Taxonomic, functional, and avian community dynamics in selected Southern Mistbelt Forests of southern KwaZulu-Natal and the Eastern Cape, South Africa

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ABSTRACT

Human population increase and landscape transformation result in the reduction of natural habitats, such as forests, causing changes in forest patch composition, habitat amount, patch size, isolation, shape, and edges. This is challenging specialist such as Orange Ground-thrush (*Geokichla gurneyi*) and Lemon Dove (*Aplopelia larvata*) species unable to survive in fragmented habitats and also influencing the composition and distribution of avian species assemblages. Therefore, the main aims of this multifaceted study were to (1) assess the habitat requirements of two forest specialised bird species, the Orange Ground-thrush (*Geokichla gurneyi*) and the Lemon Dove (*Aplopelia larvata*); (2) identify if avian assemblage diversity and species functional trait diversity show consist patterning across different landscapes in a forest ecosystem; (3) determine the influence of vegetation structures on the taxonomic and functional diversity of avian forest species, and (4) modelling how to connect forest patches of higher functional diversity. In 2018-2019, we conducted a series of camera-trap surveys of 21-day periods and fixed-radius point-count surveys at 420 sites across 94 forest patches of Southern Mistbelt Forest of southern KwaZulu-Natal and Eastern Cape, South Africa, during the breeding and non-breeding seasons in conjunction with surveys of microhabitat structural covariates. Firstly, we modelled the probability of occupancy and detection for the selected two species, which showed that forest specialist species prefer a highly diverse habitat structure. Secondly, we quantified functional diversity measures based on species' trait per patch to measure the influence of habitat and landscape configuration on each measure. This resulted in functional diversity measures which were highly influenced by patch size, the distance between patches and diverse landscape and habitat. Thirdly, we conducted RLQ analyses to examine the association between avian functional traits and microhabitat structures present at each forest patch. We found there was a significant difference in vegetation structure and species richness between forest patches. Lastly, we ranked the functional diversity measures scores of avian communities present at each forest patch to identify core habitat patches responsible for the contribution of high functional diversity measures. Protection of natural forest habitat and diverse landscapes is important in preserving avian communities.

PREFACE

The data described in this thesis were collected in the Southern Mistbelt Forest of KwaZulu-Natal and Eastern Cape Provinces, Republic of South Africa, from (May-August) and (October-February) of 2018 and 2019. Fieldwork was done 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 the College of Agriculture, Engineering, and Science, University of KwaZulu-Natal, 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.

…… [redacted] …….

Silindile T. Gumede

December 2020

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

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………………………….

Prof Colleen T. Downs (Supervisor)

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DECLARATION 1 – PLAGIARISM

I, Silindile Thobeka Gumede, 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.

Manuscript 1

S Gumede, CT Downs, DA Ehlers Smith, YC Ehlers Smith, MS Maseko

Occupancy of two forest specialist birds in the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

Author contributions:

SG, DAE and YCE conceived paper with CTD. CTD sourced funding. SG, SPN and MS collected data. SG and analysed the data, and wrote the draft paper. CTD, DAE, MSM and YCE contributed valuable comments to the manuscript.

Manuscript 2

S Gumede, CT Downs, DA Ehlers Smith, YC Ehlers Smith

What are the landscape-scale drivers of avian species richness and functional diversity in KwaZulu-Natal and Eastern Cape Mistbelt Forests?

Author contributions:

SG, DAE and YCE conceived paper with CTD. CTD sourced funding. SG, SPN and MS collected data. SG analysed the data, and wrote the draft paper. CTD, DAE, and YCE contributed valuable comments to the manuscript.

Manuscript 3

S Gumede, CT Downs, DA Ehlers Smith, YC Ehlers Smith

The influence of the microhabitat structure on avian communities of Southern Mistbelt Forest

Author contributions:

SG, DAE and YCE conceived paper with CTD. CTD sourced funding. SG, SPN and MS collected data. SG analysed the data, and wrote the draft paper. CTD, DAE and YCE contributed valuable comments to the manuscript.

Manuscript 4

S Gumede, CT Downs, DA Ehlers Smith, YC Ehlers Smith

How connected are South African Mistbelt Forests for birds? Connectivity of selected Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

Author contributions:

SG, DAE and YCE conceived paper with CTD. CTD sourced funding. SG, SPN and MS collected data. DAE and SG analysed the data. SG wrote the draft paper. CTD, DAE and YCE contributed valuable comments to the manuscript.

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Silindile Thobeka Gumede

December 2020

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"God promises to make something good out of the storms that bring devastation to your life"

Romans 8:28

Silindile Thobeka Gumede about to go in to the field to conduct the forest research she loves.

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CHAPTER 1

Introduction

1.1 Indigenous forests

Generally, the term “indigenous forest” refers to a vegetation class made up of different layers and dominated by trees, which may be evergreen, deciduous or semi-deciduous and whose combined levels have overlapping crowns (Shackleton et al., 1999). Furthermore, indigenous forests are mostly of high habitat quality with a unique microclimate, abundant leaf litter deposition and diversity (Christopher and Cameron, 2012). More than 50% of the world’s forests are located in developing countries (Becknell et al., 2015). However, global forest cover is declining as a result of various natural and anthropogenic processes, such as land-use change and agricultural expansion, overharvesting of industrial wood and fuelwood, poor harvesting practices, overgrazing, fire and extreme climatic events, such as storms (Shackleton et al., 2007; Eberle et al., 2017).

In the past, South Africa was covered by extensive indigenous forests (Eberle et al., 2017) that were previously classified into inland temperate Afromontane forests and coastal subtropical Indian Ocean types (Shackleton et al., 2007). Much of these forests were also naturally fragmented and patchily distributed as a result of biogeography and paleoclimate (Moll and White, 1978; Cooper, 1985). These two types of indigenous forests were further classified into seven main sub-groups: Southern Afrotemperate, Northern Afrotemperate, Northern Misbelt, Southern Misbelt, Scarp, Northern Coastal and Southern Coastal groups, and four azonal forests types which are Lowveld Riverine, Swamp, Mangrove and Licuati Sand Forests (Shackleton et al., 2007). These indigenous forest types make up a belt along the south and east of the country (Wilson et al., 2017). However, indigenous forests occupy a disproportionately small area in relation to that of the country as a whole as they cover approximately less than 6% of the total area of South Africa (Eeley et al., 1999; Jevon and

Shackleton, 2015; Eberle et al., 2017). Indigenous forests have historically faced an unprecedented decline in area (Mucina and Rutherford, 2006). The decline in indigenous forests has been the result of anthropogenic activities, use of fire for management, browsing and grazing pressure, clearing forest for plantations and through the invasion of alien species (Mensah et al., 2016). Forests are used by local people in pursuit of their livelihoods (Shackleton et al., 2007). South Africa has a large rural population, most of whom rely on arable and livestock agriculture and gathering of wild resources (Jevon and Shackleton, 2015).

The largest indigenous forest patches in South Africa are located along the southern coast of the Western Cape (Hope et al., 2014), and large forests fragments are also found in the Eastern Cape and KwaZulu-Natal Provinces (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Shackleton et al., 2007). Within the Eastern Cape and southern KwaZulu-Natal, there are southern Mistbelt and Coastal Forests (Eastern Cape Dune Forests) groups which comprise of different faunal and floral species, and Scarp Forest patches which comprise of a mixture of elements of these two major forest groups (Shackleton et al., 2007). These forests form the edge of the former Bantustan which refers to the ten areas of land designated by the apartheid government in the 1950s as separate ethnic zones where black people would live (Evans, 2012). Historians have noted that the key idea behind the Bantustans was that Black people would be citizens of ethnic and self-governing homelands rather than of South Africa itself (Evans, 2012; Beinart, 2012). During this time, it was illegal for Black Africans to hold individual ownership of property, in a conflict that this would erode shared land tenancy (Evans, 2012). Whereas, fifteen years later, the 1927 Native Administration Act codified African customary law in a distorted way gave traditional leaders power over the land they had not historically enjoyed, while at the same time restraining the usage, occupation and inheritance rights of most people within indigenous systems of land rights (Delius, 2008). Later on, another rule called "six native rule" passed, stating that any group of more than six Black people who had cooperated in buying land had to organise themselves as a tribe under a chief or they would lose their land (Claassens, 2008). The history of land and clashes over natural resource use has resulted in turning a blind eye to rural villagers' rights over land, and natural resources were slowly eroded (Claassens, 2008). Similarly, protected areas in South Africa served as tools of displacement and suppression parallel to the land evictions of the colonising process and apartheid rule, because rural villagers continued to be overlooked and separated from important natural and cultural resources (Khan, 1990). This history has led to a reliance on natural resources and forest products by local people. Indigenous forest patches often occur in rural areas in the Eastern Cape and southern KwaZulu-Natal, where people rely on natural resources for their daily livelihoods such as fire-woods (Lawes et al., 2004; Shackleton et al., 2007; Adie et al., 2013). Furthermore, scientific knowledge and management practices for forest persistence are mostly poor in rural areas. The understanding of conserving these natural forests may not be a priority among communities. Humans are not the only species depending on natural forests: mammals, birds and other animals are found in indigenous forests; therefore, the decline in natural forests impacts on these species (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000).

Globally, forests are simultaneously experiencing climate change, disturbance regimes and lack of management, all of which affect ecosystem function (Thom and Seidl, 2016). Ecosystem function refers to biological, geochemical and physical processes and components that take place or occur within an ecosystem (Duffy, 2003). They need to be understood to predict how communities and ecosystems respond to environmental change and to understand how declining diversity influences ecosystem services on which humans depend (Duffy, 2003; Bengtsson, 1998). Disturbances is a major driver of forest ecosystem dynamics and can change the species' structuring in various ways, depending upon the disturbance agent (Cohen et al., 2016). There have been several studies on the consequences of biodiversity loss and habitat fragmentation worldwide; however, more research is needed to clarify the understanding of this process (Laurance, 2008; Bregman et al., 2014; Breed et al., 2015; Cordeiro et al., 2015; Fahrig, 2017; Kormann et al., 2018). With the increase of the global human population, there is increased demand for resources, services and the expansion of development which has an impact on the world’s forests (Newbold et al., 2015). Thus, there is an increase in anthropogenic processes resulting in fragmentation of many natural habitats, including forests (Arroyo-Rodríguez et al., 2017). All of these processes have consequences in biodiversity, such as changes in species composition and communities. Several studies have shown that specialists’ species are more negatively affected than generalists (Laurance, 2008; Bregman et al., 2014; Ehlers Smith et al., 2015, 2018; Kormann et al., 2018). Specialist species may thrive only in a narrow range of environmental conditions or may have a restricted niche or a limited diet, while generalist species typically can thrive in a wide variety of environmental conditions and can make use of a variety of different resources (Norden et al., 2013).

South Africa is a developing country with much subsistence farming, cattle grazing, unregulated burning, commercial logging, agricultural plantations, urban developments, and dune mining – all of which contribute to forest loss (Olivier et al., 2013; Olivier and Heinecken, 2017). These forests are important for many livelihoods, and some are located in rural areas where human populations rely on natural forests for resources such as fuelwoods and medicinal plants (Leaver and Cherry, 2020). These forests are also exploited by anthropogenic activities such as deforestation, logging, road developments and plantations, which disrupt forest stability and can have long-lasting impacts on forest structure and biodiversity (Laurance, 2015). Habitat destruction may lead to the division of habitat into smaller and more isolated fragments separated by conditions of human-transformed land cover (Haddad et al., 2015) that forest-dependent species must navigate to colonise, disperse and spread genes (Fahrig, 2013). Intensive logging drastically changes the forest structure and can result in a structurally more homogeneous forest canopy (DeWalt et al., 2003). Furthermore, it typically increases edge effects, where internal forest structures are changed to external edge structures. Overall these result in forest resources, structures and associated niches changing, often favouring generalist species over specialists, and the ability for alien species to invade increases (Dillon et al., 2018; Zambrano et al., 2020; Bitencourt et al., 2020).

Consequently, changes in forest ecological and ecosystem processes undermine habitat quality and the provisioning of ecosystem services (Fahrig, 2017). Forest loss reduces the range of quality habitat and the size of fragments (Olivier and Heinecken, 2017). It also decreases habitat connectivity and exposes fragment edges to novel matrix habitats (Fahrig, 2003; Ewers et al., 2010). Thus, the loss of ecosystem services since forests are essential for the provision of a wide range of ecosystem services that are important to human well-being.

1.2 Forests ecosystem services

Ecosystem services are defined as the beneficial gain by humankind from ecosystem processes (Foley et al., 2007; Nelson et al., 2009; Gamfeldt et al., 2013) and these services are divided into four categories (Millenium Ecosystem Assessment, 2003): (1) Provisioning services, which are natural benefits directly used by humans for food, clothing, medicines, tools, or other uses; (2) Cultural services which refer to the provision of recreational opportunities, the inspiration for art and music, and spiritual value; (3) Regulating services, including pest control and carcass removal; (4) Supporting services, such as pollination, seed dispersal, water purification, and nutrient cycling, providing processes essential for ecological communities and agricultural ecosystems. Globally, ecosystem services directly support more than one billion people living in extreme poverty (World Bank, 2006); therefore, protecting ecosystems is important for economic development and poverty mitigation. In terrestrial ecosystems, the process of human-conversion of natural habitats is a dominant threat to biodiversity and ecosystem services (Millenium Ecosystem Assessment, 2005). Human dominance on the planet has led to accelerating changes in the arrangement, structure and function of ecosystems (Vitousek et al., 1997). Certain ecosystem services are exploited more than others because of the pressure of anthropogenic activities and population increase (Bennett et al., 2009). As a result, there is an increase in resource extraction, such as food and timber, and a decline in services such as flood control, genetic resources, or pollination, pest control and seed dispersal (Millenium Ecosystem Assessment, 2005). However, the perception of ecosystem services has gained growing attention from science and policy in the last decades, leading to notable development of methods to assess, spatially map and preserve ecosystem services (Seppelt et al., 2011, Burkhard et al., 2013).

Indigenous forests provide ecological, economic, social, spiritual and aesthetic ecosystem services to environmental systems and humankind (Bonan, 2008). Furthermore, they provide a refuge for biodiversity and influence and regulate climatic systems through exchanges of energy, water, carbon dioxide, and other chemical elements within the atmosphere (Bonan, 2008). Africa is rich in natural resources such as tropical forests, freshwater lakes, rivers, oil, minerals and biodiversity (Holland et al., 2012; Elbra, 2013; Green et al., 2013). However, because of forest habitat loss and change in forest structure has resulted in a continuous loss of species and genetic diversity, thus a decline in the availability of forest ecosystem services (Echeverría et al., 2007) and deterioration of the health of ecosystems. Generally, ecosystem health refers to the sustainability and maintenance of ecosystem diversity, and its strength to provide ecosystem services at a certain spatial and temporal scale (Peng et al., 2007; Costanza, 2012). In forest ecosystems and forest health, both the production of forest products and other attributes of forest ecosystems, such as species assemblage and vegetation structure is critical (Trumbore et al., 2015). Ecosystems with healthier biodiversity function more optimally and are more resistant in the face of climate and environmental change

(Cardinale, 2012; Liquete et al., 2016). However, biodiversity is not an ecosystem service, but it is connected to ecosystem services because of its functional diversity influencing the provision of ecosystem services (Millenium Ecosystem Assessment, 2005).

1.3 Forests functional diversity and disturbance

The term ‘functional diversity’ has been given several definitions but at its core, refers to a variation in distinguishing qualities or characteristics within a community (Tilman, 2001; Cadotte et al., 2011). It involves understanding communities and ecosystems based on what organisms do (Petchey and Gaston, 2006) and a key driver of ecosystem processes influencing both ecosystem function and reliability (Barbaro et al., 2014). Species sharing similar effect traits fulfil a functional role within a community; this is called a species functional diversity (Jax, 2005). A trait is a distinguishing quality or characteristic, typically one belonging to a species can influence environmental tolerances and habitats requirements depending on the exact nature of the trait measured (Cadotte et al., 2011). They may also determine many things about species such as their habitats, their interactions with other species, the form of competition, and the contribution to the ecosystem function (Steneck and Dethier, 1994; Lavorel et al., 1997). For example, avian predation contributes to the maintenance of low pest population levels and may decrease damage plant production significantly (Whelan et al., 2008). Batalha et al. (2010) mentioned that communities with a greater diversity of functional traits operate more efficiently. Functional diversity can be disintegrated into two components – functional evenness which is the equability of abundances in trait space and functional richness which is the amount of niche space occupied by the species within a community (Legras et al. 2018). Additionally, functional diversity is highly prone to disturbances (natural and anthropogenic) (Cardinale et al., 2012), therefore, because of loss of diversity after disturbances functional redundancy may perform as biological insurance (Loreau et al., 2003).

Functional redundancy occurs when niches of numerous species overlap to the extent that a portfolio of functionally corresponding species is present within an ecosystem (Yachi and Loreau 1999). In contrast, functional dispersion measures the breadth of functional roles across species (Luck et al., 2013); generally, systems with species groups indicating higher dispersion should show better functional dissimilarity (Laliberté et al., 2010; Luck et al., 2013). Therefore, functional redundancy and functional dispersion define different components of biodiversity connected to the overlap in functional roles and breadth of functions accomplished by species (Laliberté et al., 2010; Luck et al., 2013).

Landscape transformation is resulting in changes to functional communities, creating new challenges in conservation and resource management (Foley et al., 2005; Millenium Ecosystem Assessment, 2005; Lindenmayer et al., 2008). Contemporary landscapes are generally the result of generational land use and management practices, along with governmental and agricultural pressured change, which have had both a direct and indirect impact on the landscape (Varga et al., 2018). Activities such as agriculture, exotic timber plantations and urban settlements are changing the landscape structure and composition (Hansen et al., 2013; Laurance et al., 2014; Arroyo-Rodríguez et al., 2017). As a result, the composition of flora and fauna assemblages are changing through sifting species based on their traits, such as diet and habitat requirements, and their physiological and behavioural characteristics (Lefcheck et al., 2016, Barnum et al., 2017, Henderson et al., 2020). These effects of landscape transformation also cause changes in plants and animal species' functional diversity (Henderson et al., 2020). Several studies have found landscape transformation having various effects on species (Arnillas et al., 2017; Ehlers Smith et al., 2018; Ehlers Smith et al., 2017; Ehlers Smith et al., 2020; Alexander et al., 2019). Different species can show different responses to landscape transformation depending on their surviving and living requirement, making it difficult to identify general response patterns. Species reliant on forests are likely to be sensitive to changes in landscape composition (such as forest loss) and configuration (such as the increase of forest edges), (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Fahrig, 2013; Pfeifer et al., 2017) whereas non-forest-dependent species are able to utilise resources not only from the forest but also from other landscape components over larger spatial scales, therefore, less likely to be affected by forest loss within a landscape (Barnes et al., 2017).

Birds are the best-known class of vertebrate animals, found worldwide virtually in every kind of habitats, and provide many services (Whelan et al., 2008). Yet, little is known of their ecosystem-services background. Most of the critical ecological roles that birds fill involving supporting and regulating services, such as insect pest control and seed dispersal are the most difficult to measure (Farber et al., 2006; Sekercioglu, 2006; Whelan et al., 2008). In most cases, birds provide regulating and supporting services through foraging (Wenny et al., 2011). More than 50% of bird species are primarily insectivorous, and almost 75% occasionally feed on invertebrates (Sekercioglu, 2006). This behaviour in birds is beneficial to avoid insect outbreaks and plants respond with higher growth rates or crop yields (Whelan et al., 2008). Pollination and seed dispersal are critical for ecosystems. Approximately 33% of bird species disperse seeds, mostly through fruit ingestion, but also through scatter-hoarding of nuts and conifer seed crops (Vander Wall, 2001, Sekercioglu, 2006). Therefore, a large proportion of plant species benefit from bird dispersal in several ways, such as of gene flow, colonising new and favourable sites, escape from predators, or enhanced germination (Jordano and Schupp, 2000, Tomback, 2005). Although the common assumption that decomposers (i.e., microbes and insects) are largely responsible for recycling carrion biomass; vultures and many other bird species scavenge animal carcasses at least occasionally, together with raptors, seabirds, gulls, herons, rails, shorebirds, woodpeckers, and passerines (DeVault et al., 2003). Birds contribute to nutrient cycling in all habitats, but most remarkably where aquatic birds nest colonially on islands (Polis and Hurd, 1996, Anderson and Polis, 1999). Seabirds often nest in dense groups in coastal areas and on islands where they process large amounts of food in small areas (Wenny et al., 2011). In this way, seabirds are carrying nutrients from the aquatic zone to the terrestrial zone, which influence the structure and composition of plant communities (Ellis 2005; Wenny et al., 2011).

About 75% of bird species are primarily found in forested habitats (Şekercioğlu et al., 2004). Higher diversity of birds is found in lowland tropical and subtropical forests near the Equator in the Americas and Africa and 25°N in Southeast Asia; there are richness declines towards the poles (Birdlife International, 2014; Newton, 2003). Forests provide important resources to primary consumers to predators, omnivores and scavengers (Stratford and Şekercioğlu, 2015). Since birds' calorific requirements are higher and so their demands for food are also higher, which are likely to be more sensitive to changes in resources (Stratford and Şekercioğlu, 2015). Avian diet ranges from feeding on plants, animals to fruits (Şekercioğlu et al., 2004; Kissling et al., 2012; McCallum et al., 2013; Stratford and Şekercioğlu, 2015). Folivorous birds consume the vegetative parts of plants and at times, supplement their diet with insects (Şekercioğlu et al., 2004; Stratford and Şekercioğlu, 2015). Granivorous (seed-eating) birds make up the great proportion of avian biomass the Amazon (Terborgh et al., 1990), whereas, almost 600 bird species are primarily consumers of nectar and are mostly concentrated in the tropics (Brown and Hopkins, 1995). Frugivores are also common in forests, consuming fleshy pulp associated with seeds (fruits); however, relatively few species are exclusively frugivorous (Jordano and Schupp, 2000). Insectivorous birds may also feed on vertebrates (Poulin et al., 1994). They are divided into aerial and terrestrial/arboreal insectivores, based on their feeding strategies (Stratford and Şekercioğlu, 2015). Carnivorous birds, like insectivores, feed on animals. Omnivorous birds are the most opportunistic birds feeding on various types of food, and their numbers are lower in the forests because they require specialised physiology to process their diet (Kissling et al., 2012).

During forest disturbance, the area and size of habitat are reduced. Habitat connectivity also decreases, and fragment edges get exposed (Fahrig, 2003; Ewers et al., 2010). The process of fragmentation causes many changes within the habitat, such as quality, quantity and distribution of food resources in a landscape that affect species persistence (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000). This results in specialist species with narrow feeding niches less likely to make use of resources in the habitats that surround fragments than generalist species with broad feeding niches (Lees and Peres, 2008, Vetter et al., 2011). Therefore, the species that can occupy specialist feeding guilds may be less likely to sustain meta-population dynamics within fragmented landscapes (Schnell et al., 2013) and making them particularly vulnerable to habitat fragmentation and land-use change. For instance, a decline in insectivores is purported to increase insect herbivory in degraded or fragmented forests (Van Bael et al., 2008). Furthermore, avian insectivory is more prevalent at the forest edges compared with interiors (Skoczylas et al., 2007). However, other studies reported increased insectivory and decreased herbivory (Gonzalez-Gomez et al., 2006; De la Vega et al., 2012). Preceding studies have shown that avian species richness declines with forest fragment size, approximately in accordance with species-area relationships (Lees and Peres, 2006; Banks-Leite et al., 2012). In a study by Bregman et al. (2014), species richness was far higher in tropical than temperate fragments and declined with fragment size in all three major feeding guilds (insectivores, frugivores and granivores). However, the declines were the steepest in insectivores both in relation to frugivores and granivores (Bregman et al., 2014).

