Local and landscape drivers of avian diversity facets in the naturally fragmented Southern Mistbelt forests of KwaZulu-Natal and Eastern Cape, South Africa

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GENERAL ABSTRACT

Forest fragmentation is a process whereby a forest landscape is subdivided into smaller and more isolated fragments embedded within a matrix of anthropogenic land-uses. The effects of increasing anthropogenic practices surrounding forest remnants threaten species persistence as habitat fragments become further isolated by the matrix, which impedes species movement and dispersal, causing local extinctions when conditions become more unfavourable. However, naturally fragmented forest systems harbour resilient species, but the novel challenges presently experienced by these species have unknown consequences.

Here, I determined to assess local avian diversity facets in selected naturally fragmented Southern Mistbelt forests of KwaZulu-Natal and Eastern Cape provinces, South Africa. I conducted fixed-radius point-count surveys across 32 (range: 0.03 – 732.42 ha) of these Southern Mistbelt Forests. Data collection was conducted during the breeding (October-February) and non-breeding (May-August) seasons in 2018 and 2019. Firstly, I used a multifaceted approach to assess the effects of landscape composition (i.e., matrix quality), habitat fragmentation (i.e., isolation distance and fragment-size) and local habitat heterogeneity (i.e., forest-structural complexity) on avian alpha-diversity (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) of the whole community, forest-dependent (i.e. forest specialist) and non-forest-dependent (i.e. forest generalist) assemblages. Secondly, I revealed how key landscape features (i.e. habitat amount, matrix heterogeneity and average isolation distance) affected local bird diversity and determined the importance of each landscape variable using linear mixed-effect models (LMEs). Thirdly, I mapped connectivity of core Southern Mistbelt Forest patches provisioning the highest (≥ 50 %) avian phylogenetic diversity by using a hybrid of least-cost pathway and ecological circuit theory approach to identify landscape features that promote or impede habitat connectivity of a surrogate forest-specialised and dispersal-limited species (Lemon dove - *Aplopelia larvata*) to guide landscape connectivity for avian forest communities in the fragmented forest mosaic landscape.

My findings revealed that: A) 1. matrix quality was a significant positive predictor of functional (FRic, sesFRic) and phylogenetic (sesPD) diversity; 2. habitat fragmentation had significantly negative effects (i.e. increasing isolation distance and decreasing fragment size) on multiple diversity facets; and 3. diversity facets of forest-dependent species unexpectedly declined with increasing local vegetation complexity. B) Habitat amount in the landscape was the main significant positive predictor of local forest bird diversity, and there were no significant influences of the average isolation distance and landscape (matrix) heterogeneity on local avian diversity. C) Landscape connectivity of Southern Mistbelt Forest fragments is predominantly promoted by indigenous forest cover and reduced in regions of unsuitable habitat (i.e. exotic timber plantations, grassland, agriculture, and residential land-cover).

I concluded that i) positive effects of surrounding matrix quality in the landscape mediates the negative effects of habitat fragmentation on local forest bird ecological groups; ii) promoting local vegetation complexity could contribute to the loss of forest-dependent species (i.e. forest specialists); iii) habitat amount in the surrounding landscape was the predominantly important predictor of local avian diversity and promoted habitat connectivity among core forest patches of fragmented Southern Mistbelt Forest. Therefore, I recommend preserving and increasing forest cover in the landscape to ensure the long-term survival of forest species in this naturally fragmented ecosystem.

PREFACE

The data described in this thesis were collected in the Southern Mistbelt forests of KwaZulu-Natal and Eastern Cape Provinces, the Republic of South Africa, from May-August and October-February of 2018 and 2019. Fieldwork, analyses and thesis writing were carried out while registered in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs. Dr David A. Ehlers Smith and Dr Yvette C. Ehlers Smith.

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

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Samukelisiwe P. Ngcobo

February 2022

I certify that the above statement is correct, and as the candidate's main 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, Samukelisiwe Princess Ngcobo, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been re-written but the general information attributed to them has been referenced
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5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

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DECLARATION 2 - PUBLICATIONS

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

Publication 1: Landscape Ecology (in press)

SP Ngcobo, ST Gumede, M Sosibo, DA Ehlers Smith, YC Ehlers Smith & CT Downs

Using a multifaceted approach to reveal avian community responses to natural and anthropogenic effects in a fragmented Southern Mistbelt Forest system, South Africa

Author contributions:

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

Publication 2: Revised for Journal of Biogeography

SP Ngcobo, ST Gumede, M Sosibo, DA Ehlers Smith, YC Ehlers Smith & CT Downs

Landscape drivers of bird taxonomic and functional diversity in selected South African Southern Mistbelt forests

Author contributions:

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

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SP Ngcobo, ST Gumede, M Sosibo, DA Ehlers Smith, YC Ehlers Smith & CT Downs

Identifying habitat connectivity of focal Southern Mistbelt Forests within human-altered landscapes in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa

Author contributions:

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

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February 2022

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"If You Only Do What You Can,

You Will Never Be More Than You Are Now"

(Master Shifu, Kung Fu Panda)

I can honestly say that I am a changed person and have learnt the most about myself during this experience. God has been good to me throughout this entire journey, and all glory be to His name for bringing me thus far.

