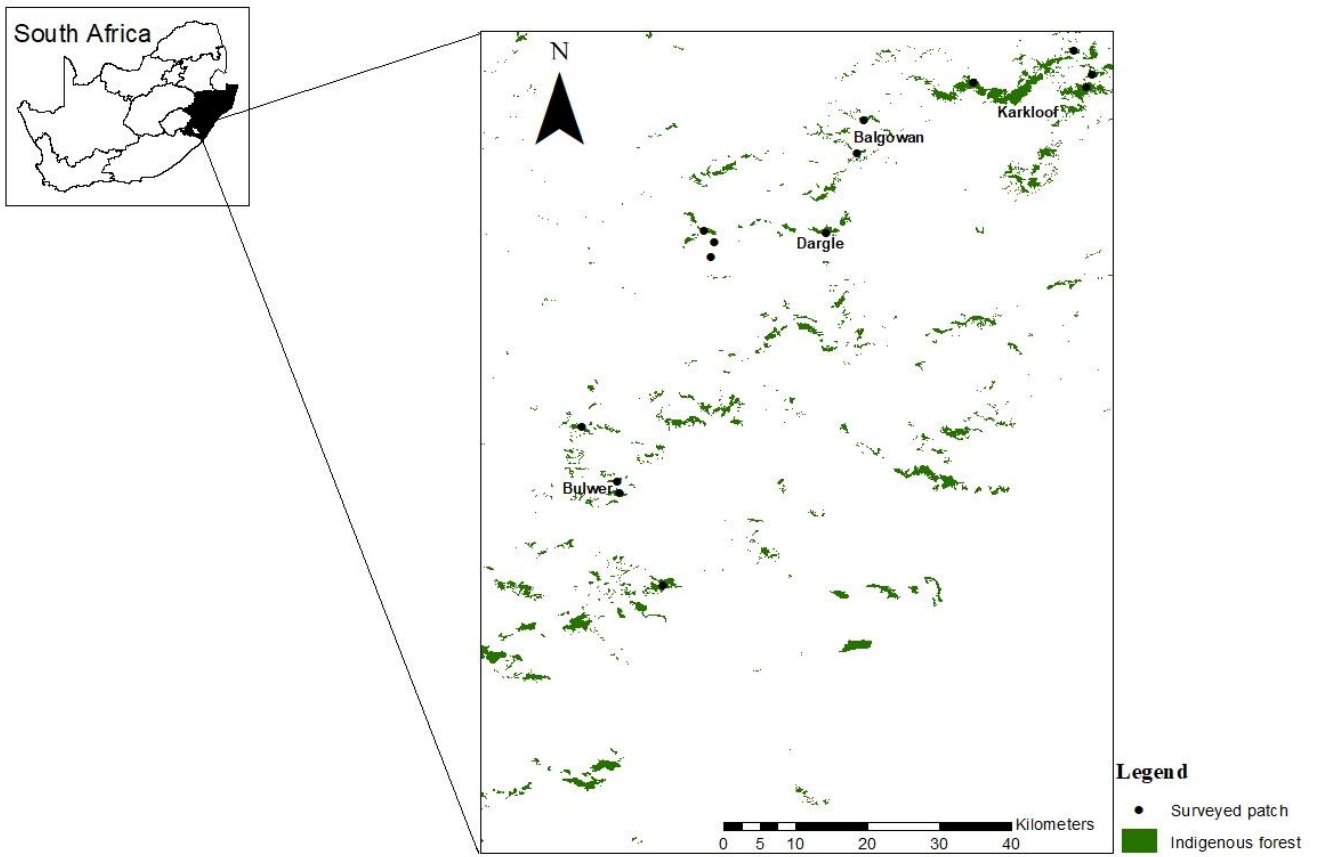


Figure 3.1 Distribution of 14 Mistbelt Forest patches of the Midlands of KwaZulu-Natal Province, South Africa, used in the present study. (Black dots represent surveyed forest patches).

Table 3.1 Studied Mistbelt Forest patches in the KwaZulu-Natal Midlands, South Africa. Superscripts indicate landownership with privately

(^a)owned and state-owned (^b) forest patches.

Region	Forest Patch	Coordinates	Patch size (ha)	Point counts (n) per season	Dominant surrounding matrix
Karkloof	Karkloof of Nature Reserve ^a	29°17'50"S; 30°13'59" E	1685	98	Grassland
	Benvie Farm ^a	29°18'08"S; 30°22'26" E	101	17	Commercial plantation
	Mbona Private Nature Reserve ^a	29°15'27"S; 30°21'29" E	679	66	Commercial plantation
	L'Abri ^a	29°17'08"S; 30°23'40" E	199	19	Commercial plantation
Dargle	Maritzdaal Forest ^a	29°29'05"S; 30°02'57" E	558	46	Grassland
	Wakefield Forest ^a	29°29'06"S; 29°54'28" E	4.5	3	Grassland
	Waterfall Forest ^a	29°30'54"S; 29°54'18" E	2.2	1	Grassland
	Sharedown (New Forest) ^a	29°28'57"S; 29°53'44" E	112	17	Grassland
Balgowan	Milestone Forest Walk ^a	29°22'57"S; 30°05'40" E	77	6	Commercial plantation
	Rameron (Boshoek complex) ^a	29°20'34"S; 30°05'43" E	207	15	Grassland
Bulwer	Ingelabantwana Nature Reserve ^b	29°43'43"S; 29°44'35"E	338	24	Grassland
	Xotsheyake Nature Reserve ^b	29°47'46"S; 29°47'16"E	98	10	Commercial plantation
	Marutswa Nature Reserve ^b	29°48'36"S; 29°47'25"E	268	22	Commercial plantation
	Nxumeni (Nkwezela State Forest) ^b	29°55'38"S; 29°50'42"E	385	27	Commercial plantation

3.3.3 Bird species survey

As per Ehlers Smith et al. (2017a) and Maseko et al. (2019), in ArcGIS 10.6 (ESRI, Redlands, CA, USA), grids of 200 x 200 m were overlaid using the recent indigenous forest layer (South African National Land-Cover 2018) for the selected 14 patches. The grid axes (i.e., the grid lines crossing points) were assigned a survey point 200 m apart in all surveyed patches. We had 371 fixed-radius point counts (Table 3.1) per season within the 14 selected forest patches, and the number of points per patch varied depending on the patch area (ha). We then projected the point counts into a global position system (GPS), then using a Garmin eTrex 10 (USA), we located these in the field. If the points were inaccessible in the field, we created a new point, ensuring it was within 50 m of the projected point. We used a fixed radius point count to identify bird species and recorded all bird species visible or audible within a 100 m radius. We recorded the number of individuals per identified bird species at each bird survey point. The point-count surveys were conducted for 3 h from sunrise, sampling each survey point for 10 min, and the number of points for each day varied depending on the openness of the forest patch. We did not record the bird species if we were unsure of the species' identification ($n = 1$). Each point count was surveyed once in each season (i.e., breeding from October 2020 to March 2021; the non-breeding from April 2021 to September 2021). We then created a matrix of functional traits (Supplementary Information Table S3.1) that captured bird functional roles in ecosystems and response to disturbance (Ehlers Smith et al., 2018; Flynn et al., 2009). The matrix included bird nesting type (i.e. ball/cup, cavity, or platform), body mass, primary diet (i.e. carnivore, frugivory, omnivory, nectarivory, granivory, or insectivory), foraging strategy (i.e. harvest, terrestrial probe, arboreal probe, glean, hawk, perch and swoop, or various), and habitat specificity (i.e. specialist or generalist) (Ehlers Smith et al., 2018; Flynn et al., 2009; Hockey et al., 2005). Species richness and abundance were calculated per surveyed point as the cumulative species number and number of individuals, respectively. Then both were pooled

as the total number of species and relative species abundance per patch (Ehlers Smith et al., 2017a).

3.3.4 Forest structure and composition sampling

Four quarters were established around each bird point survey to measure habitat structure and composition within a 20 m radius. We ran two tape measures diagonally to create the four quarters totalling 100%. Within each quarter, we visually estimated the percentage of understory cover for bare ground, leaf litter, grass, herbaceous plants, woody plant (saplings \leq 2 m) and water. We also recorded the average height of grass, herbaceous, and woody plants and the maximum tree height. We counted the number of mature live and dead trees (horizontal and vertical) at six different height classes (2-5 m, 6-10 m, 11-15 m, 16-20 m, 20-25 m, $>$ 25 m; Ehlers Smith et al., 2017a). Each point count of the 371 was sampled once during the wet (October 2021 to March 2021) and dry (April 2021 to September 2021) seasons. To determine the tree species richness and diversity, we identified all the trees within the plot to species level and identified the dominant and co-dominant plant species. The Gap Light Analysis Mobile Application (GLAMA) measured canopy openness, closure, and cover at each survey point. For every survey point, we used the mean height of all the vegetation classes (grass, herb, sapling, or tree) to calculate the height heterogeneity index and used the mean percentage cover for the structural complexity using the Shannon-Weiner Diversity Index (SWDI) as follows: $H = -\sum p_i \ln(p_i)$, where 'p_i' is the proportion of the total foliage in the *i*th layer for a chosen horizontal layer (Bibby et al., 2000).

3.3.5 Data analyses

We quantified the bird's functional diversity using three indices: functional richness (Fric), functional evenness (FEve) and functional divergence (FDiv). Functional richness quantifies

the total amount of functional space filled by a given community, which is the bird assemblage in the present study (Villéger et al., 2008). Functional richness is independent of species' relative abundance and only increases if functionally different species are added to the community utilising more resources (Mason et al., 2005; Villéger et al., 2008). Functional evenness and divergence quantify how species occupy the functional space and account for their relative abundance, FEve measures the distance between species, and FDiv measures the species to the centre of the multidimensional trait space. Similarly, we created bird species matrices for every surveyed season (breeding and non-breeding) using the abundance, presence and absence data. For each forest patch, we calculated FRic, FEve and FDiv for the whole bird community, forest specialists and forest generalists based on Gower functional dissimilarity using the function 'dbFD' in the package "FD" (Laliberté et al., 2014). Using the z-score formula, we standardised all the response variables to be comparable. Prior to analyses, we tested for spatial autocorrelation (Moran's *I*) using the package 'ape' in R (Dormann et al., 2007). Generalised linear models were performed to explore the influence of the retained explanatory variables on our response variable bird species richness (total number of species within the patch) Fric, FEve and FDiv (Supplementary Information Table S2). Using the package "performance" in R, we detected overdispersion for the count data model and used a negative binomial error distribution for all the models (Lüdecke et al., 2021). Using the Akaike Information Criterion (AIC), we defined the best model with $\leq 2 \Delta AIC$ (Burnham & Anderson, 2004). We calculated McFadden's Pseudo R^2 for all the top models.

To determine the effect of land use type (e.g., grassland, exotic tree plantation, etc.) adjacent to the forest patches and patch size on bird species composition across the 14 surveyed patches, we used a non-metric dimensional scaling (NMDS) based on bird species abundance data. Bird species occurring in only one forest patch (outliers) were removed ($n = 11$); therefore, only 85 bird species were used for the NMDS. We analysed the data using the

package “vegan” and function “metaMDS”, Bray-Curtis distance matrix with two dimensions (Okansen et al., 2022). To visualise the results, we used ggplot2. To test the difference in bird species composition in different patch sizes adjacent to different land use types, we used an analysis of similarity (ANOMIS) vegan package, Bray-Curtis and 9999 permutations. Lastly, we used the indicator species analysis in the package “indicspecies” to test for bird species that are indicators of different forest patch sizes. We report bird species < 0.05 .

To assess the effects of habitat structural and compositional characteristics on the presence of the three selected forest specialists, we performed generalised linear models assuming a binomial error distribution using the packages ‘MASS’. Collinearity was checked and tested between all the explanatory variables using the Variance Inflation factors (VIF) using the package ‘car’. After excluding variables with higher VIF > 5 and correlation ($r > 0.70$) (i.e. canopy closure, canopy cover), eight variables were retained: percentage bare ground, leaf litter, grass, herbaceous, saplings, tree species richness, dead tree density, and canopy openness. The structural characteristics were the explanatory variable, and the forest bird species' presence or absence (binary) data were used as a response variable. We used the Akaike Information for interpretation and selected the top models with $\Delta AIC \leq 2$ as the top models (Burnham & Anderson, 2003). To reduce uncertainty, we modelled averaged the parameters for all the models $\Delta AIC \leq 2$ as they are considered to be equal (Johnson & Omland, 2004).

3.4 Results

3.4.1 Tree species composition and forest structure

We identified a total of 68 tree species belonging to 35 families and 56 genera in the KwaZulu-Natal Midlands Mistbelt Forest patches (Supplementary Information Table S3.3). Three of these tree species are presently listed as vulnerable, two as endangered, and five are regarded

as declining. The most dominant tree families were Flacourtiaceae (17%), Rutaceae (14%) and Celastraceae (11%). The total number of tree species varied between 60 (Karkloof) and 25 (Balgowan) across the studied regions, and the smallest patch (Waterfall Forest) had the least number of species ($n = 5$) (Supplementary Table S3.4). Of the 68 tree species, only one species *Solanum mauritianum*, was an alien invasive plant invading 11 forest patches except for Ingelabantwana Nature Reserve in Bulwer and Waterfall and Wakefield Forests in the Dargle (Supplementary Table S3.4). The common forest tree species across sites were *Podocarpus/Afrocarpus* spp., *Xymalos monospora*, and the dominant understory species were *Carissa bispinosa*, *Diospyros whyteana*, and *Gymnosporia harveyana*. A total of 12 tree species (18%) were only identified in the Karkloof area, and six tree species (9%) were only identified in the Bulwer area (Supplementary Information Table S3.4). Some species were only found in specific sites or fewer patches, including *Peddiea africana* which was only identified in Balgowan, *Pittosporum viridiflorum* only in Bulwer and Dargle, and *Ocotea bullata* in Karkloof Nature Reserve and Marutswa Nature Reserve (Supplementary Table S3.4).

3.4.2 Bird species composition

We recorded a total of 12,949 individuals, and 96 bird species belonging to 39 families across the 14 indigenous forest patches of the Mistbelt Forest in the Midlands of KwaZulu-Natal (Supplementary Information Tables S3.1 and S3.5). Eight bird species are regionally listed as either vulnerable, endangered or near threatened, and seven are listed globally (Supplementary Information Tables S3.1 and S3.5). The recorded bird species differed in habitat association, feeding guild, body mass, feeding and nesting strategy (Supplementary Information Table S3.1). They were a total of 39 (41%) forest habitat specialists and 57 (59%) generalists (Supplementary Information Table S3.1). The most common trophic guild were insectivores (51%), and nest or cup was the dominant nesting strategy (61%) (Supplementary Information

Table S3.1). Bird body mass varied, ranging between 8 g to 4,000 g. In the breeding season, there was a total of 91 bird species, and the most dominant bird species across all the forest patches were southern boubou *Laniarius ferrugineus* (n = 657), sombre greenbul *Andropadus importunus* (n = 557) and bar-throated apalis *Apalis thoracica* (n = 487) (Supplementary Information Table S3.5). In the non-breeding season, there was a total of 68 bird species, and the most common species were the southern boubou (n = 656), southern double-collared sunbird *Cinnyris chalybeus* (n = 538) and dark-capped bulbul *Pycnonotus tricolor* (n = 475) (Supplementary Information Table S3.5).

Some bird species were only found in specific sites or patches. For example, the eastern bronze-naped pigeons *Columba delegorguei* were only in Karkloof Nature Reserve, and the crested guineafowl *Guttera edouardi* only in Karkloof forest patches. The number of bird species per forest patch were: Karkloof Nature Reserve (n = 67), Mbona Private Nature Reserve (n = 63), L'Abri (n = 45), Benvie Farm (n = 49), Rameron (n = 44), Milestone Forest Walk (n = 31), Maritzdaal (n = 64), Sharedown Forest (n = 45), Wakefield Forest (n = 20), Waterfall Forest (n = 16), Ingelabantwana Nature Reserve (n = 52), Xotsheyake Nature Reserve (n = 43), Marutswa Nature Reserve (n = 45), Nxumeni Forest (n = 53).

In the NMDS ordination based on the dissimilarity of the bird species composition around forest patches surrounded by commercial plantations and grassland matrix was not significantly different ($p = 0.74$; Figure 3.2). The bird species composition significantly differed in forest patches of different sizes ($p < 0.05$; Figure 3.2). We identified 40 bird species that are indicators for forest patches over 500 ha (Supplementary Information Table S3.6). These included 22 forest bird specialists and 20 generalist bird species. Among the top forest specialist bird species strongly associated with forest patches > 500 ha is the blue-mantle crested flycatcher (*Trochocercus cyanomela*), Knysna turaco (*Tauraco corythaix*) and grey cuckooshrike (*Coracina caesia*) (Supplementary Information Table S3.6). Forest generalists

that are top indicators for forest patches > 500 ha included the dark-capped bulbul, tawny flanked prinia (*Prinia subflava*) and terrestrial brownbul (*Phyllastrephus terrestris*). Only one bird, the forest generalist southern ground-hornbill (*Bucorvus leadbeateri*), was identified as an indicator for patches that are 200-500 ha (Supplementary Information Table S3.6).

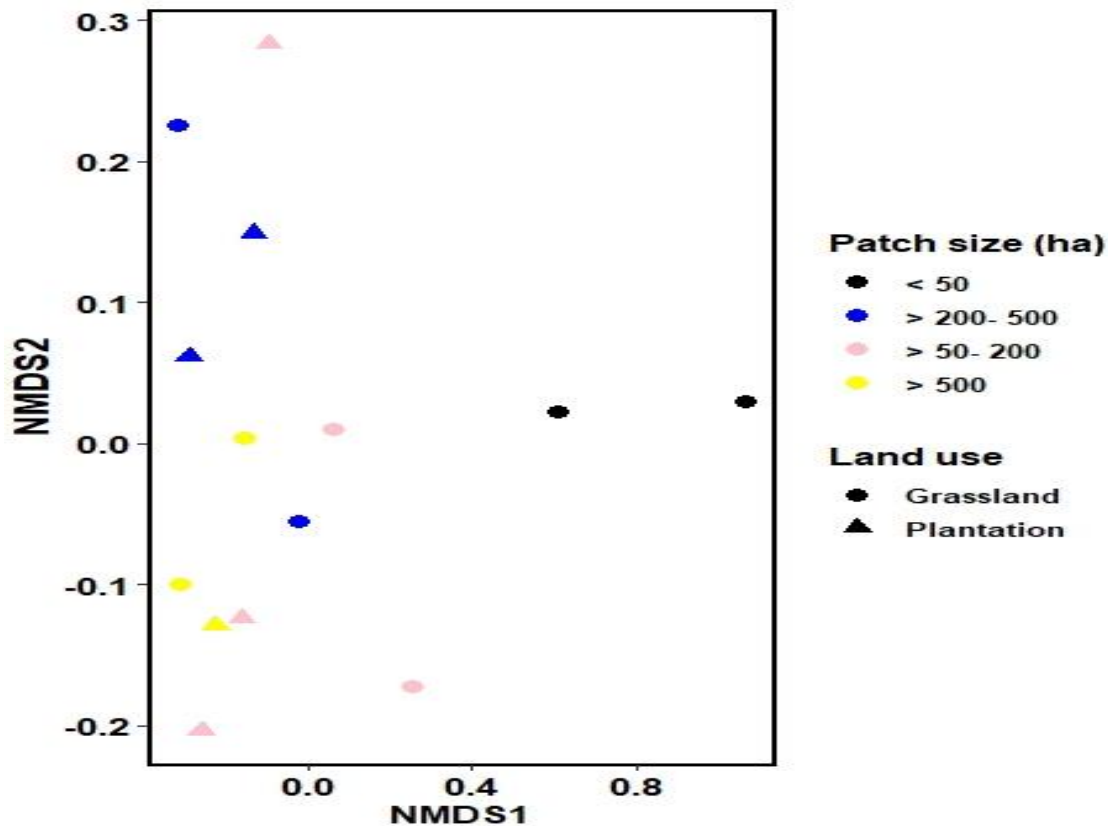


Figure 3.2 Non-metric dimensional scaling (NMDS) of the bird species composition across 14 patches in four sites in the Midlands Mistbelt forests in South Africa (stress = 0.06; k = 2).

3.4.3 Bird functional diversity and richness

The importance of the forest structure and composition characteristics influencing bird species diversity and richness differed across the surveyed seasons (Supplementary information Table S3.2). In both the breeding and non-breeding season, tree species richness positively influenced bird species richness (Table 3.2, Figure 3.3). Forest structural complexity had a significant positive influence ($p < 0.001$) on the bird species richness in the non-breeding season, and canopy cover had a non-significant positive influence in the breeding season (Figure 3.3). In

the breeding season, FRic and FDiv for the whole community had a positive association with tree species richness, while FEve had a negative association with tree species richness (Table 3.3, Supplementary Information Table S3.7). Functional divergence had an inconsistent response to tree species richness with seasonal differences.

During the breeding and non-breeding seasons, forest bird specialists' functional diversity was respectively influenced by structural complexity and tree species richness (Table 3.2; Supplementary Information Table S3.7). Forest generalists' diversity was mainly influenced by forest canopy cover and structural complexity (Table 3.2, Supplementary Information Table S3.7). During the breeding season, forest generalist bird species FDiv and FEve had a positive association with structural complexity (Table 3.2). During the non-breeding season, canopy cover had a significant ($p < 0.05$) negative influence on forest generalist birds FEve (Table 3.2). Structural complexity was an important variable for forest specialist bird species in both seasons (Table 3.2). In contrast, leaf litter was important during the breeding season and water cover during the non-breeding season (Table 3.2, Supplementary Information Table S3.7). During the breeding season, the whole bird community, forest generalists and forest specialists FDiv had a negative association with leaf litter (Supplementary Information Table S3.7). During the non-breeding season whole bird community and forest bird specialist FDiv had a negative association with water cover, while forest generalists had a positive association (Supplementary Information Table S3.7).

Table 3.2 Generalised Linear Models (GLMs) top models output based on Δ AIC rankings of the effects of tree species richness (TRic), structural complexity (SC), canopy cover (CC) and leaf litter (LL) on bird species richness and functional diversity (Fric, FEVe, FDiv) of avian communities of the Midlands Mistbelt forest patches in the breeding and non-breeding season in KwaZulu-Natal, South Africa.

	Response variable	Model structure	df	AIC	ΔAIC	Log-likelihood	R²
Non-breeding							
Bird species richness	All birds	TRic + SC (+)	11	107.43	0.00	-99.43	0.34
	FRic	SC (+)	12	61.75	0.00	-55.75	0.36
	Forest specialists	SC (+)	12	55.48	0.00	-49.48	0.37
	Forest generalists	SC (+) + CC(-)	11	55.77	0.00	-47.77	0.26
FEVe	All birds	SC (-)	12	23.94	0.00	-17.94	0.21
	Forest specialists	SC (+)	12	21.05	0.00	-16.05	0.28
	Forest generalists	CC (-)	12	22.18	0.00	-17.18	0.31
FDiv	All birds	TRic (-)	12	31.98	0.00	-25.978	0.37
	Forest specialists	SC (+)	12	31.64	0.00	-25.64	0.22
	Forest generalists	CC (-)	12	29.17	0.00	-23.15	0.23
		SC (+)	12	29.17	0.00	-23.15	0.23
Breeding							
Bird species richness	All birds	TRic (+)	12	109.20	0.00	-103.20	0.37
	FRic	TRic (+)	12	60.60	0.00	-54.60	0.21
	Forest specialists	TRic (+)	12	56.94	0.00	-50.94	0.35
	Forest generalists	TRic (+)	12	55.00	0.00	-49.00	0.33
FEVe	All birds	TRic (+)	12	25.33	0.00	-19.33	0.21
	Forest generalists	TRic (-)	12	25.18	0.00	-19.15	0.25
	Forest specialists	TRic (+)	12	23.43	0.00	-17.43	0.34
FDiv	All birds	TRic (+)	12	31.91	0.00	-25.92	0.17
		CC (-)	12	31.91	0.00	-25.92	0.17
		LL (-)	12	31.91	0.00	-25.92	0.17
		SC (-)	12	31.91	0.00	-25.91	0.17
	Forest specialists	TRIC (+)	12	32.58	0.00	-26.57	0.31
		SC (+)	12	32.58	0.00	-26.57	0.31
	Forest generalists	SC (+)	12	30.24	0.00	-24.24	0.24
		TRIC (+)	12	30.24	0.00	-24.24	0.24

Note: This table represents (Δ AIC = 0) although all top models (Δ AIC < 2) were averaged and considered further and R² indicates top model performance (McFadden's Pseudo R²).