1.4 Purpose of the study

As the inland Southern Mistbelt Forests have not been studied extensively at a landscape level in terms of avian species persistence (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Wethered and Lawes, 2003), the aims of the present study were multifaceted. Firstly, we determined the requirements and preferences, and the degree to which vegetation metrics influence on the probability of occupancy of the Orange Ground Thrush (*Geokichla gurneyi*) and the Lemon Dove (*Aplopelia larvata*), and also compare seasonal differences due to different conditions, diversity changes with richness in relatively stable, benign environments and varies with evenness under unstable, rigorous conditions (Hansen et al., 2001). Secondly, we determined how avian species richness, assemblage and functional diversity varied between patches, and how landscape structure may influence the structure of avian assemblages, their determinants is important because different functional trait distributions may imply the operation of different assembly processes (McGill et al., 2006; Cornwell et al., 2006). Thirdly, we determined the influence of microhabitat on avian functional diversity in southern Mistbelt Forests to determine the importance of conserving these forests patches. Microhabitat characteristics vary in fragmented forests; they influence the microhabitat selection of birds (Cody, 1981), suitable microhabitat provides safe shelter for bird to avoid predation and an opportunity to access reliable food resources (Li et al., 2020). Finally, we determined the potential connectivity of selected Southern Mistbelt Forests with higher avian diversity. Connectivity is a key factor in the long-term viability of populations (Keeley et al., 2018)

1.5 Study outline

Following this initial review chapter, this thesis comprises four data chapters, from Chapters 2 to 5, which can be read individually. These chapters were prepared for submission to international peer-reviewed journals (so are formatted for each). Therefore, some repetition was inevitable. The hypothesis and/or predictions are presented in each data chapter. Finally, there is a concluding chapter where the results are discussed briefly and recommendations made. The data chapters are:

Chapter 2. Occupancy of two forest specialist birds in the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa.

Chapter 3. What are the landscape-scale drivers of avian species richness and functional diversity in KwaZulu-Natal and Eastern Cape Mistbelt Forests?

Chapter 4. The influence of the microhabitat structure on avian communities of southern Mistbelt forest.

Chapter 5. Connectivity of selected Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa.

Chapter 6 is an overall conclusion and summarises all the results from the individual chapters in this study.

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CHAPTER 2

Occupancy of two forest specialist birds in the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

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Running header: Occupancy of two forest specialist birds in Southern Mistbelt Forests

2.1 Summary

Establishing the specific habitat requirements of forest specialists in fragmented natural habitats is vital for their conservation. We used camera-trap surveys and microhabitat-scale covariates to assess the habitat requirements, probability of occupancy and detection of two terrestrial forest specialist species, the Orange Ground-thrush (*Geokichla gurneyi*) and the Lemon Dove (*Aplopelia larvata*) during the breeding and non-breeding seasons of 2018 – 2019 in selected Southern Mistbelt Forests of KwaZulu-Natal and the Eastern Cape, South Africa. A series of camera-trap surveys of 21-days were conducted in conjunction with surveys of microhabitat structural covariates. During the wet season, percentage of leaf litter cover, short grass cover, short herb cover, tall herb cover and saplings 0 – 2 m, stem density of trees 6–10 m and trees 16–20 m were significant structural covariates for influencing Lemon Dove occupancy. In the dry season, stem density of 2 – 5 m and 10 – 15 m trees, percentage tall herb cover, short herb cover and 0 – 2 m saplings were significant covariates influencing Lemon Dove occupancy. Stem density of trees 2–5 m and 11–15 m, percentage of short grass cover and short herb cover were important site covariates influencing Orange Ground-thrush occupancy in the wet season. However, there was insufficient data for Orange Ground-thrush in the dry season. Our study highlighted the importance of a diverse habitat structure for both forest species. A high density of tall/mature trees was an essential microhabitat covariate, particularly for sufficient cover and food for these ground-dwelling birds. Conservation of the natural heterogeneity of their habitat is integral to management plans to prevent the decline of such species.

Keywords: Indigenous forests, Occupancy, Specialist species, Lemon Dove, Spotted Ground Thrush, Camera trap

2.2 Introduction

Human population growth continues to increase exponentially, particularly in Africa (Cohen 1995, Estrada 2016, Henn et al. 2019), exacerbating the rates at which natural habitats are transformed into anthropogenic landscapes (Laurance et al. 2014). This has resulted in significant declines biodiversity and abundance of species worldwide (Vitousek et al. 1997, Tilman et al. 2001, Sa´nchez-Bayo and Wyckhuys 2019, Piano et al. 2020). As a result, habitat patch sizes are generally decreasing and becoming isolated creating more edges/ecotones (where two adjacent ecosystems overlap) (Burkey 1995, Fahrig 1997, 2003, Haddad et al. 2015), resulting in reduced animal residency within fragments and isolated patches, and therefore, less recolonisation of fragments because of limited dispersal opportunities between them (Fahrig 1997, Collinge 2009, Fahrig 2003, Haddad et al. 2015, Hanski 2015).

Natural forest habitat supports a high proportion of biodiversity in South Africa (Geldenhuys and MacDevette 1989). Forests patches in South Africa are naturally fragmented, but anthropogenic activities, such as deforestation for agricultural land use and urbanisation, have further disconnected these landscapes, exacerbating fragmentation effects (Cromsigt et al. 2013, Jain et al. 2016). This causes significant declines in habitat heterogeneity (Bregman et al. 2014), resulting in loss and change in forest species composition (Fahrig 2003; Cooper et al., 2017). Several studies have shown a positive relationship between species diversity and habitat heterogeneity (Gaston 2000, Tews et al. 2004, Ehlers Smith et al. 2018a). Edge effects become more pronounced as fragments become smaller and more degraded, as interior structures become eroded (Magnago et al. 2017, Ruete et al. 2017, Malcolm et al. 2017). This process results in the decline of suitable habitat for interior specialists, which influences species composition, resulting in more generalists occupying the forest fragments compared with specialist species, because generalists have broader niches, and ultimately results in the decline of some ecosystem services (Şekercioğlu et al. 2004).

These pressures from loss of habitat and fragmentation lead to the extinction of some species. Many species now survive at such low densities that they can be considered nearly functionally extinct (Janzen 2001). Specialist species with narrow feeding niches may be less likely to make use of resources in the habitats that surround fragments than generalist species with broad feeding niches (Lees and Peres 2008, Vetter et al. 2011, Newbold et al. 2012, Olivier and Van Aarde 2017). Species with different dispersal capabilities may respond differently to habitat fragmentation and habitat loss (Andren 1994, Steffan-Dewenter and Tscharntke 2000), with broader range dispersers displaying less sensitivity to fragmentation (Liao et al. 2017, Ehlers Smith et al. 2018b). Birds are among the most mobile organisms, they have large/overlapping or small home ranges, but they are good indicators of habitat disturbance as a whole class because of their wide range of functional traits (Garson et al. 2002, Uezu et al. 2005). Their ability to fly allows them to cope better with the disconnection of habitat and fragmentation than other taxonomic groups (Rolstad 1991). Birds are generally easy to identify either visually or acoustically, and their habitat affinities are mostly well known (Rolstad 1991, Garson et al. 2002). Therefore, bird populations in forest ecosystems provide excellent opportunities to study the consequences of habitat fragmentation. Birds have many different responses to habitat disturbance, given their different functional traits, but forest specialists are likely to be good indicators of forest disturbance because of their specialisation. However, some bird species such as ground-dwelling and forest specialists may not be spotted easily (Ehlers Smith et al. 2017a, b, c, Maseko et al. 2017), therefore, their response to habitat disturbance might be challenging to examine.

In this study, we investigated two ground-dwelling forest bird specialists, the Lemon Dove *Aplopelia larvata* and the Orange Ground-thrush *Geokichla gurneyi* because these species are forest specialists requiring a suitable habitat and resources to persist in the ecosystem. Pigeons and doves (Columbidae) are exposed to extinction from hunting, introduced predators and habitat loss (Owens and Bennett 2000). The Orange Ground-thrush is range-restricted and a relatively scarce forest specialist (Colyn et al. 2020). Therefore, their presence or absence in camera traps may highlight the suitability of the forest patches for these species and may be indicative of the wider forest habitat quality and condition. We analysed camera-trap photographs of species combined with microhabitat variables. Lemon Dove and Orange Ground-thrush presence and absence in the photographs represent the habitat preference and requirements of these species. However, indigenous forest patches, which are composed of native trees and are not categorised as timber plantations often occur in rural areas in the Eastern Cape and southern KwaZulu-Natal (KZN) Provinces, where people rely on natural resources for their daily livelihoods such as firewood (Shackleton et al. 2007, Leaver and Cherry 2020) and hunting (Pasmans and Hebinck 2017); therefore, these forests are disturbed in different ways. Previous research in Indian Ocean Coastal Belt Forests between the Umtamvuna and Umkomasi Rivers of KZN indicates that Lemon Doves were relatively uncommon in all forests studied (Ehlers Smith et al. 2017a). In the same coastal forests, Spotted Ground-thrush *Geokichla guttata* had a strong preference for large patches, and the isolation distances of forest patches negatively influenced occupancy (Ehlers Smith et al. 2017b). Forests with an open understorey and a less-diverse habitat structure influenced Spotted Ground-thrush occupancy positively; however, bare ground and the presence of grass cover influenced detection probability negatively (Ehlers Smith et al. 2017b). The studies by Ehlers Smith et al. (2017a, b) only examined Indian Ocean Coastal and Scarp forests in southern KZN and did not include any of the KZN or Eastern Cape Province Southern Mistbelt Forests. Given the importance of forest specialists and the rate of habitat transformation, it is important to study habitat requirements of forest specialists in other South African forests to understand better the importance of protecting these species for local forest ecology and to inform local management practices across the broader landscape. Additionally, the decline of some specialist forest bird species has been documented in South Africa (Cooper et al. 2017)

Indian Ocean Coastal Belt Forest is known to be highly fragmented, disturbed, and critically endangered (Department of Environmental Affairs 2013, Ehlers Smith et al. 2017c). Currently, the KZN Indian Ocean Coastal Belt Forests are affected by a complex mosaic of extensive sugarcane fields, timber plantations and coastal holiday resorts, with scattered grasslands, Coastal Dense Bush (regenerating Coastal Forest; Mucina et al. 2006a, b, Ehlers Smith et al. 2017a, b, c). By contrast, the Southern Mistbelt Forests surveyed in the present study are mostly situated in grassland landscapes with villages and are affected by commercial and subsistence use of the indigenous forest resources (Hassan and Haveman 1997, Mucina et al. 2006a, b, Leaver et al. 2019). Additionally, timber plantations and alien invasive plant species often occur near or around these indigenous forest patches (Mucina et al. 2006a, b; authors' pers. obs.).

In this study, we therefore aimed to elucidate (1) if the Lemon Dove habitat requirements in the Southern Mistbelt Forests were similar to those in the Indian Ocean Coastal Belt Forests and (2) if the Orange Ground-thrush responded to the Southern Mistbelt Forest pressures in a similar way to the Spotted Ground-thrush does in the Indian Ocean Coastal Belt Forest. We (3) measured habitat requirements to interpret their possible habitat preferences and calculated the degree to which vegetation metrics impacted on the probability of occupancy of Lemon Doves and Orange Ground-thrushes in the Southern Mistbelt Forest patches; and (4) compared seasonal differences in the presence and absence of the species and the use of habitat during breeding and non-breeding seasons. We predicted that the Lemon Dove in the Southern Mistbelt Forests would have similar habitat requirements as in the Indian Ocean Coastal Belt Forests and the Orange Ground-thrush would respond to the Southern Mistbelt Forest pressures the same way as the Spotted Ground-thrush in the Indian Ocean Coastal Belt Forests.

2.3 Methods

2.3.1 Study area

We conducted this study in select Southern Mistbelt Forests within the provinces of KZN (28.5˚S, 30.9˚E) (Kokstad and Creighton) and the Eastern Cape (32.3˚S, 26.4˚E) (Nqadu, Mhlahlane and eLangeni forests), South Africa (Figure 2.1). Eastern Mistbelt forests are naturally fragmented and patchily distributed as a result of biogeography and paleoclimate (Moll and White 1978) and form part of the Southern Mistbelt Forest group which occurs from the Eastern Cape to KZN (Hope et al. 2014). The Mistbelt forms an irregular band through the KZN Midlands, extending from Weza in the south-west to Ngome in the north-east (Mucina et al. 2006a, b, Wilson et al. 2017). It once had a significant grassland component, but this has now been transformed into agriculture and commercial timber plantations (Mucina et al. 2006a, b). The forest component known as the Southern Mistbelt Forests consists of a series of patches occurring mainly on southern slopes effects of fire are reduced (Hope et al. 2014). The climate is moderate and humid, and mists are frequent in summer and frosts in winter. The average annual rainfall is 950–1,350 mm, falling mostly in summer. The major exploitation of the Southern Mistbelt Forests started early in colonial history and in some patches, continues illegally (Adie et al. 2013). Beneficial tree that humans used for medicinal purposes or to build shelters and as poles, such as Henkel's yellowwood *Podocarpus henkelii*, stinkwood *Ocotea bullata*, sneezewood *Ptaeroxylon obliquum* and thorn pear *Scolopia zeyheri*, were plundered. *Ocotea bullata*, an excellent provider of fruits to larger birds, is almost extinct (Adie et al.

2013).

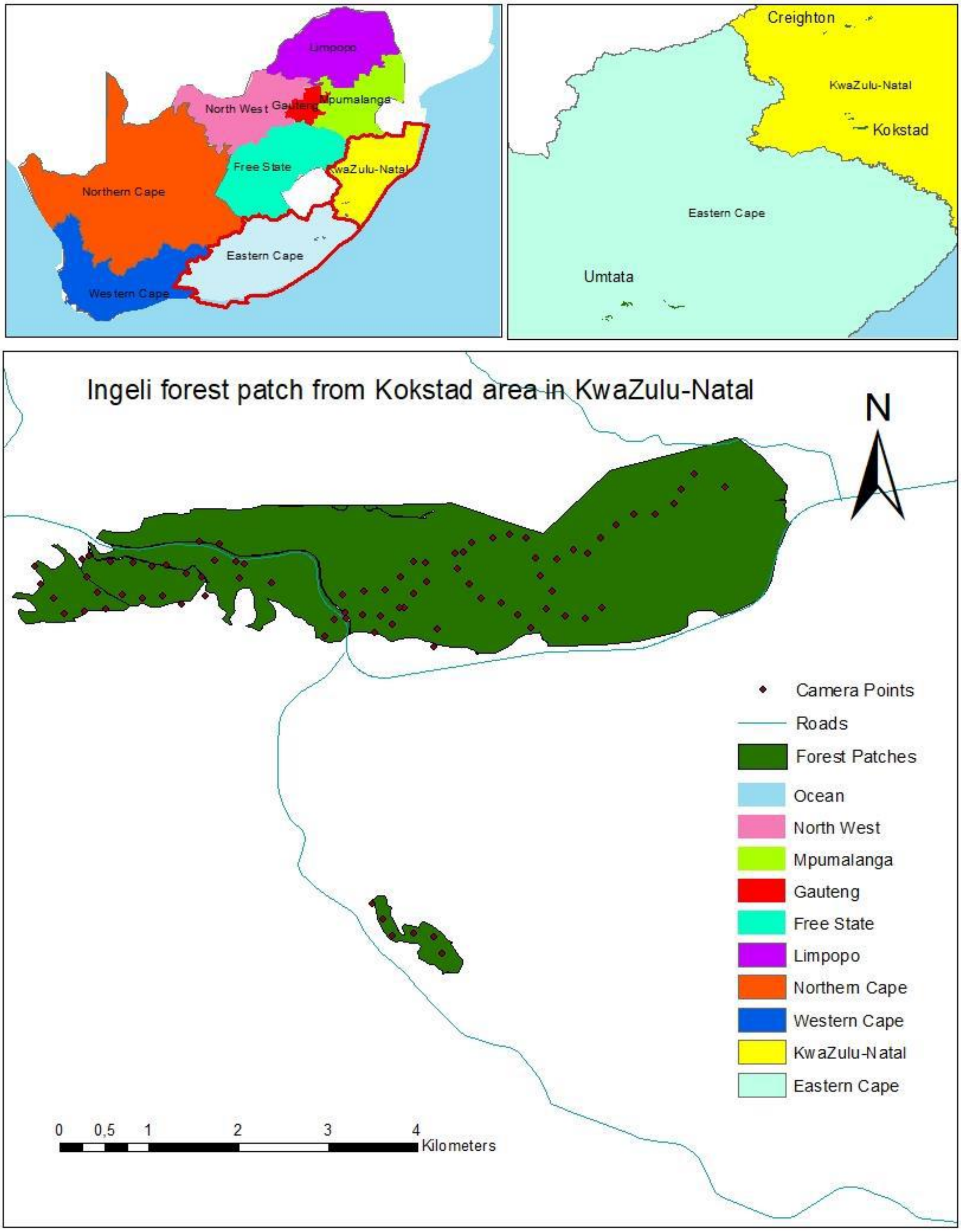

Figure 2. 1: Survey region of South Africa (insert) showing Southern Mistbelts Forest patches selected in the Eastern Cape and KwaZulu-Natal Provinces (insert), and an example of the forest patch in Kokstad showing the design of the study in the field.

2.3.2 Study species

The Lemon Dove is a medium-sized species in the family Columbidae mostly dwelling on forest floors in lowland and Afromontane forests (Hockey et al. 2005, Ehlers Smith et al. 2017d). This species is widely spread from the east of Cameroon, southern Sudan, Ethiopia, southern and eastern Africa to South Africa (Hockey et al. 2005). The diet of the Lemon Dove consists primarily of various small fallen fruits and seeds, but it may rarely feed on invertebrates (Hockey et al. 2005, Symes and Woodborne 2009). It is mostly found in pairs (monogamous) or flying solo and nesting solitarily (Hockey et al. 2005). This species is difficult to detect through traditional survey methods such as mist netting (Ehlers Smith et al. 2017a, c).

The Orange Ground-thrush is a sedentary forest bird specialist found in eastern and southern Africa (Earle and Oatley 1983). The distribution includes Kenya, western Angola, south-eastern Democratic Republic of the Congo, Tanzania, northern Malawi; and central Malawi to north-eastern South Africa respectively (Hockey et al. 2005). Orange Ground-thrush habitat is mostly in montane and Mistbelt forests. It forages for earthworms, insects, and molluscs, and rarely fruits (Earle and Oatley 1983, Hockey et al. 2005). Females are larger than males in size and are monogamous (Hockey et al. 2005). The population size of Orange Ground-thrush is currently not well known but is thought to be declining because of habitat loss (BirdLife International 2019). The IUCN Red List has listed the species as ‘Least Concern’ because it has a broad range and its population is not declining fast enough to be considered ‘Vulnerable’ (BirdLife International 2019).

2.3.3 Data collection

We collected data during non-breeding (May–August) and breeding (October–February) seasons of 2018 and 2019 for both species. We obtained the Geographic Information System (GIS) data layer maps of the Southern Mistbelt Forests in KZN and the Eastern Cape (GeoTerra Image 2014) which we then displayed in ArcGIS v10.4 (ESRI 2011) to identify suitable camera-trap site locations across the area's gradient. In our three study regions, we selected a range of Southern Mistbelt Forest patches with surrounding land uses, including timber plantations, grasslands and rural or urban developments. In each region, we selected a range of patch sizes, with the structure of source or "mainland" patch, and several surrounding satellite patches. We overlaid a 400 m x 400 m grid over each survey patch to allocate camera sites at the intersection of each gridline, following the guidelines for camera-trap survey design in KZN by Ehlers Smith et al. (2018c), and to ensure points were evenly distributed across sample areas. Some areas were not accessible upon arrival at a survey location, but we maintained a 400 m distance between survey sites. Additionally, species of similar size to our study species have a relatively large (0.4–31.9 ha) home ranges (Tweed et al. 2003, Anich et al. 2012) and Orange Ground-thrush aggregate mean home range in Tanzania is known to be 10.3±1.1 ha (Newmark et al., 2010). Therefore, the number of camera trap sites in each habitat patch was proportional to the size of each habitat patch (Bibby et al. 2000, Ehlers Smith et al. 2017a, b, c, d). We projected survey locations onto a Global Positioning System (GPS, Garmin GPS map 62; Garmin USA) to locate survey site selection in the field and ensure a minimum distance of 400 m between survey points. We used 60 camera-traps, and they were rotated to cover the whole study site. We fastened each camera-trap (Moultrie M-880 and Cuddleback 20MP) to a sturdy tree at each site at the height of 15-30 cm, covering 420 sites across 94 forest patches. We removed vegetation obstructing the sensor and left camera traps operating at each site for

21 days 24h/day, set to capture a picture whenever there was motion, with a 30-second delay between pictures.

The microhabitat structure and foliage profile were surveyed in a 20-m radius around each survey location: percentage coverage of bare ground; leaf litter; grass cover; herbaceous plants; saplings and scrub/woody plants < 2 m, and percentage of trees of 2–5 m, 6–10 m, 11–15 m, 16–20 m, 21–25 m and > 25 m in height; mean height of all plant groups, stem density of all horizontal and vertical dead trees, and stem density of all trees in each height category (Bibby et al. 2000, Ehlers Smith et al. 2015, 2017a,b,c,d). Scrub/woody vegetation was distinguished from trees and classified as ellipsoid-shaped plants with multiple branches emerging from the ground, which represent an understorey structural component (Ehlers Smith et al. 2015). Trees were classified as bare stemmed plants of height > 2 m, with upper branches containing foliage (Ehlers Smith et al. 2015). We were not able to retrieve climatic covariates in this study because of the limitations of the camera traps used.

2.3.4 Data analyses

We standardised all continuous covariates to z-scores and correlations between them were tested to avoid multicollinearity (Graham 2003, Ramesh and Downs 2014, Ehlers Smith et al. 2017d). We removed all correlated covariates and retained nine microhabitat-scale covariates (Table 2.1). Binary detection history (1 = presence, 0 = absence) was used in a single-season occupancy model (MacKenzie et al. 2006, Ehlers Smith et al. 2017a, b, c, d) to estimate the probability of occupancy (ψ) and detection (p) of habitat patches used by Lemon Doves and Orange Ground Thrushes. The detection histories of the dry and wet seasons were analysed separately. The programme PRESENCE v9.0 (Hines 2006) was used to estimate ψ and p and calculate the influence of microhabitat-scale covariates on both measures to determine if these covariates are influencing both occupancy and detection probability. Therefore, firstly we created the constant model, i.e., occupancy and detection probability without covariate influences (ψ (.)p(.)). Secondly, we created a full model encompassing all microhabitat-scale covariates. The influence of each covariate independently and in combination were modelled on ψ while keeping p constant, and vice versa, e.g. ψ(covariate)p(.) or ψ(.)p(covariate+covariate). Lastly, we tested the influence of all covariates on ψ and p at once, ψ (covariate+covariate) p(covariate+covariate). We estimated c-hat values (c-hat 1.12 and 1.17 for Lemon Dove during breeding and non-breeding respectively; 1.1 for Orange Ground Thrush for the most parameterised single-season models. We did not observe over-dispersion and the best model described covariates influence on ψ, and p was defined by the lowest Akaike's information criterion (AIC) value (Ramesh and Downs 2014, Ehlers Smith *et al*. 2017a, b, c, d).

Table 2. 1: Microhabitat-scale covariates retained in the occupancy modelling of the probability of occupancy and detection of Lemon Doves (*Aplopelia larvata*) and Orange Ground-thrushes (*Geokichla gurneyi*) in selected Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa, after removal of highly correlated covariates during multicollinearity tests.