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visits (also acknowledging all your complaints). I am most grateful to the rest of my family for their own special way of encouragement. Thank you all for loving and supporting me.

This thesis is dedicated to my late grandmother and my younger brother Lindo (who was gone too soon).

“For I Know The Thoughts That I Think Toward You, Says The LORD,
Thoughts Of Peace And Not Of Evil, To Give You A Future And A Hope”
(Jeremiah 29:11, NKJV)

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CHAPTER 1

General introduction

1.1 Background

The indigenous forest biome in South Africa covers just about 0.5 % of the total land surface area, which is the smallest of the eight biomes in the region (Low and Robelo, 1996; Berliner, 2009). South African forests often occur as clusters of fragments embedded within a natural grassland matrix, distributed along the eastern and southern margins of the country (Mucina and Geldenhuys, 2006; Rutherford et al., 2006). In South Africa, numerous forest fragments are generally less than 100 ha (Mucina and Geldenhuys, 2006). Although historically fragmented since 40,000 years BP because of paleoclimatic events of the Quaternary (Partridge et al., 1997; Eeley et al., 1999), further fragmentation events have occurred. These are driven by forest destruction (Castley and Kerley, 1996), including selective logging during colonial times (Adie et al., 2013), harvesting of forest products by informal communities (Leaver and Cherry, 2020) and matrix transformations following agricultural expansion and encroachment of commercial exotic timber plantations (Lawes et al., 2004)

Species persistence in the naturally fragmented forests consists of endemic fauna and flora, which are evolutionarily adapted to the archipelago-like distribution of forest remnants (Lawes, 1990; Lawes et al., 2000; 2007). However, the accumulative effects of increasing anthropogenic practices (land conversions for agriculture and land development) surrounding forest remnants threatens species persistence as habitat fragments become further isolated by the matrix, which impede species movement and dispersal, causing local extinctions when conditions become more unfavourable (Adie et al., 2013; Olivier et al., 2013; Leaver et al., 2019). Moreover, the generally small area of remnant forest cover (approximately 64 % between 0-10 ha; Beliner, 2005) and the restriction of forest fauna therein and the subjection of forests to increasing human pressures in the matrix; may change species vulnerability (Castley and Kerley, 1996). Therefore, this warrants an evaluation of how these present environmental changes affect biodiversity responses in remnant forest fragments.

Forest avifauna, because of their mobility and diverse ecological functions, provide the best proxy for assessing the environmental conditions of habitat patches (Lawes et al., 2007; Kissling et al., 2012). Previous studies of avian diversity in fragmented forests of South Africa, particularly Southern Mistbelt forests, have either considered responses of taxonomic diversity (i.e. richness, abundance, or Shannon-Weiner diversity) (Symes et al., 2002; Wethered and Lawes, 2003; 2005; Malan, 2014) or both taxonomic and functional diversity in relation to occupancy (Gumede et al., 2020), forest-product harvesting (Leaver et al., 2019), and the effectiveness of sampling methodologies (Mulvaney and Cherry, 2020). Assessments of avian taxonomic and functional diversity have also been determined in other South African forest types. For example, in the Indian Ocean Coastal Belt forests (IOCB) regarding patch-isolation effects (Ehlers Smith et al., 2018a; Ehlers Smith et al., 2018b), while in Scarp forest, regarding patch-isolation effects (Maseko et al., 2020) and microhabitat heterogeneity (Maseko et al., 2019). However, no research to date has assessed the various facets of avian diversity in response to local and landscape environmental changes in Southern Mistbelt forest fragments in a landscape mosaic.

1.2 Purpose of the study

This research expands the result of previous studies by addressing the multi-faceted nature of species diversity, in contrast to using a single or just a few measures of community diversity to quantify the fragmentation-diversity relationship (Chapter 3). Additionally, I provide relevant contributions to the understanding of how landscape configuration affects biodiversity and particularly important insights for ecosystems that are naturally fragmented (Chapter 4). I also identify potential drivers of habitat connectivity across focal Southern Mistbelt forest fragments since species persistence in fragmented landscapes is known to be dependent upon landscape connectivity which influences species movement, dispersal and colonisation of habitat patches (Chapter 5).