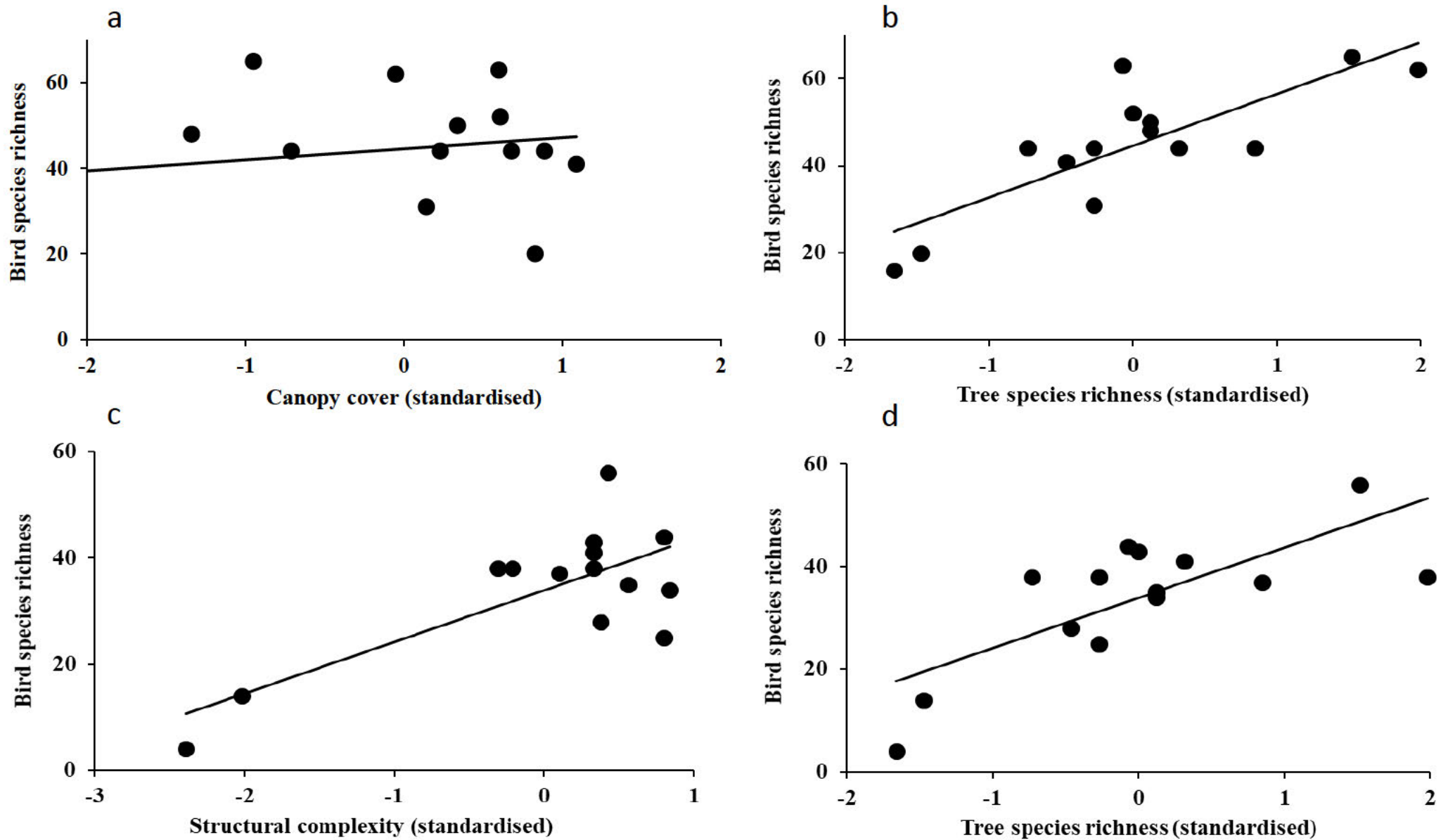


Figure 3.2 Relationship between bird species richness with (a) canopy cover, (b) tree species richness during the breeding season and (c) structural complexity and (d) tree species richness during the non-breeding season in selected Midlands Mistbelt Forest patches (n = 14) in KwaZulu-Natal, South Africa

3.4.4 Habitat use

Individual forest-dependent bird species varied in their response to forest structural characteristics and compositional characteristics (Table 3.3). The Cape parrots were only present in the Bulwer area in all four patches and were more abundant in Ingelabantwana Nature Reserve and Marutswa Nature Reserve. The percentage cover of saplings had a significant positive influence on the presence of Cape parrots, and the grass cover had a significant negative effect (Table 3.3). Also, tree species richness negatively influenced the presence of the Cape parrot, while canopy openness had a positive effect (Table 3.3). Forest patches occupied by Cape parrots were compositionally similar. The dominant tree species in these patches were: *Podocarpus/ Afrocarpus* spp., *Ptaeroxylon obliquum*, and the dominant understory were *Gymnosporia harveyana*, and *Diospyros whyteana*. The herbaceous cover and tree species richness influenced the forest canary and the orange ground-thrush presence. The forest canary was present in forest patches with different tree species compositions (Nxumeni, Karkloof Nature Reserve, Mbona Private Nature Reserve and Maritzdaal).

Table 3.3 Generalised Linear Models (GLM) top model output of the effects of forest structure and composition characteristics influencing the occurrence of three forest specialists in the Midlands Mistbelt patches in KwaZulu-Natal, South Africa.

Species	Variables	P-value	AICc	Δ AIC	ω_i
Cape parrot <i>Poicephalus robustus</i>			306.65	0.00	0.42
	Canopy openness (+)	5.32 e-06			
	Grass cover (-)	0.000			
	Tree species richness (-)	0.001			
	Snags (+)	0.07			
	Sapling cover (+)	0.001			
	Canopy openness (+)	2e-16	307.48	0.83	0.39
	Tree species richness (-)	0.001			
	Saplings (+)	0.001			
	Herbaceous cover (+)	0.22			
Forest canary <i>Crithagra scotops</i>			302.95	0.00	0.37
	Tree species richness (+)	2e-16			
	Herbaceous cover (+)	2.01e-06			
Orange ground-thrush <i>Geokichla gurneyi</i>			96.29	0.00	0.33
	Herbaceous cover (-)	0.001			
	Tree species richness (+)	3.32e-06			
	Bareground (+)	0.45	97.55	1.26	0.16
	Tree species richness (+)	3.66e-06			
	Herbaceous cover (-)	0.04			

Note: Bold indicates significance. Significant codes: < 0 ‘****’ 0.001 ‘***’ .01 ‘**’ .05

Abbreviations: AICc, Akaike’s Information Criterion; Δ AIC = Delta AIC, ω_i Akaike weights.

3.5 Discussion

As the transformation of habitats increases, changing the structure and composition of forest habitats, it is important to understand the influence on the avian community. In this study, we evaluated the responses of bird species richness, three functional diversity indices, and selected forest specialists to vegetation structure and composition characteristics. We demonstrated the importance of forest structure and composition in shaping the bird community structure, richness, functional diversity, and forest specialists' species-specific responses. Our results showed the importance of tree species richness in bird species richness and diversity. Also, we showed that species-specific responses to local scale structural and compositional attributes do not scale up to the whole community response. This supported our hypothesis that forest specialist bird species richness responds differently to vegetation structure and composition characteristics.

3.5.1 Bird species richness and forest specialists' response to forest structure and vegetation

Local tree species richness was a significant factor that positively affected bird species richness in the Mistbelt Forest patches of KwaZulu-Natal. This positive response to high tree diversity by bird species has been reported in previous studies for bird species (Gil-Tena et al., 2007; Regnery et al., 2013). Tree species richness influence on species has been shown for other taxa, including amphibians (McKenny et al., 2006; Sankararaman et al., 2021) and mammals (Regnery et al., 2013; Wells et al., 2007). Tree species richness contributes to the heterogeneity and spatial complexity of the forests by providing more microhabitats and resources. For example, increased tree species richness provides more nesting and food resources (Gil-Tena et al., 2007; Ong'ondo et al., 2022). For insectivorous species like the orange ground-thrush *G.*

gurneyi, high tree species richness increases insect abundance over different seasons (Bereczki et al., 2014). The orange ground-thrush is a generalist insectivore feeding mainly on insects and earthworms (Hockey et al. 2005); therefore, different trees provide them with different insects as different tree microhabitats are associated with different insect communities.

While it appears that forest tree species richness positively influenced the presence of forest specialist birds, the Cape parrot presence had a negative association with tree species-rich forest patches. Past studies show that the richness of tree species does not influence bird species that depend solely on a specific tree species microhabitat. Cape parrots depend primarily on *Podocarpus/ Afrocarpus* spp. for nesting and feeding (Leaver et al., 2022; Wirminghaus et al., 1999, 2001, 2002). This was corroborated in the present study by the absence of Cape parrots in forest patches with high tree diversity. Exotic pecan nut *Carya illinoensis* plantations outside forests provide Cape parrots with foraging resources during autumn (Symes & Downs, 2002; Wimberger et al., 2023). It has been argued that forest bird specialists prefer natural forests more than surrounding landscapes for supplementary resources (Ong'ondo et al., 2022; Porro et al., 2020). The present study did not consider the landscape attributes, which may be more important in habitat use by Cape parrots. Assessing the landscape context will give more insights into the factors influencing the Cape parrot's habitat use and selection. Intense logging history in the KwaZulu-Natal Midlands Mistbelt forests decreased the dominance of *Podocarpus/ Afrocarpus* spp. (Adie et al., 2013). This can explain the Cape parrot's absence in unoccupied patches in the present study. Although we did not quantify the logging intensity, Karkloof forest patches were heavily logged (J Geekie pers. comm., unpublished data). While surrounding communities used some Bulwer Forest patches, they were not exploited by the early settlers because these patches were difficult to access (King, 1941). *Podocarpus/ Afrocarpus* spp. cannot recover quickly, especially in heavily

logged forest patches, and the remaining tree species are limited by seed dispersal distances (Wirringhaus et al., 1999). Downs et al. (2014) attributed the Cape parrot decline in the Karkloof area (Benvie and Mbona Private Nature Reserve) to food and nest site shortages.

Structural complexity and canopy cover were the main forest attributes influencing bird species richness. Structural complexity has been previously linked to microhabitat formation and ecological niche availability (Castaño-Villa et al., 2014; Ehlers Smith et al., 2018). Structural heterogeneity has been related to increased available microhabitats for foraging (Şekercioğlu et al., 2002) and nesting sites (Martin et al., 2004). Structural characteristics influencing habitat utilisation by forest specialists were different for different species. These results are consistent with previous studies showing that different structural characteristics influence forest species occupancy as species have different microhabitat requirements (Braunisch et al., 2019; Gumede et al., 2022a,b). In our study, Cape parrots used forest patches with a dense shrubby understory, a high number of snags, and low grass cover. Our findings reinforce the positive relationship of the Cape parrot with dead trees/ snags, as previously reported (Downs & Symes, 2004). Our data suggested a strong negative influence of the herbaceous cover on the orange ground-thrush. Gumede et al. (2022a) showed that this species prefers an open understory with a high leaf litter cover. In our study, the herbaceous cover positively influenced the forest canary, consistent with the dietary as a granivorous bird (Hockey et al., 2005) and nesting requirements for dense leafy foliage (Tarboton, 2001). The response of forest-specialised bird species to tree diversity and forest structural characteristics cannot be generalised from functional group responses. Therefore, conservation-oriented approaches to forest management must assess species-specific and community responses (Basile et al., 2021).

3.5.2 Functional diversity response to vegetation diversity and forest structural attributes

Our results showed that bird species, local vegetation structure and diversity influence bird functional diversity. In the present study, functional richness was higher in forest patches with higher tree species richness for forest generalists and specialist birds during the breeding season. This positive response of functional richness to tree diversity is attributed to increased resource availability and stand structure complexity from different tree species (Díaz, 2006; Ehbrecht et al., 2017). During the non-breeding season, functional richness had a positive association with structural complexity for the whole bird community, while functional evenness and divergence had a negative association. A similar relationship was observed in Australia, where these bird functional diversity indices showed opposing responses to vegetation structure and tree species richness (Sitters et al., 2016). During the non-breeding season, forest structural complexity positively affected the diversity of forest bird specialists (functional evenness, divergence) and generalists (divergence) in the present study. Increased functional evenness reflects the efficiency of resource partitioning (Hillerbrand et al., 2008) and increased ecosystem functioning in structurally complex forest patches (Mason et al., 2005). These results emphasise the importance of structurally complex forest patches to allow more niches to be occupied by bird species and resource heterogeneity. Therefore, site-scale habitat destruction of forest systems will affect species diversity and the functionality of forests (Bogoni et al., 2020). Focusing on the total number of bird species without considering bird functional diversity or specific indices can lead to misleading forest management strategies because of the different responses of the diversity indices (Lelli et al., 2019; Matuoka et al., 2020).

3.5.3 Conclusions

Site scale structural and vegetation composition characteristics are important in maintaining high species richness and functional richness. Our study highlighted important local scale characteristics that can be managed to maintain bird species richness and forest specialists' occurrence. Tree species richness played an important role in maintaining high bird species richness, diversity and habitat use by forest specialists. Preserving local scale structural characteristics and promoting high tree species richness in the Midlands Mistbelt Forest will help maintain high species richness and diversity. This study indicated that forest-dependent bird species have distinct responses to vegetation composition and forest structural attributes. This indicates that management approaches that target community responses may not meet the requirement of vulnerable forest specialists. The importance of vegetation diversity and forest structural attributes varied between the forest bird species and diversity indices. Consideration of community and species-specific responses may improve conservation and biodiversity management. Our results suggest that the Bulwer Forest complex patches especially are important for the persistence of the remnant subpopulation of the endangered Cape parrot in the Midlands Mistbelt Forests of KwaZulu-Natal. Although these forest patches are protected and managed by Ezemvelo KwaZulu-Natal Wildlife (the government conservation parastatal) and the Department of Environment, Forest and Fisheries, they continue to be used by surrounding communities in the landscape mosaic, mainly for animal grazing, and these activities are not monitored (NB pers. obs.). It is important to implement sustainable use initiatives to ensure the conservation of Cape parrots in these forest patches. Our study confirmed that tree species richness should be maintained and is important in the conservation of forest specialists, bird species richness and functional richness. Assessing scale structural and vegetation characteristics is adequate for the management of forest patches at a local scale,

especially if they are privately owned (Gil-Tena et al., 2007). However, we still consider the need to explore the landscape characteristics further, especially to understand habitat selection by Cape parrots.

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3.8 Supplementary Information

Supplementary Information Table S3.1 Functional traits of the bird species by Hockey et al. (2005) in the present study.

Species name	Dietary guild							Foraging strategy						Nesting strategy			Habitat specificity			
	Body mass	Carnivory	Frugivory	Omnivory	Nectarivory	Granivory	Insectivory	Harvest	Terrestrial probe	Arboreal probe	Glean	Hawk	Perch and swoop	Various	Ground	Ball or cup	Cavity	Platform	Generalist	Specialists
<i>Andropadus importunus</i>	31	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Apalis flavida</i>	8	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Apalis thoracica</i>	10.5	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Apaloderma narina</i>	67	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1
<i>Aplopelia larvata</i>	150	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1
<i>Batis capensis</i>	12	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Bostrychia hagedash</i>	1250	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Bradypterus barratti</i>	15	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0
<i>Bucorvus leadbeateri</i>	3770	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Buteo trizonatus</i>	660	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
<i>Bycanistes bunicator</i>	644	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>Camaroptera brachyura</i>	11	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Campephaga flava</i>	32	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Campethera abingoni</i>	70	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1
<i>Campethera notata</i>	62	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1

<i>Centropus burchellii</i>	180	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Cercotrichas leucophrys</i>	17.9	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Chalcomitra amethystina</i>	15	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Chrysococcyx capreus</i>	35	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1
<i>Chrysococcyx caprius</i>	30	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Chrysococcyx klaas</i>	26	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Cinnyris chalybeus</i>	8	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Cisticola aberrans</i>	13	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Clamatar jacobinus</i>	81	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Coccygia melanotis</i>	6.5	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Colius striatus</i>	55	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Columba arquatrix</i>	407	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>Columba delegorguei</i>	160	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>Coracina caesia</i>	60	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Cossypha caffra</i>	28	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Cossypha dichroa</i>	46	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Cossypha natalensis</i>	32	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Crithagra scotops</i>	15	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Crithagra sulphurata</i>	17	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
<i>Cuculus clamosus</i>	90	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Cuculus solitarius</i>	75	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Cyanomitra olivacea</i>	11.5	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Dendropicos griseocephalus</i>	45	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1
<i>Dicrurus adsimilis</i>	43.75	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Dryoscopus cubla</i>	26	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Estrilda astrild</i>	8	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Guttera edouardii</i>	1300	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1

<i>Hedysdipna collaris</i>	8	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Indicator minor</i>	28	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0
<i>Indicator variegatus</i>	48	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1
<i>Ispidina picta</i>	15	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1
<i>Lagonostricta rhodopareia</i>	10.3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Laniarius ferrugineus</i>	60	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Lanius collaris</i>	40	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
<i>Lioptilus nigricapillus</i>	31	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Lophaetus occipitalis</i>	1055	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
<i>Lybius torquatus</i>	54	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
<i>Malaconotus blanchoti</i>	77	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Melaenornis pammelaina</i>	30	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0
<i>Muscicapa adusta</i>	11	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Muscicapa caerulescens</i>	16.5	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>Myioparus plumbeus</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Nectarinia fanosa</i>	15	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Numida meleagris</i>	1350	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Orious larvatus</i>	65	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Onychognathus morio</i>	140	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Parus niger</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0
<i>Phoeniculus purpureus</i>	76	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0
<i>Phyllastrephus terrestris</i>	31.5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Phylloscopus ruficapilla</i>	8	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Ploceous bicolor</i>	35	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Ploceous ocularis</i>	30	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Ploceus velatus</i>	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pogoniulus pusillus</i>	17	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0

<i>Pogonocichla stellata</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Poicephalus robustus</i>	300	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>Polemaetus bellicosus</i>	4000	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
<i>Prinia subflava</i>	9.5	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
<i>Pternistis natalensis</i>	445	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Pternistis afer</i>	640	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
<i>Pternistis swainsonii</i>	585	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Pycnonotus tricolor</i>	37.3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Sarothruta elegans</i>	45	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1
<i>Spermestes cucullata</i>	10	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Stephanoaetus coronatus</i>	3400	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1
<i>Streptopelia capicola</i>	150	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
<i>Streptopelia semitorquata</i>	235	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0
<i>Streptopelia senegalensis</i>	100	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Sylvietta rufescens</i>	11	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0
<i>Tauraco corythaix</i>	300	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>Telophorus olivaceus</i>	33	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Telophorus viridis</i>	37	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Terpsiphone viridis</i>	14.25	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Tockus alboterminatus</i>	225	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
<i>Treron calvus</i>	235	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
<i>Trochocercus cyanomelas</i>	10	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>Turdus olivaceus</i>	66	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Turtur tympanistria</i>	71	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Upupa africana</i>	53	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0
<i>Geokichla gurneyi</i>	68	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Zosterops virens</i>	13.5	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0

Supplementary Information Table S3.2 Generalised Linear Models (GLMs) top models output of the effects of tree species richness (TRic), structural complexity (SC), canopy cover (CC), water cover (WC) and leaf litter (LL) on bird species richness and functional diversity (Fric, FEve, FDiv) of avian communities of the Midlands Mistbelts forest patches in the breeding and non-breeding season in KwaZulu-Natal, South Africa. The models are ranked by increasing Δ AIC. Top models Δ AIC < 2 are in bolded.

Model	Explanatory variables	Significant variables (P-value)
Non Breeding		
Bird species Richness (Whole community)		
M0	TRIC+SC	TRIC (0.05); SC (0.00122**)
M1	TRIC+CC+SC	TRIC (0.02776*); SC (0.001***)
M2	SC	SC (2.83E-06***)
M3	CC*SC	SC (2.73E-06)
M4	TRIC+SC+WC	SC (0.00197***)
M5	WC*SC	WC (0.0810.); SC: WC (0.0608.)
M6	TRIC*SC	TRIC:SC (0.00572**)
M7	Global Model	TRIC (0.0280); SC (0.0021**)
M8	SC+CC	SC (2.76E-06***)
M9	SC+WC	SC (9.27e-07***)
M10	CC+SC+WC	SC (9.25E-06***)
M11	TRIC	TRIC (0.000181***)
M12	TRIC*WC	TRIC: WC (0.0658.)
M13	TRIC+CC	TRIC (4.93E-05***)
M14	TRIC+WC	TRIC (0.000343***)
M15	TRIC*CC	TRIC (0.000543***)
M16	Null Model	-
M17	WC	-
M18	CC	-
M19	CC+WC	-
M20	CC*WC	-
FRic (Whole community)		
M0	SC	-
M1	Null	-
M2	TRIC	-
M3	CC+SC	-
M4	TRIC+CC	-
M5	CC	-
M6	WC+SC	-
M7	TRIC+WC	-
M8	SC*CC	-
M9	TRIC+CC+SC	-
M10	TRIC*SC	-
M11	CC+SC+WC	-
M12	TRIC*CC	-
M14	TRIC+CC+WC	-
M15	CC+WC	-
M16	SC*WC	-
M17	TRIC*WC	-
M18	Global	-

M19	CC*WC	-
M20	SC*WC*CC	-
Forest specialists		
M0	TRIC*SC	TRIC:SC (0.0866.)
M1	SC	SC (2e-16***)
M2	TRIC+SC	SC (0.0394*)
M3	SC+WC	SC (0.0134*)
M4	SC+CC	SC (0.00989**)
M5	TRIC+CC+SC	SC (0.0414*)
M6	WC*SC	-
M7	CC*SC	SC (0.011*)
M8	CC+SC+WC	SC (0.0148*)
M9	TRIC	TRIC (0.0175*)
M10	Global Model	-
M11	TRIC*WC	-
M12	TRIC+WC	TRIC (0.0259)
M13	TRIC+CC	TRIC (0.0189*)
M14	TRIC+SC+WC	-
M15	TRIC*CC	TRIC (0.0194)
M16	Null Model	-
M17	WC	-
M18	CC*WC	-
M19	CC	-
M20	SC*WC*CC	-
	CC+WC	-
Forest generalists		
M0	SC+CC	-
M1	SC	-
M2	Null Model	-
M3	TRIC+CC	-
M4	CC*SC	-
M5	TRIC	-
M6	CC	-
M7	TRIC+CC+SC	-
M8	CC+SC+WC	-
M9	TRIC+SC	-
M10	WC	-
M11	SC+WC	-
M12	TRIC*SC	-
M13	TRIC*CC	-
M14	CC+WC	-
M15	TRIC+WC	-
M16	TRIC+SC+WC	-
M17	WC*SC	-
M18	Global Model	-
M19	TRIC*WC	-
M20	CC*WC	-
FEve (Whole community)		
M0	SC	-
M1	TRIC	-
M2	CC	-
M3	Global Model	-

M4	WC	-
M5	SC+CC	-
M6	SC+WC	-
M7	TRIC+CC	-
M8	TRIC+SC	-
M9	TRIC+WC	-
M10	CC+WC	-
M11	CC*SC	-
M12	TRIC*CC	-
M13	TRIC+CC+SC	-
M14	CC+SC+WC	-
M15	WC*SC	-
M16	TRIC+SC+WC	-
M17	TRIC*SC	-
M18	TRIC*WC	-
M19	CC*WC	-
M20	Null Model	-
Forest specialists		
M0	SC	SC (0.0254*)
M1	TRIC	-
M2	WC	-
M3	CC	-
M4	SC+CC	SC (0.0144*)
M5	SC+WC	SC (0.0196*)
M6	TRIC+SC+WC	SC (0.0158*)
M7	CC+SC+WC	SC (0.0428*)
M8	TRIC+SC	SC (0.0193*)
M9	TRIC+WC	-
M10	TRIC+CC	SC (0.0187*)
M11	CC+WC	-
M12	TRIC*SC	SC (0.0279*)
M13	Null Model	-
M14	WC*SC	SC (0.0250*)
M15	Global Model	SC (0.0119*)
M16	TRIC+CC+SC	SC (0.0174*)
M17	CC*SC	SC (0.0249*)
M18	TRIC*CC	-
M19	TRIC*WC	-
M20	CC*WC	-
Forest generalists		
M0	CC	CC (0.0127*)
M1	SC	-
M2	TRIC	-
M3	WC	-
M4	SC+CC	CC (0.0190*)
M5	TRIC+SC	-
M6	TRIC+CC	CC (0.0415*)
M7	SC+WC	-
M8	CC+WC	CC (0.0104*)
M9	TRIC+WC	-
M10	Null Model	-
M11	CC*SC	CC:SC (0.0413*)

M12	CC+SC+WC	-
M13	TRIC+CC+SC	CC (0.0136*)
M14	TRIC*SC	-
M15	TRIC*CC	CC (0.0203*)
M16	TRIC+SC+WC	-
M17	WC*SC	-
M18	CC*WC	CC (0.0397*)
M19	TRIC*WC	-
M20	Global Model	CC (0.0177*)
FDiv (Whole community)		
M0	Null Model	
M1	TRIC	-
M2	SC	-
M3	WC	-
M4	CC	
M5	TRIC+SC	-
M6	TRIC+CC	-
M7	TRIC+WC	-
M8	CC+WC	-
M9	SC+CC	-
M10	SC+WC	-
M11	TRIC*CC	-
M12	TRIC+CC+SC	-
M13	TRIC*WC	-
M14	TRIC*SC	-
M15	CC*SC	-
M16	TRIC+SC+WC	-
M17	CC*WC	-
M18	WC*SC	-
M19	CC+SC+WC	-
M20	Global Model	
Forest specialists		
M0	SC	SC (0.00039***)
M1	TRIC	-
M2	CC	-
M3	WC	-
M4	Null Model	-
M5	SC+CC	SC (0.00046***)
M6	SC+WC	-
M7	TRIC+SC	SC (0.00047***)
M8	TRIC+CC	-
M9	TRIC+WC	-
M10	CC+WC	-
M11	CC*SC	SC (0.00019***)
M12	TRIC+CC+SC	SC (0.00034***)
M13	TRIC*SC	SC (0.00017***)
M14	CC+SC+WC	SC (0.00022***)
M15	WC*SC	-
M16	TRIC*CC	-
M17	TRIC+SC+WC	SC (0.00051***)
M18	TRIC*WC	-
M19	CC*WC	-