Covariates	**Abbreviation**
% Leaf Litter	LL
% Short grass cover	SGC
% Short herb cover	SHC
% Tall herb cover/ Seedlings	THC
% Saplings 0-2 m	S2
Trees 2-5 #	T2
Trees 6-10 #	T6
Trees 11-15 #	T11
Trees 16-20 #	T16

2.4 Results

Twenty-one days of sampling in 420 sites resulted in 8,820 camera-trap nights during dry and wet seasons. This resulted in 502 captures in the wet season and 363 captures in the dry season of Lemon Dove and 122 captures in the wet season and 26 captures in the dry season of Orange Ground-thrush were obtained. The naive occupancy of the Lemon Dove was 0.25 during the wet season and 0.23 for the dry season. However, the Orange Ground-thrush naïve occupancy was 0.23 for the wet season and there was insufficient data for this species in the dry season. This could be the result of scarcity of the Orange Ground-thrush species during the non-breeding season, as the species has limited movement during the non-breeding season (Hockey et al. 2005) and moving away from breeding sites during cold months (Earle and Oatley, 1983). Thus, we only modelled occupancy for the wet season where the naïve occupancy ≥ 0.2. We produced 507 (wet season) and 519 (dry season) Lemon Dove and 155 (wet season) Orange Ground-thrush models integrating nine microhabitat covariates to estimate the occupancy of the two species; and retained three models within ΔAIC ≤ 2 thresholds (Tables 2.1, 2.2 and 2.3).

Across all top models, the mean occupancy, the standard deviation (± SD), and the probability of detection of Lemon Dove were 0.29 ± 0.05 and 0.15 ± 0.04 for the wet seasons, and 0.29 ± 0.06 and 0.19 ± 0.03 for the dry seasons. For the Orange Ground-thrush, the mean occupancy and the probability of detection were 0.51 ± 0.03 and 0.17 ± 0.02 in the wet seasons.

In the wet seasons, short grass cover (%), (β 0.32 ± 0.14 ωi= 0.92) short herb cover (%) (β 0.63 ± 0.14, ωi= 0.99), tall herb cover (%) (β 0.65 ± 0.12, ωi= 0.99), stem density of trees 2–5 m (β 0.63 ± 0.14, ωi= 0.99) and 6–10 m (β 0.15 ± 0.14, ωi= 0.09) in height had a positive influence on a probability of detection of Lemon Doves while stem density of trees 16–20 m (β 0.65 ± 0.19, ωi= 0.98) in height had a negative influence on the probability of Lemon Dove detection (Figure 2.2). Leaf litter (%) (β 1.90 ± 0.70, ωi= 0.92) had a positive influence on a probability of occupancy of Lemon Doves (Figure 2.2).

In the dry seasons, short grass cover (%) (β 0.38 ± 0.19, ωi= 0.65) had a positive influence on a probability of occupancy of Lemon Doves (Figure 2.3). Short herb cover (%) (β 0.57 ± 0.15, ωi= 1) and the stem density of trees 11 – 15 m (β 0.22 ± 0.13, ωi= 0.65) in height had a positive influence on a probability of detection of Lemon Doves, whereas saplings 0 – 2 m (%) (β 0.24 ± 0.14, ωi= 0.76), stem density of trees 2 – 5 m in height (β -0.39 ± 0.12, ωi= 1) and tall herb cover (%) (β -0.54 ± 0.11, ωi= 1) had a negative influence (Figure 2.3).

In comparison in the wet seasons, short herb cover (%) (β -0.11 ± 0.06, ωi= 0.91), saplings 0–2 m (%) (β -0.17 ± 0.07, ωi= 0.89) and stem density of trees 16–20 m in height (β -0.21 ± 0.09, ωi= 0.95) had a negative influence on the probability of detection of the Orange Ground-thrush (Figure 2.4). Stem density of trees 6–10 m (β 0.17 ± 0.07, ωi= 0.96) and 11–15 m in height (β 0.26 ± 0.06, ωi= 1) had a positive influence on a probability of detection of Orange Ground-thrush. Occupancy was positively influenced by stem density of trees 11–15 m in height (β 0.46 ± 0.18, ωi= 1) for Orange Ground-thrush (Figure 2.4).

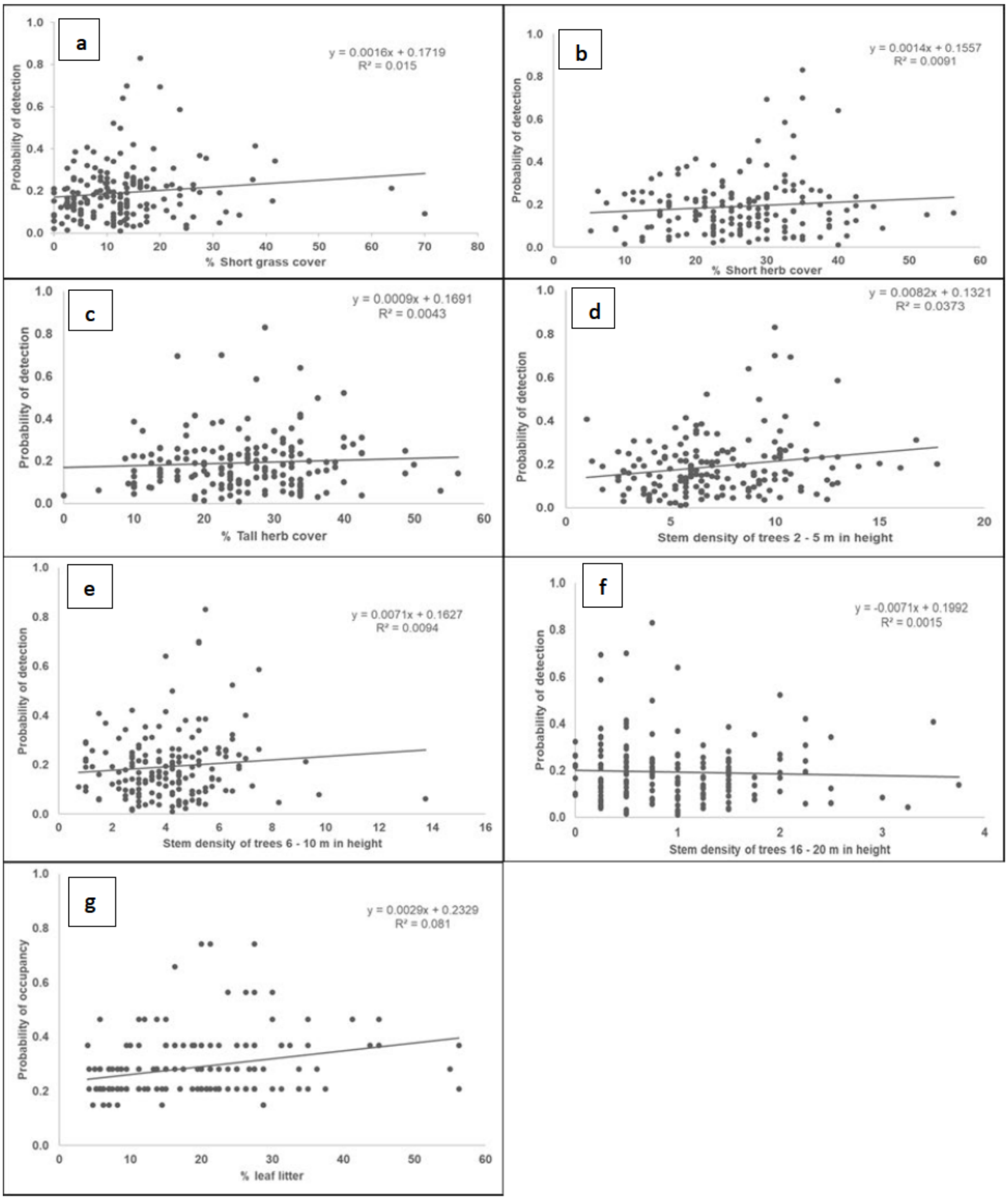

Figure 2. 2: Lemon Dove occupancy and detection estimates in relation to site covariates during the wet seasons in the present study where (a) is the percentage of short grass cover and probability of detection, (b) is the percentage of short herb cover and probability of detection, (c) is the percentage of tall herb cover with the probability of detection, (d) is the stem density of trees 2 – 5 m with the probability of detection, (e) is the stem density of trees 6 – 10 m with

probability of detection, (f) is the stem density of trees 16 – 20 m with probability of detection and (g) is the percentage of leaf litter and probability of occupancy.

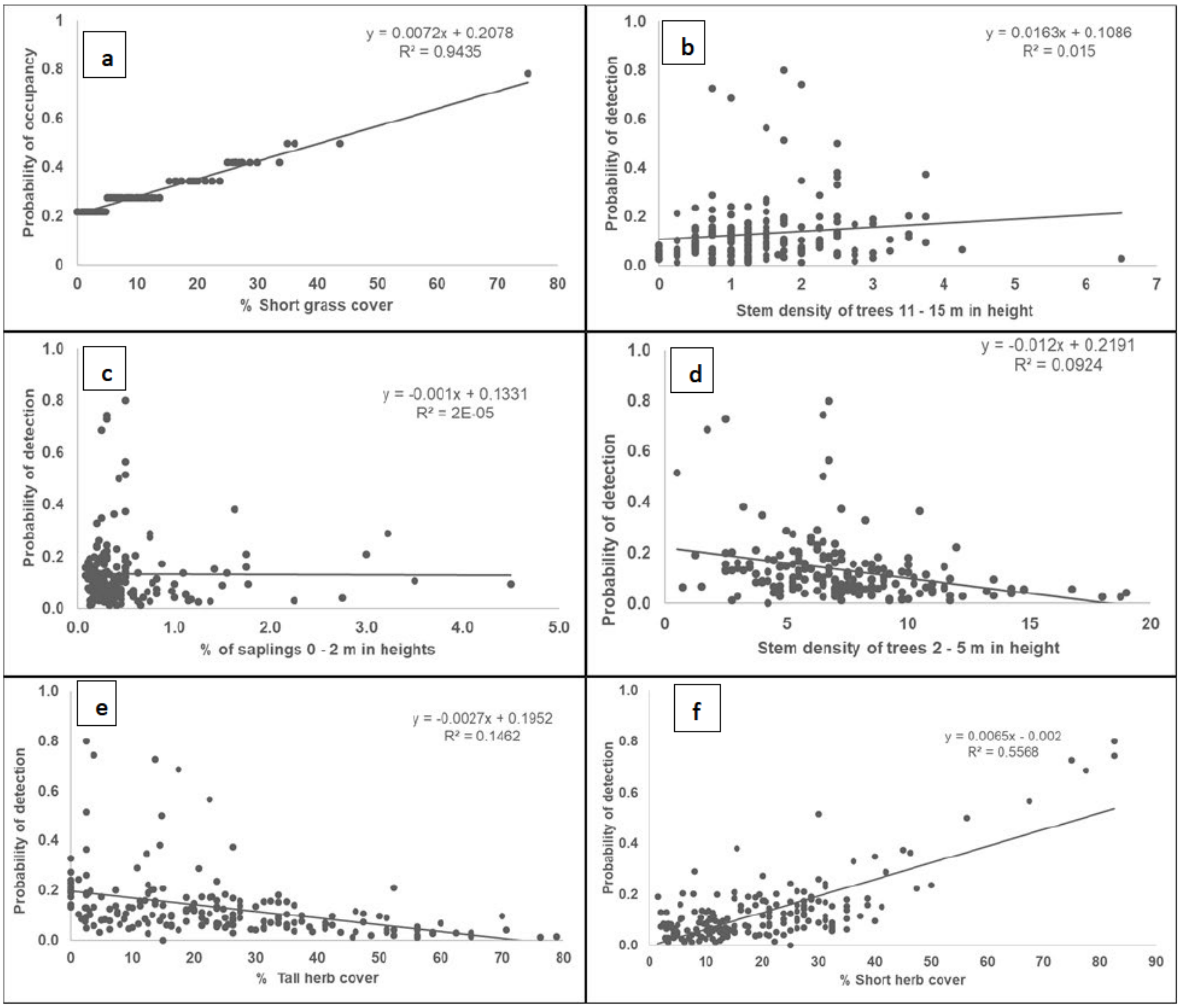

Figure 2. 3: Lemon Dove occupancy and detection estimates in relation to site covariates during the dry seasons in the present study where (a) is the percentage of short grass cover and probability of occupancy, (b) is the stem density of trees 11 – 15 m in height with probability of detection, (c) is the percentage of saplings 0 – 2 m with the probability of detection, (d) is the stem density of trees 2 – 5 m with the probability of detection, (e) is the percentage of tall herb cover with probability of detection, and (f) is the percentage of short herb cover with probability of detection.

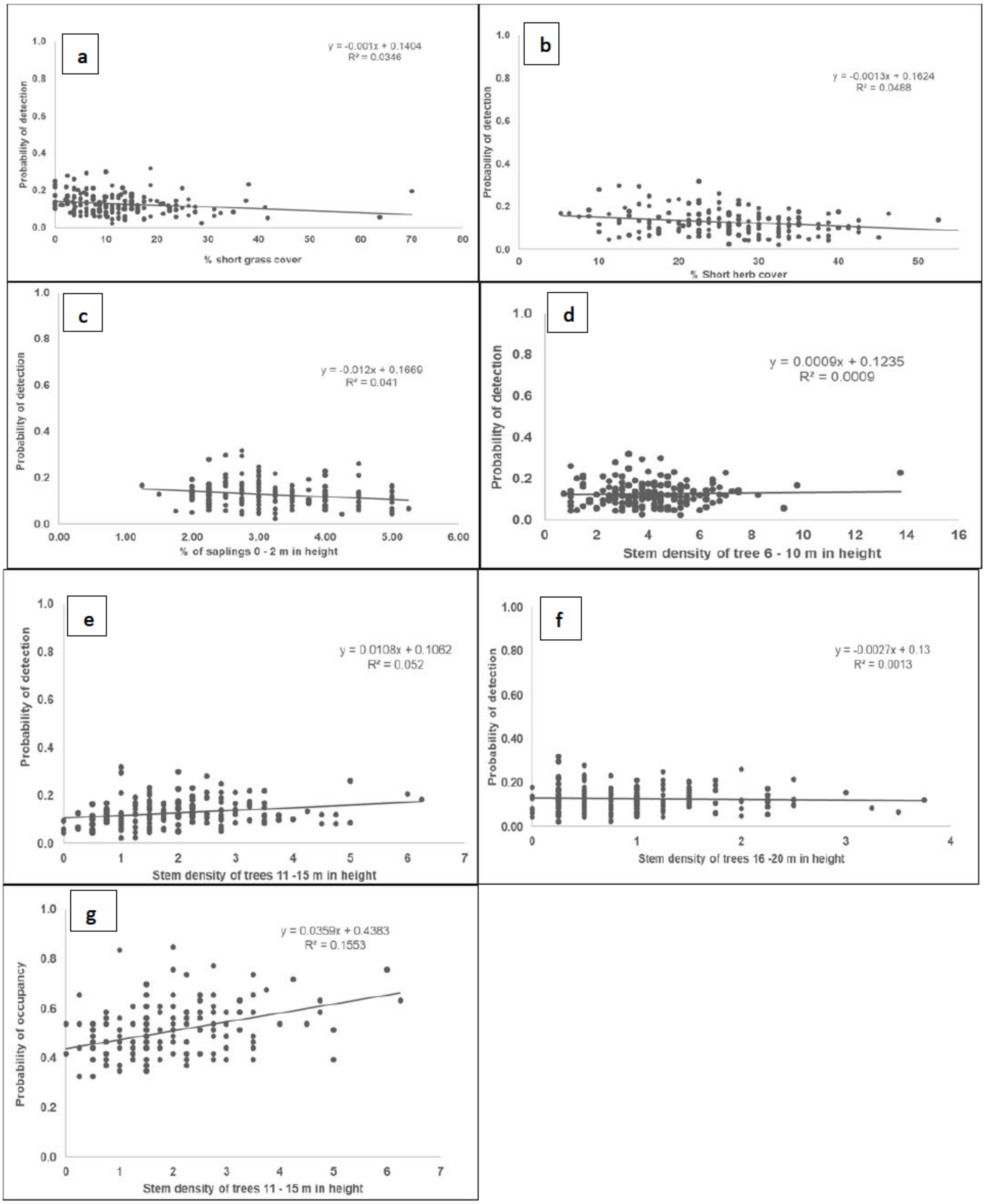

Figure 2. 4: Orange Ground-thrush occupancy and detection estimates in relation to site covariates during the wet seasons in the present study where (a) is the percentage of short grass cover and probability of detection, (b) is the percentage of short herb cover with probability of detection, (c) is the percentage of saplings 0 – 2 m with the probability of detection, (d) is the

stem density of trees 6 – 10 m with the probability of detection, (e) is the stem density of trees 11 – 15 m with the probability of detection, (f) is the stem density of trees 16 – 20 m with the probability of detection, and (g) is the stem density of trees 11 – 15 m with the probability of occupancy.

Table 2. 2: Summary of top models used to estimate occupancy and detection of Lemon Doves (*Aplopelia larvata*) and Orange Ground-thrushes (*Geokichla gurneyi*) during wet and dry seasons using nine microhabitat-scale covariates. The first two top models are for Lemon Dove during wet and dry seasons respectively, and the third model is for Orange Ground Thrush during the wet seasons.

Model	**AIC**	**Delta AIC**	**AIC Weight**	**Model Likelihood**	**No. Parameters**	**2Likelihood**
ψ(LL),p(SGC+SHC+THC+T2+T6+T16)	1099.44	0.00	0.0842	1.00	9	1081.44
ψ(SG),p(T11+S2+T2+THC+SHC)	916.05	0.00	0.0447	1.0000	8	900.05
ψ(T11),p(SGC+SHC+S2+T6+T11+T16)	1684.37	0	0.3088	1	8	1668.37

Index: LL = leaf litter, SGC = short grass cover, SHC = Short herb cover, THC = Tall herb cover, T2 = Tree height between 2 – 5 m, T6 = Tree height between 6 – 10 m, T16 = Tree height between 16 – 20 m.

2.5 Discussion

Occupancy and detection are determined by many factors such as resource availability, disturbance, the chance of survival and habitat use (O'Connell et al. 2006), which vary between seasons. The size of the species can also influence chances of detection; the larger the species, the higher the chances of detection (Randler and Kalb 2018). The Orange Ground-thrush was relatively rare during the dry season, and the photograph capture dataset was insufficient to model occupancy. However, Lemon Dove capture data were sufficient to satisfy modelling requirements for both the dry and wet seasons. Lemon Dove occupancy remained constant between the wet and dry seasons, but their detection probability was higher in the dry season than the wet season. The following covariates were significant for occupancy and detection of Lemon Doves during the wet season: percentage of leaf litter, short grass cover, short herb cover, tall herb cover, saplings 0–2 m, stem density of trees 6–10 m and trees 16–20 m. These covariates were similar to those found affecting Lemon Dove presence in the Indian Ocean Coastal Belt Forests study (Ehlers Smith et al. 2017a), excluding bare ground percentage as it was not an essential covariate in explaining Lemon Dove occupancy and detection in the present study. In the present study, the percentage of leaf litter had a positive influence on the occupancy of Lemon Doves in the wet season. Similarly, Ehlers Smith et al. (2017a) showed the positive influence of the percentage of leaf litter on the occupancy of Lemon Doves. Generally, there are more food resources in leaf litter because of invertebrates that inhabit it (Hockey et al. 2005, Ehlers Smith et al. 2017a, c, d). In the present study, leaf litter was main covariate positively influencing Lemon Dove occupancy probability, while in the Indian Ocean Coastal Belt Forests, leaf litter, as well as the percentage of bare ground and grass cover, also influenced occupancy of Lemon Doves (Ehlers Smith et al. 2017a). In the Indian Ocean Coastal Belt Forests, percentage of herbaceous cover and grass cover influenced detection probability positively during spring-summer months (Ehlers Smith et al. 2017a). Lemon Dove is a ground-dwelling bird which forages on forest floors; thus, short vegetation structure is crucial for their detection probability (Hockey et al. 2005), since they are not easily spotted.

During the dry season, the following covariates were significant for the occupancy and detection of Lemon Doves: stem density of trees 2–5 m and 11–15 m, percentage of saplings 0–2 m, tall herb cover and short herb cover. Percentage of short grass cover was a positive influence on the occupancy of Lemon Doves; it is likely that birds are finding more food where there is short grass cover. Stem density 11–15 m and a percentage of short herb cover had a positive influence on detection probability of Lemon Doves; presumably these trees are at their fruiting stage and may have fallen fruits underneath them and may also provide enough canopy cover for the species. In the Indian Ocean Coastal Belt Forests, detection probability of Lemon Doves was positively influenced by plant species richness, percentage of saplings and short woody plants during autumn-winter months (Ehlers Smith et al. 2017a). In contrast, the percentage of tall herb cover, saplings 0–2 m and stem density of trees 2–5 m negatively influenced the detection probability of Lemon Dove in the dry season in the present study. These sites may be lacking ideal and sufficient resources such as food for the species during the dry season in the Southern Mistbelt Forests compared with the Indian Ocean Coastal Belt Forests. Although Lemon Doves were more common in the Southern Mistbelt Forests compared with the Indian Ocean Coastal Belt Forests (Ehlers Smith et al. 2017a), we found their habitat requirements in both forest types had similarities. It is possible there is more anthropogenic disturbance in the Coastal Forests, which may negatively influence occupancy.

Percentage of short grass cover, percentage of short herb cover, percentage of saplings 0–2 m, stem density of trees 6–10 m, stem density of trees 11–15 m, stem density of trees 16–20 m were significant covariates for the occupancy and detection of Orange Ground-thrushes. Stem density of trees 11–15 m was a positive influence on the occupancy and probability of detection of Orange Ground-thrushes. The species primarily feeds on invertebrates and occasionally on fruits (Earle and Oatley 1983, Hockey et al. 2005), so tall trees may be beneficial for the occupancy of this species through provision of food and nesting sites. Percentage of short grass cover, short herb cover and saplings 0–2 m had a negative influence on the detection probability of the Orange Ground-thrush, indicating a preference for vegetation structure with an open understorey. Our results confirmed the habitat requirements of this species to be similar to those of Spotted Ground-thrush in the Indian Ocean Coastal Belt

Forest (Ehlers Smith et al. 2017b). These two species in both forest types seem to prefer forest patches with tall trees. However, the short herbaceous cover had a negative influence on detection probability of the Orange Ground-thrush, while it was a positive influence on detection probability of the Spotted Ground-thrush in the Indian Ocean Coastal Belt Forest (Ehlers Smith et al. 2017b). Our results showed the negative influence of short grass cover on the detection probability of the Orange Ground-thrush, which was similar to the findings of Ehlers Smith et al. (2017b). In this study, microhabitat-scale covariates revealed that both species have similar habitat requirements, regardless of the forest types within which they occur. Our study further indicated that these forest specialists prefer mature forests (Ehlers Smith et al. 2017b). Generally, forest specialists are sensitive to disturbance and negatively affected by habitat modification (Pardini et al. 2009, Ehlers Smith et al. 2017a, b, c).