1.3 Aims and objectives

The overall aim of this research was to reveal patterns of local forest bird diversity facets (i.e. the different diversity metrics which quantify the broad concept of biodiversity that cannot be fully captured by a single variable) in the naturally fragmented Southern Mistbelt forests system. Specifically:

- I used a multifaceted approach to determine the responses of local avian diversity (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) to the effects of matrix quality (landscape composition), habitat fragmentation (isolation distance and fragment-size), and local habitat heterogeneity (forest-structural complexity) in selected Southern Mistbelt Forest systems which are characterised by both natural and anthropogenic forest fragmentation.
- I investigated the effects of habitat amount, landscape heterogeneity (i.e. matrix compositional heterogeneity) and average isolation distance (i.e. distance effect of fragmentation per se) on forest bird alpha (α) taxonomic richness and functional richness of community and forest-dependent (i.e. forest specialist species) assemblages in selected

Southern Mistbelt forest fragments of KwaZulu-Natal and Eastern Cape Provinces, South Africa.

- I used a hybrid approach of least-cost pathway and ecological circuit theory to assess potential habitat connectivity of core Southern Mistbelt Forest patches provisioning ≥ 50 % avian phylogenetic diversity along southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa.

1.4 Structure of the thesis

The thesis structure is organised in the following way: The first chapter (Chapter 1) is a brief introduction which includes the motivations and aims of the study; the second chapter (Chapter 2) is a review of the relevant literature; the next three chapters (Chapter 3, 4 and 5) are data chapters with each one covering our specific objectives. The hypotheses or predictions are presented in each. The final chapter (Chapter 6) provides an overview, conclusions and recommendations. Each chapter is formatted for submission to international peer-reviewed journals. Thus, some repetition, although of little concern, was unavoidable.

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CHAPTER 2

A systematic review of forest fragmentation research in Africa: Avian biodiversity responses in fragmented landscapes

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Running header: Effects of forest fragmentation on avian biodiversity responses in Africa

2.1 Abstract

Forest fragmentation is a process where the subdivision of forest habitat results in the creation of smaller and more isolated fragments embedded within a matrix unlike the original. The reduced total area and increased isolation, as well as increased exposure to surrounding matrix landcover at habitat edges, alter the structure and function of forest remnants. Here, we aimed to systematically review the available literature to elucidate patterns of avian biodiversity responses in forest fragments across fragmented landscapes of Africa. Few studies have addressed the effects of forest fragmentation on avian biodiversity in Africa. We expected that the expression of fragmentation effects on the African continent would follow global patterns because of the variable nature of fragmentation effects. Thus, we synthesised and reviewed the literature from 28 relevant publications investigating avian biodiversity responses to forest fragmentation effects in Africa. Our selection criteria were focused solely on 'forest' bird biodiversity responses with fragmentation-related predictor variable(s) at either patch and/or landscape scales. Similar to worldwide patterns, avian biodiversity responses to forest fragmentation effects were variable: 61 % negative effects, 54 % neutral effects, and 11 % positive effects were found. The majority of the reviewed studies revealed patterns of local (within patch) biodiversity responses and at the patch-scale, but an increasing number of studies are investigating fragmentation effects also at the landscape-scale. We encourage future research in Africa to include other biodiversity components at multiple scales (i.e. landscape and regional levels) so as to obtain a more complete picture of fragmentation effects across diversity gradients to address these knowledge gaps.

Keywords: Africa; avian biodiversity; fragmented landscape; patch characteristics, scale effects

2.2 Introduction

Forests are among the dominant biomes on Earth, providing critical ecosystem services for human wellbeing and contributing largely to the conservation of global biodiversity (Turner et al., 2007; Mengist and Soromessa, 2019). Forest conversion into anthropogenic land uses (e.g. agriculture, infrastructure, etc.) causes biodiversity loss, thereby negatively impacting ecological processes and ecosystem service provisioning (Lindenmayer and Fischer, 2006; Newbold et al., 2015). Forest destruction leads to fragmentation, a process where forest habitat is divided into smaller and more isolated fragments embedded within an anthropogenic land-use matrix (Fahrig, 2003; Watling et al., 2011). The reduced total area and increased isolation, as well as increased exposure to surrounding matrix landcover at habitat edges, alters the structure and function of forest remnants (Didham et al., 2012).