M20	Global Model	SC (0.00012***)
Forest generalists		
M0	SC	-
M1	CC	CC (0.0010**)
M2	WC	-
M4	TRIC	-
M5	SC+CC	CC (0.0031**)
M6	TRIC+CC	CC (0.0014**)
M7	TRIC+SC	-
M8	SC+WC	-
M9	TRIC+WC	-
M10	TRIC+CC+SC	CC (0.00174**)
M11	CC+SC+WC	CC (0.0011**)
M12	TRIC*CC	-
M13	CC*SC	CC:SC (0.0013**)
M15	TRIC*SC	-
M16	CC*WC	-
M17	WC*SC	-
M18	TRIC+SC+WC	-
M19	TRIC*WC	-
M20	Global Model	CC (0.00321**)
Breeding		
Bird species richness		
M0	TRIC	TRIC (2.91E-06***)
M1	TRIC+CC	TRIC (8.86E-07***)
M2	TRIC*CC	TRIC (1.65E-05***)
M3	TRIC*LL	TRIC (0.08221.); TRIC:LL (0.00658**)
M4	TRIC+CC+SC	TRIC (1.77e-05***)
M5	TRIC+SC	TRIC (2e-16***)
M6	TRIC+LL	TRIC (3.89E-05***)
M7	TRIC+SC+LL	TRIC (0.00157**)
M8	TRIC*SC	TRIC (2.65e-05***)
M9	Global Model	TRIC (0.00048***)
M10	SC+LL	SC (0.0219*); LL (0.0365*)
M11	CC*SC	CC:SC (0.0465*)
M12	CC+SC+LL	SC (0.0172*); LL (0.0664.)
M13	SC	SC (0.0663.)
M14	LL*SC	LL (0.0361*); SC (0.0410)
M15	LL	-
M16	SC+CC	SC (0.0376*)
M17	Null Model	
M18	CC	-
M19	CC+LL	-
M20	CC*LL	LL (0.0996)
Fric (Whole community)		
M0	TRIC	-
M1	LL	-
M2	CC	-
M3	SC	-
M4	Null Model	-
M5	TRIC+SC	-
M6	TRIC+CC	-

M7	TRIC+LL	
M8	CC+LL	-
M9	SC+LL	-
M10	SC+CC	-
M11	TRIC+CC+SC	-
M12	TRIC*SC	-
M13	TRIC*CC	-
M14	TRIC*LL	-
M15	TRIC+SC+LL	-
M16	CC*SC	-
M17	CC+SC+LL	-
M18	CC*LL	-
M19	LL*SC	-
M20	Global Model	-
Forest specialists		
M0	TRIC	-
M2	LL	-
M3	TRIC+LL	-
M4	TRIC+SC	-
M5	TRIC+CC	-
M6	SC	-
M7	CC	-
M8	TRIC*LL	-
M9	SC+LL	-
M10	CC+LL	-
M11	TRIC+SC+LL	-
M12	TRIC*SC	-
M13	TRIC+CC+SC	-
M14	TRIC*CC	-
M15	SC+CC	-
M16	CC*SC	-
M17	CC+SC+LL	-
M18	LL*SC	-
M19	CC*LL	-
M20	Global Model	-
Forest generalists		
M0	TRIC	
M1	LL	
M2	CC	
M3	SC	
M4	TRIC*CC	
M5	TRIC+CC	
M6	TRIC+SC	
M7	TRIC+LL	
M8	CC+LL	
M9	SC+LL	
M10	SC+CC	
M11	TRIC+CC+SC	
M12	TRIC*SC	
M13	TRIC+SC+LL	
M14	TRIC*LL	
M15	Null Model	

M16	CC*SC	
M17	CC+SC+LL	
M18	CC*LL	
M19	LL*SC	
M20	Global Model	
FEve		
Whole community		
M0	TRIC	-
M1	SC	-
M2	LL	-
M3	CC	-
M4	Null Model	-
M5	TRIC+CC	-
M6	TRIC+LL	-
M7	TRIC+SC	-
M8	SC+LL	-
M9	CC+LL	-
M10	SC+CC	-
M11	TRIC*LL	-
M12	TRIC*SC	-
M13	TRIC+CC+SC	-
M14	TRIC+SC+LL	-
M15	TRIC*CC	-
M16	LL*SC	-
M17	CC+SC+LL	-
M18	CC*SC	-
M19	CC*LL	-
M20	Global Model	-
Forest specialists		
M0	TRIC	TRIC (0.0239*)
M1	LL	-
M2	CC	-
M3	SC	-
M4	SC+LL	-
M5	TRIC+CC	TRIC (0.032*)
M6	TRIC+LL	TRIC (0.0327*)
M7	TRIC+SC	TRIC (0.0349*)
M8	CC+LL	-
M9	SC+CC	-
M10	TRIC*LL	TRIC (0.0635.)
M11	CC*SC	-
M12	TRIC*CC	TRIC (0.0261*)
M13	TRIC+CC+SC	TRIC (0.0253*)
M14	TRIC*SC	TRIC (0.0409*)
M15	TRIC+SC+LL	TRIC (0.0425*)
M16	CC+SC+LL	-
M17	LL*SC	-
M18	CC*LL	-
M19	Null Model	
M20	Global Model	TRIC (0.0259*)
Forest generalists		
M0	TRIC	TRIC (0.00045***)

M1	SC	
M2	LL	LL (0.00052***)
M3	CC	
M4	Null Model	
M5	TRIC+LL	LL (0.00042***)
M6	TRIC+CC	TRIC (0.00062***)
M7	TRIC+SC	TRIC (0.00030**)
M8	SC+CC	
M9	SC+LL	LL (0.00016***)
M10	CC+LL	LL (0.0009***)
M11	TRIC+CC+SC	TRIC (0.00081***)
M12	TRIC*CC	TRIC (0.00069***)
M13	TRIC*LL	TRIC:LL (0.00012***)
M14	TRIC*SC	
M15	CC*SC	CC (0.0045**)
M16	CC*LL	LL:CC (0.00021***)
M17	LL*SC	LL (0.0009***8)
M18	CC+SC+LL	LL (0.00033***); CC (0.0014**)
M19	TRIC+SC+LL	LL (0.00061***)
M20	Global Model	TRIC (0.00042***); LL (0.00015***)
FDiv		
Whole community		
M0	TRIC	-
M1	CC	-
M2	LL	-
M3	SC	-
M4	TRIC+SC	-
M5	TRIC+CC	-
M6	SC+CC	-
M7	SC+LL	-
M8	CC+LL	-
M9	TRIC+LL	-
M10	LL*SC	-
M11	TRIC*CC	-
M12	TRIC*LL	-
M13	TRIC*SC	-
M14	CC*LL	-
M15	CC*SC	-
M16	TRIC+CC+SC	-
M17	TRIC+SC+LL	-
M18	CC+SC+LL	-
M19	Null Model	-
M20	Global Model	-
Forest specialists		
M1	TRIC	TRIC (0.00136**)
M2	SC	SC (0.0156*)
M3	LL	-
M4	CC+LL	-
M5	TRIC+CC	TRIC (0.0064**)
M6	TRIC+SC	TRIC (0.0023**); SC (0.0340*)
M7	TRIC+LL	
M8	SC+CC	SC (0.0145*)

M9	SC+LL	SC (0.0134*)
M10	TRIC*SC	TRIC (0.00321**)
M11	Null Model	-
M12	TRIC*CC	TRIC (0.0045**)
M13	TRIC*LL	TRIC (0.0045**)
M14	TRIC+CC+SC	SC (0.0437*)
M15	CC*LL	-
M16	CC*SC	-
M17	CC+SC+LL	SC (0.0183*)
M18	TRIC+SC+LL	TRIC (0.0018**); SC (0.0414*)
M19	LL*SC	-
M20	Global Model	TRIC (0.0071**); SC (0.0304*)
Forest generalists		
M0	TRIC	-
M1	SC	SC (0.0169*)
M2	CC	-
M3	LL	-
M4	SC+CC	SC (0.0243*)
M5	SC+LL	SC (0.0268*)
M6	TRIC+CC	-
M7	TRIC+SC	SC (0.0416*)
M8	CC+LL	-
M9	TRIC+LL	-
M10	TRIC*CC	-
M11	CC*SC	SC (0.0413*)
M12	CC+SC+LL	SC (0.0119*)
M13	CC*LL	-
M14	TRIC*SC	SC (0.0167*)
M15	TRIC+CC+SC	SC (0.0149*)
M16	LL*SC	SC (0.0128*)
M17	TRIC+SC+LL	SC (0.04218)
M18	TRIC*LL	-
M19	Global Model	SC (0.0314*)
M20	Null Model	-

Supplementary Information Table S3.3 Tree species in 14 selected Mistbelt Forest patches of the Midlands of KwaZulu-Natal, South Africa.

Family	Scientific name	Common name
Anacardiaceae	<i>Searsia chirindensis</i>	Red currant
Apocynaceae	<i>Carissa bispinosa</i>	Num-num
	<i>Strophanthus speciosus</i>	Forest poison-rope
Aquifoliaceae	<i>Ilex mitis</i>	Cape holly
Araliaceae	<i>Cussonia sphaerocephala</i>	Forest cabbage-tree
Buddlejaceae	<i>Nuxia floribunda</i>	Forest-elder
	<i>Elaeodendron croceum</i> ^D	Common saffron
	<i>Gymnosporia harveyana</i>	Round-fruit forest spikethorn
Celastraceae	<i>Pterocelastrus rostratus</i> ^D	Red candlewood
	<i>Salacia gerrardii</i>	Forest lemon-rope
	<i>Celtis africana</i>	White-stinkwood
Celtidaceae	<i>Trema orientalis</i>	Pigeonwood
	<i>Trimeria grandifolia</i>	Wild-mulberry
Combretaceae	<i>Combretum edwardsii</i>	Forest climbing bushwillow
Connaraceae	<i>Cnestis polyphylla</i>	Itch-pod
Ebenaceae	<i>Diospyros whyteana</i>	Bladder-nut
	<i>Drypetes gerrardii</i>	Forest ironplum
Euphorbiaceae	<i>Micrococca capensis</i>	False bead-string
	<i>Calpurnia aurea</i>	Wild laburnum
Fabaceae	<i>Dalbergia obovata</i>	Climbing flat-bean
	<i>Dovyalis lucida</i>	Glossy Kei-apple
	<i>Dovyalis rhamnoides</i>	Sourberry Kei-apple
Flacourtiaceae	<i>Kiggelaria africana</i>	Wild-peach
	<i>Scolopia flanaganii</i>	Kei thorn-pear
	<i>Scolopia mundii</i>	Red thorn-pear
	<i>Scolopia zeyheri</i>	Thorn-pear
Icacinaceae	<i>Apodytes dimidiata</i>	White-pear
	<i>Cassinopsis illicifolia</i>	Lemon-thorn
Lamiaceae	<i>Clerodendrum glabrum</i>	Cats-whiskers
	<i>Cryptocarya mrtifolia</i> ^V	Myrtle wild-quince
Lauraceae	<i>Cryptocarya woodii</i> ^D	River wild-quince
	<i>Ocotea bullatta</i> ^E	Stinkwood
Meliaceae	<i>Ekebergia capensis</i>	Cape-ash
	<i>Trichilia dregeana</i>	Forest Natal mahogany
Monimiaceae	<i>Xymalos monospora</i>	Lemonwood
Moraceae	<i>Ficus craterostoma</i>	Forest fig
Myrsinaceae	<i>Rapanea melanophloes</i> ^D	Cape-beech
Myrtaceae	<i>Eugenia zuluensis</i>	Paperbark myrtle
	<i>Syzigium gerrardii</i>	Forest umdoni
Ochnaceae	<i>Ochna arborea</i>	-

	<i>Chionanthus foveolatus</i>	Pock-ironwood
Oleaceae	<i>Chionanthus pelglerae</i>	Giant pock-ironwood
	<i>Olea capensis</i>	Ironwood
Pittosporaceae	<i>Pittosporum viridiflorum</i> ^P	Cheesewood
	<i>Afrocarpus falcatus</i> ^P	Common yellowwood
Podocarpaceae	<i>Podocarpus henkelii</i> ^P	Dropping-leaf yellowwood
	<i>Podocarpus latifolia</i> ^P	Broad-leaf yellowwood
Ptaeroxylaceae	<i>Ptaeroxylon obliquum</i>	Sneezewood
Rhamnaceae	<i>Scutia myrtina</i>	Cat-thorn
	<i>Cassipourea gummiflua</i> ^V	Large-leaf onionwood
Rhizophoraceae	<i>Cassipourea malosana</i> ^D	Onionwood
Rosaceae	<i>Prunus africana</i> ^V	Red-stinkwood
	<i>Canthium ciliatum</i>	Hairy turkey-berry
	<i>Canthium kuntzeanum</i>	Mountain turkey-berry
Rubiaceae	<i>Hypecanthus amoenus</i>	Spiny-gardenia
	<i>Tricalysia lanceolata</i> ^E	Jackal-cofee
	<i>Calodendrum capense</i>	Cape-chestnut
	<i>Clausena anisata</i>	Horsewood
Rutaceae	<i>Vepris lanceolata</i>	White-ironwood
	<i>Zanthoxylum capense</i>	Small knobwood
	<i>Zanthoxylum dayvi</i>	Forest knobwood
	<i>Allophylus africanus</i>	African false-currant
Sapindaceae	<i>Allophylus dregeanus</i>	Simple-leaf False-currant
Scrophulariaceae	<i>Halleria lucida</i>	Tree fuchsia
	<i>Solanum giganteum</i>	Healing-leaf tree
Solanaceae	* <i>Solanum mauritianum</i>	Bugweed
	<i>Dais cotinifolia</i>	Pompon tree
Thymeleaceae	<i>Peddiea africana</i>	Poison-olive

*Alien invasive

^DDeclining

^EEndangered

^PProtected

^VVulnerable

Supplementary Information Table S3.4 Tree species presence and absence in selected forest 14 patches in the Midlands of KwaZulu-Natal, South Africa.

Region Tree species	Forest Patch													
	Karkloof				Balgowan		Dargle			Bulwer				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Searsia chirindensis</i>	✓	✓	-	-	-	-	-	-	-	-	✓	-	-	-
<i>Carissa bispinosa</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	✓	✓	✓	✓
<i>Strophanthus speciosus</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	-	✓
<i>Ilex mitis</i>	✓	✓	-	✓	-	-	-	-	-	-	-	-	-	-
<i>Cussonia sphaerocephala</i>	✓	✓	✓	✓	-	-	✓	-	-	-	✓	✓	✓	✓
<i>Nuxia floribunda</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Elaeodendron croceum</i> ^D	✓	✓	✓	✓	✓	✓	-	-	-	-	✓	-	✓	✓
<i>Gymnosporia harveyana</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
<i>Pterocelastrus rostratus</i> ^D	-	-	-	-	-	-	-	-	-	-	✓	-	-	✓
<i>Salacia gerrardii</i>	✓	✓	✓	✓	✓	✓	✓	-	-	-	-	✓	✓	✓
<i>Celtis africana</i>	✓	✓	✓	✓	-	-	✓	-	-	-	✓	✓	✓	✓
<i>Trema orientalis</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trimeria grandifolia</i>	✓	✓	✓	✓	✓	✓	-	-	✓	-	✓	✓	✓	✓
<i>Combretum edwardsii</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Cnestis polyphylla</i>	✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-
<i>Diospyros whyteana</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	✓	✓	✓	✓
<i>Drypetes gerrardii</i>	-	✓	-	-	✓	✓	✓	✓	-	-	✓	-	✓	-
<i>Micrococca capensis</i>	✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-
<i>Calpurnia aurea</i>	✓	✓	✓	✓	-	-	-	-	-	-	✓	✓	✓	✓
<i>Dalbergia obovata</i>	✓	✓	✓	-	-	-	-	-	-	-	-	-	-	-
<i>Dovyalis lucida</i>	✓	✓	-	-	-	-	-	-	-	-	✓	-	-	-
<i>Dovyalis rhamnoides</i>	✓	✓	-	-	-	-	-	-	-	-	✓	-	✓	-
<i>Kiggelaria africana</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	✓	✓	✓	✓
<i>Scolopia flanaganii</i>	✓	✓	-	-	✓	✓	-	-	-	-	✓	-	-	✓
<i>Scolopia mundii</i>	-	-	-	-	-	-	-	-	-	-	-	-	✓	✓
<i>Scolopia zeyheri</i>	✓	✓	-	-	✓	✓	✓	✓	-	-	✓	✓	✓	-
<i>Apodytes dimidiata</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	-
<i>Cassinopsis illicifolia</i>	✓	✓	✓	✓	✓	✓	✓	-	-	-	-	✓	✓	-
<i>Clerodendrum glabrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Cryptocarya mrtifolia</i> ^V	✓	✓	-	✓	-	-	-	-	-	-	-	-	-	-
<i>Cryptocarya woodii</i> ^D	✓	✓	✓	✓	✓	✓	✓	-	✓	✓	✓	✓	✓	-
<i>Ocotea bullatta</i> ^E	✓	-	-	-	-	✓	-	-	-	-	-	-	✓	-
<i>Ekebergia capensis</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trichilia dregeana</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xymalos monospora</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	-	✓	✓	✓
<i>Ficus craterostoma</i>	✓	✓	✓	✓	✓	✓	✓	-	-	-	✓	-	✓	-
<i>Rapanea melanophloes</i> ^D	✓	✓	✓	✓	✓	✓	✓	✓	-	-	-	-	✓	✓
<i>Eugenia zuluensis</i>	✓	✓	✓	✓	✓	✓	✓	-	✓	✓	✓	✓	✓	✓
<i>Syzigium gerrardii</i>	✓	✓	✓	✓	-	-	-	-	-	-	-	-	-	-
<i>Ochna arborea</i>	✓	✓	✓	✓	-	-	-	✓	-	-	-	-	✓	-
<i>Chionanthus foveolatus</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	-
<i>Chionanthus pelglerae</i>	-	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Olea capensis</i>	✓	✓	-	-	-	-	✓	-	-	-	-	-	-	-

<i>Pittosporum viridiflorum</i> ^P	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	✓
<i>Afrocarpus falcatus</i> ^P	✓	✓	✓	✓	✓	✓	✓	✓	✓	-	✓	✓	✓	✓
<i>Podocarpus henkelii</i> ^P	✓	✓	✓	-	✓	✓	✓	-	-	-	✓	✓	✓	✓
<i>Podocarpus latifolia</i> ^P	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	-
<i>Ptaeroxylon obliquum</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	✓	✓	✓	✓
<i>Scutia myrtina</i>	✓	✓	-	-	✓	✓	-	✓	-	-	-	-	✓	✓
<i>Cassipourea gummiflua</i> ^V	-	✓	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassipourea malosana</i> ^D	✓	✓	-	-	-	-	✓	-	-	-	-	-	-	-
<i>Prunus africana</i> ^V	✓	✓	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Canthium ciliatum</i>	-	✓	-	-	-	-	-	-	-	-	-	✓	✓	-
<i>Canthium kuntzeanum</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	✓
<i>Hypecanthus amoenus</i>	✓	✓	✓	✓	-	-	-	-	-	-	-	✓	-	✓
<i>Tricalysia lanceolata</i> ^E	-	✓	✓	✓	-	-	-	-	-	-	-	-	-	-
<i>Calodendrum capense</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	-	-	✓	✓
<i>Clausena anisata</i>	✓	✓	✓	✓	-	-	✓	-	-	-	✓	-	✓	✓
<i>Vepris lanceolata</i>	-	✓	✓	✓	-	-	-	-	-	-	-	-	-	-
<i>Zanthoxylum capense</i>	✓	✓	✓	✓	-	-	-	✓	-	-	✓	✓	✓	✓
<i>Zanthoxylum dayvi</i>	✓	✓	-	-	-	-	✓	-	-	-	-	-	✓	✓
<i>Allophylus africanus</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Allophylus dregeanus</i>	-	✓	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Halleria lucida</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	-	✓	✓
<i>Solanum giganteum</i>	-	✓	-	✓	-	-	-	-	-	-	-	-	-	-
* <i>Solanum mauritianum</i>	✓	✓	✓	✓	✓	✓	✓	✓	-	-	-	✓	✓	✓
<i>Dais cotinifolia</i>	✓	✓	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Peddiea africana</i>	-	-	-	-	✓	-	-	-	-	-	-	-	-	-
Species richness	52	59	33	32	24	25	27	18	7	5	30	22	41	30

1= Karkloof Nature Reserve, 2 = Mbona Private Nature Reserve, 3 = L'Abri, 4= Benvie Farm, 5 = Rameron, 6 = Milestone Forest Walk, 7 = Maritzdaal, 8 = Sharedown Forest, 9 = Wakefield Forest, 10=Waterfall Forest, 11 = Ingelabantwana Nature Reserve, 12 = Xotsheyake Nature Reserve, 13 = Marutswa Nature Reserve, 14 = Nxumeni Forest

*Alien invasive

^D Declining

^E Endangered

^P Protected

^V Vulnerable

Supplementary Information Table S3.5 Bird species recorded and seasonal counts in 14 selected Mistbelt Forest patches of the Midlands of KwaZulu-Natal, South Africa

Family	Scientific name	Breeding season (n)	Non-breeding season (n)	
Accipitridae	<i>Buteo trizonatus</i> ^{NT}	10	0	
	<i>Lophaetus occipitalis</i>	16	27	
	<i>Polemaetus bellicosus</i> ^{E;V}	0	3	
	<i>Stephanoaetus coronatus</i>	5	0	
Alcedinidae	<i>Ispidina picta</i>	3	0	
Bucerotidae	<i>Bycanistes bunicator</i>	28	7	
	<i>Tockus alboteerminatus</i> ^{V;NT}	4	8	
Bucorvidae	<i>Bucorvus leadbeateri</i> ^{E;V}	10	14	
Campephagidae	<i>Campephaga flava</i>	8	7	
	<i>Coracina caesia</i>	89	71	
Cisticolidae	<i>Apalis flavida</i>	37	7	
	<i>Apalis thoracica</i>	487	328	
	<i>Camaroptera brachyura</i>	423	253	
	<i>Cisticola aberrans</i>	2	0	
	<i>Prinia subflava</i>	46	61	
Coliidae	<i>Colius striatus</i>	18	48	
Columbidae	<i>Aplopelia larvata</i>	79	75	
	<i>Columba arquatrix</i>	231	117	
	<i>Columba delegorguei</i> ^E	5	0	
	<i>Streptopelia capicola</i>	51	38	
	<i>Streptopelia semitorquata</i>	96	124	
	<i>Streptopelia senegalensis</i>	4	2	
	<i>Treron calvus</i>	2	0	
	<i>Turtur tympanistria</i>	12	6	
	<i>Centropus burchellii</i>	2	0	
Cuculidae	<i>Chrysococcyx capreus</i>	90	1	
	<i>Chrysococcyx caprius</i>	13	0	
	<i>Chrysococcyx klaas</i>	2	0	
	<i>Clamatar jacobinus</i>	7	0	
	<i>Dicrurus adsimilis</i>	91	73	
	<i>Cuculus clamosus</i>	41	0	
	<i>Cuculus solitarius</i>	196	0	
	Estrelidae	<i>Coccygia melanotis</i>	1	1
		<i>Estrilda astrild</i>	0	24
<i>Lagonosticta rhodopareia</i>		39	246	
<i>Spermestes cucullata</i>		6	3	
Fringillidae	<i>Crithagra scotops</i>	30	16	
	<i>Crithagra sulphurata</i>	3	0	
Indicatoridae	<i>Indicator minor</i>	7	0	

	<i>Indicator variegatus</i>	13	0
Laniidae	<i>Lanius collaris</i>	0	1
Locustellidae	<i>Bradypterus barratti</i>	20	28
Lybiidae	<i>Pogoniulus pusillus</i>	1	0
	<i>Lybius torquatus</i>	0	1
Macrosphenidae	<i>Sylvietta rufescens</i>	1	0
Malaconotidae	<i>Dryoscopus cubla</i>	84	11
	<i>Laniarius ferrugineus</i>	657	656
	<i>Malaconotus blanchoti</i>	3	0
	<i>Telophorus olivaceus</i>	86	70
	<i>Telophorus viridis</i>	2	0
Mornachidae	<i>Trochocercus cyanomelas</i>	80	55
	<i>Terpsiphone viridis</i>	44	12
Muscicapidae	<i>Cercotrichas leucophrys</i>	5	5
	<i>Cossypha caffra</i>	86	113
	<i>Cossypha dichroa</i>	144	10
	<i>Cossypha natalensis</i>	8	14
	<i>Melaenornis pammelaina</i>	1	0
	<i>Muscicapa adusta</i>	46	10
	<i>Muscicapa caerulescens</i>	6	0
	<i>Myioparus plumbeus</i>	5	0
	<i>Pogonocichla stellata</i>	76	10
	<i>Tauraco corythaix</i>	183	245
Oriolidae	<i>Oriolus larvatus</i>	190	73
Nectariniidae	<i>Cinnyris chalybeus</i>	271	538
	<i>Chalcomitra amethystina</i>	87	5
	<i>Cyanomitra olivacea</i>	22	0
	<i>Hedysdipna collaris</i>	153	47
	<i>Nectarinia fanosa</i>	9	0
Numididae	<i>Guttera edouardii</i>	103	67
	<i>Numida meleagris</i>	25	10
Paridae	<i>Parus niger</i>	3	0
Phasianidae	<i>Pternistis natalensis</i>	5	0
	<i>Pternistsis afer</i>	28	16
	<i>Pternistsis swainsonii</i>	17	0
Phoeniculidae	<i>Phoeniculus purpureus</i>	24	8
Phylloscopidae	<i>Phylloscopus ruficapilla</i>	102	0
Picidae	<i>Campethera abingoni</i>	7	0
	<i>Campethera notata</i> ^{NT}	4	46
	<i>Dendropicos griseocephalus</i>	56	78
Platysteiridae	<i>Batis capensis</i>	191	140
Ploceidae	<i>Ploceous bicolor</i>	65	40
	<i>Ploceous ocularis</i>	1	3
	<i>Ploceus velatus</i>	1	2

Psittacidae	<i>Poicephalus robustus</i> ^{E;V}	40	95
Pycnonotidae	<i>Andropadus importunus</i>	557	327
	<i>Phyllastrephus terrestris</i>	192	374
	<i>Pycnonotus tricolor</i>	127	475
	<i>Sarothruta elegans</i>	49	7
Slyviidae	<i>Lioptilus nigricapillus</i> ^V	14	12
Strurndiae	<i>Onychognathus morio</i>	0	27
Threskiornithidae	<i>Bostrychia hagedash</i>	284	316
Trogonidae	<i>Apaloderma narina</i>	84	6
Turdidae	<i>Turdus olivaceous</i>	42	20
	<i>Geokichla gurneyi</i> ^{NT}	57	50
Upupidae	<i>Upupa africana</i>	4	0
Zosteropidae	<i>Zosterops virens</i>	373	420

^E Endangered

^{NT} Near-threatened

^V Vulnerable

Supplementary Information Table S3.6 Indicator bird species for selected Southern Mistbelt forest patches of sizes 200-500 and >500 ha in the Midlands of KwaZulu-Natal, South Africa.