The present study highlighted the importance of diverse habitat structures for the Orange Ground-thrush and the Lemon Dove. Heterogeneous habitats provide more resources and species diversity (Tscharntke et al. 2005). Since Lemon Doves are generally not easily detected, they prefer interior forest areas implying that they are likely to be negatively affected by edge effects and anthropogenic activities such as logging (Ehlers Smith et al. 2017a). Lemon Doves showed a preference for patches with dense understorey and a diverse habitat structure (Malan 2011, Ehlers Smith et al. 2017a) which highlights the importance of conserving natural forests in their natural condition. Orange Ground-thrush showed a preference for forests with an open understorey. Understorey insectivores are mainly known to be sensitive to habitat disturbance and fragmentation (Powell et al. 2015), and negatively affected by edge effects (Beier et al. 2002)

Efforts to conserve natural forests are necessary to ensure the survival of these forest specialist species as they are beneficial to local communities. Many cultures perceive doves as a sign of peace and they are believed to invite good luck, happiness, and protection against evil spirits (Nengovhela 2010), thus providing cultural ecosystem services to local communities. The present study showed the importance of a diverse habitat structure for both of these forest species. Unfortunately, 41% of the KZN Mistbelt region had been converted into timber plantations by the turn of the millennium, which is the most predominant anthropogenic land-use in this region (Armstrong et al. 1998). As a consequence, homogeneous vegetation structure threatens forest species requiring diverse habitat structure. Moreover, the isolation of certain Mistbelt forest patches results in isolated populations, and thus, reduced population sizes, which threaten range-restricted species (Armstrong et al. 1998) such as the Orange Ground-thrush. A high density of tall trees in this study was an essential microhabitat covariate, particularly for sufficient cover and food source for these ground-dwelling birds. Therefore, directing attention towards conserving mature natural forests and restoring those degraded is a critical conservation management strategy to maintain species diversity and habitat heterogeneity.

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CHAPTER 3

What are the landscape-scale drivers of avian species richness and functional diversity in KwaZulu-Natal and Eastern Cape Mistbelt Forests?

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Running header: Landscape-scale drivers of avian species richness and functional diversity in Mistbelt Forests

3.1 Abstract

Context

Landscape configuration influences the distribution and abundance of species, and its transformation through anthropogenic developments affects biodiversity through various processes (including dispersal, competition, reproductive pressures and local extinction). Landscape transformation results in changes to natural forest habitats causing changes in forest patch composition, habitat amount, patch size, isolation, shape, and edge dynamics. Therefore, avian species assemblages and distribution are expected to be influenced by changes in the landscape.

Objectives

To identify whether avian assemblage diversity and species functional trait diversity show consistent patterning across different landscapes in a forest ecosystem mosaic, particularly to examine the landscape-scale drivers of avian community composition.

Methods

We surveyed bird communities in 58 distinct patches of the Mistbelt Forests of KwaZulu-Natal and Eastern Cape Provinces, South Africa during the breeding and non-breeding seasons. We quantified avian species richness and various measures of functional diversity based on species' traits per forest patch. We measured the influence of forest patch size, habitat structural complexity, isolation effects (distance between patches, habitat amount) and landscape configuration on each diversity measure. We performed Bayesian generalised linear models to determine how the landscape influenced the diversity of avian communities in the forest**.**

Results

Distance between forest patches, patch diversity, indigenous forested areas, patch shape index and exotic timber plantations were drivers of most diversity measures. Amount of indigenous forest had a significant influence on species richness. Forest patch diversity had a significant positive influence whereas, amount of timber plantations surrounded forest patches were significant negative influence on avian functional richness, evenness and dispersion across seasons. Avian beta diversity was significantly driven by the reduction in forest patch size and habitat structural complexity.

Conclusions

Reduction in forest size and complexity reduced avian species richness and functional diversity. Increasing isolation distance negatively influenced avian diversity. Therefore, protection of natural forest habitats and diverse landscape mosaics is recommended for preserving avian communities. Consideration of forest connectivity should be given in further timber plantation management plans.

Keywords: Indigenous forest; fragmentation; beta diversity; functional diversity; avian communities

3.2 Introduction

Human population growth is increasing pressure to transform natural habitats to support demand for resources. Anthropogenic activities such as natural habitat conversion for agriculture, exotic timber plantations and urban settlements are altering the landscape structure and composition (Hansen et al. 2013; Laurance et al. 2014; Arroyo-Rodríguez et al. 2017). Landscape refers to a spatially diverse land area encompassing a mixture of land cover patches differentiated by biotic and abiotic structure or composition (Benton et al. 2003; Arroyo-Rodríguez et al. 2017). Landscape structure and composition describe the heterogeneity of a landscape and may have different (negative, positive, or neutral) impacts on biodiversity (Fahrig, 2003; Fahrig et al. 2011; Tscharntke et al. 2012). Transforming landscapes causes changes in natural habitats, including the configuration of the landscape matrix: ‘habitat amount’ (c.f. Fahrig 2013), habitat patch size, isolation, patch shape, and edge dynamics

(Burkey 1995; Fahrig 1997; Fahrig 2003; Fahrig 2013; Haddad et al. 2015). Generally, habitat patches or land cover types are embedded in a matrix at the landscape level (Niebuhr et al. 2015): for example, agriculture, plantations or settlements surround natural forest, savanna or grassland patches. Changes in the landscape affect biodiversity in various ways, including increasing species mortality, reducing dispersal potential, disrupting reproduction, increasing local extinction, and disrupting the interaction of species at different spatial scales (Reynolds 2010; Smith et al. 2011; Carrara et al. 2015; Niebuhr et al. 2015). The distribution and abundance of species in transformed landscapes seem to mostly depend on preferences for higher quality fragments and the ability to move between patches (Moilanen and Hanski 1998; Mazerolle and Villard 1999; Fleishman et al. 2002; Niebuhr et al. 2015). For this reason, landscape configuration may strongly influence changes in movement patterns, affecting patch colonisation, increasing mortality risk during dispersal, and changing predator-prey interactions within the matrix, ultimately influencing survival and reproductive success within habitat patches (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Kupfer et al. 2006; Fahrig 2002; Niebuhr et al. 2015). The ability to disperse is also considered a major driver of the variation in species composition among local communities. The difference between the species composition within a region (ɣ diversity) and that found within specific local sites (α diversity) is known collectively as β diversity (Whittaker 1960; Baselga 2010; Vannette and Fukami 2017). This variation across space and time is influenced by two distinct processes: the loss or gain of species (Ferger et al. 2017). This may be further decomposed into its two additive components: turnover (species replacement) and nestedness (community assemblage being a nested subset of the larger/gamma species pool (Baselga 2010).

Many natural habitats, such as forests, are highly fragmented, either naturally because of climate, geographic barriers, topography, or through anthropogenic processes, but may still support high proportions of biodiversity (Geldenhuys and MacDevette 1989; Gibson et al.

2011). However, some forest patches are negatively affected by deforestation, exotic timber plantations and agricultural activities, aggravated by landscape transformation (Lawes, 1990; Swart and Lawes, 1996; Turner 1996; Lawes et al., 2000). This often results in indigenous forest patches nested in rural landscapes where people rely on natural resources for their livelihoods (Lawes et al. 2004; Shackleton et al. 2007; Adie et al. 2013). Consequently, forest patch sizes are decreasing, forest edge amounts have increased, habitat structural complexity is reduced, and isolation pressures increase, causing a shift in species composition, distribution and abundance within the patches (Murcia 1995; Turner 1996; Fahrig 2003). Forest edges contain different species' communities from those of forest interiors because of a change in habitat structural complexity, altered climate with higher light availability, loss of soil moisture, and increased incursion of predators and competitors (Murcia 1995; Ewers and Didham 2006). Community dynamics within remnant forest patches are often complex and driven by multiple factors. For example, ant abundance and diversity are higher at the edges compared with the forest interior (Gonzalez et al. 2018). However, the species richness and diversity of ground beetles is not significantly higher at forest edges compared with the interior (Magura 2017). Furthermore, transformed landscapes may be surrounded by poor quality matrix compositions with inhospitable or impenetrable features, resulting in the elimination of certain vulnerable species and affecting the interactions between plants and animals (Cordeiro and Howe 2003). A matrix landscape that presents harsh abiotic conditions may hinder species' dispersal and patch colonisation causing local extinction, whereas a matrix with suitable composition may supplement local resources and species can forage for alternative supplies (Brotons et al. 2003, Rand et al. 2006; Kuefler et al. 2010).

Individual species respond differently to landscape transformation, depending on their biological traits. Functional traits refer to features of each species required for them to survive and reproduce (Mason et al. 2005; Croci et al. 2008). Variation in environmental characteristics such as the structure and resources availabilities are reflected by variation in communitycomposition, as species with diverse traits fill various niches based on resources and habitat structures (Magalhaes et al. 2002). Consequently, specific responses in community traits may be able to predict differences in environmental processes or conditions (Adler et al. 2013). In avian communities, the results of fragmentation differ, depending on factors such as the time the fragmentation occurred, size of remaining fragments, shapes and distance between remnants (Saunders et al. 1991, Hansen and Urban 1992; Fahrig 2019). Functional traits determine the avian response to landscape transformation (Şekercioğlu et al. 2012; Odling-Smee et al. 2013; Banks et al. 2017). These traits differ among communities, and these differences can cause communities to respond uniquely to a given landscape change (Dolman et al. 2007). Species with generalised traits react differently to landscape transformation than do those with specialised traits (Zhang et al. 2016; Adu-Acheampong and Samways 2019). Since generalists are capable of exploiting several habitat types, resources or structures in the landscape matrix, they tend to be less affected by changes in habitat than specialists, which are more dependent on a specific or a few habitat types and their specialised structures and resources therein (Bonier et al. 2007; Carrara et al. 2015; Zhang et al. 2016). Some avian communities are specialised to forest interior habitats; others prefer forest edges habitats (Terraube et al. 2016). Therefore, there are various factors likely to be essential drivers of avian communities in transformed landscapes.

In this study, we investigated whether avian assemblage diversity and species functional trait diversity showed a discrepancy across different landscapes in a forest ecosystem mosaic and aimed to elucidate landscape-scale drivers of avian community composition. Hence, different species respond differently to landscape transformation depending on their traits. Therefore, we hypothesised that bird species assemblages and functional diversity would show significant changes: forest patches dominated by a few highly abundant species adapted to landscape transformation. We studied the avian assemblage found in various patches of the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape Provinces, South Africa, which are naturally and anthropogenically fragmented, surrounded by exotic timber plantations, grasslands and villages. We analysed the data from both breeding and nonbreeding seasons to eliminate factors such as resource availability, migration and immigration. We aimed to determine how avian species richness, assemblage and functional diversity differed among patches, and how landscape configuration may drive the structure of avian assemblages. We predicted that (1) avian β diversity would be higher between forest patches of decreasing size and complexity, and increasing isolation (2) patches surrounded by timber plantations that were isolated would have low avian species richness and functional diversity (3) species richness and functional richness would increase with patch structural diversity, size and habitat amount (total amount of that habitat in the landscape, c.f. Fahrig [2013]) (4) functional richness would increase with patch size, habitat amount and indigenous forest proportions and decrease with the increased isolation metrics.

3.3 Methods

3.3.1 Study area

We conducted the study in three different regions (Umtata, Kokstad and Creighton) that contained Afrotemperate Southern Mistbelts Forests, located within inland KwaZulu-Natal and Eastern Cape Provinces of South Africa (Fig. 3.1). KwaZulu-Natal is approximately 92,100 km^2 in area and is situated from the east coast of South Africa, reaching a maximum inland elevation at 3,451 m. The climate is subtropical along the coast and becomes temperate towards the inland regions at high altitude. KwaZulu-Natal contains areas rich in biodiversity and houses several UNESCO World Heritage sites. The Eastern Cape is in the south-east of South Africa and covers approximately 168,966 km^2. Its climate is highly diverse: the west is dry and arid year-round, with sub-zero temperatures in winter and > 40 °C in summer. The east of the province experiences more rainfall and humidity and becomes subtropical along its northern coast with relatively higher summer rainfall.

The Southern Mistbelt Forests were historically fragmented across the landscape but anthropogenic land-use change and activities have further affected them (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Lawes et al., 2004; Adie et al., 2013). A mix of *Afrocarpus* and *Podocarpus* tree species dominates the Southern Mistbelt Forests of our study region (Cooper, 1985; Wilson et al. 2017). They occur at 800 – 1500 m altitude, on steep, south-facing slopes on dolerite ridges and receive frequent mist in the summer, and a mean annual rainfall of > 1000 mm with highest temperatures of ~37°C and lowest of ~4°C (Moll, 1972). Other characteristic tree species are *Cussonia chartacea, Cryptocarya myrtifolia, Prunus africanus, Xymalos monospora, Kiggelaria africana* and *Combretum kraussii, Ptaeroxylon obliquum, Celtis africana, Calodendrum capense*, and *Olea capensis* (Moll, 1972).

3.3.2 Survey-site selection

In our three study regions, we selected a range of indigenous forests patches with varying surrounding land uses, including timber plantations, grasslands and rural or urban developments. At each area, we chose a variety of forest patch sizes, with the structure of 1 – 3 source or "mainland" forest patches, and several surrounding satellite forest patches. We identified all Mistbelt Forests within the study region using the latest landcover maps (GeoTerra Image 2015) displayed in Geographic Information System (GIS) programme, ArcGIS v10.4 (ESRI, 2011). We overlaid a 200 m x 200 m grid over each survey forest patch identified to allocate survey points at the intersection of each gridline, to ensure they were distributed evenly across sample areas. Therefore, the numbers of points in each habitat patch were proportional to the size of each habitat patch (Bibby et al. 2000; Ehlers Smith et al. 2018). Survey locations were then projected using a Global Positioning System (GPS, Garmin GPS map 62; Garmin USA) to locate survey-site selection in the field and maintain a minimum distance of 200 m between survey points.

3.3.4 Bird surveys

We conducted surveys during the avian non-breeding season of southern Africa between May – July 2018 and the breeding season between October 2018 – February 2019. We conducted fixed-radius point-count surveys of all avian species audible or visible within a 50 m radius. We calculated species richness as the accumulative number of species recorded at each survey location, and then pooled the total species richness and relative abundance per forest patch. We also recorded relative abundance as the total number of individuals of each species at each survey location (Bibby et al. 2000; Ehlers Smith et al. 2018). Surveys occurred during sunrise + 3 h and lasted 10 min at each point. We did not record nocturnal birds because of the timing of our surveys. All individuals for which the species was not identified, were discarded.

3.3.5 Functional traits of the avian community

As per Ehlers Smith et al. (2018), we constructed a list of functional traits, comprising: primary diet (carnivory, frugivory, granivory, insectivory, nectarivory, omnivory), main foraging strategy (harvest [fruit/seed/nectar], terrestrial probe, arboreal probe, glean, hawk, perch and swoop, various [omnivory]), movements (altitudinal migrant, breeding migrant, nomadic, partial migrant, sedentary, sedentary/altitudinal migrant), nesting requirement (cup/ball/bowl, cavity, ground, platform). These traits indicate resource use and habitat provisioning (Flynn et al. 2009), and we created a species-trait matrix incorporating these traits.

3.3.6 Microhabitat covariate surveys

The microhabitat structure and foliage profile were surveyed in a 20 m radius around each survey location point thus: percentage coverage of bare ground; leaf litter; grass cover; herbaceous plants; saplings and scrub/woody plants <2 m, and percentage of trees of 2–5 m, 6–10 m, 11–15 m, 16–20 m, 21–25 m and above 25 m heights; mean height of all plant groups, stem density of all horizontal and vertical dead trees, and stem density of all trees in each height category (Bibby et al. 2000; c.f. Ehlers Smith et al. 2015, 2017). Scrub/woody vegetation was distinguished from trees and classified as ellipsoid-shaped plants with multiple branches emerging from the ground, which represent an understory structural component (Ehlers Smith et al. 2015). We classified trees as bare-stemmed plants of height >2 m, with upper branches containing foliage (Ehlers Smith et al. 2015). We calculated the Shannon Wiener Diversity Index (SWDI) to investigate the habitat structural complexity in our survey forest patches using the formula:

$$H = -\sum_{i-1}^{s} pi \ln(pi)$$

We firstly converted mean height scores for each vegetation class into foliage height index, and *pi* is the proportion of the total foliage lying in the *ith* layer of the chosen horizontal layer (Bibby et al., 2000; Ehlers Smith et al. 2015).

To analyse landscape-scale configuration, we calculated (a) the gross sizes of all surveyed forest patches (patch size) and identified all forest patches greater than 90 ha as ‘mainland’/core patches and all forest patches less than 90 ha as fragments (c.f Ehlers Smith et al. 2018); (b) the distance of all smaller forest patches to the mainland patch as the isolation distance; (c) the amount of habitat in the surrounding matrix of a survey forest patch within a radius of 540 m (the mean distance of the dispersal limit for avian sedentary forest specialists, c.f. Ehlers Smith [2018]), together with the area of the survey patch itself (habitat amount).

3.3.7 Analyses

To avoid multi-collinearity, we created a correlation matrix to test for significant correlations between explanatory covariates with a correlation threshold of $r \geq 0.7$ (Garden et al. 2010). After removing correlated covariates, we retained ten landscape covariates. We created a species-presence matrix based on the total avian species richness recorded in each forest patch, a primary functional presence matrix based on avian species primary source of diet, foraging strategy, nesting requirements and migratory strategy. We classified species α-diversity as the accumulative number of species documented in each forest patch, and functional α-diversity as the functional space involving several dimensions occupied by all functional and biological traits present in the avian community in a forest patch (Ehlers Smith et al. 2018). We calculated species richness as the total number of species in each site (SR); functional richness as the amount of niche space occupied by the species within a community (FRic) (Legras et al. 2018). We calculated functional evenness (FEve) as an abundance-weighted consistency of density distribution in the filled niche volume of species (Mason et al. 2005; Ibarra and Martin 2015), which is expected to be equal to one in the case of perfect distributions of species (Villéger et al. 2008). Functional divergence (FDiv) was calculated as an abundance-weighted taxonomic distinctness and the functional dispersion (FDis) as an abundance-weighted version of functional richness (Cooke et al. 2019). Each measure was calculated for each given forest patch using a principle coordinate analysis (PCoA) on a distance matrix of functional traits of each species recorded in the avian and tree community (Villéger et al. 2008). Pairwise distance scores of species' traits were calculated in the community based on Gower's distance (Gower 1966) which allows for a combination of continuous data and a binary matrix, calculated in the FD package (Laliberté and Legendre 2010) using the statistical software programme R v3.3.1 (R Core Team 2015). We retained the first two PCoA axes which explained 73.1%, and 72.3%

of the total inertia in the avian community during the non-breeding season and breeding season, respectively. The Betapart package (Baselga and Orme 2012) was used to partition β diversity into its spatial turnover and nestedness resultant components (nestedness), applying the Sørensen dissimilarity index to pairwise species traits to describe overall species and functional β diversity, the Simpson's dissimilarity index to describe the effect of turnover, and their difference to describe nestedness (Baselga 2010) in R v3.3.1. We then calculated the ratio as a proportion of nestedness component to overall β-diversity. We generated distance matrices of forest patch sizes differences as the independent variable. We analysed the effect of forest patch size on taxonomic and functional β-diversities components by conducting multiple regression of distance matrices (Lichstein 2007). All p-values were calculated by permutation test (9,999 runs) to avoid the outcome of non-independence between cases on p-values. We conducted analyses using packages ade4, arm, ecodist and lme4 (Dray and Dufour 2007; Gelman et al. 2015; Goslee and Urban 2007; Bates et al. 2015) in R v3.3.1 (R Core Team 2015). We also created Bayesian generalised linear models (BayesGLM) for taxonomic, functional and guild diversity against site and land-use covariates. We ran maximum likelihood models to define the best model fit of the influence of site covariates and landscape configuration on avian diversity measures in our study sites. Shannon Wiener Index (SWDI) which is a measure of diversity that combines the number of species in a given area, in this study referred to forest patch diversity and their relative abundance, isolation (distance between patches), forest patch size and habitat amount were converted to log (non-normal distribution: Kolmogorov–Smirnov test, $p < 0.001$). Model selection concluded by the Akaike information criterion (AIC); models with <2 AIC differences were considered of similar explanatory power (Burnham and Anderson 2004).

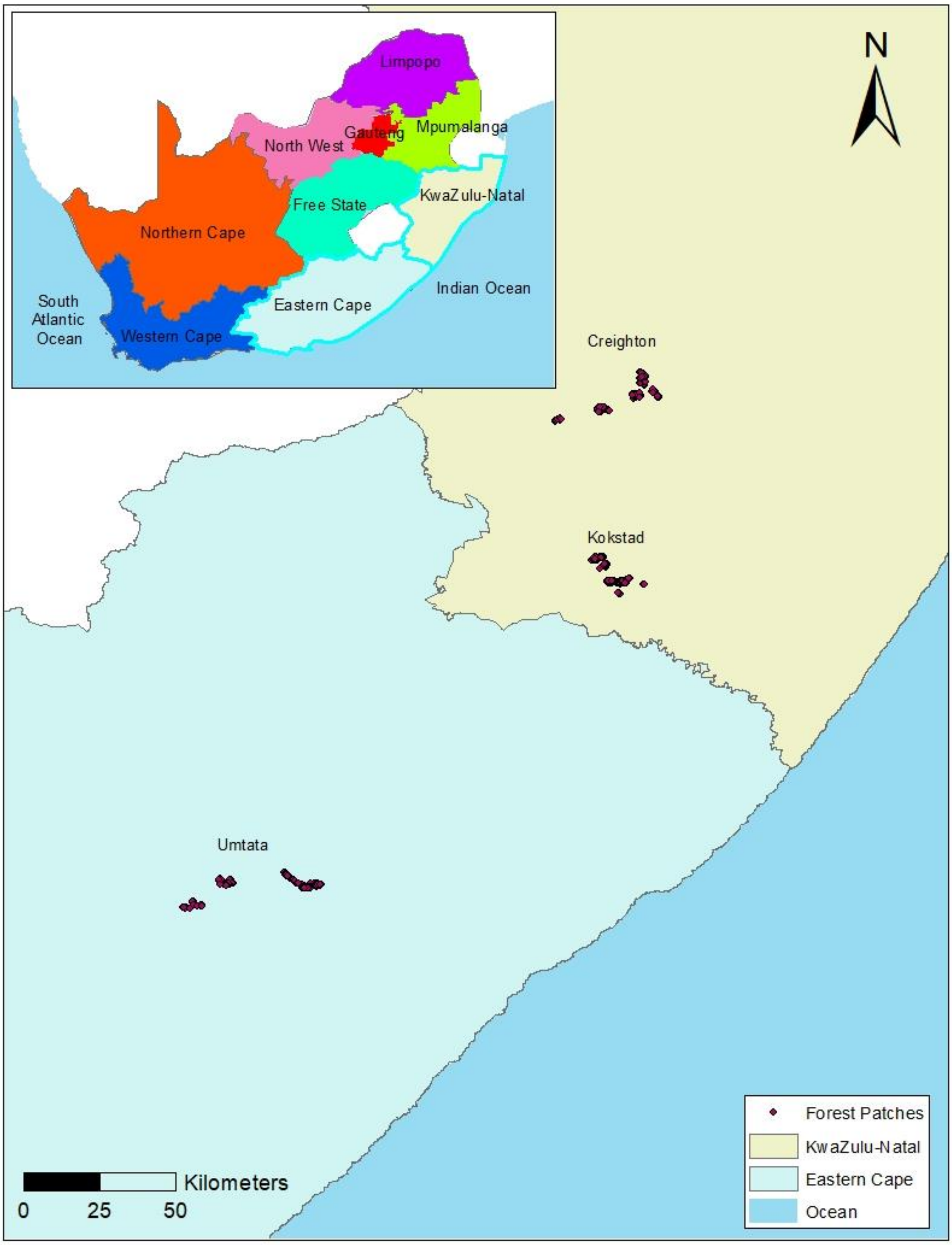

Figure 3. 1: Mistbelt Forest patches in KwaZulu-Natal and Eastern Cape Provinces, South Africa, where we selected a range of indigenous forests patches as our study sites in Umtata, Kokstad and Creighton.