Forest fragmentation effects operate at multiple spatial scales (i.e. patch to landscape scale; Wilson et al., 2016; Bhakti et al., 2018). At the patch scale, fragmentation changes forest patch configuration factors, such as local habitat amount and quality, location of habitat patches in the landscape and their degree of connectivity to other patches (Long et al., 2010). These patch dynamics can affect population viability and potential species loss, colonisation of adjacent localities, and assembly processes of local-level communities (Didham, 2010; Chase et al., 2020). In comparison, forest cover and configuration (forest spatial arrangement) are driven by fragmentation effects at the landscape scale. Thus, loss of forest cover in the landscape may reduce habitat availability, impacting species dispersal and metapopulation dynamics in remaining forest fragments (Niebuhr et al., 2015). Further, landscape configuration attributes can alter the abiotic environment caused by increased exposure to external factors through edge effects (Laurance et al., 2011; Haddad et al., 2015; Pfeifer et al., 2017).

Fragment communities have to persist in forest remnants increasingly isolated by the surrounding anthropogenic matrix in fragmented landscapes. However, landscape forest cover and the degree of matrix contrast along forest fragment edges can affect species occupancy and abundance by influencing dispersal ability, potential colonisation, availability of additional resources and risk of mortality (Kupfer et al., 2006; Fahrig et al., 2011; Boesing et al., 2018). Fragmentation effects on forest species are highly variable (Fahrig, 2017; Fahrig et al., 2019), with sensitivity to fragmentation being dependent on species-specific morphological and ecological traits (Newbold et al., 2013; Bregman et al., 2014; Bueno et al., 2018). Specifically, large-bodied, long-lived, sedentary, and diet and habitat specialised species tend to decline the most in forest fragments, but vagile and generalist species (with broader habitat and diet breadth) proliferate in modified, fragmented landscapes (Neuschulz et al., 2013; Morante-Filho et al., 2018; Kuipers et al., 2019).

Here, we aimed to systematically review the available literature to elucidate patterns of avian biodiversity responses in forest fragments across fragmented landscapes of Africa. Our objectives were to synthesise the available literature to identify the present knowledge and any potential gaps that warrant further study.

2.3 Methods

A systematic review was conducted using guidelines from the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA- Moher et al., 2009; O'Dea et al., 2021). PRISMA guidelines improve literature reporting quality and ensure that article selection process used in the systematic review is clearly defined (Moher et al., 2009; O'Dea et al., 2021). We conducted keyword searches to locate peer-reviewed studies in the Thomson Reuters' Web of

Science database (accessible as of the 04 January 2022) for literature on biodiversity responses to forest fragmentation research in Africa. To ensure that we obtain all available articles, we intentionally 'cast a wide net' because of the patchy availability of fragmentation research in this region. However, we specifically sought to review the literature on avian biodiversity responses. The following search terms were included: forest fragmentation OR habitat fragmentation OR fragmented forest OR forest fragment OR forest remnant, AND biodiversity OR diversity OR community composition OR assemblage, AND fragmented landscapes OR fragmented forest landscapes OR human-modified forest landscape AND Africa. We did not specify the publication date in our literature search. Additionally, we used the same search terms in the Google Scholar search engine to identify other potentially useful articles that would have been missed from the Web of Science database. Duplicated studies were thus removed. For the article inclusion criteria (Fig. 2.1), we required studies that investigated avian responses (other vertebrate taxa were excluded) to forest fragmentation (biomes other than 'forests' were excluded) in Africa (other regions outside Africa were excluded); specifically, studies primarily focussed on 'forest' bird biodiversity responses and assessing fragmentation-related predictor variable(s) at patch or landscape scales.