Forest patch size (ha)	Bird species	Habitat specificity	Stat	p-value
>200-500	<i>Bucorvus leadbeateri</i>	Generalist	0.827	0.04
>500	<i>Trochocercus cyanomela</i>	Specialist	0.930	0.001
	<i>Prinia subflava</i>	Generalist	0.926	0.001
	<i>Tauraco corythaix</i>	Specialist	0.918	0.001
	<i>Pycnonotus tricolor</i>	Generalist	0.910	0.01
	<i>Cossypha caffra</i>	Generalist	0.906	0.01
	<i>Phyllastrephus terrestris</i>	Generalist	0.905	0.01
	<i>Cinnyris chalbeus</i>	Generalist	0.899	0.001
	<i>Ploceus bicolor</i>	Specialist	0.893	0.001
	<i>Apalis flavida</i>	Generalist	0.888	0.01
	<i>Camaroptera brachyura</i>	Specialist	0.875	0.01
	<i>Laniarius ferrugineus</i>	Generalist	0.870	0.01
	<i>Batis capensis</i>	Specialist	0.869	0.01
	<i>Chlorophoneus olivaceus</i>	Specialist	0.865	0.001
	<i>Andropadus importunus</i>	Generalist	0.858	0.01
	<i>Dendropicos griseocephalus</i>	Specialist	0.855	0.001
	<i>Cossypha natalensis</i>	Specialist	0.850	0.01
	<i>Bradypterus barratti</i>	Generalist	0.837	0.02
	<i>Apalis thoracica</i>	Specialist	0.833	0.01
	<i>Lophaetus occipitalis</i>	Generalist	0.820	0.01
	<i>Chalcomitra amethystina</i>	Generalist	0.819	0.01
	<i>Zosterops capensis</i>	Generalist	0.817	0.01
	<i>Oriolus larvatus</i>	Generalist	0.813	0.01
	<i>Coracina caesia</i>	Specialist	0.810	0.001
	<i>Hedypina collaris</i>	Specialist	0.804	0.01
	<i>Chrysococcyx cupreus</i>	Specialist	0.784	0.01
	<i>Upupa africana</i>	Generalist	0.775	0.04
	<i>Columba larvata</i>	Specialist	0.767	0.01
	<i>Pogonocichla stellata</i>	Specialist	0.759	0.01
	<i>Dicrucus admilis</i>	Generalist	0.755	0.03
	<i>Cuculus solitarius</i>	Specialist	0.748	0.01
	<i>Apaloderma narina</i>	Specialist	0.735	0.02
	<i>Cyanomitra olivacea</i>	Specialist	0.732	0.03
	<i>Campephaga flava</i>	Generalist	0.721	0.04
	<i>Geokichla gurneyi</i>	Specialist	0.718	0.04
	<i>Dryoscopus cubla</i>	Generalist	0.718	0.02
	<i>Cossypha dichroa</i>	Specialist	0.702	0.03
	<i>Terpsiphone viridis</i>	Specialist	0.687	0.03
	<i>Chrysococcyx caprius</i>	Generalist	0.668	0.04
	<i>Sarothrura elegans</i>	Specialist	0.663	0.04
	<i>Phylloscopus ruficapilla</i>	Specialist	0.661	0.03

Supplementary Information Table S3.7 Modelled-averaged coefficients for the GLM top models of the effects of tree species richness (TRic), structural complexity (SC), canopy cover (CC), water cover (WC) and leaf litter (LL) on bird species richness and functional diversity (Fric, FEve, FDiv) of avian communities of the Midlands Mistbelts forest patches in the breeding and non-breeding season in KwaZulu-Natal, South Africa.

Non-breeding					
Response	Variable	Estimate	Std error	z-value	p-value
Bird species richness	Tree species richness	0.165	0.056	2.985	0.0028
	Structural complexity	0.286	0.064	5.667	5.16e-06
	Canopy cover	-0.064	0.021	1.092	0.232
	Water cover	0.014	0.004	0.383	0.651
FRic (All)	Structural complexity	0.163	0.012	1.434	0.155
	Tree species richness	0.142	0.010	1.300	0.114
	Canopy cover	-0.053	0.011	0.839	0.394
FRic (Specialists)	Tree species richness	0.245	0.173	1.376	0.019
	Structural complexity	0.523	0.290	1.653	0.036
Fric (Generalists)	Structural complexity	0.264	0.192	1.384	0.178
	Canopy cover	-0.246	0.169	1.438	0.155
	Tree species richness	0.1883	0.1629	1.165	0.260
	Water cover	-0.047	0.143	0.328	0.743
	Structural complexity	-0.144	0.048	0.354	0.726
FEve (All)	Tree species richness	0.119	0.052	0.143	0.882
	Canopy cover	0.081	0.044	0.120	0.867
	Water cover	-0.033	0.045	0.071	0.948
	Structural complexity	0.596	0.299	0.102	0.014
FEve (Specialists)	Tree species richness	0.157	0.055	0.342	0.730
	Water cover	1.295	0.126	0.173	0.863
	Canopy cover	-0.115	0.046	0.249	0.804
	Canopy cover	-0.152	0.041	0.126	0.008
	Structural complexity	-0.102	0.038	0.265	0.790
FEve (Generalists)	Tree species richness	-0.166	0.424	0.392	0.695
	Water cover	-1.819	0.206	0.093	0.926
	Tree species richness	-0.038	0.304	0.124	0.901
	Structural complexity	0.403	0.286	0.610	0.042
FDiv (All)	Tree species richness	0.150	0.130	0.401	0.313
	Canopy Cover	-0.125	0.030	0.210	0.068
	Water cover	-2.625	1.463	0.351	0.844
	Structural complexity	0.223	0.166	0.544	0.654
FDiv (Specialists)	Canopy Cover	-0.231	0.131	0.519	0.001
	Water cover	0.035	0.037	0.153	0.944
	Tree species richness	0.135	0.091	0.274	0.788
Breeding					
Response	Variable				
Bird species richness	Tree species richness	0.261	0.052	4.337	4.24e-05
	Canopy cover	0.079	0.063	1.264	0.226
	Leaf Litter	0.031	0.067	0.413	0.737
	Structural complexity	0.052	0.035	0.733	0.435
Fric(All)	Tree species richness	0.179	0.108	0.727	0.467
	Leaf Litter	-0.016	0.010	0.150	0.882

	Canopy cover	0.115	0.104	0.148	0.882
	Structural complexity	0.121	0.111	0.171	0.866
Forest specialists	Tree species richness	0.167	0.137	1.385	0.190
	Structural complexity	-0.177	0.144	0.534	0.594
	Canopy cover	-0.109	0.130	0.070	0.944
	Leaf litter	-0.501	0.133	0.513	0.619
Forest generalists	Tree species richness	0.153	0.134	0.740	0.256
	Canopy cover	0.276	0.212	0.528	0.598
	Leaf litter	-0.044	1.343	0.291	0.777
	Structural complexity	-0.141	0.140	0.270	0.793
FEve (All)	Tree species richness	0.139	0.447	0.311	0.756
	Canopy cover	0.167	0.107	0.040	0.968
	Leaf Litter	0.135	0.132	0.086	0.932
	Structural complexity	-0.133	0.160	0.082	0.935
Forest specialists	Tree species richness	0.417	0.008	0.024	0.004
	Leaf litter	0.041	0.015	0.090	0.999
	Canopy cover	0.101	0.015	0.002	0.929
	Structural complexity	0.109	0.130	0.024	0.981
Forest generalists	Structural complexity	0.216	0.031	0.135	0.001
	Tree species richness	0.112	0.135	0.054	0.210
	Leaf litter	0.123	0.021	0.192	0.801
	Canopy cover	2.124	1.114	0.168	0.621
FDiv (All)	Tree species richness	1.014	0.320	0.044	0.965
	Structural complexity	-1.014	0.302	0.042	0.966
	Canopy cover	-1.010	0.308	0.034	0.972
	Leaf Litter	-1.015	0.321	0.045	0.964
Forest specialists	Tree species richness	0.160	0.029	0.054	0.002
	Leaf litter	-1.010	0.293	0.036	0.971
	Canopy cover	-1.002	0.293	0.005	0.996
	Structural complexity	0.150	0.022	0.052	0.010
Forest generalists	Tree species richness	0.036	0.003	0.112	0.923
	Structural complexity	0.344	0.041	0.129	0.001
	Canopy cover	1.085	0.355	0.243	0.808
	Leaf litter	-1.023	0.335	0.073	0.941

CHAPTER 4

Microhabitat requirements and occupancy of understorey bird forest specialists in Southern Mistbelt Forests of KwaZulu-Natal, South Africa

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Running header: Occupancy of forest understorey bird specialists

4.1 Abstract

Monitoring species' habitat selection and microhabitat requirements is vital for conservation and management, though studies on bird species' habitat selection at relatively fine scales are often limited. Camera traps are useful techniques for studying bird communities, particularly elusive species that are challenging to document using traditional survey techniques. Here, we installed 184 camera traps during the non-breeding and breeding seasons to study understory forest-specialist birds' habitat requirements in 14 selected Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa. We conducted foliage profile and forest structure surveys and an inventory of tree species richness to characterise forest microhabitat. Over 7182 trap days, we had 615 detections of ten understory forest-specialists, most of which were insectivores. We modelled the occupancy of Lemon Doves (*Aplopelia larvata*), Chorister Robin-chats (*Cossypha dichroa*), Crested Guineafowls (*Guttera pucherani*), and Red-necked Spurfowls (*Pternistis afer*) to determine microhabitat characteristics that influenced detection probability and occupancy. The main microhabitat characteristics influencing forest-specialist understory birds were tree species richness, leaf litter, and water cover. Forest structural characteristics that influenced the occupancy of the selected understory forest-specialists were those within 5 m of the forest floor. Microhabitat requirements for the birds were species-specific, with seasonal variation for Lemon Doves. Conservation strategies should maintain undisturbed forest understory to allow for the persistence of understory forest-specialist bird species.

Keywords: camera trap, forest-specialist birds, microhabitat, Mistbelt Forest, occupancy

4.2 Introduction

Biodiversity is under threat from human-driven habitat alterations at a global scale (Ceballos et al., 2015; Barlow et al., 2016). In forest systems, habitat destruction is one of the main drivers of biodiversity loss (Harper et al., 2007). These changes in biodiversity have motivated the need for biodiversity monitoring for effective conservation and management. Monitoring biodiversity is essential for evaluating species status (Nielsen et al., 2009), community structure (Favila and Halffter, 1997), responses to global environmental change (Bellard et al., 2014) and identifying areas to be prioritised for conservation (Sutter et al., 2015). Various habitat characteristics influence species' habitat selection at different spatial scales and are often associated with habitat quality (Wiens et al., 1987; Mateo-Sánchez et al., 2016). For biodiversity monitoring efforts to be successful and practical, different spatial scales must be considered in assessing species' habitat selection (Poiani et al., 2000). For habitat-specialised species, local-scale characteristics are often more important than landscape characteristics in influencing habitat selection (Graham and Blake, 2001). Despite acknowledging the importance of microhabitat-level studies, they are often limited. Monitoring species' habitat preference at a relatively fine-scale is highly demanding, time-consuming, and expensive. Therefore, it is essential to identify effective approaches for monitoring species microhabitat requirements of habitat-specialised species for conservation management.

In recent years, camera traps have become widely used to assess species occurrence, distribution (Wevers et al., 2021), density (Wearn et al., 2022) and behavioural activity (Fontúrbel et al., 2021; Jean-Pierre et al., 2022). Compared with traditional survey techniques, camera traps have many advantages, including collecting continuous data without observer interference (Liu et al., 2018). For bird species studies, camera traps are useful for monitoring understory bird species, especially those that are elusive and difficult to document using traditional methods (Fontúrbel et al., 2020). A recent review that assessed camera trap use in

Africa showed that bird species were among the taxonomic groups that have received relatively little attention (Cordier et al., 2022).

Avian communities play an essential role in the ecosystem and contribute to ecosystem services and the maintenance of ecosystem functioning (Bregman et al., 2015; Benedetti et al., 2020). As a group, bird species are sensitive to habitat change, particularly the conversion of forest habitat into other land-use types (Dunn, 2004; Aratrakorn et al., 2006; Zurita et al., 2006). Among bird species, understorey forest-dependent birds are more vulnerable to habitat disturbance (Laurance, 2004; Vergara and Simonetti, 2006; Visco et al., 2015). Microhabitat specialisation (Peters et al., 2008), nesting strategies, limited dispersal ability (Castellón and Sieving, 2006; Korfanta et al., 2012) and rarity (Newmark, 1991) are among the traits that contribute to the increased sensitivity of this group. Understorey forest-specialist bird species (hereafter, understorey forest specialists) have been shown to be strongly associated with microhabitat characteristics in different forest types (Stratford and Stouffer, 2015; Gumede et al., 2022). Consequently, effective management for these bird species requires understanding habitat requirements at micro-scale levels.

In South Africa, the forest biome is the smallest of the eight biomes (e.g., grasslands), occupying < 1% of the land surface but supporting 14% of bird species (Geldenhuys and MacDevette, 1989). Also, these forests support more threatened bird species than any other South African biome. The Southern Mistbelt Forests are naturally fragmented and embedded in a grassland mosaic (Eeley et al., 1999). Anthropogenic activities have further fragmented these forest patches. In the past, European settlers exploited these forest patches for timber for about 150 years, which were then left to recover naturally (Rycroft, 1944; Mucina et al., 2006). Though these forests seem to have recovered through successional processes (Adie et al., 2013), the regeneration has been slow (Grieve and Downs, 2015) and is estimated to be 40% of their original size (Lawes, 1992). Present threats to the Southern Mistbelt Forests are

mismanaged fires, grazing, deforestation and transforming the surrounding natural grasslands to commercial exotic tree plantations and agriculture (Rycroft, 1944; Mucina et al., 2006; Mensah et al., 2018). In the KwaZulu-Natal Midlands, most of the Mistbelt forest patches are privately owned, while some are state owned. Although protected, some of the forest patches that are surrounded by communal lands are used to meet the livelihood needs of surrounding communities (Mucina et al., 2006). About 50% of forest-specialist bird species in South African forests have experienced range declines (Cooper et al., 2017). Despite this knowledge, factors influencing the habitat selection of most forest-specialist bird species have not yet been studied.

Previous studies of selected understorey forest-specialists have shown the effectiveness of camera trap surveys for elusive forest specialist bird species (Ehlers Smith et al. 2017a, b; Gumede et al., 2022). In South African forest systems, the few occupancy studies that have used camera trap data to study forest-specialist birds have focused typically on one bird species (e.g., Ehlers Smith et al. 2017a, b; Chibesa and Downs, 2017; Maseko et al., 2017). To our knowledge, the only occupancy study of the Southern Mistbelt Forests of KwaZulu-Natal is Lawes et al. (2006), which used other bird survey techniques (e.g., interviews, vocalisation playback, etc.) focusing on landscape-level characteristics (e.g., land-use matrix, logging history). Therefore, the microhabitat requirements for understorey forest-specialists have not been identified in the studied region to inform management. Also, to our knowledge, understorey forest-specialists in South African forests have not been studied at a community level using camera traps.

Considering this knowledge gap, this study uses camera trap surveys to explore the community of understorey forest-specialist community in the Southern Mistbelt Forests of the Midlands of KwaZulu-Natal, South Africa. The objectives of the study were to identify (1) understorey forest-specialists using the forest understorey of Southern Mistbelt Forest patches,

(2) microhabitat characteristics influencing the occupancy and detectability of these understorey forest-specialists, (3) seasonal differences in microhabitat requirements. We hypothesised that microhabitat characteristics influencing the bird species occupancy would (1) be species-specific (Murphy et al., 2018; Gumede et al., 2022) and vary seasonally (c.f. Ehlers Smith et al., 2017a).

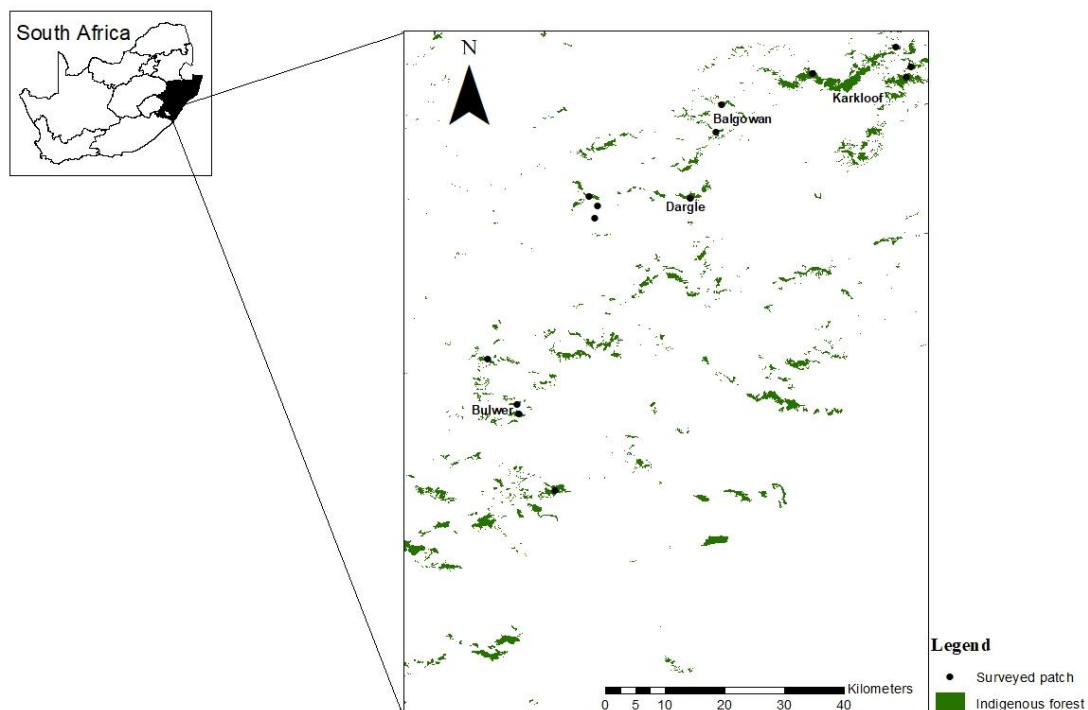


Figure 4.1 Location of the study area and the distribution of the sampled 14 Mistbelt Forest patches in the Midland of KwaZulu-Natal, South Africa. (The black dots indicate the surveyed forest patches).

4.3 Methods

4.3.1 Study area

We sampled 14 Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa, between October 2020 and September 2021 (Fig. 4.1). The selected forest

patches occur on southeast-facing slopes dominated by *Podocarpus/ Afrocarpus* species and have been classified as the Southern Mistbelt Forest type (Mucina and Rutherford, 2011). These forests are generally found at elevations of 1500 - 1800 m a.s.l. (King 1941) where the mean annual rainfall is 800-1000 mm, mainly during the summer (November – January) (Wethered and Lawes, 2003). The Southern Mistbelt Forest patches vary in size and are dominated by relatively few large patches (> 500 ha) and many small patches (> 0.01 ha). We randomly selected forest patches of varying patch sizes ranging between 2.23 – 1685 ha. In each studied region, we selected one of the patches as the mainland patch (> 200 ha).

Table 4.1 Sampling effort and location of the 14 surveyed Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Region	Patch	Coordinates	Camera sites (n) per season	Patch size (ha)
Karkloof	Karkloof Nature Reserve	29°17'50" S; 30°13'59" E	51	1685
	Mbona Private Nature Reserve	29°18'08" S; 30°22'26" E	28	679
	Benvie Farm	29°15'27" S; 30°21'29" E	8	101
	L'Abri	29°17'08" S; 30°23'40" E	10	199
Balgowan	Milestone Forest Walk	29°22'57" S; 30°05'40" E	3	77
	Rameron (Boeshoek complex)	29°20'34" S; 30°05'43" E	8	207
Dargle	Maritzdaal Forest	29°29'06" S; 30°02'57" E	21	558
	Wakefield Forest	29°29'06" S; 29°54'28" E	2	4.5
	Waterfall Forest	29°30'54" S; 29°54'18" E	1	2.2
	Sharedown (New Forest)	29°28'57" S; 29°53'44" E	9	112
Bulwer	Ingelabantwana Nature Reserve	29°43'43" S; 29°44'35" E	13	338
	Xotsheyake Nature Reserve	29°47'46" S; 29°47'16" E	5	98
	Marutswa Nature Reserve	29°48'36" S; 29°47'25" E	11	268
	Nxumeni (Nkwezela State Forest)	29°55'38" S; 29°50'42" E	14	385

4.3.2 Camera trapping

The camera trap surveys were conducted in the avian breeding (October 2020 – March 2021) and non-breeding seasons (April 2021 – September 2021). We used ArcMap in ArcGIS 10.8.1 (ESRI, Redlands, CA, USA) to create systematic 400 x 400 m grids to predetermine camera trap sites. We used the Garmin eTrex 10 (USA) outdoor handheld global positioning system (GPS) unit to locate the points. We set out 184 camera traps per season (Table 4.1) using a systematic camera trapping technique following the Ehlers Smith et al. (2017a, b) camera trapping protocol. The number of camera traps per forest patch was proportional to the sampled patch size (ha) (Table 4.1). Each camera site was surveyed once per season (i.e., breeding, and non-breeding), surveying for 24 h for a minimum of 21 consecutive days. The camera traps were placed on tree trunks ~30 cm above the ground and set to a 30s motion delay detect setting. If the selected tree was not naturally open, we cleared vegetation around it to minimise camera sensor obstruction and avoid blank shots.

4.3.3 Covariates

We quantified vegetation structure at each camera point survey within a radius of 20 m of the camera site. Measured microhabitat characteristics included percentage cover of water, bare ground, leaf litter, grass short (0 - 0.25m), grass tall (> 0.25m), herbaceous short (0 - 0.25m), herbaceous tall (> 0.25 cm) and saplings (≤ 2 m) (Table 4.1). We also recorded the number of live and dead trees in six different height classes (2 - 5 m, 6 - 10 m, 11 - 15 m, 16 - 20 m, 20 - 25 m, and > 25 m). We identified all trees to species level. We calculated the height heterogeneity index by converting the mean height scores of all the vegetation classes (e.g., short grass, tall grass) using the Shannon-Weiner formula (Ehlers Smith et al., 2015). The formula follows $H = -\sum p_i \ln(p_i)$ where 'p_i' is the proportion of the total foliage in the *i*th layer for a chosen horizontal layer (Bibby et al., 2000).

4.3.4 Data analyses

To test the data for multicollinearity, we used the variance inflation factor (VIF) in the ‘car’ package in R (R core Team, 2020). We removed covariates with higher VIF and retained covariates with $VIF < 3$ (Zuur and Elpick, 2010). In the breeding season, we removed canopy openness, canopy closure, short herbaceous cover, heterogeneity index, stem density of trees 21 - 25 m and stem density of trees > 25 m. In the non-breeding season, we removed canopy closure, canopy openness, tall herbaceous cover, stem density of trees 16-20 m, tree density of trees 21 - 25 m and tree density of trees > 25 m. After excluding these variables, with were left with 14 uncorrelated covariates in both seasons (Table 4.2). Before analysis, all the covariates were standardised to z-scores (Cooch and White, 2005). Captured photographs of the bird species were considered independent captures if they were obtained 30 min apart (Murphy et al., 2018).

The naïve occupancy for all the recorded bird species across all surveyed forest patches was < 0.20 . Consequently, we only considered bird species occupying at least 20% of the camera sites in detected forest patches for further occupancy analysis (O’Connell et al., 2006; Ehlers Smith et al., 2018). For each bird species targeted in this study, we created a binary matrix (absence = 0; presence = 1) for the detection history for 21 consecutive nights for each survey site (camera site). We used a single-season occupancy model (MacKenzie et al., 2006) for each bird species to estimate occupancy (ψ) and detection probability (p) in the breeding and non-breeding seasons using Program PRESENCE version 13.47 (Hines, 2006). Initially, we started with occupancy modelling by running a null model (i.e., $\psi(\cdot)$, $p(\cdot)$) with both occupancy and detection probability constant, followed by a global model containing all potential covariates. We then followed with models of each of the covariates separately, keeping the detection probability constant (e.g., $\psi(\text{covariate})$, $p(\cdot)$). Following a two-step procedure, we modelled occupancy (ψ) and then detection (p) by running all potential

combinations of covariates keeping the detection probability constant (i.e., ψ (covariate + covariate), $p(\cdot)$). Lastly, we constructed models for occupancy (ψ) and detection probability together (i.e., ψ (covariate+covariate), $p(\text{covariate+covariate})$). For model selection and comparison, we used the Akaike Information Criterion (AIC) and considered models with a delta (Δ) AIC < 2 as having equivalent explanatory power for estimating detection probability (p) and occupancy (ψ) of the studied bird species (Burnham and Anderson, 2002). We used 10,000 bootstrap iterations in the final model to test the goodness-of-fit to produce a mean overdispersion parameter (c-cap) (Ramesh and Downs, 2014). Models with a c-cap value of ~ 1 were the best models with non-dispersion (Burnham and Anderson, 2002). To assess the contribution of each covariate in the top model, we summed the Akaike weight (ω) based on the representation across the final models.