3.4 Results

We recorded 9,037 individual birds from 747 surveys in 58 distinct habitat forest patches which totalled 82 avian species for the breeding and non-breeding seasons. This assemblage comprised of 75 avian species during the non-breeding season and 68 avian species during the breeding season. Most species were recorded in both seasons. In the breeding season, overall species β-diversity was not significantly influenced by forest patch size and isolation ($F = 7.97$; $P > 0.05$; $r^2 = 0.011$). The avian species nestedness significantly increased with increasing forest patch size and decreased with increasing isolation ($F = 97.40$; $P < 0.05$; $r^2 = 0.120$). Avian species turnover increased with decreasing forest patch size and isolation ($F = 84.36$; $P < 0.05$; $r^2 = 0.105$). Overall avian functional β-diversity was not significantly influenced ($F = 8.36$; $P > 0.05$; $r^2 = 0.115$), nor was avian functional nestedness ($F = 4.55$; $P > 0.05$; $r^2 = 0.006$) by forest patch size and isolation but avian functional turnover ($F = 27.97$; $P < 0.05$; $r^2 = 0.037$) increased with increasing forest patch size and isolation.

During the non-breeding season, the overall avian species β-diversity was not significantly influenced by forest patch size and isolation ($F = 15.74$; $P > 0.05$; $r^2 = 0.025$). Avian nestedness increased with increasing forest patch size and decreased with increasing isolation ($F = 264.33$; $P < 0.05$; $r^2 = 0.301$), and turnover decreased with increasing forest patch size and increased with increasing isolation ($F = 180.59$; $P < 0.05$; $r^2 = 0.228$). Overall avian functional β-diversity was not significantly influenced by forest patch size and isolation ($F = 0.377$; $P > 0.05$; $r^2 = 0.001$. Avian functional nestedness increased with increasing forest patch size and decreased with increasing isolation ($F = 22.087$; $P < 0.05$; $r^2 = 0.035$). Avian functional turnover decreased with increasing forest patch size and increased with decreasing isolation ($F = 42{,}906$; $P < 0.05$; $r^2 = 0.066$).

During the breeding season, the Bayesian generalised linear models indicated that the indigenous forested area and the variation in the vegetation that is captured by the index significantly (($F = 42$; $P < 0.05$ $r^2 = 0.035$) influenced avian species richness positively (Fig. 3.2a, b). The the variation in the vegetation that is captured by the index (SWDI)significantly ($F= 42$; $P < 0.05$; $r^2 = 0.191$ influenced the avian functional richness positively, while timber plantations significantly ($P < 0.05$) influenced avian functional richness negatively (Fig. 3.2c, d). Isolation distance and timber plantation both had a non-significant ($P > 0.05$) influence on the avian functional evenness, whereas variation in the vegetation that is captured by the index (SWDI) had a significant ($F = 34$; $P < 0.05$; $r^{2\,=}$ 0.008 positive influence (Fig. 3.2e, f and g). Isolation distance and variation in the vegetation that is captured by the index(SWDI) both had a non-significant ($F = 42$; $P > 0.05$; $r^2 = 0.999$ influence avian functional divergence (Fig. 3.2h and i). Woodland open bush and isolation distance both had a non-significant ($F = 42$; $P >.05$; $r^2 = 0.091$ influence on the avian functional dispersion (Fig. 3.2k and l).

During the non-breeding season, the isolation distance had a significant negative influence on avian species richness, and indigenous forest had a significant (($F = 34$; $P < 0.05$; $r^2 = 0.053$) positive influence (Fig. 3.3a, b). The variation in the vegetation that is captured by the index(SWDI) and forest patch shape index both had a significant ($F = 34$; $P < 0.05$; $r^2= 0.180$) positive influence, whereas timber plantations had a significant negative ($P < 0.05$) influence on avian functional richness (Fig. 3.3c, d and e). Avian functional evenness was significantly ($F = 34$; $P < 0.05$; $r^2= 0.007$ negatively influenced by indigenous forests but positively influenced by variation in the vegetation that is captured by the index(SWDI) (Fig. 3.3f, g and h). Timber plantations and forest patch shape index both had a non-significant ($F = 34$; $P > 0.05$; $r^2= 0.993$) influence on avian functional divergence (Fig. 3.3i, j). Timber plantations and isolation distance both had a non-significant ($F = 34$; $P > 0.05$; $r^2= 0.125$) influence on functional dispersion (Fig. 3.3k, l).

Table 3. 1: Summary of top Bayesian General Linear Models showing the influence of landscape and forest patch configuration on avian diversity measures of avian communities in Mistbelts Forest of KwaZulu-Natal and Eastern Cape Provinces, South Africa, using ten covariates during the breeding season

Response Variable	**Model**	**AIC**	**Delta AIC**	**AIC Weight**	**Model Likelihood**	**No. Parameters**
Species richness	IF + SWDI	362.4	0	0.00643	1	2
Functional richness	SWDI + PL	323.37	0	0.006440	1	2
Functional evenness	Iso + SWDI + PL	80.908	0	0.006437	1	3
Functional divergence	Iso + SWDI	113.73	0	0.006387	1	2
Functional dispersion	Wood + Iso	157.99	0	0.006379	1	2

Index: SWDI = Shannon Wiener Diversity Index; IF = Indigenous forests; PL = Timber Plantations; CUL = Cultivated area; Iso = Isolation distance; Wood = Woodland open bush.

Table 3. 2: Summary of top Bayesian General Linear Models showing the influence of landscape and forest patch configuration on avian diversity measures of avian communities in Mistbelts Forest of KwaZulu-Natal and Eastern Cape Provinces, South Africa, using ten covariates during the non-breeding season.

Response Variable	**Model**	**AIC**	**Delta AIC**	**AIC Weight**	**Model Likelihood**	**No. Parameters**
Species richness	Iso + IF	280.84	0	0.006333	1	2
Functional richness	SWDI + PL + SI	228.71	0	0.006257	1	3
Functional evenness	IF + SWDI	76.922	0	0.006342	1	2
Functional divergence	PL + SI	92.732	0	0.006329	1	2
Functional dispersion	PL + Iso	121.09	0	0.006110	1	2

Index: SWDI = Shannon Wiener Diversity Index; IF = Indigenous forests; PL = Timber Plantations; CUL = Cultivated area; Iso = Isolation distance; SI = Patch Shape Index.

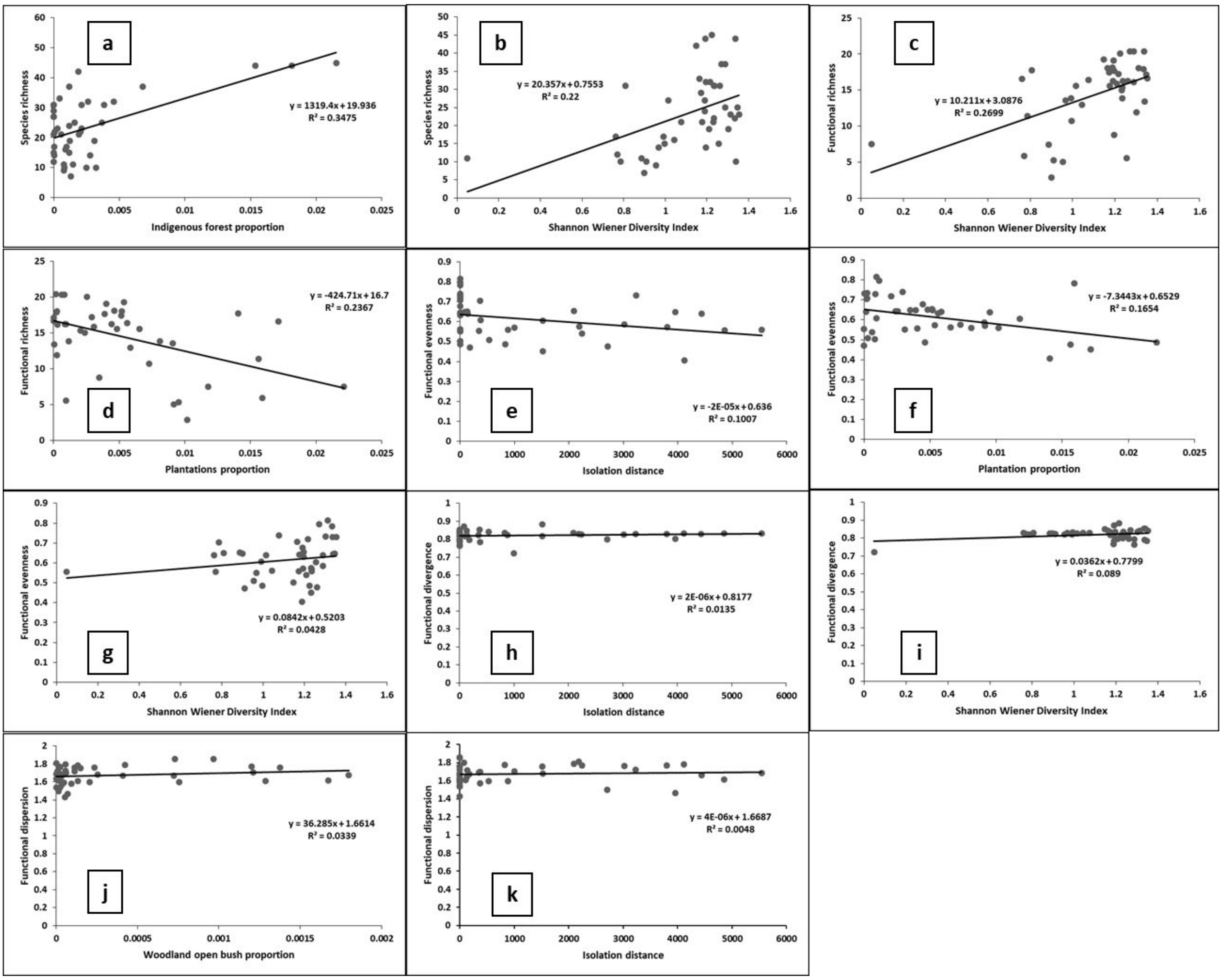

Figure 3. 2: Graphical display of top models connecting bird diversity measures to landscape covariates during the breeding season where (a) is avian species richness and indigenous forest proportion, (b) avian species richness and forest patch diversity (SWDI), (c) avian functional richness and forest patch diversity (SWDI), (d) avian functional richness and timber plantation proportions, (e) avian functional evenness and forest patch isolation distance, (f) avian functional evenness and forest patch diversity (SWDI), (g) avian functional evenness and timber plantation proportions, (h) avian functional divergence and forest patch isolation distance, (i) avian functional divergence and forest patch diversity (SWDI), (j) avian functional dispersion and woodland open bush proportions, and (k) avian functional dispersion and log forest patch isolation distance.

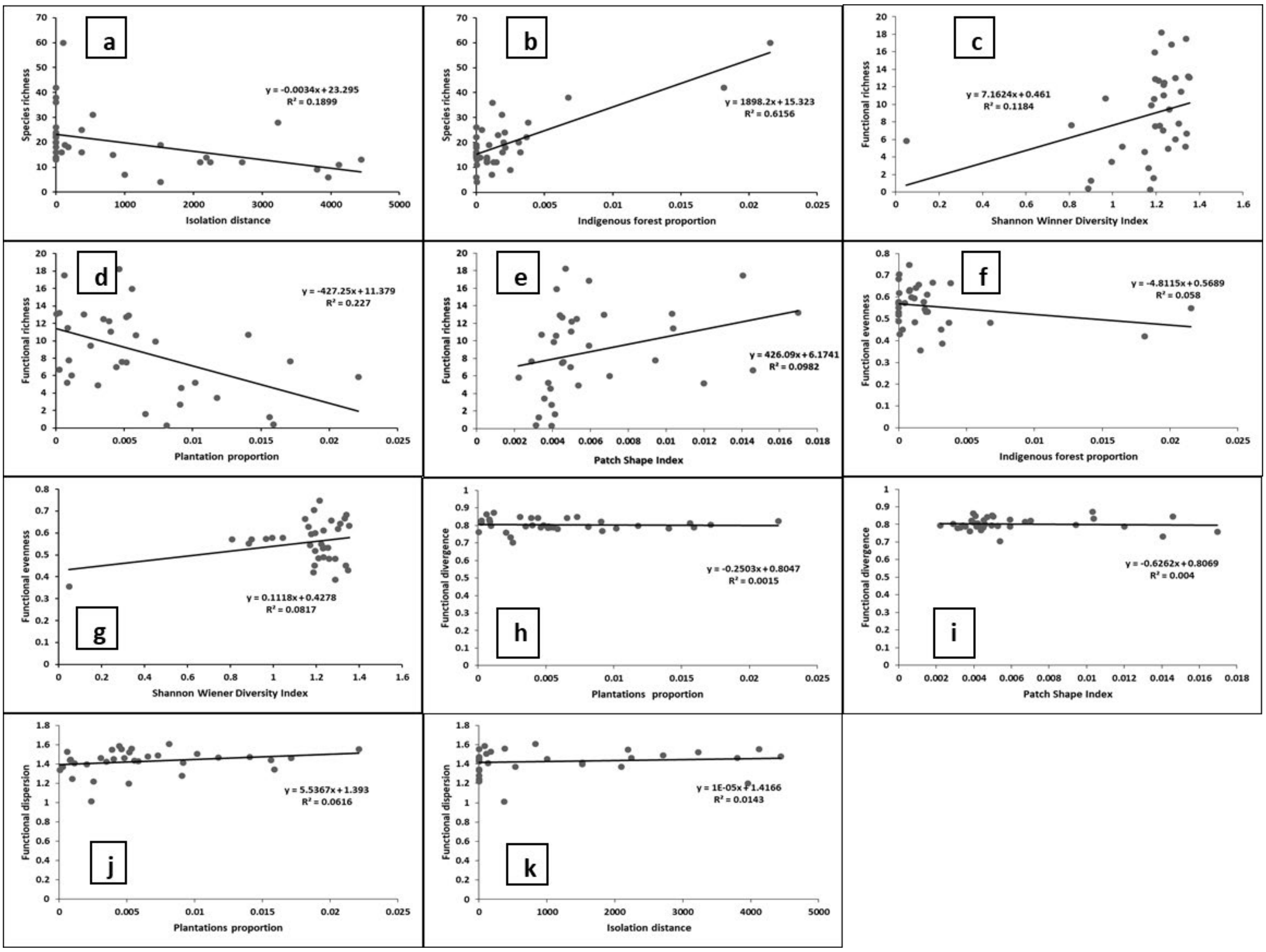

Figure 3. 3: Graphical display of top models connecting bird diversity measures to landscape covariates during the non-breeding season where (a) is avian species richness and indigenous forest proportion, (b) avian species richness and forest patch diversity (SWDI), (c) avian functional richness and forest patch diversity (SWDI), (d) avian functional richness and timber plantation proportions, (e) avian functional evenness and forest patch isolation distance, (f) avian functional evenness and forest patch diversity (SWDI), (g) avian functional evenness and timber plantation proportions, (h) avian functional divergence and forest patch isolation distance, (i) avian functional divergence and forest patch diversity (SWDI), (j) avian functional dispersion and woodland open bush proportions, and (k) avian functional dispersion and log forest patch isolation distance.

3.5 Discussion

Our results showed that avian species richness and functional α-diversity increased with forest patch size; the increase in patch size resulted in high species richness and functional diversity during breeding and non-breeding seasons, supporting our predictions. Our results also support the study conducted by Ehlers Smith et al. (2018) in Indian Ocean Coastal Belt Forest, where decreasing forest patch size had a negative influence on avian species richness and functional α-diversity. Si et al. (2016), similarly described avian species richness and functional α-diversities increasing with habitat area. This could be related to the increased structural complexity of the vegetation in larger forest patches since avian species richness, and functional diversity is based on traits that represent the use of environmental resources by species (Carscadden and Mirotchnick 2011; Magioli et al. 2015; Ehlers Smith et al. 2018). A larger and more complex habitat patch likely provides more resources and structural diversity for species of varying traits (Magioli et al. 2015). Therefore, we recommend sustainable use and protection of larger forest patches to ensure continued support of avian communities by preventing the reduction in niches, and therefore homogenisation of species richness.

Avian species richness and functional diversity were negatively influenced by forest patch isolation distance; the increase in the distance between forest patches resulted in low species richness and functional diversity across seasons, supporting our prediction. This is congruent with the avian community in Indian Ocean Coastal Belt Forest, where the distance had a negative impact on avian communities across seasons (Ehlers Smith et al. 2018). *Eucalyptus* monocultures were found containing lower α-diversity in the study by Barros et al. (2019) because homogenous timber plantations differ from natural forests in vegetation complexity, structure and species composition. Therefore, our results explain the importance of high-quality matrix as the connection between habitats or forest patches to promote the species dispersal and patch colonisation.

Separating β-diversity into turnover (i.e. species replacement) and nestedness (i.e. subsets of species of the greater overall species pool) between sites improves the understanding of the mechanisms behind the drivers determining species composition across spatial scales (Baselga et al. 2010; Si et al. 2015). Our results showed a significant change in avian species richness across the matrix across seasons. Avian species nestedness was significantly driven by forest patch size and isolation distance across seasons, and avian functional nestedness was driven by forest patch size but was only significant during the non-breeding season. Avian species in smaller forest patches were taxonomically and functionally the subsets of larger patches. Numerous processes have been proposed to result in nested patterns of species assemblages (Ulrich et al. 2009), including differential colonisation and extinction histories caused by species-specific traits, such as the ability to disperse (Srinivasan et al. 2014), and patch or habitat heterogeneity or quality linked with species changing in their degree of specialisation (Wright and Reeves 1992).

Avian species turnover during the breeding season significantly decreased as the forest patch size, and isolation distance increased. Replacement of species is problematic as fragmentation gradients become more severe, as it may result in a homogenisation of species in communities (Morelli et al. 2016), where range-restricted or specialist species usually exhibit low resilience to disturbance (Salisbury et al. 2012) and are more likely to go extinct and be replaced (Sekercioglu 2011). For conservation purposes, this finding is key to showing that large forest patches are also crucial for avian diversity.

During both seasons, avian species richness across landscapes with higher proportions of indigenous forested areas was higher, which supported our prediction. Our results are congruent with previous studies that show higher species richness in natural forests (O’Dea and Whittaker 2007; Neuschulz et al. 2011; Goded et al. 2019). Furthermore, Weathered and Lawes (2003) found relatively low avian species richness in Mistbelt Forest patches in a timber plantation matrix. Forests habitats may be providing breeding niches and food resources such as insects and fruits which are essential for avian communities. This is supported by the increase in avian species richness with forest patch diversity, indicating that diverse patches within the matrix accommodated multiple species, thus, supporting our prediction. Diverse habitats are expected to provide more ecological niches or complementary resources and thus increase the diversity of plants and animals (Rosenziweig 1995; Lee and Martin 2017; Maseko et al. 2020). During the non-breeding season, the distance between forest patches had a significant influence on avian species richness.

Avian functional richness significantly increased with forest patch diversity and decreased with patch shape index across the landscapes, in support of our prediction. Generally, larger forest patches hold high complexity in relation to less homogenised edge vs. more complex interior structures (Murcia 1995; Mandal and Chattarjee 2020) and provision for high functional diversity (Villard et al. 2014). In our study, avian functional richness significantly decreased where exotic timber plantation landscapes were predominantly bordering forests, across seasons. Exotic timber plantations are known to reduce the species richness and modify the composition of species assemblages (Lees et al. 2015), likely because of their homogenous structure.

Avian functional evenness was less evenly distributed among species across landscapes where timber plantations were dominant, but it increased with forest patch diversity and indigenous forested areas. It is likely that the spread of resources such as breeding niches and food resources across our study system, implying niches were utilised in large, diverse indigenous forests. Our results indicated that complex habitat structures allowed even distribution of traits among avian species, which may be because these habitats are providing niche and resource diversity (Mason et al. 2005). Furthermore, avian species may be occupying less disturbed areas since the functional evenness of a given community decreases along a disturbance gradient (Grime 2006; Mouillot et al. 2013).

Avian functional divergence increased with increasing forest patch isolation distance, implying that species' traits became more divergent across cultivated landscapes and in forest patches far from each other, with irregular patch shape. This pattern of avian species distribution showed that forest patches far from each other with irregular shapes shared only very specialised or very generalised species. Additionally, in a previous study, timber plantations appeared to support the wider distribution of generalist species and the loss of some specialists' species from large forest patches (Weathered and Lawes 2003). A high functional divergence specifies a high degree of niche variation (Mason et al. 2005), and thus, lower resource competition, and possibly has consequences for the increased ecosystem function because of more efficient resource use. In our study, avian functional dispersion increased with the distance between forest patches across seasons, implying a high potential for avian species immigration to forest patches that were close to each other. The possible explanation for this finding is likely to be high resources and niches available in forest patches less severely affected by the fragmentation gradient (Neuschultz et al. 2013).

In conclusion, in KwaZulu-Natal and Eastern Cape Mistbelt Forests, indigenous forest patch size and amount, and patch structural diversity were critical for provisioning avian species richness and functional diversity, while timber plantations and isolation distances between forest patches decreased avian species richness and functional diversity, and but drove functional dispersion to favour divergent traits. Our study also confirmed the importance of diverse landscape structure for the conservation of avian diversity and richness. The diversity of the avian community in the Mistbelts Forests is compromised in less diverse forest patches at greater isolation distances. Armstrong et al. (1996), also found exotic pine *Pinus* spp. plantations reduced the number of species compared with indigenous vegetation.

Consequently, we recommend the identification of protected corridors to promote connectivity and enabling the dispersal of species between the forest patches. By preserving both maximal avian functional diversity and richness, we suggest connectivity between these patches be a management and future research priority.

3.6 Acknowledgements

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CHAPTER 4

The influence of microhabitat structure on the avian communities of Southern Mistbelt Forests of South Africa

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Running header: Influence of microhabitat structure on the avian communities of Southern Mistbelt Forests

4.1 Abstract

Changes in natural environments as a consequence of human population growth are a major threat to biodiversity. Natural habitat modifications have resulted in decreased species richness and functional diversity. The changes in vegetation structure of natural habitats, and microhabitat conditions, have resulted in the endangerment of many species. Species' distributions and abundance are generally reliant on habitat suitability. Therefore, we determined the influence of microhabitat structure on avian communities in Southern Mistbelt Forests in the provinces of KwaZulu-Natal and Eastern Cape, South Africa across a variety of forest patches. We conducted bird point-count surveys and quantified the microhabitat foliage profile in 58 distinct forest patches in three study areas. We also quantified avian species richness and functional diversity per forest patch. The use of multivariate analyses showed significant differences between forests patches in vegetation structure and subsequent avian species richness and functional diversity across the study areas. Microhabitat structure appeared to be shaping the avian community across all sites based on their functional traits. We recommend the further improvement of regulatory standards concerning the sustainable utilisation of forest resources to promote a healthy and diverse habitat structure and safeguard the avian community.

Keywords: Vegetation; birds' diversity; habitat structure; indigenous forests; microhabitats

HIGHLIGHTS

- Species' dissemination and abundance are generally dependent on habitat suitability.
- Microhabitat structure influence on birds' diversity was examined across three study sites.
- Microhabitat structure and species richness were different across all the study sites.
- Species richness was higher in sites with complex microhabitat structure.

4.2 Introduction

Habitat loss and fragmentation are commonly regarded as being among the greatest threats to global biodiversity (Carr and Fahrig, 2001). When these processes take place, it reduces the amount of habitat, changes the habitat structure, and natural environments are replaced by habitats created and maintained by anthropogenic activities (Fahrig, 2002). Commonly, anthropogenic pressures are driving the failure of natural habitats within many ecosystems; deforestation on forests, fire regimes on savannas and coastal alterations to wetlands (Nepstad et al., 1999; Mitsch and Hernandez, 2013; Enright et al., 2015; Scheiter et al., 2015), thus, changing species composition and vegetation structure in ecosystems. Generally, habitat selection for species is influenced by several factors, including food resources, competitive interactions, predation, and vegetation structure (Nordberg and Schwarzkopf, 2019), which are indicators of suitable habitats. Therefore, with natural habitat quality deterioration, these demands for species are not always met. Consequently, some ecological niches will be entirely removed, resulting in a decline in species (flora and fauna) diversity and likely extinction of some species (McKinney, 2002; Maseko et al., 2017). The distribution and abundance of species across landscapes mostly are reliant on habitat suitability (Moilanen and Hanski, 1998; Fleishman et al., 2002; Niebuhr et al., 2015).