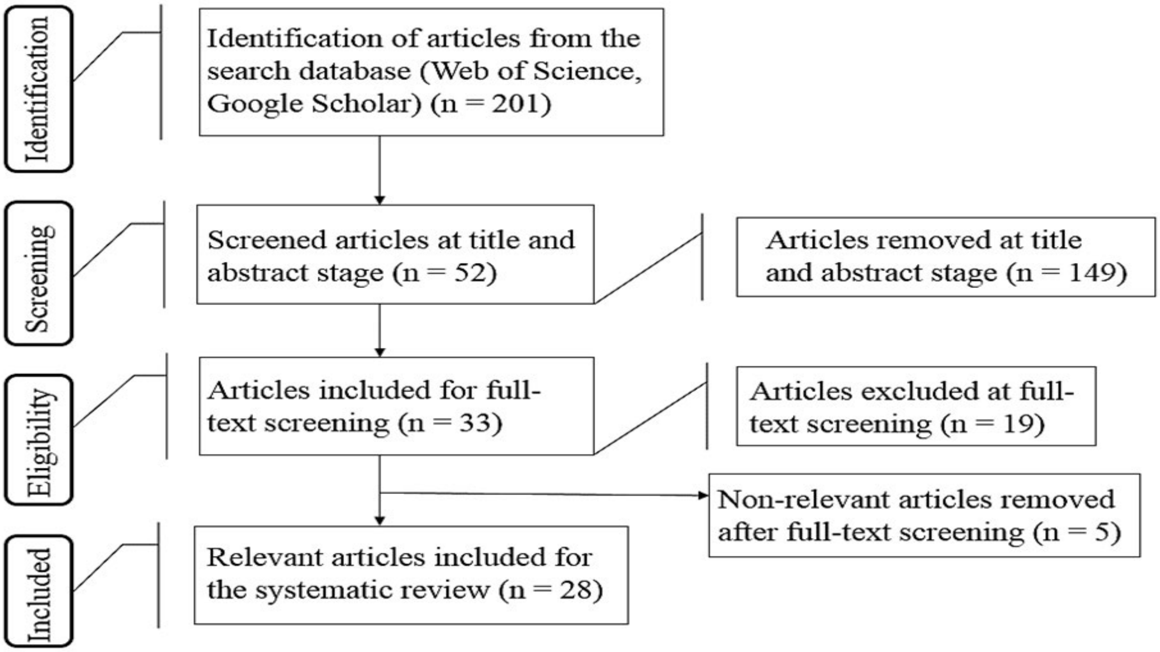

Fig. 2.1. Article inclusion and exclusion criteria following the PRISMA guideline flow chart (O'Dea et al., 2021)