Table 4.2 Microhabitat variables used for occupancy models of selected understorey forest v specialist bird species detected across 14 Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Variable	Description
Bare ground (BG)	Percentage cover of bare ground (%)
Leaf litter (LL)	Percentage cover leaf litter (%)
Short grass (SG)	Percentage cover of short grass (0-0.25 m) (%)
Tall grass (TG)	Percentage cover of tall grass (>0.25 m) (%)
Short herbaceous (SH)	Percentage cover of short herbaceous (0-0.25 m) (%)
Tall herbaceous (TH)	Percentage cover of tall herbaceous (>0.25 m) (%)
Sapling cover (SC)	Percentage cover of saplings (≤ 0.20) (%)
Water cover (WC)	Water body – percentage area cover with water (%)
Stem density 2-5 (SD2-5)	Total number of trees 2-5 m
Stem density 6-10 (SD 6-10)	Total number of trees 6-10 m
Stem density 11-15 (SD11-15)	Total number of trees 11-15 m
Stem density 16-20 (SD16-20)	Total number of trees 16-20 m
Snag density	Number of vertical dead trees (≥ 2 m)
Height Heterogeneity Index (HHI)	Converted mean height scores
Canopy cover	Percentage of canopy cover (%)
Tree species richness (TSR)	Total number of tree species

4.4 Results

Excluding the camera traps that were either stolen, malfunctioned, or had a dead battery during the survey period, the sampling effort was 7182 trap days. During the surveyed period, there were 871 independent captures of understorey bird species. Of these photographs, 615 captures were of understorey forest-specialist bird species. We recorded ten forest specialists representing eight avian families across the 14 surveyed forest patches (Fig. 4.2). Of the total bird forest-specialist species, five (50%) of the detected birds were insectivores, followed by frugivores (20%), omnivores (20%) and a granivore (10%) (Supplementary Information Table

S1). The detected bird body size ranged between 16 - 50 cm, and the body mass ranged between 21 - 1300 g (Supplementary Information Table S4.1). Bird species richness varied slightly between the breeding and non-breeding seasons. Seven of the ten detected bird species were detected in both seasons, two only in the non-breeding season Olive Woodpecker (*Dendropicos griseocephalus*), African Olive Pigeon (*Columba arquatrix*) and one only in the breeding season (Knysna Turaco *Tauraco corythaix*). The Lemon Dove (*Aplopelia larvata*) was the most abundant bird species, accounting for 46% of the total independent captures (Fig. 4.3). The Knysna Turaco and Olive Woodpecker had the lowest independent capture ($n = 1$) (Fig. 4.3). The Lemon Dove, Chorister Robin-chat (*Cossypha dichroa*), White-starred Robin (*Pogonocichla stellata*) and Orange Ground-thrush (*Geokichla gurneyi*) were detected across all the surveyed regions (Supplementary Information Table S4.2). The Crested Guineafowl (*Guttera edouardi*) was only detected in the Karkloof region. In the non-breeding season, the Crested Guineafowl was observed in groups of 1 - 19, while in the breeding season, it was in groups of 1 - 4 birds. The Red-necked Spurfowl (*Pternistis afer*) and Lemon Dove were detected in pairs or singly in both seasons. The African Olive Pigeon was observed in groups of 1 - 5 individuals.



Figure 4.2 Understorey forest-specialist bird species detected during the breeding and non-breeding season in 14 Mistbelt Forest patches in KwaZulu-Natal, South Africa.

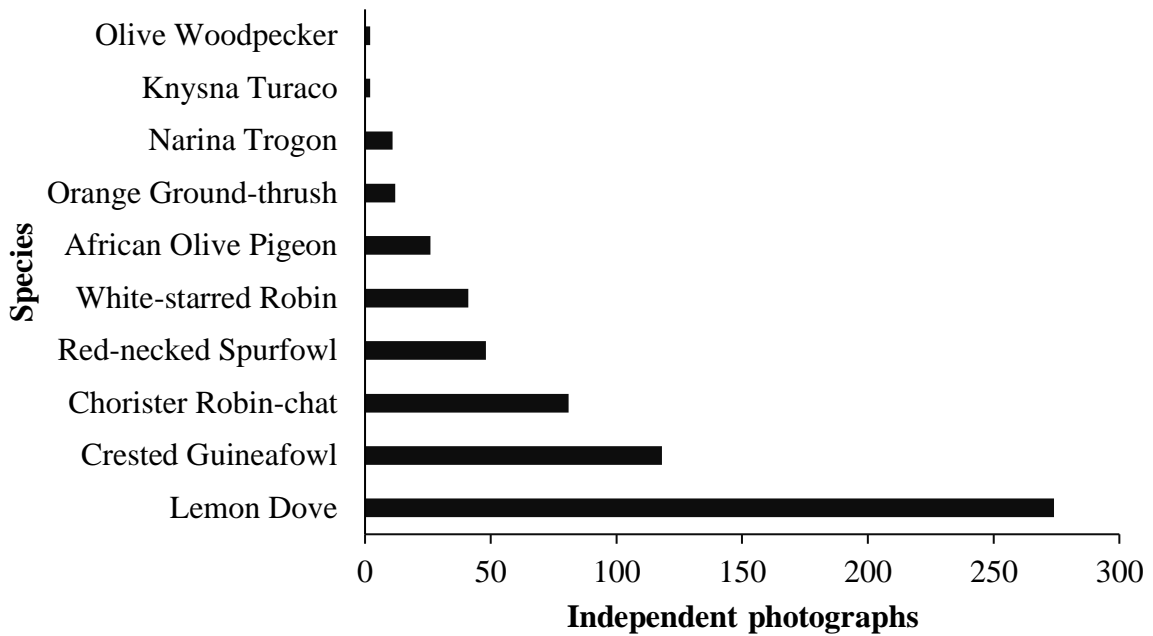


Figure 4.3 Total independent photographs of understory bird species detected in selected Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Of the detected bird species, only four were detected sufficiently frequently (≥ 0.20) to be considered for occupancy modelling (Table 4.3). Due to the low detection rates of bird species, we could only assess seasonal requirements for Lemon Dove (Table 4.3).

In the non-breeding season, tree species richness was the most common covariate influencing the bird species occupancy, except for Crested Guineafowl (Table 4.4). During the non-breeding season, tree species richness influenced the occupancy of Red-necked Spurfowl and Lemon Dove negatively, while it positively influenced Chorister Robin-chat. Also, leaf litter was consistently in the top models during the non-breeding season, influencing the occupancy of all birds except for the Lemon Dove (Table 4.4). Tree species stem density and the height heterogeneity index influenced the detection probability of all bird species except for Red-necked Spurfowl.

During the non-breeding season, stem density of 2 - 5 m trees, leaf litter and water cover had a positive influence on the occupancy of Crested Guineafowl (Fig. 4.4). The detection probability of Crested Guineafowl was negatively influenced by the percentage cover of bare ground, snag density and height heterogeneity index while the percentage cover of saplings and tall grass positively influenced the detection probability (Supplementary Information Fig. 4.1, Table 4.5). The occupancy of Red-necked Spurfowl was positively influenced by the percentage cover of leaf litter and negatively influenced by tree species richness and the percentage cover of saplings (Fig. 4.4, Table 4.5). The detection probability of Red-necked Spurfowl was influenced positively by the percentage cover of saplings. In contrast, the herbaceous short percentage cover had a negative influence (Supplementary Information Fig. S4.1, Table 4.5). Occupancy of Chorister Robin-chat was positively influenced by the percentage cover of short herbaceous and negatively influenced by forest canopy cover (Fig. 4.4). Percentage cover of short grass stem density of trees 2-5 m and height heterogeneity index had a positive influence on the detection probability of Chorister Robin-chat.

During the non-breeding season, the occupancy of Lemon Dove was influenced positively by tree species richness and percentage cover of water, while the percentage cover of short grass negatively influenced occupancy (Fig. 4.5; Table 4.5). During the non-breeding season, the detection probability of Lemon Dove was positively influenced by canopy cover and the stem density of trees of 11-15 m and influenced negatively by the stem density of trees 6-10 m, tree species richness and heterogeneity index (Fig. 4.6, Table 4.5). In contrast, during the breeding season, the occupancy of Lemon dove was positively influenced by snag density and percentage of leaf litter cover, while tree species richness had a negative influence (Table 4.5). The percentage of short grass cover negatively influenced the detection probability and positively influenced by canopy cover and percentage cover of tall grass (Table 4.5).

Table 4.3 Number of detection and naïve occupancy of understory forest-specialist bird species detected on camera traps during the breeding and non-breeding season in 14 Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Season	Scientific name	Common name	n	Naïve occupancy
Breeding	<i>Guttera edouardi</i>	Crested Guineafowl	72	0.14
	<i>Aplopelia larvata</i>	Lemon Dove	142	0.27
	<i>Pternistis afer</i>	Red-necked Spurfowl	13	0.12
	<i>Cossypha dichroa</i>	Chorister Robin-chat	14	0.09
Non-breeding	<i>Guttera edouardi</i>	Crested Guineafowl	76	0.22
	<i>Aplopelia larvata</i>	Lemon Dove	149	0.28
	<i>Pternistis afer</i>	Red-necked Spurfowl	34	0.28
	<i>Cossypha dichroa</i>	Chorister Robin-chat	76	0.22

Table 4.4 Species-specific top occupancy models ($\Delta AIC < 2$) showing forest microhabitat characteristics influence on the occupancy (ψ) and detection probability (p) of four understorey forest-specialist bird species detected in the breeding and non-breeding season in selected Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

Season	Species	Model	AIC	ΔAIC	ω_i	k	Model Likelihood	c-hat
Non-breeding	<i>Aplopelia larvata</i>	ψ (WC+TSR+SG), p (SD6+SD11+TSR+HHI+CC)	605.16	0.00	0.20	10	1.00	1.12
		ψ (WC+TSR+CC), p (SD6+SD11+TSR+HHI+CC)	606.94	1.78	0.08	10	0.49	
	<i>Cossypha dichroa</i>	ψ (SH+CC), p (SG+SD2+HHI)	181.97	0.00	0.19	7	1.00	0.99
		ψ (SH+TSR+LL), p (SG+SD2+HHI)	183.26	1.29	0.10	8	0.52	
		ψ (SH+SC+WC), p (SG+SD2+SD6+HI)	183.48	1.51	0.09	9	0.47	
	<i>Guttera edouardi</i>	ψ (LL+SD2+WC), p (BG+ TG+SC+HHI+Snags)	266.50	0.00	0.41	10	1.00	1.02
	<i>Pternistis afer</i>	ψ (LL+TSR+SC), p (SH+SC)	130.08	0.00	0.26	7	1.00	0.93
Breeding	<i>Aplopelia larvata</i>	ψ (LL+TSR+Snags), p (SG+TG+CC)	424.61	0.00	0.20	8	1.00	1.03
		ψ (LL+SG+TSR), p (TG+SD11+CC)	425.37	0.76	0.13	8	0.69	
		ψ (TSR+LL), p (GS+TG+SD11+CC)	425.94	1.33	0.11	8	0.38	

Note: k = the number of parameters. BG = bare ground cover (%). LL = leaf litter cover (%). SG = short grass cover (%). TG = tall grass cover (%). SH = short herbaceous cover (%). SC= saplings cover (%). SD2 = stem density of trees 2-5 m. SD11= stem density of trees 11-15 m. TSR = tree species richness. HI = vegetation structure index. ω_i = Akaike weight. c-hat = goodness of fit and overdispersion parameter.

Table 4.5 Parameter estimates for the microhabitat variables from the best occupancy and detection probability models ($\Delta AIC < 2$) for four forest understorey specialists birds during the breeding and non-breeding season in the surveyed Mistbelt forest patches in the Midlands of KwaZulu-Natal, South Africa.

Species	Site occupancy			Detection probability		
	Covariate	Estimate \pm Std. error	ω_i	Covariate	Estimate \pm Std. error	ω_i
<i>Non-breeding</i>						
Chorister Robin-chat	SH	7.86 \pm 4.73	0.89	SD 2-5	0.27 \pm 0.20	0.83
	CC	-1.91 \pm 0.32	0.48	HHI	0.05 \pm 0.02	0.87
Crested Guineafowl	SD 2-5	1.31 \pm 0.58	0.97	BG	-2.04 \pm 0.51	0.98
	LL	2.47 \pm 2.44	0.69	Snags	-0.56 \pm 0.29	0.98
	WC	2.08 \pm 1.63	0.42	HHI	-0.05 \pm 0.03	0.88
				SC	1.45 \pm 0.43	0.98
Lemon Dove	TSR	0.48 \pm 0.27	0.87	TG	0.89 \pm 0.26	
				CC	0.19 \pm 0.09	0.73
	WC	0.72 \pm 0.49	0.60	SD 11-15	0.43 \pm 0.09	0.98
	SG	-0.58 \pm 0.28	0.93	SD 6-10	-0.43 \pm 0.17	0.89
				TSR	0.35 \pm 0.17	0.87
				HHI	-0.06 \pm 0.01	0.98
Red-necked Spurfowl	LL	2.73 \pm 1.68	0.70	SC	1.16 \pm 0.33	0.80
	TSR	-4.08 \pm 2.64	0.50	HC	-1.21 \pm 0.99	0.45
	SC	-3.74 \pm 2.12	0.80	SG	0.73 \pm 0.36	0.70
<i>Breeding</i>						
Lemon Dove	Snags	0.36 \pm 0.26	0.46	SG	-0.79 \pm 0.47	0.95
	LL	3.03 \pm 1.76	0.94	CC	0.48 \pm 0.19	0.93
	TSR	-0.92 \pm 0.39	0.94	TG	0.32 \pm 0.20	0.88

Note: k = the number of parameters. BG = bare ground cover (%). LL = leaf litter cover (%). SG = short grass cover (%). TG = tall grass cover (%). SH = short herbaceous cover (%). SC = saplings cover (%). SD2 = stem density of trees 2-5 m. SD11 = stem density of trees 11-15 m. TSR = tree species richness. HI = vegetation structure index. ω_i = Akaike weight.

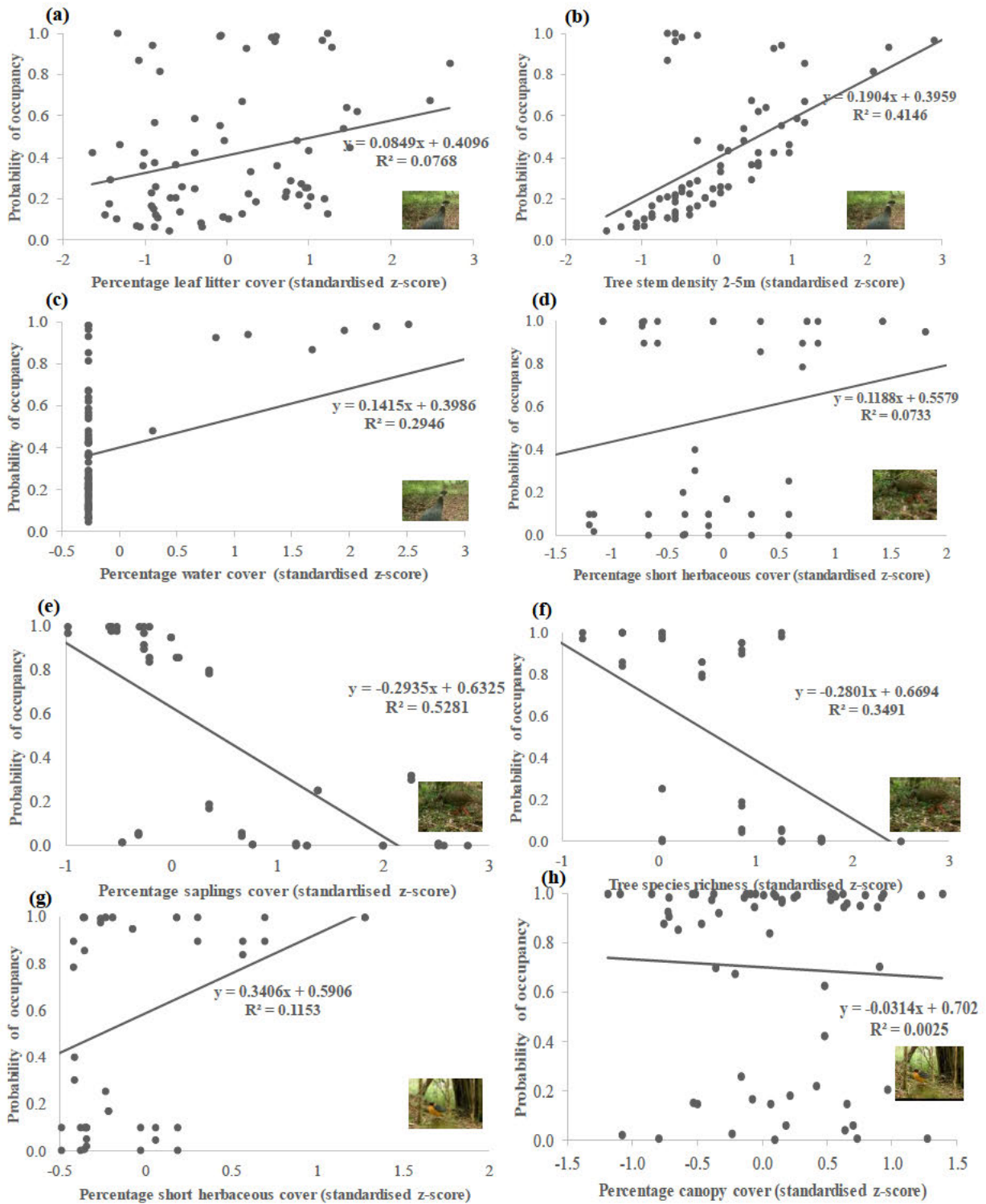


Figure 4.4 Relationship of microhabitat characteristics with the occupancy of Crested Guineafowl (*Guttera edouardi*) (a-c), Red-necked Spurfowl (*Pternistis afer*) (d-f) and (*Cossypha dichroa*) Chorister Robin-chat (g-h) during the non-breeding season in the Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa.

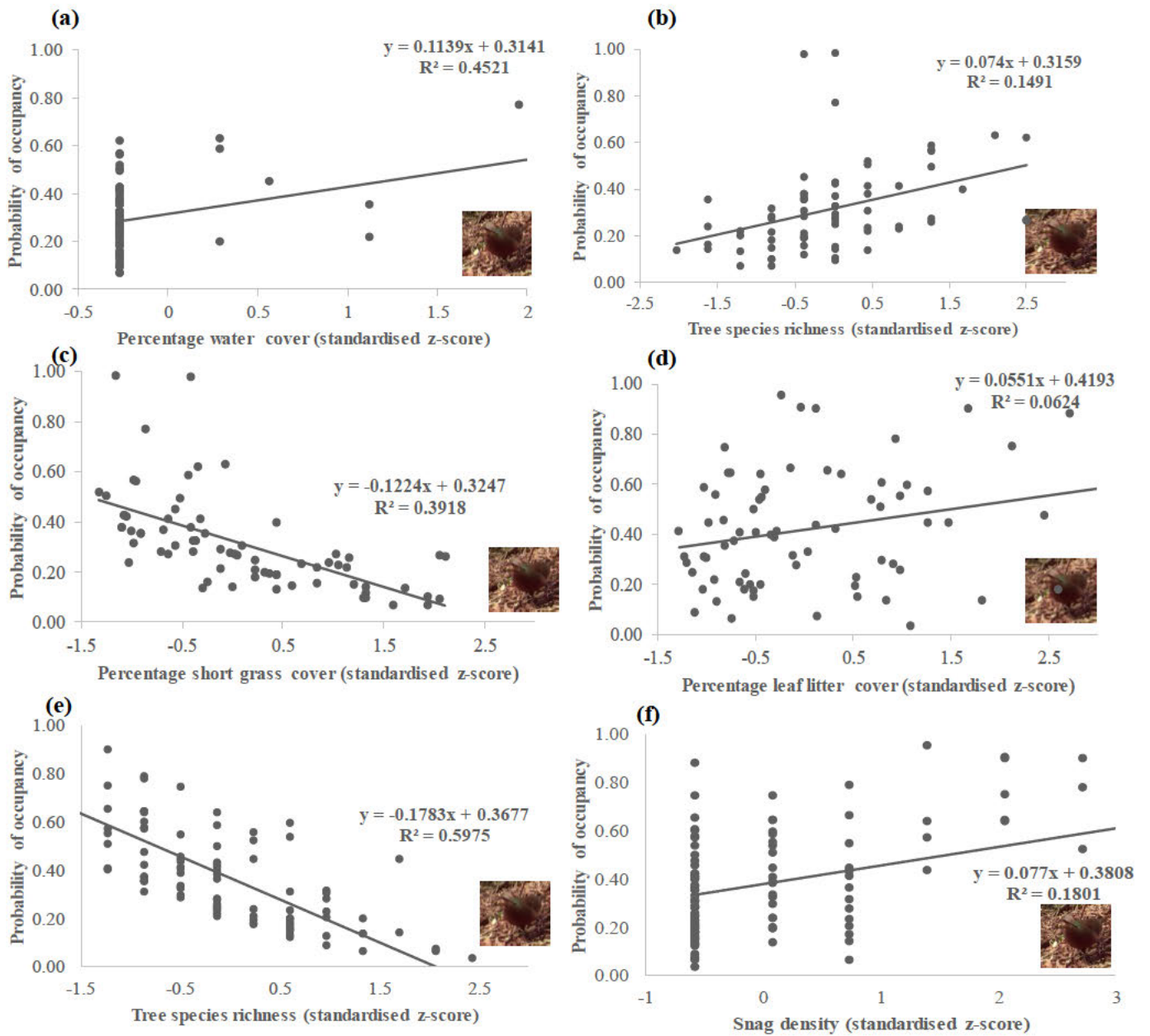


Figure 4.5 Relationship of microhabitat characteristics with the occupancy of Lemon Dove (*Aplopelia larvata*) during the breeding (a-c) and non-breeding season (d-f) detected in the Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa.

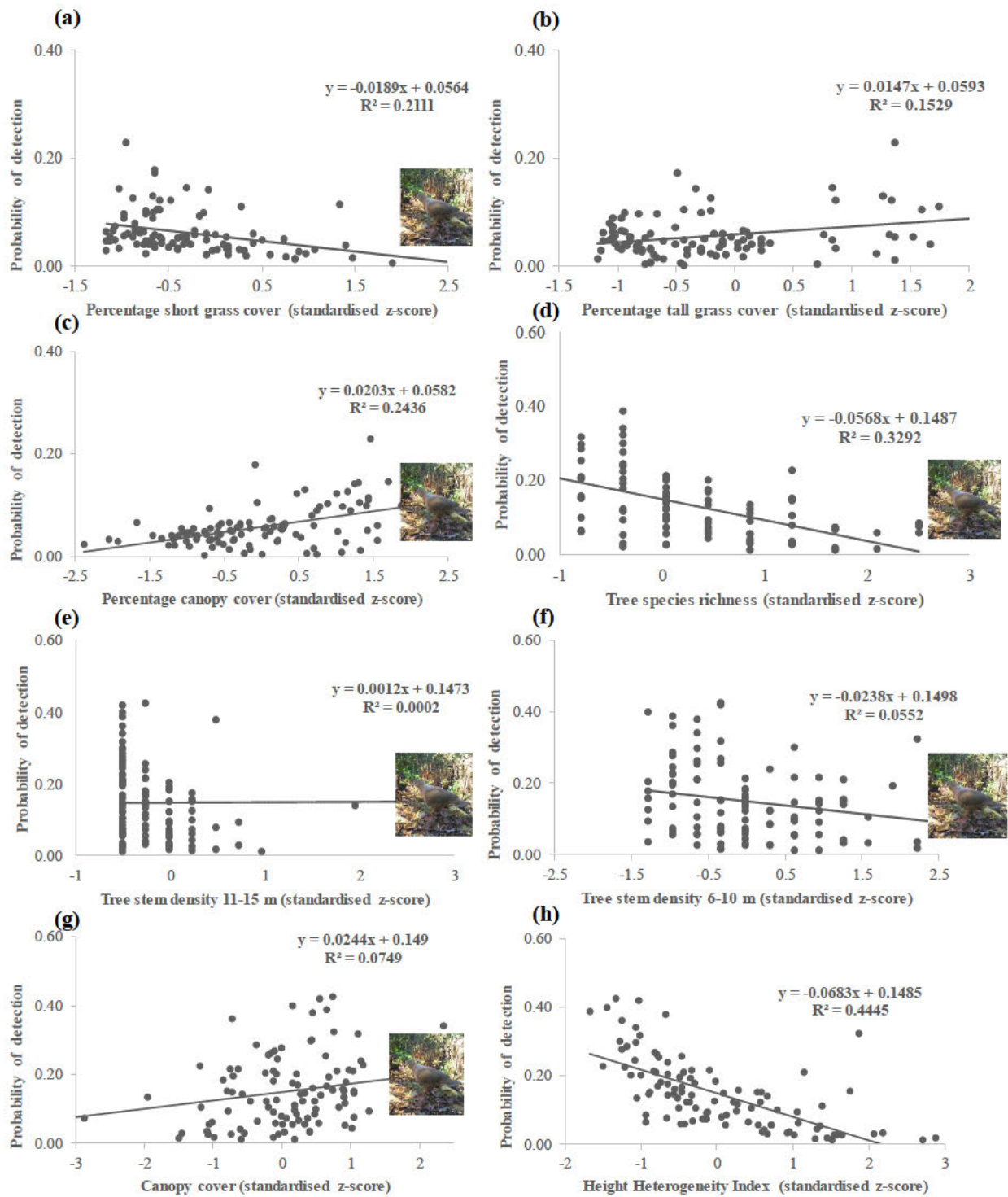


Figure 4.6 Relationship of microhabitat characteristics with the detection probability of Lemon Dove (*Aplopelia larvata*) during the breeding (a-c) and non-breeding season (d-h) detected in the Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa.