Ecosystem health refers to the sustainability and maintenance of ecosystem diversity, and its strength to provide ecosystem services at a particular spatial and temporal scale (Costanza, 2012; Peng et al., 2007). In forest ecosystems and forest health, both the production of forest products and other attributes of forest ecosystems, such as species assemblage and vegetation structure is very much important (Trumbore et al., 2015). Fragmentation results in several changes within fragments and microhabitats (Fahrig, 2013; Haddad et al., 2015) and so typically shaping the species composition. Variations in temperature, insolation, humidity, the amount of sunlight and wind (Didham and Lawton, 1999; Kapos et al., 1997; Murcia, 1995) within these fragments and microhabitats may inhibit their use by some species. For example, in forest fragments, higher light levels may hinder understory insectivores use of these habitats (Stratford and Robinson, 2005; Pollock et al., 2015). Furthermore, typically mature trees, canopy cover, the amount of seedlings to saplings and leaf litter also influence the habitat preference of vertebrate species in forest species (Kreutzweiser et al., 2020; Ehlers Smith et al., 2017a; 2017b). Therefore, increased tree mortality and changes in vegetation structure may alter habitat suitability for some species (Arellano et al., 2019). Many species depend on tree microhabitats during their life-cycles for food, shelter, and breeding habitat (Larrieu et al., 2013). The variations in habitat conditions filter out non-compatible suites of traits so that only a subset of species with tolerance traits can occupy that habitat (Lavorel et al., 2007; Biswas and Mallik, 2011). Hence, forest structural complexity is important for species diversity. Different microhabitats and their spatial arrangement are significant factors shaping species and trait distribution (Massicotte et al., 2014; Biswas et al., 2019).

Avian species are considered excellent indicators of ecological function because of their response to habitat change at various spatial scales, high position in the food chain and the relative ease at which they may be studied (Bryce et al., 2002; Lindbladh et al., 2020). Characteristics of avian communities such as species diversity, species richness and composition are shaped by various environmental factors, with interactions amongst species, habitat qualities and weather patterns (Imai and Nakashizuka, 2010; Gianuca et al., 2013; Paker et al., 2014). Both physical and vegetation structure influence bird species composition at both spatial scales and their relative influences are species-specific, predominantly in regions where forest habitat is comparatively homogeneous (Schmiegelow and Mönkkönen, 2002). Furthermore, in these habitats, there is generally a correlation between changes in avian species composition, abundance, their presence or absence patterns and the aspects of physical structure across landscapes including foliage height diversity, mean tree height, stem density, and canopy cover (Lee and Rotenberry, 2005; McElhinny et al., 2005). Habitat structural complexity influences many ecological interactions, including foraging efficiency and species coexistence (Werner and Hall, 1976; Vitt et al., 1997; Darling et al., 2017). Consequently, the structural complexity of habitats can influence ecological interactions and community dynamics. Some studies have found significant relations between assemblage diversity and habitat complexity (Carpenter et al., 1981; McCormick, 1994). The 'habitat complexity hypothesis assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Bazzaz, 1975; Moreno et al., 2014). Whereas, homogenised habitats result in the decline of traits and therefore low functional diversity (Britton et al., 2009)

In this study, we investigated the influence of microhabitat on avian functional diversity in Southern Mistbelt Forests to determine the importance of conserving these forests patches. Since we understand that habitat suitability in species is influenced by several factors, we investigated if three study clusters are different in terms of microhabitat structure. We hypothesised that species richness would be significantly correlated with changes in microhabitat structure. Secondly, to determine the relationship between avian species functional traits and their microhabitat, we hypothesised that microhabitat would structure avian functional communities. We predicted that less complex microhabitat structures would support low functional diversity.

4.3 Methods

4.3.1 Study areas

Our study was conducted in selected patches of Southern Mistbelt Forests in the provinces of KwaZulu-Natal (KZN) (28.5° S, 30.9° E) (Creighton and Ingeli) and the Eastern Cape (32.3° S, 26.4° E) (Umthatha), South Africa (Fig. 4.1). Eastern Mistbelt Forests form a part of the

Southern Mistbelt Forest group occurring from the Eastern Cape to KwaZulu-Natal (Hope et al., 2014). These forest patches are dominated by a mix of *Afrocarpus* and *Podocarpus* tree species (Cooper, 1985; Wilson et al., 2017) and are patchily distributed because of biogeography and paleoclimate (Moll and White, 1978; Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000). They are typically located on south-facing slopes, where the effects of fire are reduced (Hope et al., 2014). In summer, they receive frequent mist, and a mean annual rainfall of > 1000 mm with highest temperatures of ~37°C and lowest of ~4°C (Moll, 1972). Currently, they are transformed by agriculture and commercial timber plantations; however, in the past; they had a substantial grassland component (Mucina et al., 2006). The Southern Mistbelt Forests have been exploited since very early in colonial history, which continues illegally in some patches (Adie et al., 2013).

Many rural and peri-urban communities in the Eastern Cape depend on natural resources either to supplement their income or for their subsistence (Leaver and Cherry, 2020). Furthermore, land ownership and associated land management practices have a strong effect on vegetation degradation, with traditional villages exhibiting much higher vegetation degradation than commercial farms (Kakembo 2001). In KwaZulu-Natal, 7.6% of the natural habitat was lost due to anthropogenic transformation of the landscape, counting agriculture, timber plantations, urban areas, dams, and mines (Jewitt et al., 2015). Apart from the direct loss of natural habitat, the anthropogenically transformed land covers all pose additional negative impacts for biodiversity remaining in these or surrounding areas (Souza et al., 2015). Landscape matrix surrounding forest patches within the Umthatha cluster are composed mainly of communal areas and low levels of commercial forestry. While fragments within the Creighton cluster are surrounded by agricultural areas of commercial plantations and fewer communal areas. And the Ingeli cluster forest patches are surrounded by commercial plantations and minor levels of communal lands.

4.3.2 Survey-site selection

We selected a range (54 patches) of indigenous Southern Mistbelt forests with different surrounding land uses (commercial timber plantations, grasslands and rural or urban developments) in our three study areas. We selected a range of forest patch sizes from each study area and named the biggest patches as our "mainland" patches, and numerous surrounding as satellite patches. Within the study areas, we identified all Southern Mistbelt Forests using the latest landcover maps (Geoterraimage, 2015) using ArcGIS v10.4 (ESRI, 2011). We allocated survey points at the intersection of 200 m x 200 m grid overlaid over each survey forest patch identified, to ensure they were distributed evenly across sample areas. As a result, in each patch, the number of points was proportional to the size of the patch (Bibby et al., 2000; Ehlers Smith et al., 2018, 2017, a, b, c). We then projected all survey locations using a Global Positioning System (GPS, Garmin GPS map 62; Garmin USA) to locate survey-site in the field and keep a minimum distance of 200 m between survey points.

4.3.3 Bird surveys

We conducted bird surveys during the avian non-breeding season of southern Africa (May – July 2018) and during the breeding season (October 2018 – February 2019). We conducted fixed-radius point-count surveys of all birds' species audible or visible within a 50 m radius. Species richness as the accumulative number of species recorded at each survey point was calculated and then combined as the total species richness and relative abundance per forest patch. We also recorded relative abundance as the total number of individuals of each species at each survey location (Bibby et al., 2000; Ehlers Smith et al., 2018). All the surveys occurred from sunrise to 3 h after sunrise, with each sample point surveyed for 10 min. Nocturnal birds were not recorded because of the timing of our surveys. Any individuals for which the species could not be identified was not included in the analyses.

4.3.4 Microhabitat covariate surveys

We surveyed the microhabitat structure and foliage profile in a 20 m radius around each survey location using the following vegetation classes: the proportion of bare ground; leaf litter; grass cover; herbaceous plants; saplings and scrub/woody plants < 2 m, and the number of trees of 2 – 5 m, 6 – 10 m, 11 – 15 m, 16 – 20 m, 21 – 25 m and > 25 m heights; mean height of all plant groups, stem density of all horizontal and vertical dead trees, and stem density of all trees in each height category (Bibby et al., 2000, Ehlers Smith et al., 2015, 2017). We also distinguished scrub/woody foliage from trees and classified ellipsoid-shaped plants with many branches surfacing from the ground representing an understorey structural component (Ehlers Smith et al., 2015). We classified trees as bare-stemmed plants of height >2 m, with upper branches containing foliage (Ehlers Smith et al., 2015).

4.3.5 Data analyses

To examine the habitat diversity of each survey site, we converted foliage profile of vegetation classes into height diversity using the Shannon-Weiner Formula (SWDI), $H = - \sum_{i-1}^{s} pi \ln(pi)$ where p is a portion of the total foliage in the ith layer (Bibby et al., 2000). We conducted correlation analyses between the covariates using Pearson’s correlation coefficient to avoid multi-collinearity before the analyses after which nine microhabitat-scale covariates were retained for analyses (Table 4.1). We identified the differences/similarities between our forest patches structure using Principal Component Analysis (PCA). Principal component analyses were used to envision the distribution of forest patches in relation to their microhabitat structure and distribution of forest specialists in relation to their functional traits using ‘ggplot’ and ‘factoextra’ in R Statistical Software (R Core Team). We conducted non-metric multidimensional scaling (nMDS) and similarity percentage analysis (SIMPER) in the programme PAST (Harper and Ryan, 2001). We used the presence/absence data of our avian communities (Jaccard index) and nMDS to display differences between all three survey areas and SIMPER to show birds species responsible for the similarities and differences between our study areas. Furthermore, we conducted a two-way ANOVA to determine if the species richness was significantly different between all three areas and one-way MANOVA to determine if microhabitats covariates were significantly different in SPSS.

4.4. Results

We conducted a total of 747 point-count surveys and recorded 9,037 individual birds in 58 distinct habitat forest patches which totalled 82 avian species across all three areas. The first two axes of PCA of the nine microhabitat covariates explained 40.3% of the variation (Fig. 4.2, Table 4.2). The first PCA axis was negatively correlated with leaf litter, trees of 2 – 5 m, 6 – 10 m and 11 – 15 m in height, and positively correlated with short grass cover, tall herb cover and saplings (Fig. 4.2, Table 4.2). The second PCA axis was negatively correlated with short grass cover, saplings, trees of 2 – 5 m and 6 – 10 m in height, and positively correlated with leaf litter, short herb cover, tall herb cover, trees of 11 – 15 m and 16 – 20 m in height. Forest patches from the Umthatha study area had a high proportion of leaf litter and taller trees (Fig. 4.2, Table 4.2). Creighton and Ingeli forest patches had more herbaceous cover, medium-sized trees, and saplings (Fig. 4.2). We observed a 38.3% similarity in avian species between all three study areas (Umthatha, Ingeli and Creighton) (Table 4.2). Cape Parrots (*Poicephalus robustus*), Olive Bushshrikes (*Chlorophoneus olivaceus*) and Green-backed Camaropteras (*Camaroptera brachyuran*) contributed the most to the average similarity between all three study areas (Table. 4.2). Overall there was a significant difference ($F = 32.147$; $p < .0005$; Wilk's $\Lambda = 0.300$; partial $\eta^2 = 0.36$) in species richness and microhabitat covariates between the three study areas.

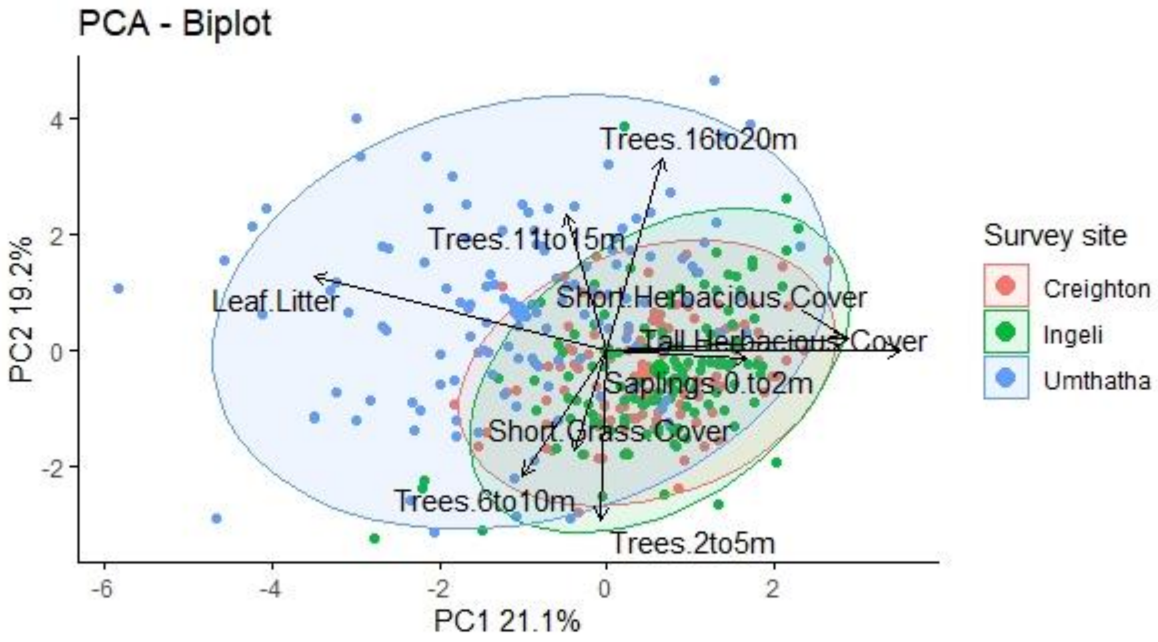

Figure 4. 1: First two axes of Principle Component Analysis axes constructed using nine microhabitat covariates and survey areas (Creighton, Ingeli and Umthatha) of Southern Mistbelt Forests. The axes described 40.3% of variance using PC1 and PC2.

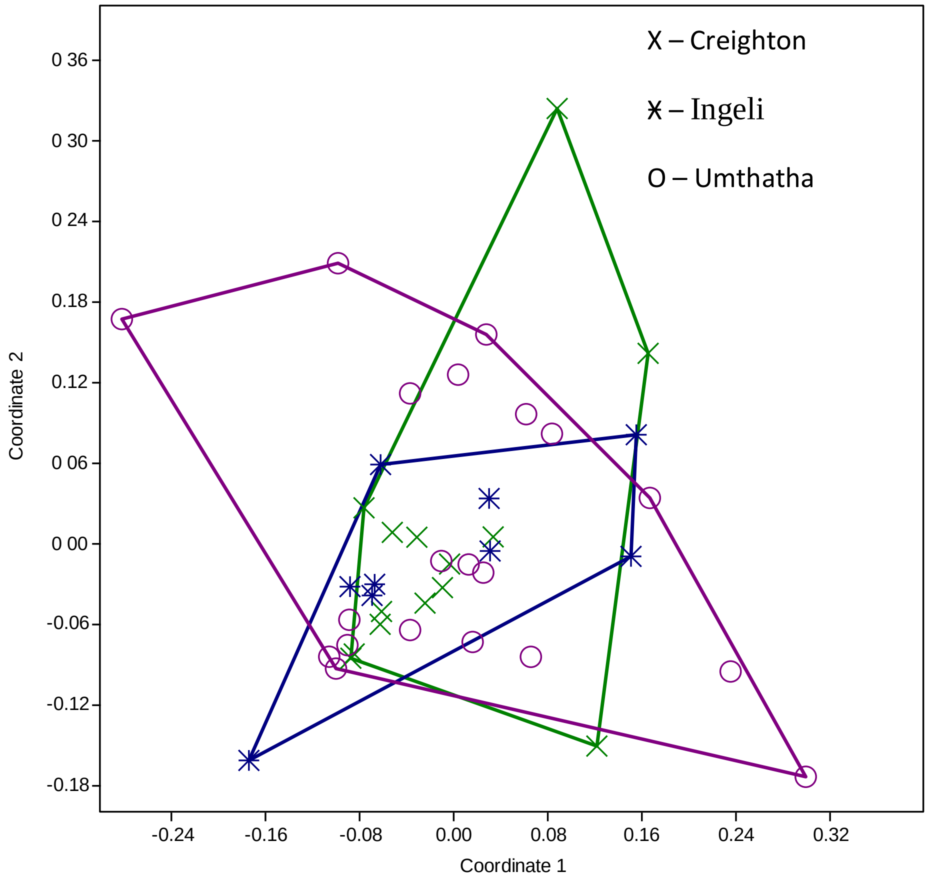

Figure 4.2: Non-metric multidimensional scaling (nMDS) displaying distinctive grouping of our three study areas (Umthatha, Ingeli and Creighton) based on the presence and absence of avian species.

Table 4. 1 Eigenvector scores of microhabitat covariates of selected Southern Mistbelt Forest (Umtata, Ingeli and Creighton) study areas and avian species functional traits based on the first two axes of the Principle Component Analysis (PCA) in the present study.

Forest microhabitat covariates	**PC1 (21.1%)**	**PC2 (19.2%)**
Leaf Litter	-0.57	0.23
Short grass cover	-0.06	-0.29
Short herbaceous cover	0.47	0.03
Tall herbaceous cover	0.57	0.001
Saplings 0 -2m	0.27	-0.03
Trees 2 - 5m	-0.01	-0.50
Trees 6 - 10m	-0.17	-0.37
Trees 11-15m	-0.08	0.40
Trees 16 -20 m	0.11	0.57

Table 4. 2 SIMPER analysis results showing the top ten of significant avian species responsible for the similarity between our three study areas (Umthatha, Ingeli and Creighton).

Scientific names	**Common names**	**Av. dissimilarity**[a]	**Contrib (%)**[b]	**Cumulative (%)**[c]
Poicephalus robustus	Cape Parrot	1.09	2.843	2.843
Chlorophoneus olivaceus	Olive Bushshrike	0.9792	2.554	5.397
Camaroptera brachyura	Green-backed Camaroptera	0.9687	2.526	7.923
Apaloderma narina	Narina Trogon	0.9471	2.47	10.39
Dendropicos griseocephalus	Olive Woodpecker	0.93	2.425	12.82
Chalcomitra amethystine	Amethyst Sunbird	0.9284	2.421	15.24
Apalis flavida	Yellow-breasted Apalis	0.9274	2.419	17.66
Streptopelia semitorquata	Red-eyed Dove	0.9149	2.386	20.04
Trochocercus cyanomelas	Blue-mantled Crested Flycatcher	0.9028	2.354	22.4
Pogonocichla stellate	White-starred Robin	0.8907	2.323	24.72

a Average dissimilarity between vegetation classes.

b Percentage contribution to dissimilarity.

c Cumulative percentage dissimilarity

4.5 Discussion

In the process of understanding the influence of species composition to find effective management tools and strategies in protecting them, the physical structure of the habitat cannot be disregarded. Our study aimed to understand the influence of microhabitat structure on avian communities in Southern Mistbelt Forests using a functional trait-based method. Our results highlighted the differences in forest structures and avian communities across three study areas. Patches in the Umthatha study area had predominantly open understory, while Creighton had patches with closed understory and Ingeli had a mixture of open and closed understory forest patches (Fig. 4.1). These results were confirmed by the grouping of study areas based on the presence and absence of species. The Ingeli study area had a mixture of avian species present in Creighton and Umthatha. Therefore, our results indicated that the presence and absence of avian species were influenced by the vegetation structure of the patches. These results are supported by other studies that have shown that vegetation structure is of relative importance across foraging guilds (MacArthur and MacArthur, 1961, Kissling et al., 2008, Munro et al., 2010, Jankowski et al., 2013). Studies have found both vegetation structure and vegetation species composition to predict bird assemblages and guild abundance (Cubley et al., 2020). Vegetation structural diversity benefits a wider range of bird species by increasing microhabitat diversity, therefore providing enough food and cover for species (Whittaker et al., 2001; Hill et al., 2004). Microhabitat covariates such as foliage height diversity and canopy cover may have an impact on food resources, microclimate, and predation (Jones, 2001). Furthermore, vegetation structure has been shown to be an important factor for other taxa as well (e.g. Saalfeld et al., 2016; Alvarenga et al., 2020; de Abreu Pestana et al., 2020).

Our results highlighted a significant difference in functional and species richness between all three study areas. These results align with the vegetation structure across our study areas, which were significantly different. Therefore, this supports our prediction that microhabitat would influence avian communities across the study site and increase with habitat complexity. Generally, structurally more complex and heterogeneous habitats can accommodate more avian species and a broader suite of functional traits (Ozdemir et al., 2018). These results may be because of enough cover and resources in structurally complex habitats or microhabitats. Studies show that the distribution of species based on their foraging strategy may have direct associations with particular plant species (Hanzelka and Reif, 2016). Our results showed that the Ingeli site had a higher functional and species richness compared with Creighton and Umthatha. This pattern is likely driven by the vegetation structure of this site, which had a diversity of strata, allowing diverse avian communities to occupy these patches. Avian species responsible for the similarity between our three study areas were dominated by insectivorous species (Olive Bushrike, Green-backed Camaroptera, Narina Trogon, Olive Woodpecker, Amethyst Sunbird, Yellow-breasted Apalis, Blue-mantled Crested Flycatcher and White-starred Robin) (Table 4.2). The presence or absence of a given species or group of species in a particular environment can be used to define normal or baseline environmental conditions and to determine the degree to which communities have been affected (Cadotte and Tucker, 2017). Insectivorous species may be more specialized than other groups, and, therefore, more sensitive to changes in the particular populations they feed upon (Mansor et al., 2019). Therefore, our three sites microhabitat may be similar in terms of providing resources for insectivorous guild. Additionally, the species with the highest contribution was the frugivorous Cape Parrot (Table 4.2). Cape Parrots are known to primarily feed on Yellowwood (*Afrocarpus falcatus* and *Podocarpus latifolius*) fruits (Wirminghaus et al., 2002), which is one of the dominant tree species in all three of our study areas (Moll, 1972; pers. obs).

One aspect that was unexplored in our analyses was the influence of tree species composition on bird communities. Generally, avian species feeding primarily on a plant-based diet (e.g. frugivores and nectarivores) are more closely associated with tree species composition (Hasui et al., 2007). Several studies explore this method for different species (Lee and Rotenberry et al., 2005; Fleishman et al., 2003; Jankowski et al., 2013; da Silva et al., 2020; Iezzi et al., 2020; Laurent et al., 2020; Meloni et al., 2020). According to previous studies, tree species richness varies across Southern Mistbelt Forests (Downs and Symes, 2004; Hart et al., 2013; Wilson et al., 2017) depending on the study site. However, Southern Mistbelt Forests are expected to have keystone tree species that are important for avian diversity (Bleher et al., 2003). Generally, Southern Mistbelt Forests in the Creighton district have experienced a history of logging of large trees and continue to be harvested by local communities (Downs and Symes, 2004; Adie et al., 2013). As a result, forest patches in this area are highly disturbed, resulting in low avian species richness in Creighton forest patches. Therefore, we might expect tree species composition influencing avian communities in Southern Mistbelt Forests patches.

In conclusion, our results confirm the general influence of a diverse microhabitat structure driving diverse avian species and functional communities. Avian species show a discrepancy in breeding, foraging, and nesting habitat preferences and they require different resources and use of different strategies (Whittingham and Evans, 2004; Petit, 2000). Therefore, the results of this study have implications for the conservation of Southern Mistbelts Forests or protecting these patches from logging because of their vital role in avian communities. It is also contributing to understanding the causes of species distributions and their response to habitat change. Microhabitat structure appeared to be important for different avian communities, depending on their functional traits. Complex vegetation structure within forests should be sustained as they are vital for avian functional diversity and richness. Consequently, we recommend the sustainable use of forest products and tree species to promote a diverse habitat structure and conservation of our avian species. Furthermore, groups of stakeholders could possibly be used for further improvement of regulatory standards in relation to the sustainable utilisation of forest resources.