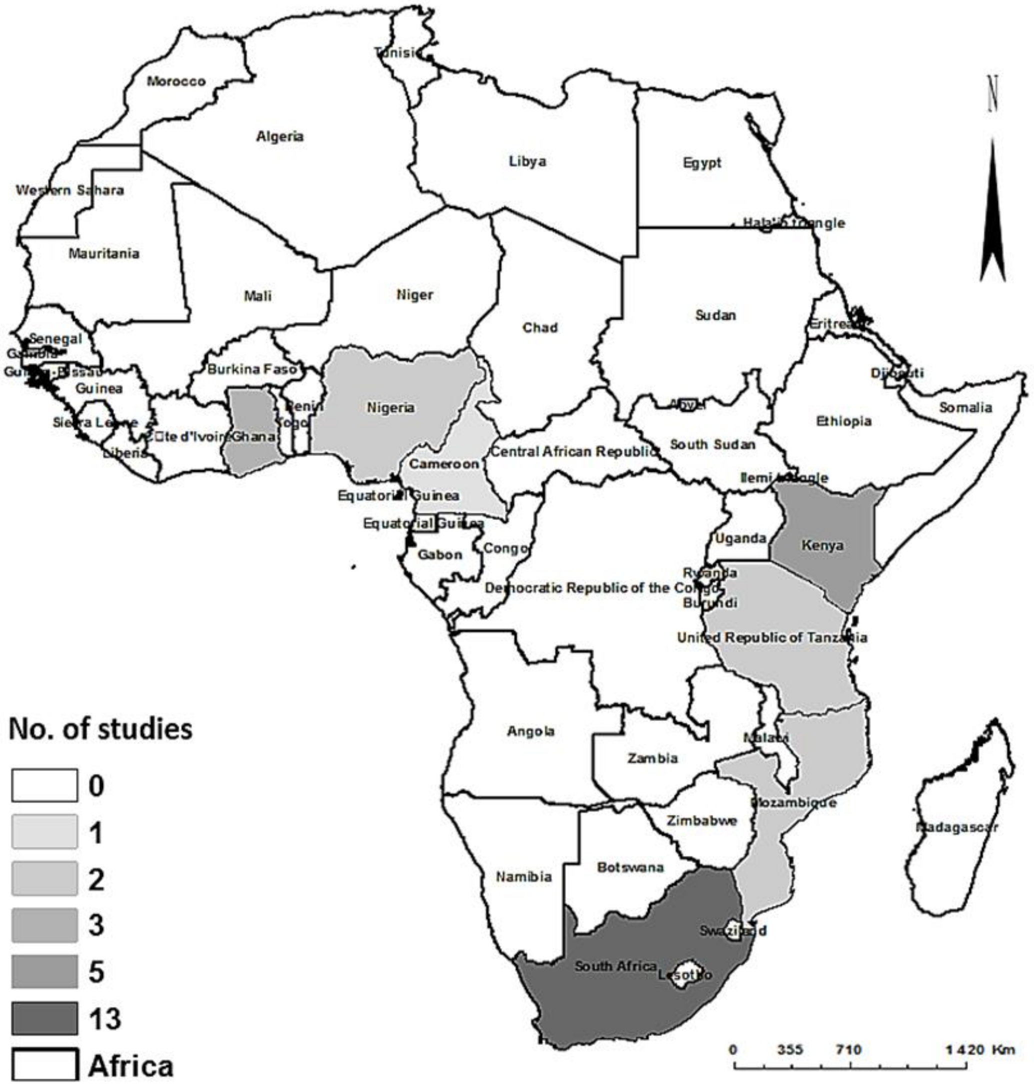

Fig. 2.2. Study locations of articles included on the systematic review. Study locations highlighted based on the number of articles found: South Africa (n = 13); Kenya (n = 5); Ghana (n = 3); Mozambique (n = 2); Nigeria (n = 2); Tanzania (n = 2); Cameroon (n = 1); other African countries (n = 0)

Table 2.1: Summary of publications in Africa used for the review (n = 28)

Taxon	Year	Study location	Fragmentation scale	Biodiversity response	Source
Negative effects:					
Community	2021	Kenya	Both	Taxonomic (richness and abundance)	Mulwa et al., 2021
Community	2020	South Africa	Patch	Taxonomic richness, Functional richness	Maseko et al., 2020
Diversity, forest specialists	2018	South Africa	Patch, landscape	Taxonomic diversity, Functional diversity	Ehlers Smith et al., 2018a
Diversity	2018	South Africa	Patch	Taxonomic diversity, Functional diversity	Ehlers Smith et al., 2018b
Species-area relationship	2018	South Africa	Patch	Taxonomic diversity	Freeman et al., 2018
Feeding guilds	2017	South Africa	Patch, landscape	Taxonomic diversity	Olivier and van Aarde, 2017
Community	2016	Tanzania	Patch	Taxonomic diversity	Modest et al., 2016
Mixed-species flocks	2015	Tanzania	Patch	Taxonomic diversity	Cordeiro et al., 2015

Insectivorous birds	2015	South Africa	Patch, landscape	Taxonomic diversity	Peter et al., 2015
Songbird community	2014	Cameroon	Patch	Occupancy	Sedláček et al., 2014
Community	2014	Ghana	Patch, landscape	Taxonomic diversity	Deikumah et al., 2014
Community	2013	Nigeria	Patch	Taxonomic diversity	Dami et al., 2013
Ecosystem processes	2011	Kenya	Patch	Taxonomic diversity	Schleuning et al., 2011
Community composition	2007	Nigeria	Patch, landscape	Taxonomic diversity	Manu et al., 2007
Community	2007	Mozambique	Patch	Taxonomic diversity	Wilson et al., 2007
Forest specialist	2006	South Africa	Patch	Occupancy	Lawes et al., 2007
Assemblages	2005	South Africa	Patch	Taxonomic diversity	Wethered and Lawes, 2005
Neutral effects:					
Community	2021	Kenya	Patch, landscape	Taxonomic (richness and abundance)	Mulwa et al., 2021
Community	2020	Ghana	Patch	Taxonomic (richness and abundance)	Dakwa et al., 2020
Community	2020	South Africa	Patch	Taxonomic richness, Functional richness	Maseko et al., 2020

Diversity, forest specialists	2018	South Africa	Patch, landscape	Taxonomic diversity, Functional diversity	Ehlers Smith et al., 2018a
Bird communities	2016	Kenya	Patch, landscape	Taxonomic diversity, Functional diversity	Ulrich et al., 2016
Frugivore communities	2014	South Africa	Patch	Frugivory	Berens et al., 2014
Frugivore communities	2013	South Africa	Patch	Frugivory	Chama et al., 2013
Community composition	2013	South Africa	Patch, landscape	Movement	Neuschulz et al., 2013
Community composition	2011	South Africa	Patch, landscape	Frugivory	Neuschulz et al., 2011
Community composition	2010	Mozambique	Patch	Taxonomic diversity	Guldemond and van Aarde, 2010
Frugivore species	2009	Kenya	Patch	Frugivory/movement	Lehouck et al., 2009
Community composition	2007	Nigeria	Patch, landscape	Taxonomic diversity	Manu et al., 2007
Community	2007	Mozambique	Patch	Taxonomic diversity	Wilson et al., 2007
Forest specialist	2006	South Africa	Patch	Occupancy	Lawes et al., 2007
Community	2002	Ghana	Patch, landscape	Taxonomic diversity	Beier et al., 2002
Positive effects:					