4.5 Discussion

Understanding the microhabitat requirements of bird species is important for bird species conservation and management. Here, we used camera traps to explore the occupancy and microhabitat requirements of the understorey forest-specialist communities in the Mistbelt forests. Our study is one of a few to examine understorey bird communities using camera traps and the first in South African forest systems. This study has shown which forest-specialist bird species are using the understorey of Southern Mistbelt Forest patches. Insectivores were the dominant trophic guild in the understorey of Southern Mistbelt Forest patches, as has been shown by many bird studies in forest fragments, including Costa Rica (Blake and Loiselle, 2001), Mexico (e.g. Ruiz-Guerra et al., 2012) and China (Xie et al., 2016). In this study, bird species richness did not vary seasonally. The lack of seasonal differences in species richness may be a consequence of all the detected bird species being forest residents. A previous study also showed only slight seasonal variation in bird species richness if detected bird species are mostly resident (Pandey et al., 2020). Our modelling showed that different microhabitat characteristics influenced understorey forest-specialists occurrence. Our results are consistent with previous studies showing that understorey forest-specialists' microhabitat requirements are species-specific (Gumede et al., 2022). In this study, different forest structural characteristics influenced the occupancy and detection of the studied understorey forest bird specialists. For example, during the non-breeding season, stem density was important for the occupancy of the Crested Guinea fowl, while the Chorister Robin-chat was mainly influenced by short herbaceous cover. We could only compare seasonal data for Lemon Doves to show seasonal variations in microhabitat requirements. These results confirmed our hypothesis that understorey forest-specialist bird species have specific seasonal microhabitat requirements (Ehlers Smith et al., 2017a; Gumede et al., 2022).

4.5.1 Microhabitat characteristics influencing occupancy

In this study, tree species richness and leaf litter were the main microhabitat characteristics that influenced the occupancy of understorey forest specialist species. These results corroborate a previous bird occupancy study in Canada, showing that forest composition and structure are driving factors in bird habitat selection (Zhang et al., 2013). Tree species (Holmes and Robinson, 1981; Gil-Tena et al., 2007) and leaf litter (Stratford and Stouffer, 1999; Ehlers Smith et al., 2017a, b) are often considered an essential microhabitat characteristic in diverse forest systems and have been shown to influence understorey forest birds worldwide. The positive influence of leaf litter and tree species richness in the occupancy of forest bird species is attributed to increased invertebrate abundance and diversity; forest sites with abundant and diverse understorey invertebrates are associated with increased bird abundance (Vergara et al., 2021). The influence of tree species richness and leaf litter varied for different forest bird species. For example, tree species richness influenced the occupancy of Chorister Robin-chats negatively, while it positively influenced that of Red-necked Spurfowls and Lemon Doves during the non-breeding season. The differences in response to tree species richness could be associated with the dietary guild of the bird species. A previous study on local habitat selection of forest birds in Canada showed that bird trophic guilds respond differently to tree species richness, with insectivores responding more strongly than omnivorous bird species (Zhang et al., 2013). Moreover, leaf litter positively influenced the occupancy of Crested Guineafowls and Red-necked Spurfowls, while it negatively influenced Chorister Robin-chats during the non-breeding season. This relationship indicates the Chorister Robin-chat prefers dense understorey in the studied region.

Water cover was also an important variable affecting the occupancy of the understorey forest specialist in this study. The occupancy of the Lemon Dove, Chorister Robin-chat and

Crested Guineafowl was affected positively by the increased water cover during the non-breeding season. Previous studies in the Amazonian (Beja et al., 2010; Bueno et al., 2012) and Caribbean (Wunderle et al., 1987) forests have reported water cover influence on understory bird species. The strong association of these bird species with water during the non-breeding season may be linked to food availability. For example, understory forest birds increase their foraging range during the non-breeding season by using areas near water sources when food resources are limited (Beja et al., 2010). According to Karr and Freemark (1983), forest understory birds' selection for moist microclimate can also be linked to their physiological needs, which are equally important as food availability.

In the present study, tree stem density was less important in the occupancy of the understory forest-specialists, except for Crested Guineafowls. The lack of importance of this variable indicated that the vegetation influenced most understory forest bird specialists, especially cover closer to the ground < 2 m. Therefore, changes in the forest understory structure will significantly impact the occupancy of the forest-specialist species in Southern Mistbelt Forest patches. In contrast, the positive effect of tree stem density on Crested Guineafowls may be attributed to the species' preference for a denser understory to reduce visibility (Urban, 1986).

4.5.2 Microhabitat characteristics influencing detection probability

Microhabitat characteristics that influenced the detection probability of the Crested Guineafowl, Chorister Robin-chat and Red-necked Spurfowl were likely linked to the nesting strategy of these bird species. For example, increased tall grass and saplings cover influenced the detection probability of Crested Guineafowls positively. Also, the detection of Chorister Robin-chats increased with an increase in stem density of trees between 2 - 5 m. The Crested Guineafowl prefers using thick tall grass to conceal their nest, while the Chorister Robin-chat

uses forest trees about 5 m tall (Tarboton, 2001; Tarboton and Roberts, 2011). The Red-necked Spurfowl has also been shown to use shrub cover as a nest substrate (Tarboton and Roberts, 2011). The height heterogeneity index negatively influenced the detection probability of the understorey forest specialist species. Other studies have also reported this relationship using camera traps for forest birds (Moore et al., 2020; Godoy-Güinao et al., 2023). Generally, forest bird species are influenced by the forest's structural characteristics, not height itself (Díaz et al., 2005).

4.5.3 Seasonal microhabitat requirements of the Lemon Dove

Microhabitat requirements of the Lemon Dove varied seasonally. For example, in this study, tree species richness influenced the occupancy of the Lemon Dove positively during the breeding season and negatively during the non-breeding season. Also, leaf litter was an important variable during the breeding season, whereas water was an important variable during the non-breeding season. Similarly, a previous study on the Lemon Dove seasonal requirements in the Indian Ocean Coastal Forests of KwaZulu-Natal, South Africa, showed seasonal variations in the microhabitat requirements of the Lemon Dove (Ehlers Smith et al., 2017a). Seasonal differences in habitat selection have been reported for other taxa, including mammals (Naxara et al., 2009; Richard et al., 2022) and amphibians (Basile et al., 2015) in forest systems. These changes in habitat selection could be related to bird habitat needs during the breeding or non-breeding seasons. For example, bird habitat selection can vary seasonally influenced by the species' shift in feeding resources (Karr, 1976). Therefore, the seasonal variation could be attributed to the seasonal changes in available resources in the studied region. The variation in microhabitat requirements in forests during the breeding and non-breeding seasons of bird species demonstrates the importance of considering multi-season data to guide the management of understorey bird species (McClure et al., 2012).

4.5.4 Conclusions

Overall, assessing the understorey forest-specialist bird species community in selected Southern Mistbelt Forest patches of South Africa showed that resident specialists over non-resident dominate the forest patches in the area. Understorey forest-specialists in Southern Mistbelt Forests have species-specific microhabitat requirements with potential seasonal variations. This makes this group be of conservation concern as any changes to the forest understorey structure and composition may have major effects on these bird species. The main microhabitat characteristics influencing bird species occupancy were tree species richness, leaf litter and water cover. Effective conservation and ensuring the persistence of these birds in the studied region will require management to prioritise maintaining the forest understorey undisturbed, particularly within 5 m of the forest floor. This is particularly important for the Bulwer Forest patches that are surrounded by rural communities and are using the surveyed patches for livestock grazing despite being state protected and managed (Bitani et al., 2023). Considering the ongoing uncontrolled forest use these patches need to be monitored closely for sustainable resource use by the responsible authorities. Different microhabitat characteristics influenced the bird species occupancy and detection probability related to bird resource use. Consequently, multiple microhabitats characteristics relating to understorey forest-specialists should be considered to manage their forest habitats.

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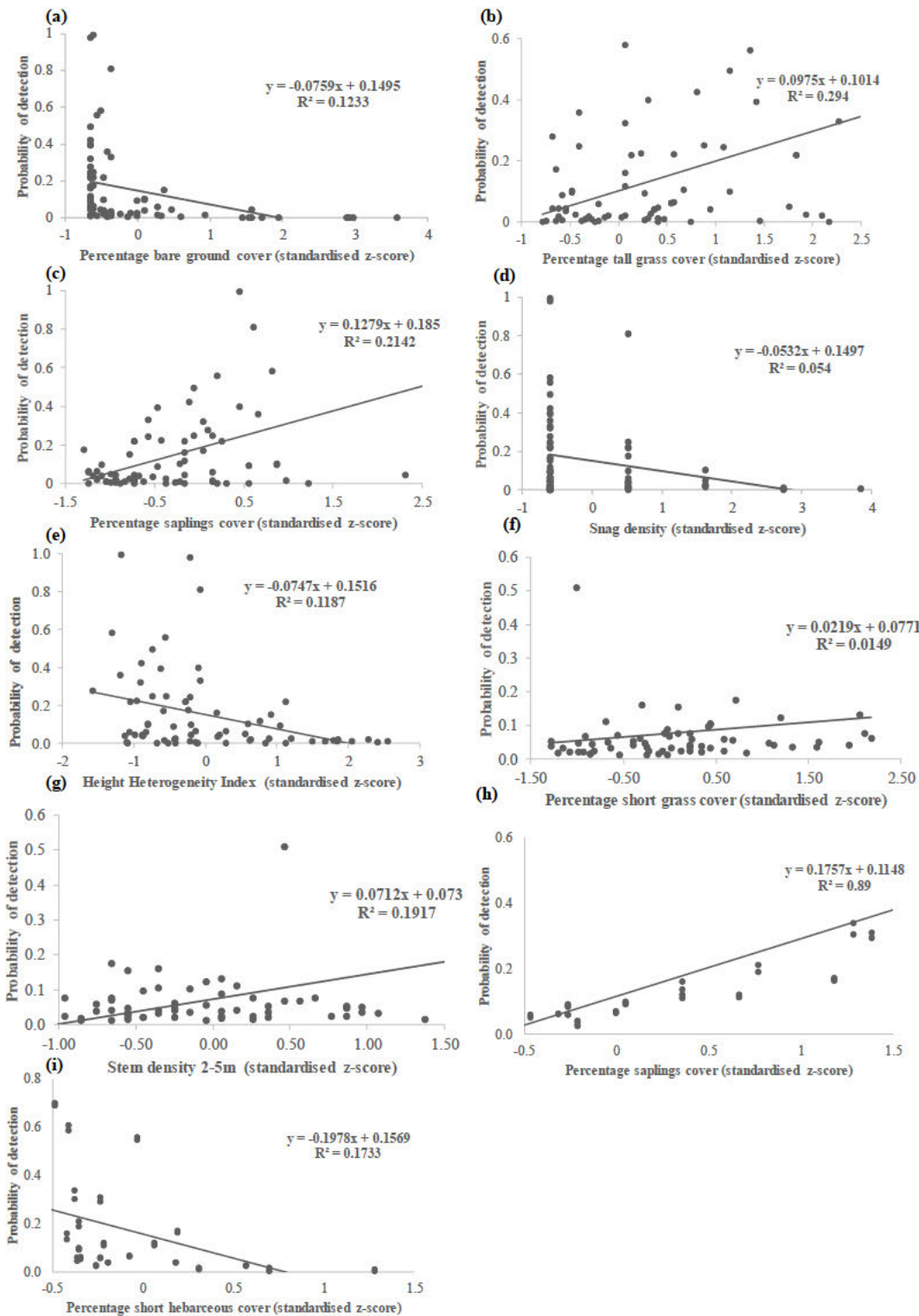
4.8 Supporting information

Supplementary Information Table S4.1 Body size, body mass and dietary feeding guild based on Hockey et al. (2005) of the understory forest-specialist bird species detected in Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa.

Bird species	Mean body size (cm)	Mean body mass (g)	Trophic guild	Endemic	Status
<i>Apaloderma narina</i>	32	67	Insectivore	-	Fairly common resident
<i>Aplopelia larvata</i>	28	150	Granivore	-	Fairly common resident
<i>Columba guinea</i>	40	407	Frugivore	-	Fairly common resident
<i>Cossypha dichroa</i>	18	46	Insectivore	✓	Common resident
<i>Dendropicos griseocephalus</i>	20	45	Insectivore	-	Fairly common resident
<i>Guttera edouardi</i>	50	1300	Omnivore	-	Locally common resident
<i>Tauraco corythaix</i>	46	310	Frugivore	✓	Fairly common resident
<i>Geokichla gurneyi</i>	22	68	Insectivore	-	Uncommon resident
<i>Pternistis afer</i>	36	617	Omnivore	-	Fairly common resident
<i>Pogonochla stellata</i>	16	21	Insectivore	-	Common resident

Supplementary Information Table S4.2 Understorey forest-specialist bird species detected in 14 selected Southern Mistbelt Forest patches across four regions in the Midlands of KwaZulu-Natal, South Africa.

Bird species	Karkloof				Balgowan			Dargle			Bulwer			
	Karkloof Nature Reserve	Mbona Private Nature Reserve	Benvie Farm	L'Abri	Milestone Forest Walk	Rameron	Maritzdaal	Shakedown (New Forest)	Wakefield Farm	Waterfall Forest	Xosheyake Nature Reserve	Ingelabantwana Nature Reserve	Marutswa Nature Reserve	Nxumeni
<i>Apaloderma narina</i>	-	✓	-	-	-	-	✓	-	-	-	-	-	✓	-
<i>Aplopelia larvata</i>	✓	✓	✓	✓	-	✓	✓	✓	-	-	✓	-	✓	✓
<i>Columba guinea</i>	✓	✓	-	-	-	-	✓	-	-	-	-	-	-	-
<i>Cossypha dichroa</i>	✓	✓	✓	✓	✓	✓	-	-	-	-	-	-	✓	-
<i>Dendropicos griseocephalus</i>	-	-	-	-	✓	-	-	-	-	-	-	-	-	-
<i>Guttera edouardi</i>	✓	✓	✓	✓	-	-	-	-	-	-	-	-	-	-
<i>Pogonocichla stellata</i>	-	✓	-	-	-	✓	✓	✓	-	-	-	-	✓	-
<i>Pternistis afer</i>	-	-	-	-	-	✓	✓	-	-	-	-	-	✓	-
<i>Tauraco corythaix</i>	-	-	-	-	-	-	-	-	-	-	-	-	✓	-
<i>Geokichla gurneyi</i>	-	✓	✓	-	-	-	-	-	-	-	-	-	✓	✓



Supplementary Information Figure S4.1. Relationship of forest microhabitat characteristics with the probability of occupancy of Crested Guineafowl (a-), Chorister Robin-chat (f-g) and Red-necked Spurfowl (h-i) during the non-breeding season in selected Southern Mistbelt Forest patches of KwaZulu-Natal, South Africa.

CHAPTER 5

Responses of bird functional communities in Southern Mistbelt Forests in the Midlands of KwaZulu-Natal, South Africa, to anthropogenic disturbances

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Running header: bird communities; forest disturbance; functional diversity

5.1 Abstract

Forest disturbance has major threats to biodiversity and forest ecosystem processes. Understanding bird species' responses to disturbed forests is important for species conservation and forest management. Here, we assessed the impact of selective logging history (~150 years), livestock grazing, alien plant invasion and adjacent matrix-type surrounding forest patches on bird species richness and functional diversity in 14 Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa. The bird communities were surveyed using point-counts. Functional diversity was quantified using functional richness, functional divergence and functional evenness estimated using bird functional traits. Bird species richness was not affected by all the assessed disturbance types. Bird species composition was affected by forest patch size. The orange ground-thrush (*Geokichla gurneyi*), forest canary (*Crithagra scotops*) and Cape parrot (*Poicephalus robustus*) were used as focal species to understand species-specific responses. Species-specific responses to forest disturbances vary dependent on the type of disturbance, intensity and the bird species habitat use. The orange ground-thrush and forest canary were affected by livestock grazing intensity, while the Cape Parrot was influenced by the selective logging history. For functional diversity, FRic was significantly higher in disturbed forest patches for forest specialists, insectivores and cup or ball-nesting birds. Functional evenness for the forest sensitive groups like forest specialists and insectivores was significantly lower in disturbed sites. The results of this study showed that functional communities and forest specialist bird species responses varied dependent on disturbance type and intensity. We recommend that future studies assessing forest disturbance impacts on bird species use taxonomic proxies with different functional diversity indices for forest bird species conservation and management.

Keywords: Forest bird species; species richness, functional diversity, Southern Mistbelt Forests, Anthropogenic disturbance

5.2 Introduction

Worldwide, anthropogenic disturbances are key threats to terrestrial biodiversity (Arnan et al., 2018; Gorczynski et al., 2021; Polyakov et al., 2008). Biodiversity loss driven by anthropogenic activities is associated with irreversible changes, economic loss, and human well-being impacts (Balmford and Bond, 2005; Benedetti et al., 2020). The main human activity affecting biodiversity in forest ecosystems is land-use change, resulting in habitat loss and degradation (Hausner et al., 2003; Mestre et al., 2020; Sala et al., 2000). Habitat loss and destruction results in small, highly fragmented forest patches with reduced habitat quality and this pattern is evident across different forest types worldwide (Bender et al., 1998; Fahrig, 1997; Kupfer et al., 2006). Anthropogenic disturbance significantly impacts ecosystem functionality by damaging the forest structure, changing species composition, niche diversity and resource availability (Moir et al., 2021). The habitat quality of the remaining forest fragments continues to decline because of anthropogenic stressors such as livestock grazing (Arnan et al., 2018; Feng et al., 2021; Shakeri et al., 2021), selective logging (França et al., 2017; Mestre et al., 2020) and alien invasive plants (Hansen et al., 2018; Sundaram and Hiremath, 2012;). Therefore, studies need to continue quantifying disturbance impacts on species for conservation (Mouillot et al., 2013).

Avian communities play an essential role in the ecosystem and contribute to ecosystem services and maintenance of ecosystem functioning (Benedetti et al., 2020; Bregman et al., 2015; Ehlers Smith et al., 2017). The avian taxon has been identified as an essential indicator of biodiversity and ecological integrity across different forest types (e.g., Boulinier et al., 2001; Ehlers Smith et al., 2017; Thompson et al., 2002). Birds provide important ecosystem services, including seed dispersal, pollination, and pest control (Sekercioglu, 2006, 2012; Whelan et al., 2015). Therefore, birds are an important taxon on which to study landscape structural change

(Janousek et al., 2019) as they perform essential ecosystem services, have well-described traits that are linked to ecological functions and are good indicators of environmental change (Boesing et al., 2018; Cosset et al., 2020). Until recently, studies assessing anthropogenic impacts on species across different taxa have focused on taxonomic responses such as species richness (Lindenmayer et al., 2006; Pavoine et al., 2011). A recent global review showed this is true even for birds, one of the most studied vertebrate groups (Matuoka et al., 2020). Although species richness is an informative diversity measure, alternative measures of species response are more helpful, especially if the community has threatened and sensitive species (Russell et al., 2009). Recently, studies assessing the impacts of forest disturbance on species have adopted a functional diversity approach (Benítez et al., 2018; Katovai et al., 2012; Maeshiro et al., 2013; Nasi et al., 2023; Ngcobo et al., 2022). This alternative approach has been motivated by the understanding that it allows for evaluating potential ecological impacts on functional communities and ecosystem changes, especially for species that are more sensitive to disturbance (Katovai et al., 2012; Mouillot et al., 2013). However, a few studies have assessed different functional communities' responses to habitat loss and destruction. Consequently, relatively little is known about the responses of different functional groups to forest disturbance.

Focal bird species in forest systems have been used to study and monitor species-specific responses to global environmental changes (Angelstam et al., 2004; Colyn et al., 2020; Lõhmus et al., 2020). Assessing species-specific responses using focal species reveals bird species responses that can be concealed when focusing on functional communities. This approach aims to protect biodiversity based on the habitat requirements of sensitive bird species (Angelstam et al., 2004). Most studies assessing anthropogenic impacts select focal species mainly based on habitat specificity (i.e., forest specialised) (e.g., Carvajal et al., 2018; Colyn et al., 2020; Ficetola et al., 2007; de Zwaan et al., 2022). This approach does not account for

the three-dimensionality of forest systems as it fails to consider the vertical stratification in habitat use by forest specialists species in forest systems (Godoy-Güinao et al., 2023; Moore et al., 2020). Assessing forest specialist bird species responses accounting for the vertical habitat use by the birds may give more insight and a more realistic projection of the anthropogenic impacts on birds.

The forest biome in South Africa is the smallest (0.41%) (Deng et al., 2020) but contributes significantly to the country's biological diversity (Geldenhuys and MacDevette, 1989). Naturally, the South African forests are fragmented because of historic climatic fluctuation (Eeley et al., 1999) and comprised of small forest patches (~ 1 km²) (Low and Rebelo, 1996). These are located mostly on steep slopes surrounded by natural grasslands, commercial plantations, and sugarcane (Lawes et al., 2004). Anthropogenic impacts have further contributed to some forests being fragmented and reduced in size. Unlike in the Indian Ocean Coastal Belt Forests, where agricultural activity is the main anthropogenic threat, the steep and rocky topography in the Southern Mistbelt Forests has generally precluded agricultural activities (Adie et al., 2013). The Southern Mistbelt Forest patches have been converted into commercial plantations, and the remaining patches are subjected to varying degrees of anthropogenic disturbance (Hansen et al., 2018; Lawes et al., 2004). Therefore, the Southern Mistbelt Forests in South Africa are a good system to assess habitat loss and anthropogenic disturbance on bird species diversity.

Understanding the variations and responses of bird functional communities along a disturbance gradient provides insights into the ecological changes occurring in anthropogenically modified forest ecosystems. This knowledge is important for biodiversity conservation and forest management (Cosset and Edwards, 2017; Sassen and Sheil, 2013). Despite the knowledge of the negative impacts associated with forest loss, fragmentation and disturbance, the implications for ecological processes and changes in avian communities are

less well understood (Matuoka et al., 2020). We selected three forest-specialised birds with different habitat use within the vertical strata of the forest as focal species to explore species-specific responses to anthropogenic impacts. The selected species were the forest ground-dwelling orange ground-thrush (*Geokichla gurneyi*), understory forest canary (*Crithagra scotops*) and the canopy Cape parrot (*Poicephalus robustus*). The range of the selected bird species has declined drastically in the Southern Mistbelt Forests, and the declines were attributed to habitat loss and destruction (Cooper et al., 2017). Therefore, we assumed these species are valuable as focal species to assess the impacts of forest loss and disturbance.

Our study aimed to assess the effects of anthropogenic impacts on bird functional communities in the Southern Mistbelt Forests in the Midlands of KwaZulu-Natal, South Africa. We investigated (1) how bird functional communities respond to forest logging history, alien plant invasion, livestock grazing and matrix type; (2) whether the vulnerability of forest specialists to disturbance varies for species using the forest at different strata; and (3) which birds and functional group characterise disturbed forests. Previous studies assessing anthropogenic impacts on species have shown that species' responses to anthropogenic impacts vary depending on species' functional groups and the type and intensity of disturbance (Lindenmayer et al., 2012; Luck et al., 2013; Thorn et al., 2016). Therefore, we hypothesised that (1) bird functional communities (i.e., forest specialists, insectivores) are sensitive to disturbance so will be strongly negatively impacted by anthropogenic impacts, (2) bird functional communities' response to disturbance will be dependent on the type, and the intensity of the disturbance and (3) focal forest specialists bird species using different strata of the forest will respond differently to disturbance.

5.3 Methods

5.3.1 Study area

This study was conducted in 14 forest patches in four regions in the Midlands of KwaZulu-Natal, South Africa (Figure 5.1). The selected forest patches are classified as the Southern Mistbelt Forests, one of the eight forest types in South Africa (Mucina et al., 2006). These forest patches are embedded in a grassland mosaic on east-facing slopes. In the past, the Southern Mistbelt Forest patches of KwaZulu-Natal were heavily exploited by European settlers for timber for about 150 years (Adie et al., 2013). Timber extraction ended in the early 1940s (McCracken et al., 2004; Wirminghaus et al., 1999), and the system was left to recover naturally (Adie et al., 2013). Despite being protected, in recent years, uncontrolled timber extraction by local inhabitants has continued (Grieve and Downs, 2015; Lawes et al., 2007; Robertson and Lawes, 2005). The Southern Mistbelt Forest patches are species-rich (von Maltitz et al., 2003) and tall (15-27 m) (Moll, 1976). The selected forest patches are within an elevation ranging between 1000-1500 (von Maltitz, 2003) on steep slopes. The total area of the surveyed patches was 4744,14 ha, ranging between 2,23 to 1685 ha. The region receives a mean annual rainfall of 800-1000 mm, mainly in summer (Nov to Jan).

Table 5.1 Studied Southern Mistbelt Forest patches in four regions in the Midlands of KwaZulu-Natal, South Africa.