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CHAPTER 5

How connected are South African Mistbelt Forests for birds? Habitat connectivity in selected forest patches of KwaZulu-Natal and Eastern Cape Mistbelt forests

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Running header: Habitat connectivity for selected forest patches of KwaZulu-Natal and Eastern Cape forests

5.1 Abstract

Anthropogenic processes are altering and modifying natural environments; consequently, wildlife communities are decreasing. Fragmentation reduces natural habitats and threatens biological diversity. Due to this process, natural habitats are disconnected, which impede dispersal and other ecological movements of species between fragments. Connectivity is influenced both by the geographic location of habitat patches and characteristics of the surrounding environment. Forest loss and human-modified habitats are critical issues reducing habitat amount and connectivity of forests habitats. In this study, we evaluated potential connectivity for avian forest communities in three clusters of the Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape Provinces, South Africa. We conducted a hybrid of least-cost corridors and ecological circuit theory between forest patches of high avian functional diversity to encourage connectivity across the landscape. We found forests had large isolation distances between clusters, and the quality of the matrix had a significant influence on habitat connectivity. One forest cluster was highly affected by connectivity barriers. Therefore, we recommend rehabilitation within and around these forests patches to safeguard and conserve their avian species communities.

Keywords: Indigenous forest; habitat connectivity; fragmentation; matrix; ecological barriers

5.2 Introduction

As the anthropogenic use of the environment increases, the amount of habitat available for natural wildlife communities will continue to decrease (Fahrig, 2003; Thomas et al., 2004; Pereira et al., 2010; Butchart et al., 2010; Pimm et al., 2014). As a result, natural habitats are becoming bisected and reduced, leaving small habitat islands isolated from each other surrounded by human-altered environments, and this process is called fragmentation (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Fahrig, 2003; Fletcher et al., 2018; Fahrig et al., 2019). Fragmentation results in various natural environment changes, including reduced habitat amount and an increased number of smaller and more disconnected patches (Burkey, 1995, Fahrig, 1997, Fahrig, 2003, Haddad et al., 2015). These effects from fragmentation contribute to a decline in biological diversity within the original habitat (Fahrig, 2003). However, in some landscapes, the habitat was historically naturally fragmented, for example, Southern Mistbelt forest patches in South Africa (Lawes, 1990).

The results of these effects on biological diversity depend on the response of each species and the scale (individual patch or at landscape level) of the occurrence (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Steffan-Dewenter and Tscharntke, 2000; Liao et al., 2017). Fragmentation, however, may result in reduced competition, higher diversity, and increased movement between patches (Fahrig et al., 2019), which are positive responses from the fragmentation process. Therefore, several studies challenge the perceptions of the negative impacts of fragmentation on biodiversity (Fahrig, 2013, 2017, 2019; Fahrig et al., 2019). The review by Fahrig (2003) showed that habitat loss and fragmentation are two different processes and suggested that habitat loss had more significant negative impacts compared with fragmentation, which was also shown in several other studies (Trzcinski et al., 1999; Uezu and Metzger, 2011; De Camargo et al., 2018). In contrast, some studies have shown fragmentation to have positive impacts on biodiversity (Fahrig et al., 2019; Miller-Rushing et al., 2019)

Habitat connectivity plays a critical role in maintaining the biodiversity of fragmented landscapes (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Wilkosz, 2010; Shafer, 2015; Thatte et al., 2018). Connectivity dictates dispersal and population dynamics, permitting or precluding species' persistence in fragmented landscapes (Baggio et al., 2011; Correa Ayram et al., 2016; Córdova-Lepe et al., 2018). Connectivity is defined as the magnitude to which the landscape enables species movement among resource patches (Taylor et al., 1993; Bélisle, 2005) through a matrix of unsuitable habitat or land-use types.

There are two types of landscape connectivity: i) structural connectivity, which defines the physical relationships between habitat patches such as distance between the patches and the quality of the matrix, and ii) functional connectivity, which refers to organisms' responses to both the landscape structure and the landscape matrix (Tischendorf and Fahrig, 2000a,b; Meiklejohn et al., 2009; Mühlner et al., 2010). Consequently, connectivity is influenced both by the geographic location of habitat patches and the surrounding habitat matrix's characteristics (Prevedello and Vieira, 2010). Effects of habitat connectivity on different taxa differ at various scales (Bailey et al., 2010). Landscape structure enhances the functional connectivity amongst patches, which increases the flow of individuals or genes and permits the recolonisation and reduce local extinctions (Sarremejane et al., 2017; van Strien et al., 2018).

Globally, there has been a loss of forest habitats because of the rapid expansion of agriculture, exotic tree plantations and urban expansion, and the exponential rise in deforestation is putting pressure on remaining natural forests (Delang, 2002; Lawes et al., 2004; Lambin and Meyfroidt, 2011; Zemp et al., 2017). Deforestation and fragmentation threaten biodiversity within forests, including invertebrates, mammals, birds, amphibians, and plants (Betts et al., 2017); many of these species are endemic to natural forests. The reduction of forest patch sizes and increase in forest patch isolation results in less colonisation of patches and dispersal challenges for species (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Beier et al., 2008), which reduces biodiversity functioning and provisioning of ecosystem services (Brockerhoff et al., 2017; Rudman et al., 2017). Consequently, communities within disconnected patches may become homogenised, gene flow may be reduced, and some functional traits may be lost because of limited movement of dispersal-challenged species between isolated patches (Tonkin et al., 2018). Connectivity may be a key driver of the diversity of functional traits within communities because of some traits' susceptibility to isolation pressures, which may, therefore, disappear (Thiele et al., 2018). Functional traits regulate and determine species’ habitat associations, interactions with other species, competition among communities and their contribution to ecosystem functioning (Steneck and Dethier, 1994). Functional diversity refers to components of biodiversity traits that determine how ecosystems function (Tilman, 2001). Therefore, ecosystems need to remain functionally connected, maintain dispersal, colonisation, gene flow and ecosystem functioning (Hanski, 1998).

Understanding the importance to connect naturally fragmented patches of forest is essential. Although bird communities have long inhabited and fragmented landscapes, connectivity is a key factor in the long-term viability of populations (Keeley et al., 2018). In this study, we assessed possible connections for forest bird communities in the inland Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape Provinces, South Africa. These forests were naturally fragmented but, over time, are also affected by anthropogenic land-use changes and activities (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Lawes et al., 2004; Adie et al., 2013). We conducted a hybrid of least-cost corridors and ecological circuit theory to map connectivity between forest patches in which we conducted avian surveys and calculated the value of patches for maintaining avian functional diversity.

5.3 Methods

5.3.1 Study area

Our study was conducted in three different regions (Umtata, Kokstad and Creighton) that contained Afrotemperate Southern Mistbelts Forests, located within inland Eastern Cape and KwaZulu-Natal Provinces of South Africa. The Eastern Cape covers approximately 168,966 km^2 in the south-east of South Africa. The Eastern Cape climate is highly diverse: the west is dry and arid year-round, with temperatures <0°C in winter and summer > 40 °C. The province's eastern region experiences more rainfall and humidity and becomes subtropical along its northern coast with fairly high summer rainfall. KwaZulu-Natal is approximately 92,100 km^2 in area and is located on the east coast of South Africa, reaching a maximum inland elevation at 3,451 m. Along the coast of KwaZulu-Natal, the climate is subtropical but becomes colder towards high altitude inland regions. It contains areas rich in biodiversity and contains several UNESCO World Heritage sites.

Southern Mistbelt Forests of our study region are naturally and anthropogenically fragmented (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000). They are dominated by a mix of *Afrocarpus* and *Podocarpus* species (Cooper, 1985). These forests occur at 800–1500 m altitude, on steep, south-facing slopes on dolerite ridges and receive frequent mist in the summer, and a mean annual rainfall of > 1000 mm with highest temperatures of ~37°C and lowest of ~4°C (Moll, 1972). Other distinctive tree species in these forests are *Cussonia chartacea, Cryptocarya myrtifolia, Prunus africanus, Xymalos monospora, Kiggelaria africana* and *Combretum kraussii, Ptaeroxylon obliquum, Celtis africana, Calodendrum capense,* and *Olea capensis* (Moll, 1972).

5.3.2 Survey-site selection

We selected a range of indigenous forests patches with surrounding land uses, including exotic tree plantations, grasslands and rural or urban developments. We chose a variety of patch sizes, with the structure of 1 – 3 source or "mainland" patches, and several surrounding satellite patches at each area. Within the study region, we identified all Southern Mistbelt Forests using the latest landcover maps (GeoTerra Image, 2015) displayed in Geographic Information System (GIS) programme, ArcGIS v10.4 (ESRI, 2011). Over each survey patch identified, we overlaid a 200 m x 200 m grid patch to allocate avian survey points at each gridline's intersection to ensure even distribution across sample areas. Thus, the numbers of points in each habitat patch were proportional to each habitat patch's size (Bibby et al., 2000; Ehlers

Smith et al., 2017). We projected survey locations onto a Global Positioning System (GPS, Garmin GPS map 62; Garmin USA) to monitor survey-site selection in the field and to ensure survey points were 200 m apart (Chapter 3).

5.3.3 *Bird surveys*

Our forest bird surveys were conducted during the avian non-breeding season between (May-August 2018) and breeding season (October 2018-February 2019) of southern Africa via fixed-radius point-count surveys of all avian species audible or visible within a 50 m radius (Chapter 3). We calculated taxonomic diversity as richness, i.e. the accumulative number of species recorded at each survey location (Chapter 3). We also recorded relative abundance as the total number of individuals of each species at each survey location (Bibby et al., 2000; Ehlers Smith et al., 2017; Chapter 3). Species richness and abundance were then pooled by forest patch. All surveys occurred at sunrise + 3 h for 10 min. at each point. We did not record nocturnal birds because of the timing of our surveys (Chapter 3).

5.3.4 *Mapping and connecting core habitat patches of high functional diversity*

We sought to create connectivity between patches of Southern Mistbelt Forest that provisioned the highest avian functional diversity; patches that provisioned > 80% of the total avian functional diversity of the region were used as core patches to be connected. Fourteen patches of the 43 patches surveyed were reserved as core patches to be connected. We created habitat suitability maps and landscape resistance maps using Gnarly Landscape Utilities v0.1.0 (McRae et al., 2012), a plug-in toolbox for ArcGIS v10.4, informed by the ecology of the lemon dove (*Aplopelia larvata*). This species was used to inform the connectivity mapping as it is a forest specialist with potentially low dispersal capabilities (Ehlers Smith et al., 2018). Thus, we considered it an effective model for the minimum dispersal potential in this avian community (see also Alexander et al., 2019). Landscape and microhabitat covariates that positively or negatively influenced lemon dove patch occupancy (c.f. Ehlers Smith et al., 2017b; Gumede et al., 2020) were used to populate the habitat suitability and landscape resistance scores required by Gnarly Landscape Utilities (McRae et al., 2012). Habitat suitability ranges from 0 (least suitable) to 1 (most suitable), and resistance ranges from 1 (no resistance) to 101 (maximal resistance). We used the sum function to simulate compounding resistance landscapes adjacent to one another. We added a value of 1 to each land-use class to ensure least-cost distances were equal to Euclidean distances (McRae et al., 2012).

We then used Linkage Mapper Linkage Mapper v1.1 (McRae and Kavanagh, 2011), to create Least-Cost Pathway mapping based on cost-weighted and Euclidean distances, which were set to 12 km, the effective distance between mainland patches and the outlying satellite patches surveyed. We refined least-cost pathways using Pinchpoint Mapper v1.1 (McRae, 2012) to identify and locate pinch points within the resultant least-cost corridors. Pinchpoint Mapper is a plug-in tool that forms part of the Linkage Mapper toolbox, which performs Circuitscape algorithms (Circuit Theory; McRae and Shah, 2009). The tool highlights areas of highest density, such as the most connected pathways, which identifies small landscape features disproportionately contributing to landscape connectivity, which can then be prioritised in landscape management plans. We also calculated raster centrality using Circuitscape via the “pairwise” function. We then sought to identify barriers to connectivity, and potential regions that may improve connectivity through land rehabilitation or improvement, using the Barrier Mapper to identify barriers along with the corridor network that considerably influence the quality and location of respective corridors (McRae, 2012). Barrier Mapper settings incorporated minimum and maximum detection radii of 500 m and 2,000 m, with a radius step-up of 500 m. We set these radii based on a conservative estimate of the minimum and maximum strip of land that could be realistically rehabilitated within the region (McRae, 2012; Colyn et al., 2020).

5.4 Results

In regions of low suitable habitat, resistance increased, mostly in cultivated and urbanised regions (Fig. 5.1). Cost-weighted Distance scores (0 = maximal connectivity and 2,59852 = no connectivity) showed that connectivity decreased with increasing distance between patches in Southern Mistbelts Forests and that forest patches in our study regions were connected within each region but not between regions (Fig. 5.2). Pinchpoint Mapper efficiently emphasised regions of best (5200619) and no connectivity (0) between all three regions (Fig. 5.3). Pinchpoint Mapper also highlighted the best connectivity (200000) and no connectivity (0) within each region (Fig. 5.3). Connectivity pinch points identified those corridors most constrained. Barrier Mapper identified maximal (27.2455) and lowest (0.000015625) barriers across study sites (Fig. 5.4). Creighton study site had the highest barriers, followed by Kokstad and Umthatha, which had the lowest (Fig. 5.5 and 5.6). The best connectivity occurred in areas with indigenous forest and between patches close to each other and reduced in regions of increased plantations, grasslands and urban land cover. Connectivity across our study area was restricted by agriculture, grasslands and mostly by exotic tree plantations surrounding forest patches.

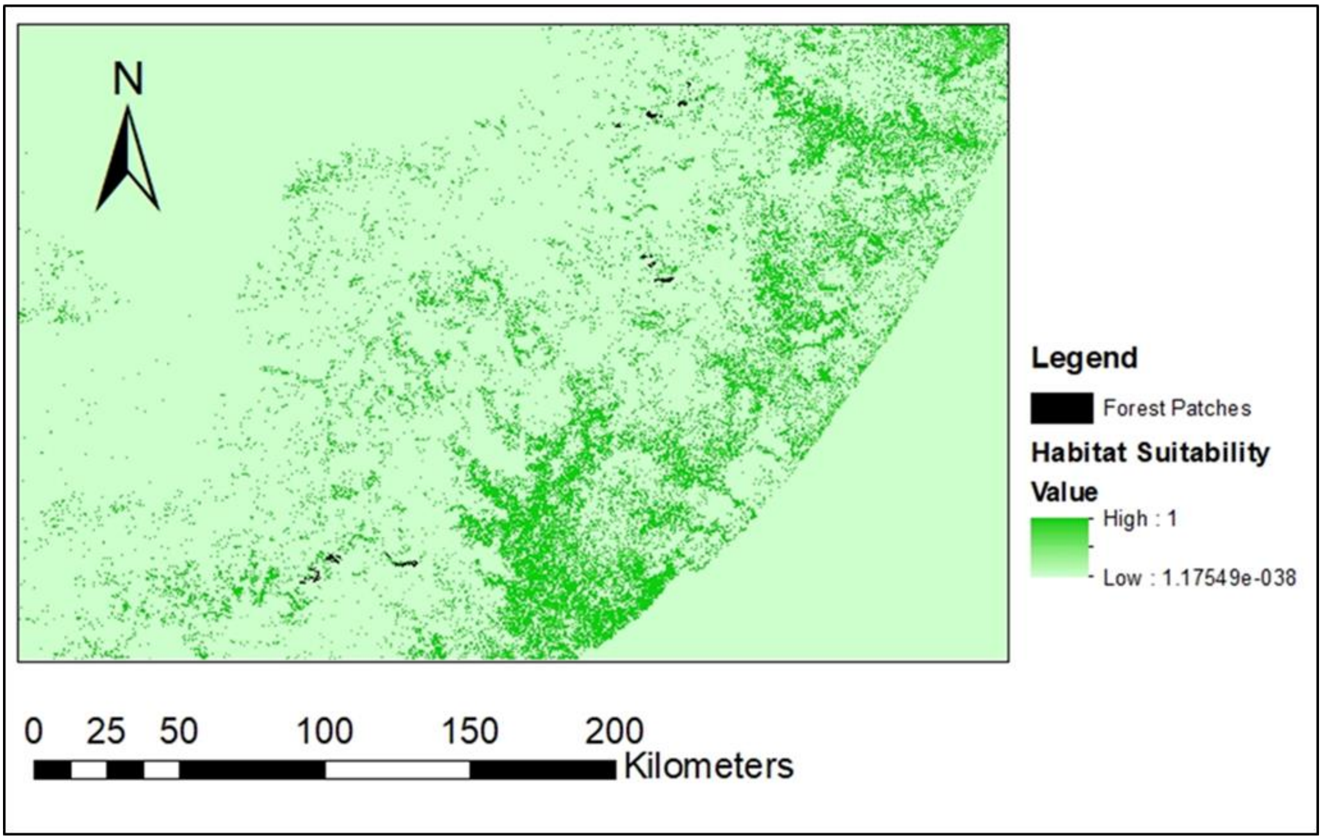

Figure 5. 1: Habitat suitability of lemon dove (*Aplopelia larvata*) in KwaZulu-Natal and Eastern Cape, South Africa, based on its ecological requirements and dispersal limitations. (Calculated using Gnarly Landscape Utilities (McRae et al., 2015)).

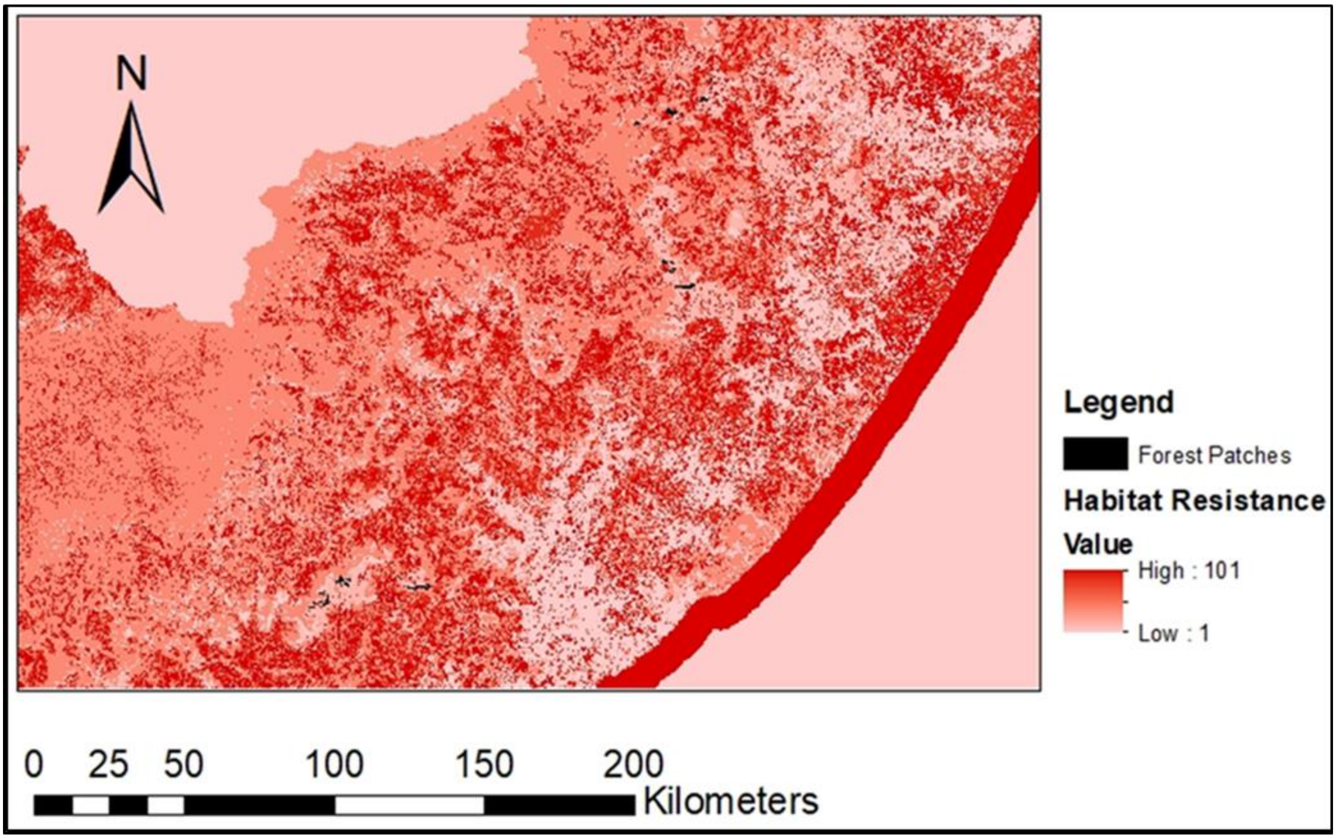

Figure 5. 2: Landscape resistance based on the ecology of the lemon dove (*Aplopelia larvata*) and its ecological requirements and dispersal limitations, as calculated using Gnarly Landscape Utilities (McRae et al., 2015).

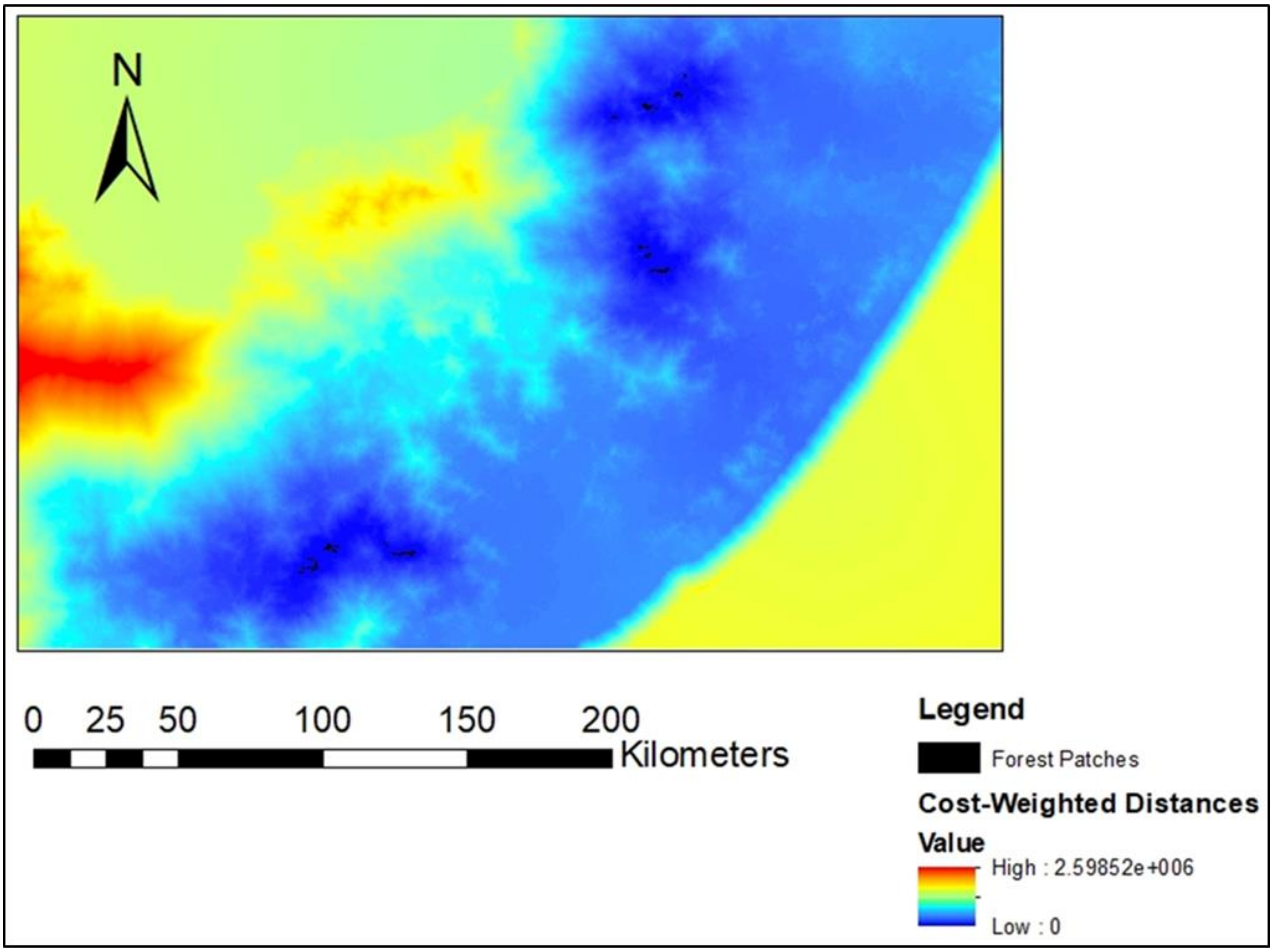

Figure 5. 3: Cost-weighted Distances between Southern Mistbelt Forest patches containing maximal avian functional diversity, showing regions of maximal (0) and no (2.59852) connectivity in KwaZulu-Natal and Eastern Cape, South Africa, constructed from landscape resistance and habitat suitability maps. (Calculated using Linkage Mapper (McRae and Kavanagh, 2011)).