Community	2009	Kenya	Patch	Nest predation	Spanhove et al., 2009
Assemblages	2005	South Africa	Patch	Taxonomic diversity	Wethered and Lawes, 2005
Assemblages	2003	South Africa	Patch	Taxonomic diversity	Wethered and Lawes, 2003

Note: some studies have been duplicated because they found varying biodiversity responses in their investigation, thus proportions will not be equal to 100 %

2.4 Results and Discussion

We synthesised literature of 28 relevant publications investigating avian biodiversity responses to forest fragmentation in Africa (Fig. 2.2; Table 2.1). Similar to the worldwide pattern, avian biodiversity responses to forest fragmentation effects were variable: 61 % (17 of 28- negative effects); 54 % (15 of 28- neutral effects); and 11 % (3 of 28- positive effects) of the reviewed studies in fragmented landscapes of Africa (Table 2.1). The majority of the reviewed studies revealed patterns of local (within patch) biodiversity responses and at the patch-scale, but most studies also investigate landscape-scale in addition to patch-scale processes (Table 2.1).

2.4.1 Local biodiversity response to patch characteristics (patch scale):

Studies that revealed negative effects indicated that i) patch characteristics (decreasing patch-size and increasing isolation distance): determined species-specific characteristics most sensitive to habitat fragmentation were large-bodied, forest specialist frugivore species in Mozambique (Wilson et al., 2007), insectivore species richness (Olivier and van Aarde, 2017), forest-dependent species (patch-size effect; Lawes et al., 2006) and taxonomic and functional diversity of forest bird communities in South Africa (patch-size effect; Ehlers Smith et al. 2018b; Maseko et al., 2020). Also, caused by the patch size effect, mixed-species bird flock assemblages were greatly distinct in composition within forest fragments relative to continuous forest, with a higher proportion of forest generalists and open habitat species in the former in Tanzania (Cordeiro et al., 2015). Patch-size effects drove changes in predation rates by antbirds and decomposition rates related to changes in species composition in small forest fragments in Kenya (Schleuning et al., 2011). Whereas, isolation effects caused declines of forest bird communities in Nigeria (Manu et al., 2007; Dami et al., 2013), and distance-dependent dispersal of a) sedentary forest specialists which were unable to disperse across isolation distances greater than 500 m in South Africa (Ehlers Smith et al., 2018a), and b) forest bird occupancy which declined with increasing gaps between forest fragments in Tanzania (Modest et al., 2016). ii) Edge effects: forest bird richness and abundance decreased with increasing distance to fragment edge in Nigeria (Manu et al. 2007), and increased nesting failure (i.e. high nest predation) of small forest understorey passerines along fragment edges in small forest fragments in Cameroon (Sedláček et al., 2014). iii) Matrix effects: a) natural grassland versus plantation matrix: forest fragments embedded within exotic timber plantation matrix experienced loss of specialist species in the larger (> 50 ha) forest patches and the proliferation of generalist species in the smaller patches(< 50 ha) in South Africa (Wethered and Lawes, 2005); b) anthropogenic versus natural matrix: species-area relationships in forest fragments embedded within anthropogenic matrices were strong predictors of forest specialist species which conformed to island biogeographic predictions, but these effects were weak in natural matrices and for generalist species (both matrix types) in South Africa and Mozambique (Freeman et al., 2018); c) agriculture versus surface mining matrix: high matrix contrast (forest-surface mining) caused declines in populations of forest-dependent birds (Deikumah et al., 2014).

Reviewed neutral fragmentation effects revealed that: i) patch characteristics (patch size and isolation) could not explain forest bird community structure in forest fragments because of the non-nested assemblage structure induced by the presence of rare and endemic species in fragments (Ghana- Beier et al., 2002; Mozambique- Guldemond and van Aarde, 2010). Patch size and/or number of patches had no effects on a) forest bird taxonomic diversity (richness and abundance) in Ghana (Dakwa et al. 2020) and Nigeria (Manu et al., 2007), possibly because of turnover of habitat edge species, spillover of species from larger reserves and species utilising several habitat patches (Dakwa et al., 2020), and presumably because of the historical extinction filtering of area-sensitive species (Manu et al., 2007), b) functional diversity after controlling for species richness, c) community assembly patterns which were reported to shift from competition-dominated to colonisation-driven structure as patch-size decreased in Kenya (Ulrich et al., 2016), d) on movement patterns of forest birds because of the high vagility of forest communities in fragmented landscapes of South Africa (Neuschulz et al., 2013), e) maintenance of seed dispersal processes because of complementation driven by the complex interactions between disperser behaviour and environment in South Africa (Lehouck et al., 2009), and f) because similar frugivore communities were observed in both continuous forests and fragments in South Africa; because of availability of fruit resources (Berens et al., 2014) which is known as an important determinant of the structure of plant-frugivore networks (Chama et al., 2013). Furthermore, isolation distance effects had no significant effects on forest bird taxonomic and functional diversity (Maseko et al., 2020), migratory forest specialists (Ehlers Smith et al., 2018a), and occupancy probability of a forest-dependent species (*Guttera edouardi*; Lawes et al., 2007) in South Africa, because of the resilience of forest fauna to the naturally archipelago-like distribution of indigenous forest in South Africa (Lawes et al., 2007) and the vagility of migratory forest specialists (Ehlers Smith et al., 2018a).