Region	Forest Patch	Coordinates	Patch size (ha)
Karkloof	Karkloof Nature Reserve	29°17'50"S; 30°13'59" E	1685
	Mbona Private Nature Reserve	29°15'27"S; 30°21'29" E	679
	Benvie Farm	29°18'08"S; 30°22'26" E	101
	L'Abri	29°17'08"S; 30°23'40" E	199
Balgowan	Rameron (Boshoek complex)	29°20'34"S; 30°05'43" E	207
	Milestone Forest Walk	29°22'57"S; 30°05'40" E	77
Dargle	Maritzdaal Forest	29°29'05"S; 30°02'57" E	558
	Sharedown (New Forest)	29°28'57"S; 29°53'44" E	112
	Wakefield Forest	29°29'06"S; 29°54'28" E	4.47
	Waterfall Forest	29°30'54"S; 29°54'18" E	2.23
Bulwer	Xotsheyake Nature Reserve	29°47'46"S; 29°47'16" E	98
	Ingelabantwana Nature Reserve	29°43'43"S; 29°44'35" E	338
	Marutswa Nature Reserve	29°48'36"S; 29°47'25" E	268
	Nxumeni (Nkwezela State Forest)	29°55'38"S; 29°50'42" E	385

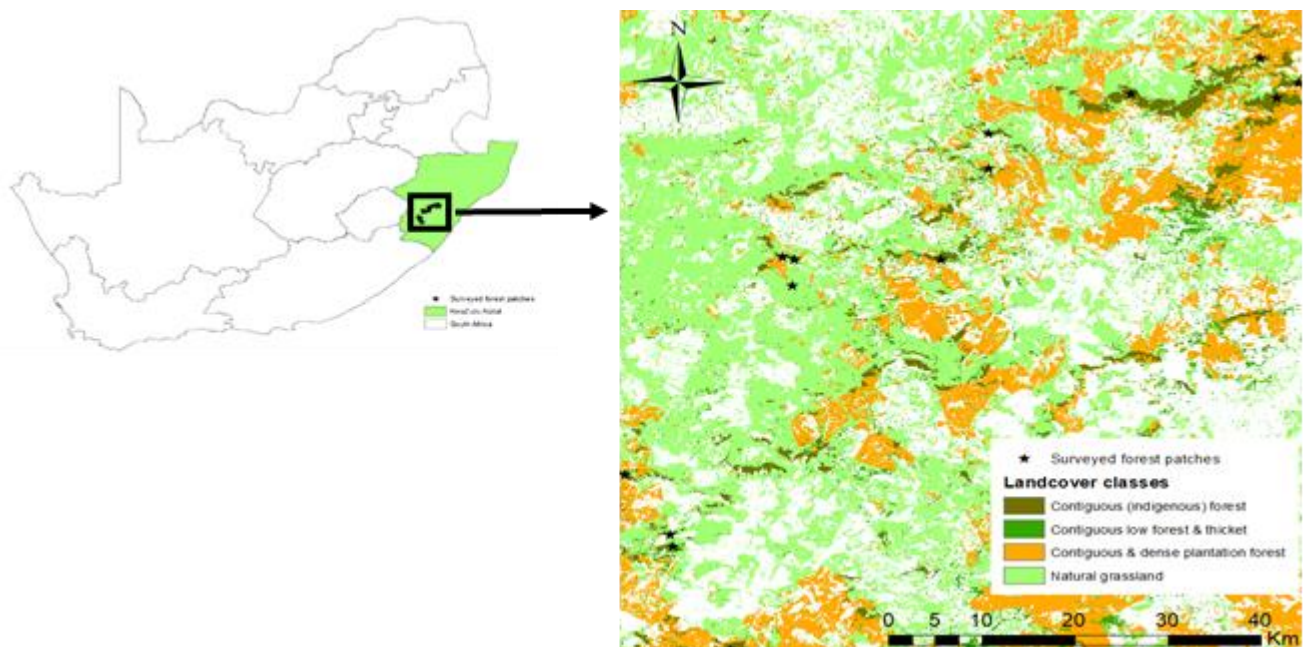


Figure 5.1 Location of 14 selected and studied Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

5.3.2 Study species

The orange ground-thrush (*Geokichla gurneyi*) is a near-threatened, medium (64 g, 21-23 cm) ground-dwelling forest specialist bird species (Hockey et al., 2005). The distribution of the orange ground-thrush includes Kenya, Tanzania, Democratic Republic of Congo, Malawi, Mozambique, Zimbabwe and South Africa. It is found in four provinces in South Africa, including Mpumalanga, Limpopo, Eastern Cape, and KwaZulu-Natal (Hockey et al., 2005). Generally, the orange ground-thrush (*G. gurneyi*) is an uncommon, solitary, insectivorous bird that forages on the ground, mostly on earthworms. It nests in a bulky bowl-shaped cup placed from the ground to 3.7 m from the forest floor (Hockey et al., 2005; Tarboton and Roberts, 2011). It prefers open areas within the forest and carpets of leaf litter with little or no vegetation (Earle and Oatley, 1983; Gumede et al., 2022). In South African forests, the average range decline on the orange ground-thrush is estimated at 8.3% (Cooper et al., 2017).

The forest canary (*Crithagra scotops*) is a small (15 g, 12-13 cm) forest understorey specialist. It is nearly endemic to South Africa and extends marginally into Lesotho and Swaziland (Hockey et al., 2005). In South Africa, it is found in forest patches in three provinces: Limpopo, KwaZulu-Natal, and Western Cape. It forages mainly on seeds in the mid to upper canopy of the forest. A nest is a bulky cup (60 mm) of mostly mosses or *Usnea*, hidden in foliage placed 1-6 m above ground (Hockey et al., 2005; Tarboton and Roberts, 2011). In South African forests, the average range decline in the forest canary is estimated at 10.2% (Cooper et al., 2017).

The Cape parrot (*Poicephalus robustus*) is a relatively large (300 mm, 300 g) endangered forest specialist bird species. It is endemic to the Afromontane Forest of South Africa, primarily in the canopy of *Afrocarpus* or *Podocarpus* spp. It feeds mainly on endocarps of *Afrocarpus* or *Podocarpus* spp with seasonal changes in diet to include other fruits like *Celtis africana* and exotics outside the forest when food is unavailable (Hockey et al., 2005;

Wimberger et al., 2023; Wirminghaus et al., 2001). The Cape parrot (*P. robustus*) nests in tree cavities of tall and large yellowwood forest trees about 15 m from the forest floor (Leaver et al., 2023; Tarboton and Roberts, 2011; Wirminghaus et al., 2001). The percentage range decline in South African forests is estimated at 58.3% (Copper et al., 2017).

5.3.4 Bird surveys

Systematic grids of 200 x 200 m were overlaid using the recent South African indigenous forest cover (South African National Land-Cover 2020) for the selected forest patches in ArcGIS v10.6 (Ehlers Smith et al., 2017). The axes of the grid were assigned a survey point, and the points were 200 m apart. In total, we had a total of 742 fixed radius point counts (371 per season) within the 14 studied forest patches. The points were then projected into a global position system (GPS) and a Garmin eTrex 10 (USA) used to locate the points in the field. If the projected points were inaccessible in the field, a new survey point was created within 50 m of the original point. Within each point, we used a fixed-radius of 100 m to record all bird species detected visually or audibly during the 10 min sampling period. The point counts were conducted within 3 h from sunrise. The number of individuals for each identified bird was recorded for each survey point. All the points were surveyed once during the seasons of breeding (Oct 2020 – Mar 2021) and non-breeding (May 2021-Sept 2021).

5.3.5 Vegetation sampling, logging history and livestock grazing

To quantify alien plant invasion in the surveyed forest patches, we conducted vegetation surveys at each point-count within a radius of 20 m. The surveys were conducted during the wet (breeding season) and dry (non-breeding season). At each point, we identified all the tree species, including the dominant and co-dominant tree species. Using the vegetation data of alien invasive plants, we categorised the remnant forest patches into alien plant-invaded, and

non-invaded forest patches. In the surveyed Southern Mistbelt Forest patches, *Solanum mauritianum* (bugweed) was the only invasive plant invading these forests. Therefore, the forest invasion categories were based on invasion by bugweed.

We identified the logging history of the surveyed forest patches through literature and based on the knowledge of the current landowners or conservation managers. Even though there are presently no historical records of the amount of timber extracted in the Southern Mistbelt Forests (Adie et al., 2013), the exploitation in the Karkloof region was intensive (Rycroft, 1944). Some of the Southern Mistbelt Forests in the Midlands of KwaZulu-Natal were unlogged either because of inaccessibility (King 1941) or privately owned (J. Geekies pers. comm.). Since 1940, the studied forest patches have not been selectively logged (Lawes et al., 2004). Thus, the forest patches were categorised into logged (naturally regenerating) and unlogged patches based on the selective logging history of 150 years.

To assess livestock grazing, we used bycatch data from camera trap surveys. The camera traps were initially set out to assess bird and mammalian communities in the studied forest patches. The camera traps (Cuddeback 20 MP and Moultrie M-880) were conducted from October 2020 to September 2021. The cameras were set out systematically using 400 x 400 m grids that were created using ArcGIS 10.8.1 (ESRI, Redlands, CA, USA). At each site, the camera was out for at least 21 days surveying 24 hours. The camera traps were placed on tree trunks approximately 30 cm above the ground and set to a 30 s setting delay. In total, we set out 368 camera traps, 184 per season. If the selected tree species were not naturally open, vegetation was cleared to minimise sensor obstruction. To quantify livestock intensity, we calculated RAI per forest patch as follows: $RAI = A/N*100$ (Li et al., 2022; O'Brien et al., 2003;). A represents the total number of captures, and N is the total camera days. Livestock captures of the same species were considered independent photographs if they were captured

over 30 min apart (O'Brien et al., 2003). The forest patches were then categorised into a grazing disturbance gradient ranging from high grazing intensity to no grazing.

The Southern Mistbelt Forest patches are naturally nested in a grassland matrix, at least since ca. 18 000 years BP (Meadows and Linder, 1993). Therefore, forest patches adjacent to other land use types (i.e., exotic plantations) have shrunk forest margins (Lawes et al., 2004). In our study region, the dominant land-use type surrounding the surveyed forest patches in exotic plantations and grassland. Thus, we categorised the surveyed forest patches' adjacent land use into two matrix land use categories: exotic timber plantation (converted) (n = 7) and grassland-dominated matrix (n = 7).



Figure 5.2 Records of grazing by cattle and goats in selected Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

5.3.6 Bird functional diversity

We created a functional trait matrix (Supplementary Information Table S5.1) for each bird species that relates to the species' functional roles and responses to habitat disturbance (Flynn et al., 2009). We focused on bird species' primary diet, body mass, foraging strategy, habitat specificity and nesting type as the key functional traits (Flynn et al., 2009; Hockey et al., 2005). Functional diversity was quantified using three indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) based on Gower functional dissimilarity using 'dbFD' function in 'FD' package. Functional richness quantifies the functional space occupied by a given community (Villéger et al., 2008) and increases as unique trait combinations are present in a community, filling a larger volume. Functional evenness measures the regularity of species dissimilarities and abundance in the multidimensional space (Villéger et al., 2008). This index increases if the functional trait space is evenly occupied (Mason et al., 2013). Functional divergence measures niche differentiation in a community by considering abundance distribution within the functional space of a species within the community (Villéger et al., 2008). We created a bird abundance and presence/ absence matrix for each surveyed patch. We then calculated FDiv, FEve and FDiv for the whole bird community, forest specialists, forest generalists, insectivores, omnivores, cavity and ball or cup nesters. The functional diversity indices calculations were based on Gower functional dissimilarity using the function 'dbFD' in the package "FD" (Laliberté et al., 2014).

Table 5.2 Functional traits used in this study to characterise functional diversity of birds in selected Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa

Functional trait	Trait type	Categories or range
Body mass	Continuous	7- 4000 g
Foraging strategy	Categorical	Arboreal probe, glean, harvest, hawk, perch and swoop, terrestrial probe or various
Habitat specificity	Categorical	Generalist, specialist
Nesting type	Categorical	Ball/cup, cavity, or platform
Primary diet	Categorical	Carnivory, frugivory, granivore, insectivory, nectarivory, omnivory

5.3.7 Data analyses

To assess the influence of selective logging history, matrix type, invasion and livestock grazing on bird species richness for the whole community we used linear mixed-effects models using the package "lme4" in R. Spatial autocorrelation for all the indices was tested using *Moran's I* using the package "ape" in R (Paradis et al., 2004). The models were constructed separately for all the functional communities (i.e. whole community, forest specialists, forest generalists, insectivores, omnivores, cup or ball and cavity nesters) and functional diversity indices (Fric, FEve and FDiv). The forest patch region was included as a random effect. The model with the lowest AIC value was selected as the best model. All the analyses were in R version 4.2.0 (R core Team, 2022).

5.4 Results

5.4.1 Taxonomic diversity

A total of 96 bird species (12 947 individuals) were recorded across the selected forest fragments. Of the 96 species, 39 were forest specialists, and 57 were forest generalists ranging between 7 to 4000 g in body size (Supplementary Information Table S5.1). The most abundant forest generalist bird species were southern boubou (*Laniarius ferrugineus*) (n = 1313), sombre greenbul (*Andropadus importunus*) (n = 884) and southern double-collared sunbird (*Cinnyris chalybeus*) (n = 809) combined across seasons. The most abundant forest specialist bird species were bar-throated apalis (*Apalis thoracica*) (n = 815), green-backed camaroptera (*Camaroptera brachyura*) (n = 676) and Knysna turaco (*Tauraco corythaix*) (n = 428). In selectively logged forest patches, the southern boubou (n = 738), sombre greenbul (n = 530) and the Cape white-eye (*Zosterops virens*) (n = 504) were the most abundant generalist bird species. In unlogged forest patches, the abundant birds were the southern boubou (n = 575), southern double-collared sunbird (n = 399) and bar-throated apalis (n = 364). The most abundant forest generalists in forest patches adjacent to a grassland and exotic plantation matrix were southern boubou, sombre greenbul and southern double-collared sunbird. Insectivores were the most common dietary guild (51%), followed by omnivores (15%) and frugivores (14%). Cup and ball nesters (61%) were the dominant, followed by cavity (15%) and ground nesters (11%).

The orange ground-thrush (*Geokichla gurneyi*) was present in ten of the 14 surveyed forest patches. Four of the ten patches were historically logged, *Solanum mauritianum* had invaded nine and five were livestock grazed (i.e., 3 = low intensity; 2 = high intensity). The orange-ground thrush was more abundant in Karkloof Nature Reserve (n = 28) and least abundant in Rameron Forest (n = 3). The forest canary (*Crithagra scotops*) was present in five of the 14 survey patches. Of the five, two patches were historically logged, four were alien

plants invaded, and three were grazed by livestock. The forest canary was most abundant in Karkloof Nature Reserve (n = 9). The Cape parrot (*Poicephalus robustus*) was only present in four of the 14 surveyed Southern Mistbelt Forest patches. All the remnant forest patches in which the Cape Parrot was present were in the Bulwer region with no historical logging history by European settlers. Of the four, three are invaded by *Solanum mauritianum*, except Ingelabantwana Nature Reserve, and all four are livestock grazed. Three of the four patches were adjacent to the exotic commercial tree plantation, and one (i.e., Ingelabantwana Nature Reserve) was adjacent to a grassland. The Cape parrot was most abundant in Ingelabantwana Nature Reserve (n = 74) and least abundant in Xotsheyake Nature Reserve (n = 4).

Bird species richness for the whole bird community did not differ significantly in varying livestock grazing intensities ($p = 0.44$, Figure 5.3). Historically, selectively logged forest patches had a significantly higher bird diversity than unlogged patches, and invaded forest patches had significantly higher bird species richness ($p < 0.05$; Figure 5.3).

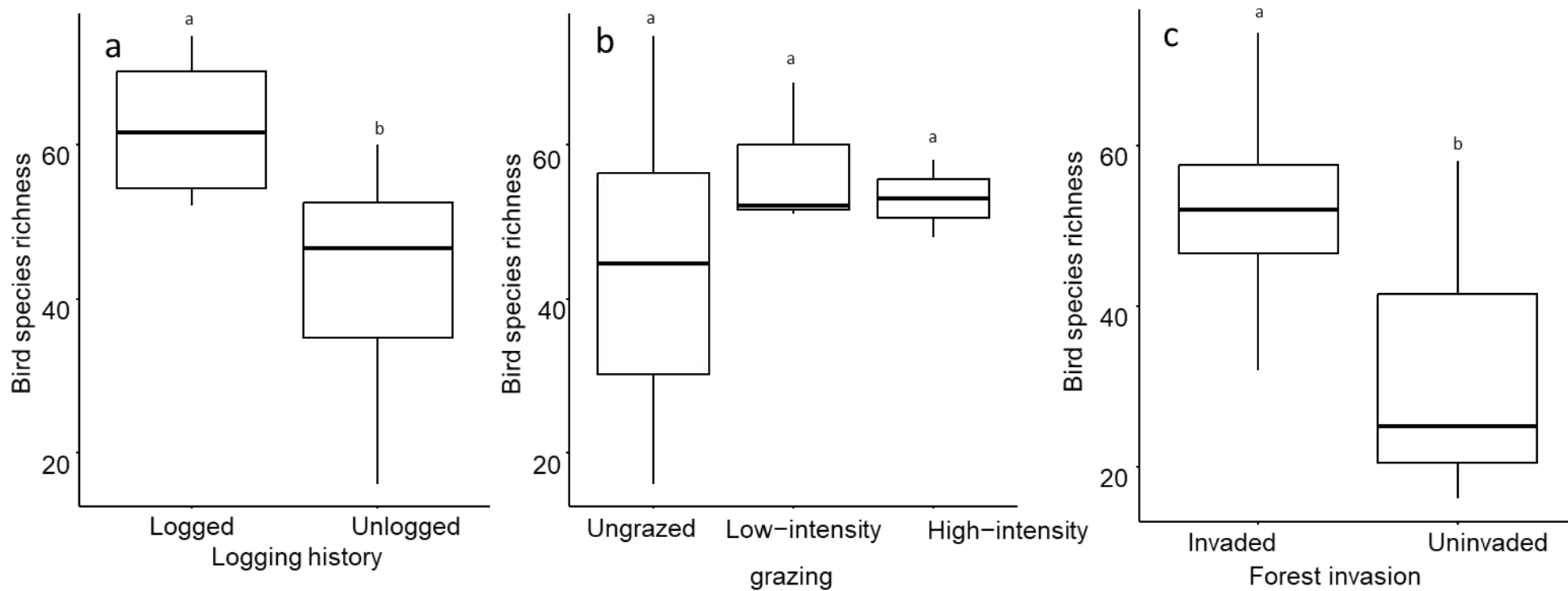


Figure 5.3 Bird species richness in selected 14 Southern Mistbelt Forest patches with different selective logging history (a) and livestock grazing (b) and invasion by *Solanum mauritianum* in the Midlands of KwaZulu-Natal, South Africa. (Significant ($p < 0.05$) are indicated using different letters (i.e. a, b)).

5.4.2 Functional diversity

Functional Richness

Functional richness for omnivores and insectivores was significantly higher in forest patches with high-intensity livestock grazing ($p < 0.05$; Figure 5.4). Selectively logged forest patches had significantly higher FRic for forest specialists, omnivores and cup or ball nesters (Figure 5.5). Functional richness for the whole bird community was significantly influenced by unlogged forest patches (-0.15 ± 0.04) and forest patches adjacent to plantations (-0.14 ± 0.05). Forest bird specialist functional richness was negatively influenced by forest patches adjacent to plantations (-0.92 ± 0.17), low-intensity grazed forest patches (-0.43 ± 0.20), and forest patches uninvaded by *Solanum mauritianum* (-1.23 ± 0.17). Unlogged forest patches were significantly ($p < 0.001$) not associated with generalists' functional richness (-0.76 ± 0.34). Uninvaded forest patches significantly negatively influenced the functional richness of generalists functional richness (-0.63 ± 0.39). Insectivorous bird species were negatively influenced by forest patches adjacent plantations (-2.00 ± 0.59), uninvaded forest patches (-2.76 ± 0.58) and ungrazed patches (-2.46 ± 0.57). Similarly, omnivorous birds were negatively influenced by forest patches adjacent to exotic plantations (-1.53 ± 0.88) and uninvaded forest patches (-1.15 ± 0.87). Cup or ball nesters were negatively influenced by unlogged forest patches (-2.85) and positively influenced by high-intensity grazing (1.22 ± 0.61). Cavity nesters' functional richness was positively influenced by high-intensity grazing (2.15 ± 0.80). The functional richness of all ecological groups were positively influenced by forest patches adjacent to a grassland matrix and patches invaded by *Solanum mauritianum*.

Functional evenness

Functional evenness of cavity nesters was significantly higher in forest patches adjacent to the exotic plantation ($p < 0.05$; Figure 5.6). For forest specialists, FEve was higher in unlogged forest patches, while for cavity nesters FEve was higher in logged forest patches ($p < 0.05$; Figure 5.6). Functional evenness for the whole bird community was significantly ($p < 0.05$) negatively influenced by high-intensity grazing and positively influenced by low-intensity grazing (0.05 ± 0.023), while unlogged forest patches (0.06 ± 0.01) had a positive influence on functional evenness. For forest specialists, functional evenness was negatively influenced by forest patches adjacent to plantations (-0.72 ± 0.39) and positively influenced by uninvaded forest patches (0.39 ± 0.24). While forest generalists, bird species functional evenness was positively significantly influenced by forest patches adjacent to plantations (0.71 ± 0.14) and positively influenced by uninvaded forest patches (0.28 ± 0.13). Insectivorous forest bird functional evenness was significantly ($p < 0.05$) negatively influenced by forest patches adjacent to plantations (-0.52 ± 0.31) and unlogged forest patches (-0.62 ± 0.27). While functional for omnivorous bird species, functional evenness was positively influenced by unlogged forest patches (0.14 ± 0.06). Functional evenness for cup or ball nesters was negatively influenced by low-intensity grazing (-0.55 ± 0.08) and positively influenced by forest patches adjacent to plantations (0.05 ± 0.04) and uninvaded forest patches (0.49 ± 0.47). Similarly, for cavity nesters, low-intensity grazing (-0.10 ± 0.09) negatively influenced functional evenness. Forest patches adjacent to a plantation matrix (-0.21 ± 0.08) and uninvaded forest patches negatively influenced the functional evenness of cavity-nesting forest birds.

Functional divergence

Functional divergence for forest specialist species was significantly lower in low intensely grazed forest patches ($p < 0.05$; Figure 5.4). For cavity nesters, FDiv was significantly higher in highly grazed forest patches ($p < 0.05$; Figure 5.4). Forest specialists had significantly higher FDiv in forest patches adjacent to a grassland matrix than generalist bird species (Figure 5.6). Functional divergence for the cup or ball nesters was significantly higher in ungrazed forest patches ($p < 0.05$; Figure 5.5). Functional divergence for the whole bird community was positively influenced by uninvaded forest patches (0.18 ± 0.16) while unlogged (-0.31 ± 0.14), adjacent to plantations (-0.23 ± 0.16), and low-intensity grazed (-0.39 ± 0.18) had a negative influence on FDiv. For forest specialists, unlogged (0.39 ± 0.14) and uninvaded forest patches had a positive influence on FDiv, while forest patches adjacent to plantations (-0.41 ± 0.15) and low-intensity grazed (-0.97 ± 0.18) patches had a negative influence on FDiv. Similarly, forest generalist FDiv was negatively influenced by forests adjacent to plantations (-0.80 ± 0.34). For generalists, bird species FDiv was positively influenced by low-intensity grazing (0.37 ± 0.20) and negatively influenced by unlogged forest patches (-0.49 ± 0.30). Functional divergence for insectivorous birds was negatively influenced by forest matrix adjacent to plantations (-0.47 ± 0.18), unlogged (0.40 ± 0.08) and uninvaded forest patches (-0.46 ± 0.17). Similarly, omnivores were negatively influenced by the plantations matrix (-0.26 ± 0.16), unlogged forests (-0.22 ± 0.14), and uninvaded forest patches (-0.74 ± 0.16). Functional divergence for cup or ball nesters was negatively influenced by plantation matrix (-0.16 ± 0.04), unlogged (-0.10 ± 0.04) and uninvaded (-0.54 ± 0.46) forest patches. Similarly, forest cavity-nesting birds FDiv was negatively influenced by ungrazed (-0.53 ± 0.10), uninvaded (-0.49 ± 0.11) and forest patches in a plantation-dominated matrix (-0.23 ± 0.11).