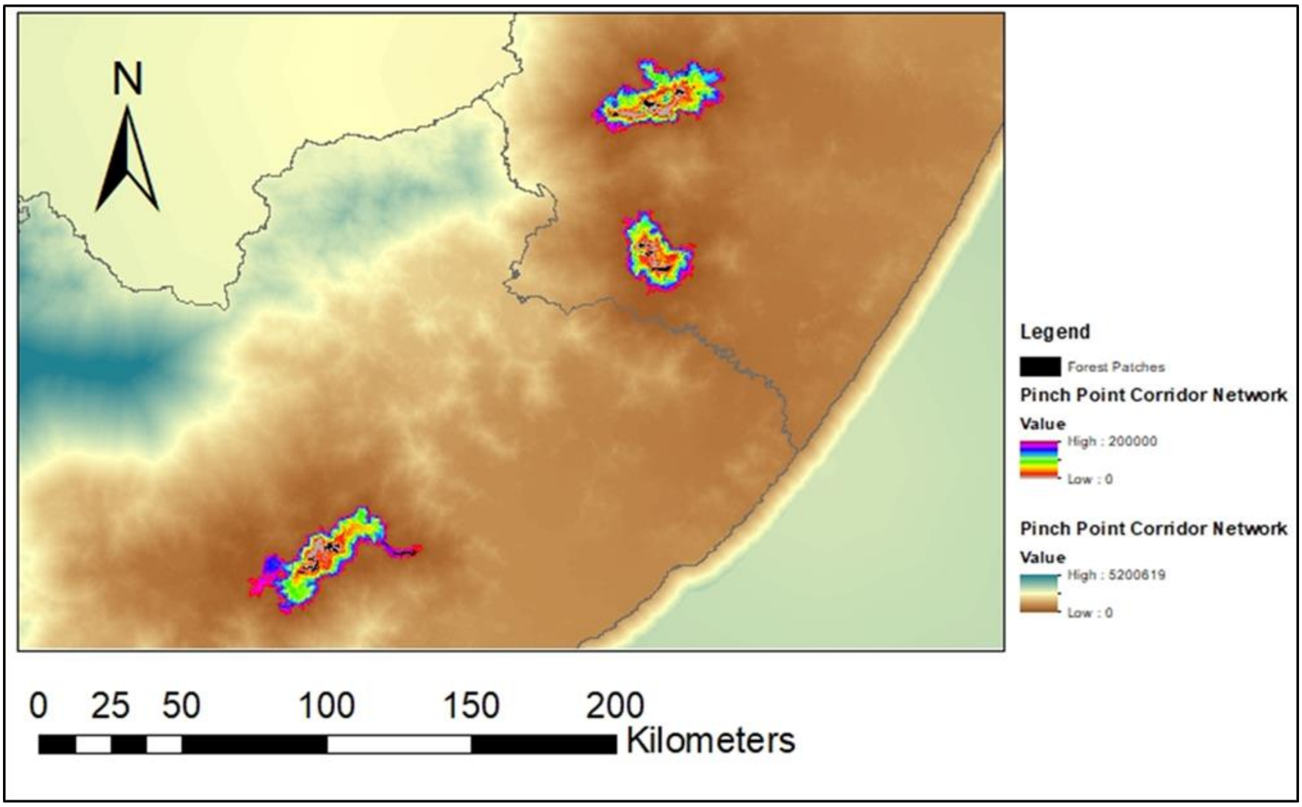

Figure 5. 4: Pinch-point connectivity between core habitats (forest patches containing maximal avian functional diversity) in Eastern Cape and KwaZulu-Natal Mistbelt forests in South Africa showing areas of maximal (5200619) and no connectivity (0) and also pinch-point connectivity within all three study regions (Creighton, Kokstad and Umthatha) at maximal (200,000) and no connectivity (0). Connectivity pinch points identify those corridors most constrained. (Calculated using Pinchpoint Mapper (McRae, 2012)).

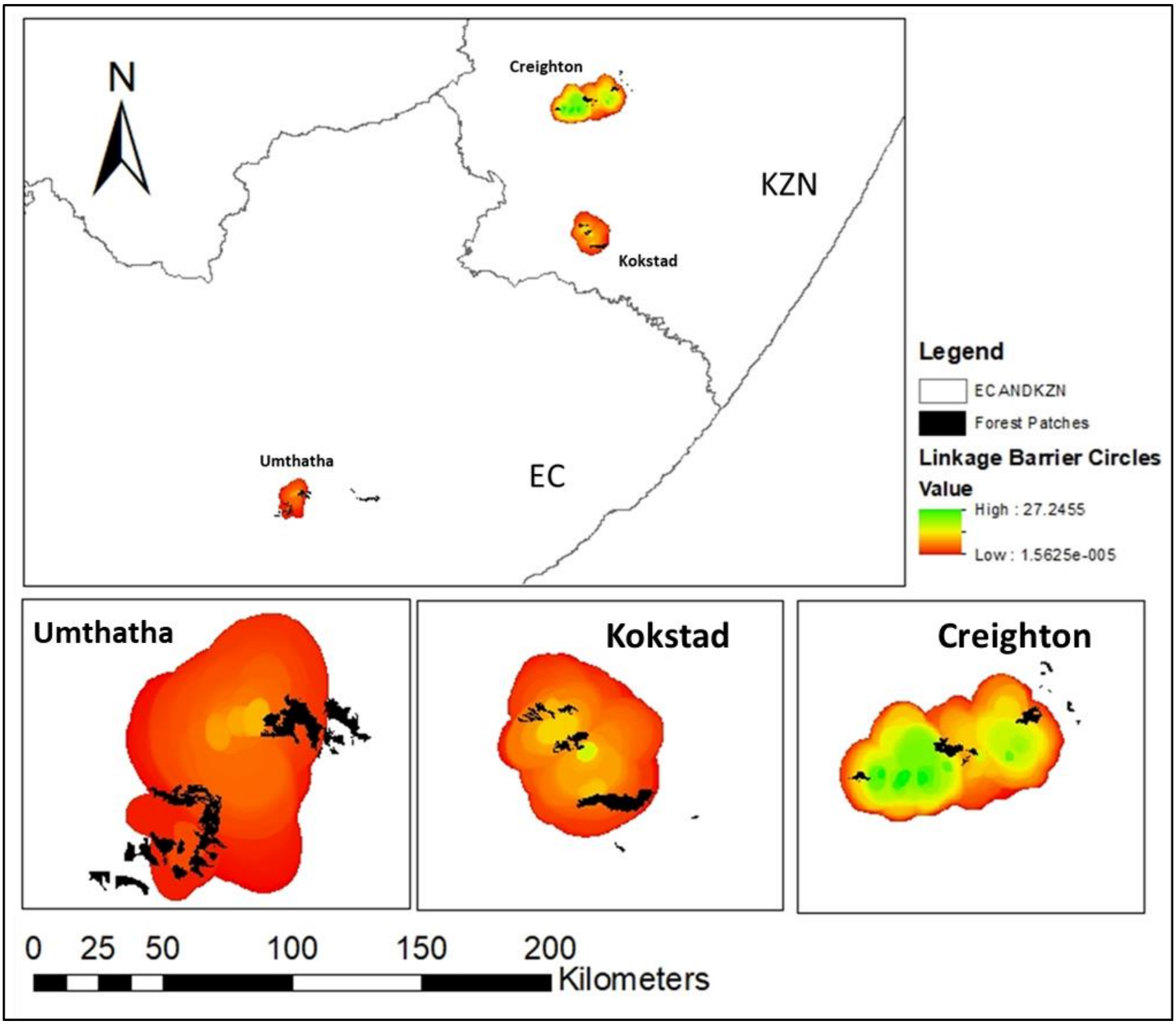

Figure 5. 5: Corridor connectivity, a maximal a maximal (27.2455) and lowest (0.000015625) barriers circles displaying where the rehabilitation of high resistance areas would benefit connectivity the most as determined in the present study. (Calculated using Barrier Mapper).

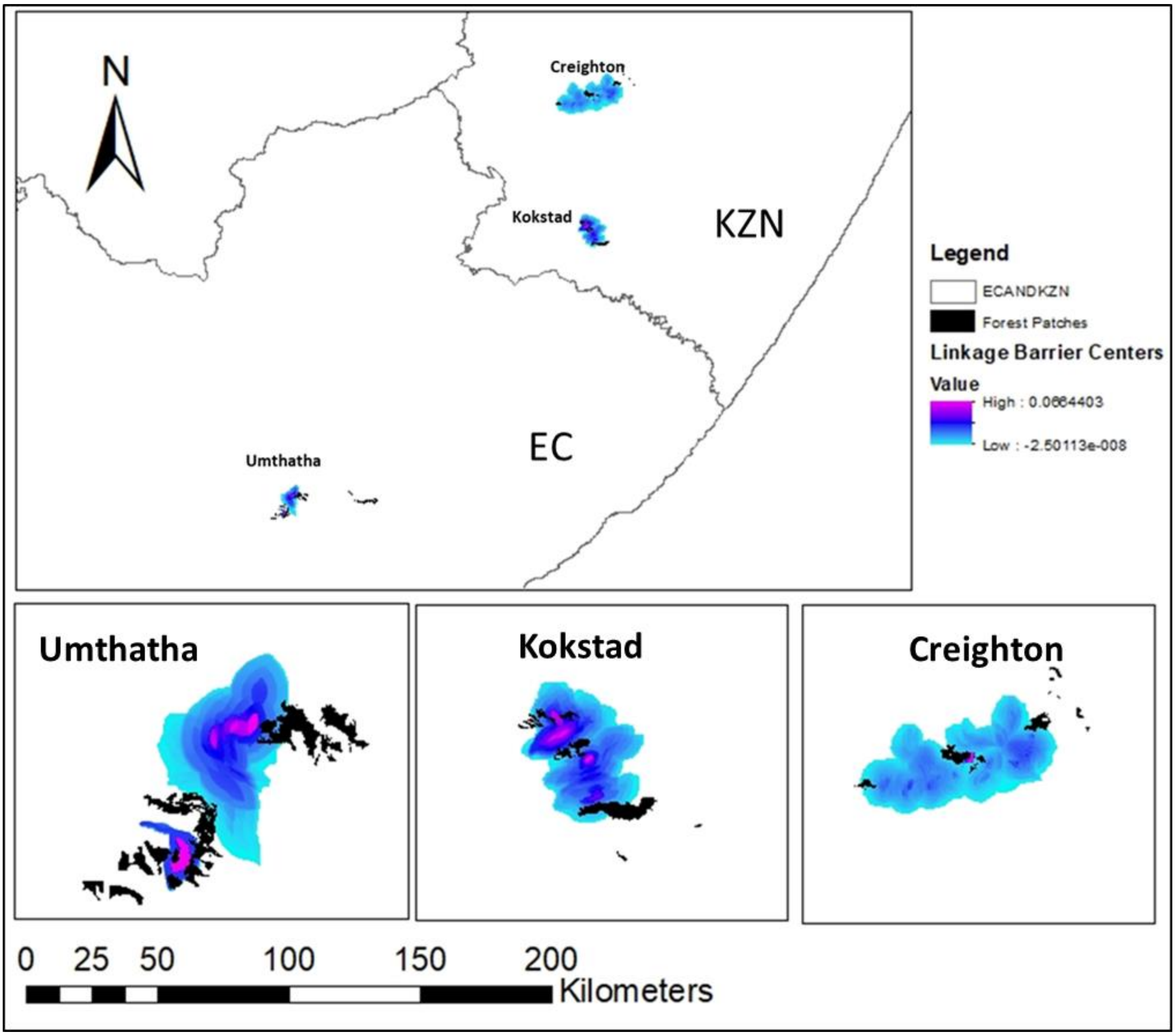

Figure 5. 6: Corridor connectivity, a maximal (0.0664403) and lowest (-0.0000000250113) barriers centres across study sites displaying where the rehabilitation of high resistance areas would benefit connectivity the most in the present study. (Calculated using Barrier Mapper).

5.5 Discussion

Our study was conducted to identify suitable habitat patches and connectivity of the Lemon Dove as a forest specialist in Southern Mistbelt Forests. Our results can assist in managing and protecting avian communities by conserving the critical habitat patches and areas with high connectivity. Connectivity allows movement and dispersal of species in between habitats, which permits genetic flow to sustain species persistence (Crooks and Sanjayan, 2006). Our study highlighted that Southern Mistbelt Forests patches in the Creighton and Kokstad areas were highly connected. However, the Umthatha cluster was not well connected to the Creighton and Kokstad clusters, because of the isolation distance between these three study areas. The matrix of land uses in between these study areas may have reduced the connectivity.

Southern Mistbelt Forests are naturally fragmented and patchily distributed because of biogeography and paleoclimate (Moll and White, 1978; White, 1978; Cooper, 1985; Lawes, 1990; Lawes et al., 2000); however, this is compounded by a complex landscape matrix in between these patches, comprised of resisting land-uses of exotic tree plantations, grasslands, urban areas and agricultural crops (Armstrong et al., 1996; Eeley et al., 1999). Generally, forest patches surrounded by poor quality matrix restrict species' movement (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Lindenmayer, 2000) and reduce the connectivity between these patches. Forest-specialised species are generally declining in patches surrounded by an exotic tree plantation matrix, which possibly favours generalist species (Graham and Blake, 2001). Commercial exotic tree plantations dominated the landscape matrix, covering 41% of the Southern Mistbelt region (Armstrong et al., 1998). Despite offering canopy cover, the monoculture of homogenised structures and limited resources is likely one of the reasons for forest disconnection for forest-specialised species. However, KwaZulu-Natal Mistbelt Forest patches were better connected than those in the Eastern Cape. This was possibly because of a higher proportion of less resistant habitats such as thicket/ dense bush, which supports avian functional diversity (Ehlers Smith et al., 2017), facilitating connectivity between the forest patches (Grafius et al., 2017). This emphasises the importance of thicket/dense bush in fragmented landscapes for their contribution to linking patches with one another (Thiele et al., 2018). Our study also highlighted the location of barriers across our study region to show where the rehabilitation of high resistance areas would benefit connectivity the most. These barriers point to regions that potentially result in the loss of core breeding and foraging habitats, thus impacting genetic diversity through habitat fragmentation (Redford et al., 2011).

Models of connectivity have shown valuable direction towards conservation planning efforts and predicting species' movement (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Colyn et al., 2020). However, most studies mostly emphasise and identify areas facilitating, rather than obstructing the movement of species (Vasudev et al., 2015; LaPoint et al., 2015). The present study's analyses indicated that the relatively high density of grasslands surrounding forest patches might be a barrier to avian forest specialist species movement. Various species are unable to migrate along with their habitat conditions where dispersal barriers are impossible (Lawes, 1990; Noss, 1991; Swart and Lawes, 1996; Lawes et al., 2000). Our analyses were performed using the Lemon Dove as a surrogate species. It is a ground-dwelling forest specialist; therefore, it mirrors the requirements of functionally similar and generalist species (Rudnick et al., 2012). Consequently, these barriers showed a lack of suitable habitat conditions.

Our results suggest that forest patches, cannot be managed as an isolated unit since habitat connectivity is decreasing with changes in land cover and the distance between the forest patches. These changes have different ecological effects (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Curran et al., 2004; DeFries et al., 2005), mainly the development of migration corridors for wildlife, improvement of edge effects and changes in the patch size of forest types (Vester et al., 2007; Gude et al., 2007; Hansen and DeFries, 2007). Several studies have shown that in many cases, indigenous people perform a variety of management practices, such as protecting certain forest patches, planting desirable species, introducing new species, eradicating competing species, protecting forests from fire and stimulating fruit production (Anderson, 1990; Gomez-Pompa, 1991; Campbell et al., 1993), to promote connectivity and conserve forest patches. Furthermore, many forested areas form corridors between the protected areas, allowing species movement between them or buffer zones to provide a layer of protection for the biodiversity and other values the area contains (Dudley and Phillips, 2006). However, conservation in such areas is generally attained through time-limited voluntary conservation agreements without permanent commitment (Dudley and Phillips, 2006). Additionally, we suggest restorations and/or rehabilitation within and around these forest patches. Restoring degraded patches/ fragments includes (1) vegetation structure, such as promoting diverse vegetation structure by encouraging forest resources' sustainable use. Various studies confirmed the association of diverse habitat structure with higher species functional diversity (Pease et al., 2012; Seymour et al., 2015). This is because of diverse habitats structure provisioning of different resources such as nesting and feeding (Tscharntke et al., 2005; Evans et al., 2009). (2) Managing the surroundings (matrix) of forests patches; reducing destructive forces in the surrounding landscape will benefit and sustain the restoration done within the degraded patch/ fragment (Aronson et al., 1993). Therefore, creating a permeable matrix by leaving or creating many small areas similar to native habitats in the matrix facilitates species movement, especially avian species, between patches and promoting connectivity between these habitats.

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CHAPTER 6

Conclusions

6.1 Introduction

Indigenous forest cover is generally decreasing in South Africa and currently confined to a belt along the south and east side of the country (Mucina and Rutherford, 2006; Eberle et al., 2017; Wilson et al., 2017). Although they occupy a relatively small area, they play an important role in providing resources to humans and biodiversity (Eberle et al., 2017). As a result, forests have been and continue to be exploited and sometimes left in an exhausted condition, particularly in rural areas (Shackleton et al., 2007). Amongst other disturbances in indigenous forests, climate change and lack of management affect the functioning of the ecosystem (Thom and Seidl, 2016). Disturbances is one of the major drivers of forest ecosystem dynamics and results in changes in species communities in several ways depending upon the agent of the disturbance (Cohen et al., 2016). Southern Mistbelt Forests are naturally fragmented and located in rural areas where people are reliant on them for their livelihoods (Moll and White, 1978; Cooper, 1985; Lawes, 1990; Lawes et al., 2000). Therefore, they are exposed to logging, deforestation and exotic tree plantations which are disrupting to forest stability, structure and biodiversity (Shackleton et al., 2007; Adie et al., 2013; Eberle et al., 2017). These disturbances cause reduced ecosystem services, habitat amount, habitat connectivity, transformed landscape structure and poor quality matrix (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000;Fahrig, 2003; Ewers et al., 2010; Carrara et al., 2015; Fahrig, 2017). Consequently, change in functional diversity within the ecosystem. However, different species respond differently to these changes depending on their traits (Mason et al. 2005; Croci et al. 2008). Therefore, this thesis aimed to highlight the influence of disturbances and fragmentation in taxonomic, functional and meta-population dynamics of the avian communities in selected Southern Mistbelt Forests in the Eastern Cape and KwaZulu-Natal Provinces, South Africa.

6.2 Research findings

As the inland Southern Mistbelt Forests have not been studied extensively at a landscape level in terms of avian species persistence (Lawes, 1990; Swart and Lawes, 1996; Lawes et al., 2000; Wethered and Lawes, 2003), the aims of the present study were multifaceted. Firstly, we determined the requirements and preferences, and the degree to which vegetation metrics influence on the probability of occupancy of the orange ground thrush (*Geokichla gurneyi*) and the lemon dove (*Aplopelia larvata*), and also compare seasonal differences. During the wet season, leaf litter, short grass, herbaceous cover, saplings, and trees were significant covariates for influencing lemon dove occupancy (Chapter 2). Whereas in the dry season herbaceous cover, saplings, short and medium trees were significant covariates for influencing lemon dove occupancy (Chapter 2). Orange ground thrush occupancy in the wet season was significantly influenced by short grass, short herbaceous cover, short and medium trees (Chapter 2). These results highlighted the significance of a diverse structure for both forest avian specialist species (Chapter 2). Diverse habitat structures typically provide more resources and the diversity of species (Tscharntke et al. 2005)

In determining the landscape-scale drivers of avian community composition in Southern Mistbelts Forests, we found distance between forest patches, patch diversity, indigenous forested areas, patch shape index and exotic timber plantations were drivers of most avian diversity measures (Chapter 3). Avian species richness was significantly influenced by the amount of indigenous forest (Chapter 3). Furthermore, the diversity of the forest structure and the number of timber plantations surrounding forest patches were significant influences on avian functional richness, evenness and dispersion across seasons (Chapter 3). The reduction in patch size and habitat structural diversity significantly influenced avian beta diversity (Chapter 3).

We also determined the microhabitat structure influence on avian communities in Southern Mistbelt Forests across a variety of forest patches (Chapter 4). Our results, showed these forests patches to be significantly different in vegetation and subsequent avian species richness in vegetation structure, avian species richness and functional diversity across the study areas (Chapter 4).

Finally, we mapped least-cost corridors between Southern Mistbelt Forest patches of high avian species richness to promote connectivity across the landscape (Chapter 5). Our results showed forests patches at a greater distance were not connected, and the quality of the matrix had a major influence on habitat connectivity (Chapter, 5). Additionally, forests patches in Creighton had the highest barriers compared with all three clusters (Kokstad and Umthatha).

6.3 Conclusions and recommendations

It is important to conserve indigenous forests to safeguard the survival of forest biodiversity, particularly avian communities. Our study showed the importance of a diverse habitat structure for avian forest species. Therefore, homogeneous vegetation structure threatens forest species requiring complex habitat structures. We also highlighted the significance of diverse landscape structure for the conservation of avian diversity and richness. Southern Mistbelts Forests avian communities' diversity was compromised in forest patches at greater isolation distances and with less diverse forest structure (Chapter 3). Diverse microhabitat structure was also found to be important for avian species diversity and functional communities (Chapter 4). Therefore, the findings of this study have inferences for the conservation of southern Mistbelts Forests or guarding these patches from logging because of their significant role in avian communities. Our findings also contribute to understanding the drivers of species distributions and how avian communities are responding to habitat transformation in Southern Mistbelts Forests (Chapters 2-4).

As a consequence of our findings, we recommend the sustainable use of forest products and tree species to promote a diverse habitat structure and conservation of our avian species. Furthermore, local communities and groups of stakeholders may perhaps participate in protecting these forest patches for further improvement of regulatory standards in relation to the sustainable use of forest resources.

Already, 41% of the KwaZulu-Natal Mistbelt region had been transformed into exotic timber plantations, which is the main anthropogenic land-use (Armstrong et al. 1998). Identification of protected corridors is therefore recommended to stimulate the connectivity and allowing the dispersal of species between the forest patches (Chapter 5). We propose connectivity between these patches be management and future research priorities. Finally, we recommend directing the attention towards conserving mature natural forests and restoring those degraded is a critical conservation management strategy to maintain species functional diversity, richness and habitat heterogeneity.

6.4 References

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