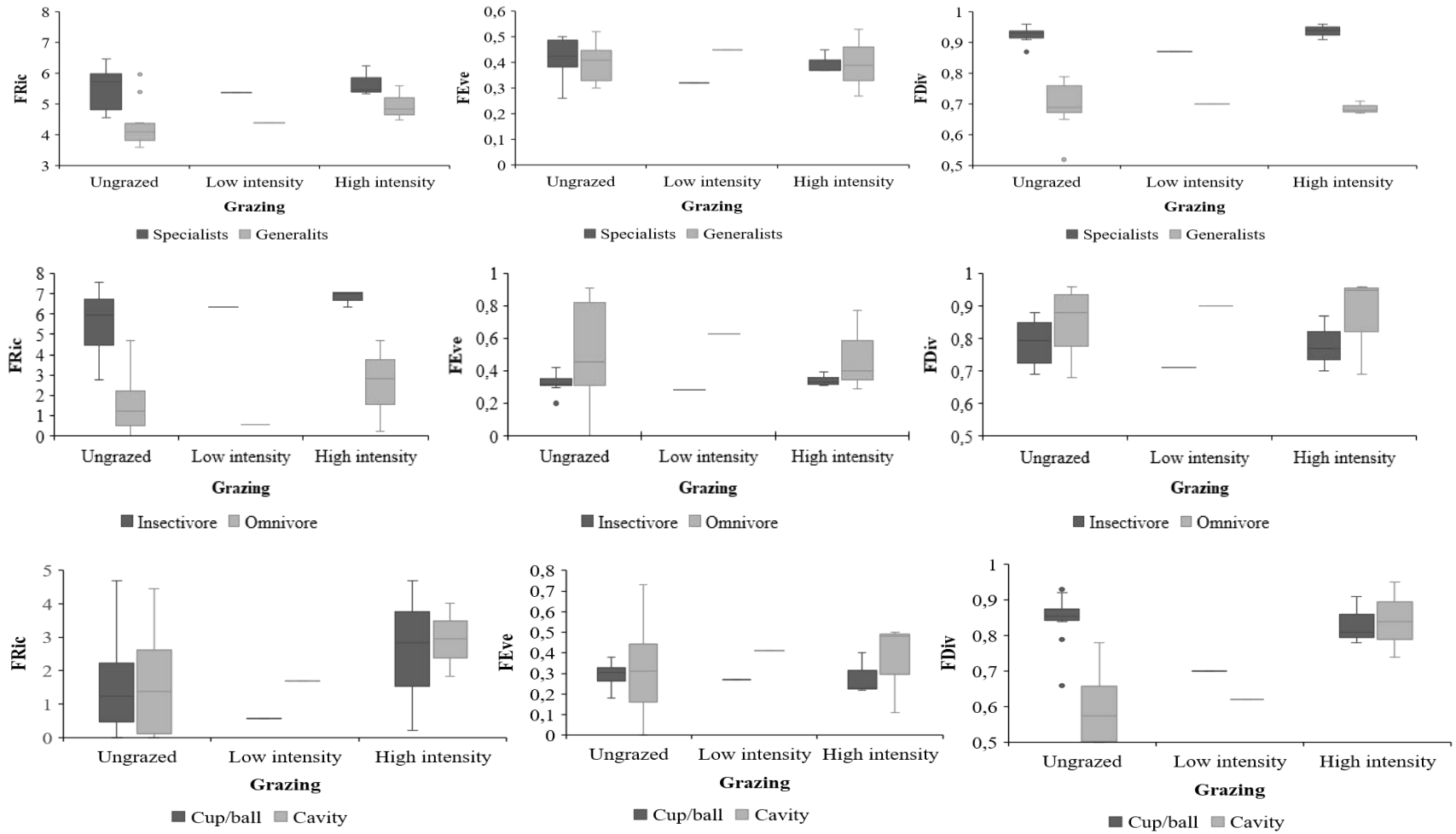


Figure 5.4 The influence of livestock grazing on bird functional communities in the Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

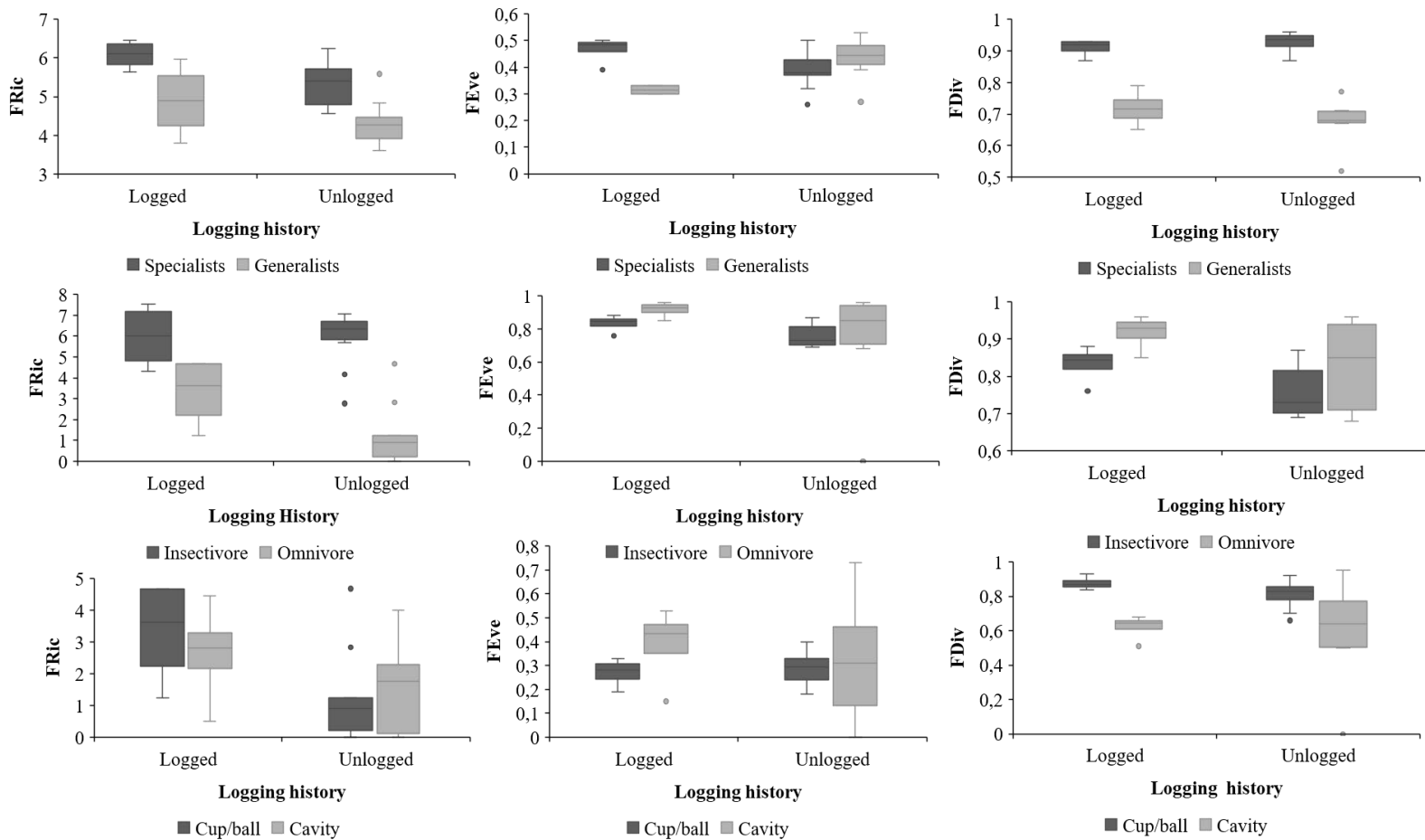


Figure 5.5 The influence of logging history on bird functional communities in the Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

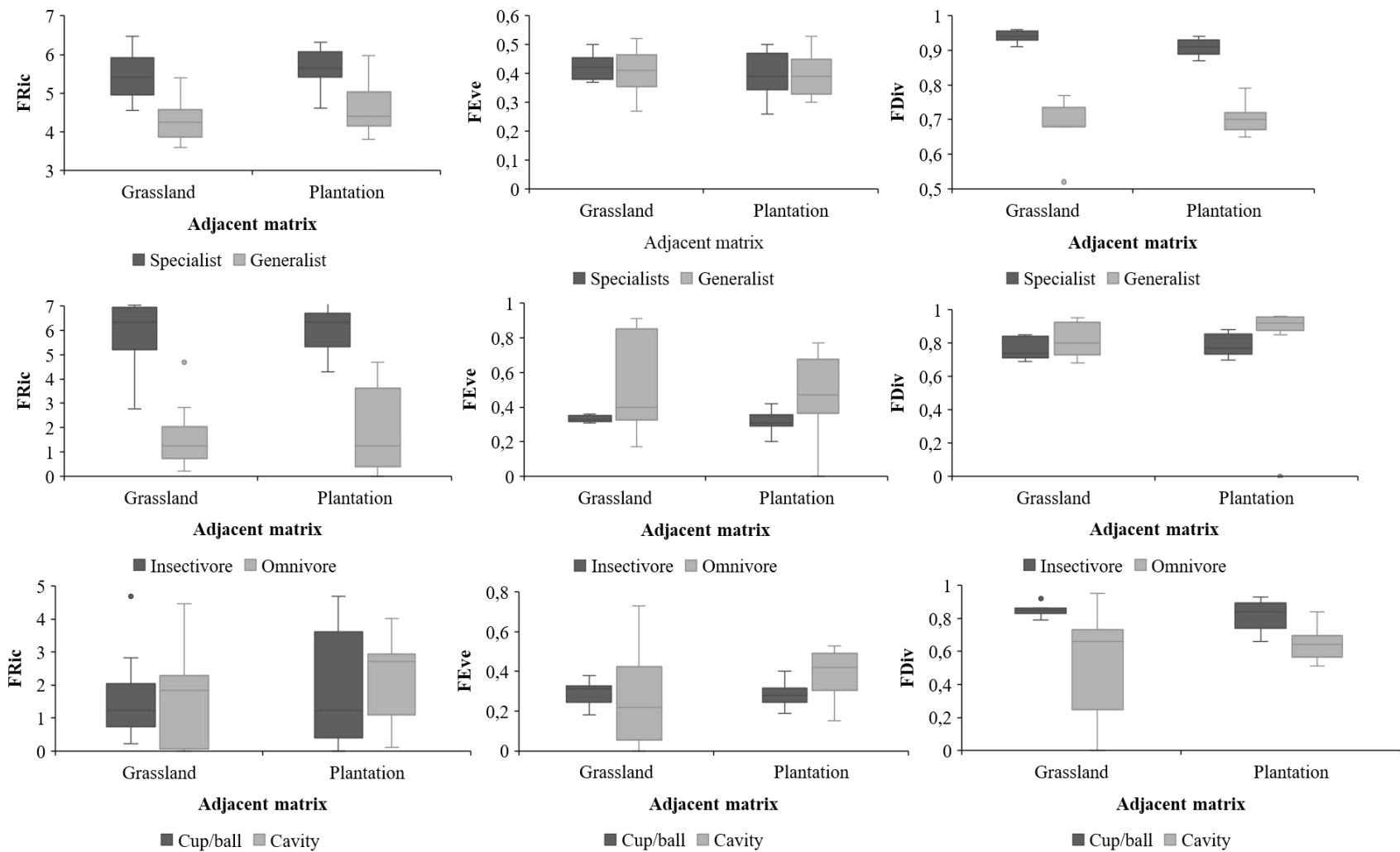


Figure 5.6 The influence of adjacent matrix on bird functional communities in the Southern Mistbelt Forest patches in the Midlands of KwaZulu-Natal, South Africa.

5.5 Discussion

Understanding anthropogenic disturbances' effects on forest communities has become increasingly important for conservation and responses to global environmental changes (Cosset and Edwards, 2017; de Bello et al., 2013; Vieira et al., 2009). Here, we assessed the effects of livestock grazing, alien plant invasions, selective logging history and matrix-type adjacent to forests on bird species richness, functional diversity and forest specialist bird species. As predicted, our results showed how the richness of forest bird species, species-specific responses, and functional communities vary with disturbance type and, in some instances, disturbance intensity. Previous studies have also shown the variation in bird functional communities' response to forest disturbance (Gray et al., 2007; Lindenmayer et al., 2006). Our results emphasise the importance of simultaneously assessing the responses of different functional communities to understand the effects of forest disturbance better.

Bird species richness was significantly higher in invaded and selectively logged forest patches. Previous studies have shown that species richness of birds and other taxa recover from disturbance as species composition changes to more open-habitat species in forest systems (Carreño-Rocabado et al., 2012; Ernst et al., 2006; García-Morale et al., 2016; Holbech, 2005; Mulwa et al., 2021; Pearce and Venier, 2006). Consequently, it has been argued that species richness as a response proxy is not an excellent ecological indicator for assessing species responses to disturbance (Bongers et al., 2009). These results emphasise using different diversity indicators so one method can inform conservation and forest management if one method does not reveal potential responses (Lindenmayer et al., 2000).

The Cape parrots were absent in historically selectively logged forest patches. This is contrary to the findings of Rea et al. (2023), who showed that Cape parrots were present in

previously logged forest patches. The Karkloof region forest patches were intensively logged (Rycroft, 1944), with potential changes to the habitat quality and microhabitat changes because of tree removal. For example, in the Karkloof region, about 14 million cubic feet of timber was removed in the 1860s, estimated to have been £ 150 000 at that time, owned by W.R. Shaw (McCracken 1986). The selective logging in the Southern Mistbelt Forest mainly targeted large tree species (Seydack and Vermuelen, 2004) and decreased *Podocarpus/ Afrocarpus* spp. (Downs, 2005a, b; Downs et al., 2014). It is essential to note the sensitivity of these birds to habitat destruction, particularly the loss of *Podocarpus /Afrocarpus* spp. Therefore, Cape parrots being absent in the Karkloof forest patches may be an indication of non-recovery in previously intensively logged forest patches because of reduced microhabitats for foraging and nesting maintain populations in the Karkloof area. Contrarily, the orange ground-thrush and forest canary were influenced by the livestock grazing intensity. Livestock grazing has been shown to affect ground-dwelling forest species in xerophytic forests in Argentina (Dardanelli et al., 2022). The effects of grazing on small ground foraging birds are because of the habit change in structure, composition and complexity (Baldi et al., 2005; Holbech, 2005; Val et al., 2018). Also, cattle might also trample nests of ground-nesters.

Contrary to our expectations FRic for forest bird specialists was higher in invaded and previously selectively logged patches. These results indicate that forest invasion by *S. mauritanum* is not a strong filter for bird communities in the Southern Mistbelt Forest patches. Forest specialists may be increasing their resources by *S. mauritanum* when resources are limited. These results were contrary to previous studies that have shown that alien invasive plant species negatively affect forest specialists (Avarind et al., 2010; Ayup et al., 2014; Hood-Nowotny et al., 2023). It has been argued that invasive plant species can contribute to the heterogeneity of forests,

increasing food or nesting resources (Chabrerie et al., 2009). Also, the high species richness of generalists and least sensitive groups (e.g., omnivores; generalists) in disturbed forest patches can contribute to high FRic or the few specialist bird species with high abundance (e.g. Knysna turaco, bar-throated apalis). Neuschulz et al. (2011) showed that in the scarp forest in KwaZulu-Natal, higher bird abundance in the disturbed site was because of the high abundance of generalists. Previous studies have shown that FRic and species richness correlate, increasing trait space volume (Villéger et al., 2008; Ding et al., 2013). Forest generalists FRic increased in highly intensely grazed and previously logged forest patches. Similarly, in South Asian forests, functional richness for forest generalists was higher in logged forest patches (Edwards et al., 2014). This was expected as forest generalist bird species increased in disturbed forest patches (Hanzelka and Reif, 2015; Bitani et al., 2020).

For forest specialists, FEve was higher significantly in unlogged forest patches, while for cavity nesters and forest generalists, FEve was higher in logged forest patches. Similar to our results, Rea et al. (2023) showed that cavity nesters were not affected by the logging history of about 25 years. Higher FEve relates to the even exploitation of resources (Mason et al., 2005). The high FEve for forest generalists and cavity nesters in disturbed forest patches can be linked to lower structural complexity in disturbed habitats (Schleuter et al., 2010). However, for forest specialists, higher FEve values can result from evenly distributed and efficient use of resources resulting from high structural heterogeneity in unlogged forest patches. These results indicate that in unlogged forest patches, forest specialist bird species can exploit specialised niches (Davies and Asner, 2014). In previously selectively logged patches, forest specialists are low in abundance because of the decline in resources and edge effects (Newmark, 2006). Cavity nesters had higher FDiv in highly grazed forest patches. Also, insectivores and omnivores were relatively higher in

previously logged forest patches. High FDiv values indicate high competition for resources in disturbed patches (Mason et al., 2005).

The general pattern in this study, forest disturbance mainly influenced bird species FEve than FRic and species richness. This pattern has also been reported in other studies where disturbance does not affect FRic and bird species richness (Edwards et al., 2014; Leaver et al., 2019). Also, FRic responds more like species richness than other functional diversity indices. In this study, FEve was a good indicator of the responses of functional communities in the present study. Therefore, species' functional diversity will depend on the specific aspect explored.

5.5.1 Conclusions

This study's primary goal was to assess the effects of landscape characteristics on bird functional communities in the Southern Mistbelt Forests. From this study's main findings, different functional communities responded differently to different types of remnant forest patches of the Southern Mistbelt Forest patches. Also, forest specialist bird responses to disturbance were species-specific depending on the anthropogenic disturbance type and intensity for some species. Furthermore, for sensitive bird species like forest specialists and insectivores, forest disturbance mainly affected FEve more than FRic. Cape parrots have not recovered from the intense selective logging in the Karkloof for approximately 78 years of natural recovery. This highlights the importance of protecting primary undisturbed forests, as not all species can recover from forest selective logging. Bird species richness response could not have provided an understanding of the potential impacts on different ecological communities. Therefore, to have a holistic understanding of the disturbance effects on bird functional communities, studies must concurrently assess different disturbance types and functional diversity indices to make informed conservation decisions. Studies assessing

the responses of bird functional communities should use taxonomic indicators complementary to functional diversity indices to maintain ecosystem processes with forests.

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5.8 Supplementary Information

Supplementary Information Table S5.1: Functional trait matrix of bird species recorded in selected Southern Mistbelt Forest patches in South Africa.

Species name	Body mass	Dietary guild							Foraging strategy					Nesting strategy				Habitat specificity		
		Carnivory	Frugivory	Omnivory	Nectarivory	Granivory	Insectivory	Harvest	Terrestrial probe	Arboreal probe	Glean	Hawk	Perch and swoop	Various	Ground	Ball or cup	Cavity	Platform	Generalist	Specialists
<i>Andropadus importunus</i>	31	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Apalis flavida</i>	8	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Apalis thoracica</i>	10.5	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Apaloderma narina</i>	67	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1
<i>Aplopelia larvata</i>	150	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1
<i>Batis capensis</i>	12	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Bostrychia hagedash</i>	1250	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Bradypterus barratti</i>	15	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0
<i>Bucorvus leadbeateri</i>	3770	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Buteo trizonatus</i>	660	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
<i>Bycanistes bunicator</i>	644	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>Camaroptera brachyura</i>	11	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Campephaga flava</i>	32	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Campethera abingoni</i>	70	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1
<i>Campethera notata</i>	62	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1
<i>Centropus burchellii</i>	180	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Cercotrichas leucophrys</i>	17.9	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Chalcomitra amethystina</i>	15	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Chrysococcyx cupreus</i>	35	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1

<i>Chrysococcyx caprius</i>	30	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Chrysococcyx klaas</i>	26	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Cinnyris chalybeus</i>	8	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Cisticola aberrans</i>	13	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Clamatar jacobinus</i>	81	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Coccopygia melanotis</i>	6.5	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Colius striatus</i>	55	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Columba arquatrix</i>	407	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>Columba delegorguei</i>	160	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
<i>Coracina caesia</i>	60	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Cossypha caffra</i>	28	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Cossypha dichroa</i>	46	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Cossypha natalensis</i>	32	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1
<i>Crithagra scotops</i>	15	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Crithagra sulphurata</i>	17	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
<i>Cuculus clamosus</i>	90	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Cuculus solitarius</i>	75	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Cyanomitra olivacea</i>	11.5	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Dendropicos griseocephalus</i>	45	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1
<i>Dicrurus adsimilis</i>	43.8	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Dryoscopus cubla</i>	26	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Elstrida astrilid</i>	8	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Guttera edouardii</i>	1300	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
<i>Hedysdipna collaris</i>	8	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
<i>Indicator minor</i>	28	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0
<i>Indicator variegatus</i>	48	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1
<i>Ispidina picta</i>	15	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1
<i>Lagonostriкта rhodopareia</i>	10.3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Laniarius ferrugineus</i>	60	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Lanius collaris</i>	40	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1

<i>Lioptilus nigricapillus</i>	31	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	
<i>Lophaetus occipitalis</i>	1055	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
<i>Lybius torquatus</i>	54	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	
<i>Malaconotus blanchoti</i>	77	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	
<i>Melaenornis pammelaina</i>	30	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0
<i>Muscicapa adusta</i>	11	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0
<i>Muscicapa caerulescens</i>	16.5	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>Myioparus plumbeus</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0
<i>Nectarinia fanosa</i>	15	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0
<i>Numida meleagris</i>	1350	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Orious larvatus</i>	65	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Onychognathus morio</i>	140	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Parus niger</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0
<i>Phoeniculus purpureus</i>	76	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0
<i>Phyllastrephus terrestris</i>	31.5	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
<i>Phylloscopus ruficapilla</i>	8	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Ploceous bicolor</i>	35	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Ploceous ocularis</i>	30	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Ploceus velatus</i>	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pogoniulus pusillus</i>	17	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
<i>Pogonocichla stellata</i>	21	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1
<i>Poicephalus robustus</i>	300	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>Polemaetus bellicosus</i>	4000	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
<i>Prinia subflava</i>	9.5	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
<i>Pternistis natalensis</i>	445	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Pternistis afer</i>	640	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
<i>Pternistis swainsonii</i>	585	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
<i>Pycnonotus tricolor</i>	37.3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Sarothruta elegans</i>	45	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1
<i>Spermestes cucullata</i>	10	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0
<i>Stephanoaetus coronatus</i>	3400	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1

<i>Streptopelia capicola</i>	150	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
<i>Streptopelia semitorquata</i>	235	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
<i>Streptopelia senegalensis</i>	100	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
<i>Sylvietta rufescens</i>	11	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0
<i>Tauraco corythaix</i>	300	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Chlorophoneus olivaceus</i>	33	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1
<i>Telophorus viridis</i>	37	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0
<i>Terpsiphone viridis</i>	14.3	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0
<i>Tockus nasutus</i>	225	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
<i>Treron calvus</i>	235	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Trochocercus cyanomelas</i>	10	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Turdus olivaceus</i>	66	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
<i>Turtur tympanistria</i>	71	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Upupa africana</i>	53	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0
<i>Geokichla gurneyi</i>	68	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Zosterops virens</i>	13.5	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0

CHAPTER 6

Conclusions and recommendations

6.1 Introduction

Forests are threatened globally by land use changes driving species distribution and composition shifts (Watt et al., 2002; Martínez et al., 2009; de Castro Solar et al., 2016). This structural damage leads to habitat loss or small fragmented patches with reduced habitat quality (Bueno et al., 2018; Lindenmayer et al., 2020). Like any other part of the world, South African forests are threatened by anthropogenic impacts, mainly habitat destruction (Leaver et al., 2019) and forest conversion to exotic tree plantations (Freeman et al., 2018). Anthropogenic impacts on species are space scale-dependent as different factors drive habitat selection at different scales (Pennington & Blair, 2011; Hingee et al., 2022). Consequently, it is important to understand the drivers of habitat selection at landscape and local scales for biodiversity conservation. This study aimed to assess the influence of local patch characteristics and landscape factors influencing avian species communities. The objectives of the study were to determine (1) threats to avian communities in African forests and their responses, (2) microhabitat structural drivers and influences on bird species richness and functional diversity, (3) Microhabitat requirements and occupancy of understory forest bird specialists using camera traps, and (4) landscape attributes influencing avian species functional communities.

6.2 Threats to avian in African forests

Forest destruction is a major threat to biodiversity and ecosystem functionality. The success of conservation strategies depends on a better understanding of the main driver of bird species and their responses to global environmental change. Synthesising existing knowledge is important as

it contributes to the knowledge and understanding effort that has been done in that specific subject (Lim et al., 2022; Varjani et al., 2019; Kraus et al., 2022). Anthropogenic impacts on avian communities were assessed by synthesizing published literature systematically using the PRIMSA methodology (Chapter 2). The results showed the research interest in understanding anthropogenic impacts on avian communities in Africa has gradually grown. Studies showed a geographic bias with more studies in South Africa and eastern African countries (e.g., Madagascar). The main anthropogenic impacts in Africa can be broadly categorised into habitat fragmentation and degradation. Some activities that have contributed to this disturbance are the conversion of forests to exotic commercial tree plantations, agriculture and selective logging (Chapter 2). Generally, forest-dependent species were the most sensitive group to habitat quality changes. Species responses varied depending on spatial scale, ecological group and were species-specific. Despite progress, our understanding of anthropogenic impacts on bird functional diversity is still limited (Chapter 2).

6.3 Influence of forest structure and tree diversity on birds

Understanding avian community habitat use and the effect of forest composition and structure allows for the development of conservation management plans to conserve species microhabitats (Díaz et al., 2005). In the Southern Mistbelt Forest in the Midlands of KwaZulu-Natal, there is a lack of studies assessing the effects of structural characteristics on avian communities. Effects of forest composition and structure on bird species community structure, habitat use and functional diversity were assessed (Chapter 3). The findings of the study showed that bird community and forest specialist species' responses to tree species richness vary. Bird functional diversity was influenced mainly by forest structural complexity, canopy cover and tree species richness (Chapter

3). Forest patches with high complexity and tree species richness had higher functional richness. For bird species-specific responses orange ground-thrush (*Geokichla gurneyi*) and forest canary (*Crithagra scotops*) were positively influenced by trees species richness, while Cape parrots (*Poicephalus robustus*) were not influenced by tree species richness (Chapter 3). The present study confirmed that tree species richness should be maintained and is important in conserving forest specialists, bird species richness and functional richness (Chapter 3).

6.4 Microhabitat requirements and occupancy of forest specialists

Resources often limit studies on species habitat selection at the micro-scale level. Camera traps have become an important tool to assess bird species microhabitat requirements, especially for elusive species (Ehlers Smith et al. 2017a, b). The microhabitat requirements of understorey forest specialists were assessed using camera traps in the Southern Mistbelt Forest patches (Chapter 4). The results showed that the microhabitat requirements of forest bird specialists are species-specific (Chapter 4). Also, there is a potential seasonal variation in microhabitat requirements. The most important structural characteristics influencing understorey forest specialists are within 15 m of the forest floor (Chapter 4). Therefore, to maintain the population of understorey forest specialists in the remnant Mistbelt Forest patches, the forest must be protected from further disturbance (Chapter 4).

6.5 Response of bird functional communities to anthropogenic impacts

Understanding the responses of bird functional groups is important for biodiversity conservation and managing forests (Sassen and Sheil, 2013; Cosset and Edwards, 2017). The effects of anthropogenic impacts on bird functional communities and forest habitat use were assessed

(Chapter 5). The results of this study showed that responses to disturbance varied for the different functional groups and disturbance types are species-specific. Disturbed forest habitats had comparable species richness and functional richness to undisturbed forest patches. Functional evenness for forest specialists and insectivores is influenced by disturbance and the intensity of disturbance. (Chapter 5) Therefore, it is important to use taxonomic and functional diversity indicators to have insight into the influence of anthropogenic impacts (Chapter 5).

6.6 Final conclusions and recommendations

This study aimed to assess local and landscape drivers of bird species richness, habitat use and functional diversity. The study showed bird species' habitat use, and selection are influenced by different factors at different spatial scales. Also, this study revealed that species responses at a finer scale or landscape level cannot be generalised as these are species-specific, even in species with the same ecological group. The Southern Mistbelt Forests in the Midlands of KwaZulu-Natal are important for maintaining the high bird functional richness and the persistence of the endangered Cape parrots. In our study region, privately owned patches are more protected and better managed than state-owned patches. Though protected, there need to be practical strategies on how the Bulwer forest patches can be managed from the ongoing disturbance. Also, research efforts in the Southern Mistbelt in the Midlands of KwaZulu-Natal have mainly focused on the Karkloof area; therefore, we recommend exploring the Bulwer patches, especially for the Cape parrot conservation. Also, we did not quantify the logging intensity in this study. Therefore, studies in the future should be expanded to understand the impacts of the past logging history.

6.7 References

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