Positive effects revealed by these studies indicated that patch-scale dynamics such as i) edge effects: reduced nest predation rates at edges relative to interiors in Kenya (Spanhove et al., 2009); and ii) matrix effects: exotic plantation matrix (compared with the natural grassland matrix) promoted colonisation and immigration rates in small forest fragments, facilitating dispersal across the landscape and favouring the proliferation of generalist species in South Africa (Wethered and Lawes, 2003; 2005).

2.4.2 Local biodiversity response to landscape characteristics (landscape scale):

At the landscape scale, studies revealed that i) forest fragmentation (perimeter to area ratio): negatively affected insectivore bird-herbivory trophic interactions through loss of forest-dependent insectivorous birds and concomitant increase in herbivory in South Africa (Peter et al., 2015) ii) across a forest degradation gradient (near-primary, degraded forest fragments, agricultural matrix): forest bird communities declined with increasing degradation, with forest-dependent species found exclusively at the near-natural forest block and bird communities in small fragments resembling those in the agricultural matrix habitat in Kenya (Mulwa et al., 2021). While neutral forest fragmentation effects indicated that i) landscape composition: surrounding habitat amount was not an important driver of taxonomic and functional diversity of forest communities in South Africa (Maseko et al., 2020) and Kenya (taxonomic diversity; Ulrich et al., 2016); ii) landscape configuration: landscape texture (i.e. clumpiness) had a marginal effect on local species composition in Kenya (Mulwa et al., 2021); iii) across a forest modification gradient (continuous forest, secondary forest, forest fragments, agricultural matrix): species richness did not differ across habitat types, but species abundance was highest in forest fragments and secondary forest because of turnover of forest generalists and open habitat species compensating the loss of forest-dependent species in South Africa (Neuschulz et al., 2011). Positive effects revealed that forest amount (landscape composition) was a positive driver of taxonomic and functional diversity of forest assemblages in South Africa (Ehlers Smith et al., 2018a).

2.5 Conclusions

Despite the patchy availability of fragmentation studies in the region, several patterns were observed: Negative responses to fragmentation tended to affect species-specific characteristics and resulted in the loss of species characterised by traits making them vulnerable. For example, loss of forest specialist species and large-bodied frugivores (Wilson et al., 2007), sedentary species (Ehlers Smith et al. 2018a), and insectivores (Olivier and van Aarde, 2017), etc. Additionally, ecological processes may also be threatened in forest fragments: For instance, insectivore-herbivory trophic interactions are disrupted because of the loss of insectivorous specialists and concomitant increase in herbivory (Peter et al., 2015); and changes in antbird predation rates and decomposition rates in fragments caused by species compositional changes (Mulwa et al., 2021). Neutral responses may be driven by turnover and proliferation of generalist and open habitat species in forest fragments; behavioural flexibility (resilience) and vagility of species (e.g. frugivore species; Lehouck et al., 2009; Neuschulz et al., 2013); availability of matrix resource complementation/ supplementation (Chama et al., 2013; Berens et al., 2014).

Positive responses could be because of the low contrasting matrix (i.e. matrix quality) surrounding habitat patches and forest cover in the landscape of fragmented landscapes (Ehlers Smith et al., 2018a). Therefore, the quality of the surrounding matrix appears to be vital for improving forest connectivity and facilitating movement across fragmented landscapes, especially for frugivorous species (Lehouck et al., 2009; Neuschulz et al., 2013). High quality matrices include forest cover, vegetation structure, and other landscape features that promote avian biodiversity persistence in forest fragments. For example, natural matrices weakened the area-dependent predictions of forest specialists in forest fragments (Freeman et al., 2018); exotic timber plantation matrix facilitated dispersal and promoted metapopulation dynamics in small forest fragments (Wethered and Lawes, 2003; 2005). In Africa, forest fragmentation studies on avian biodiversity patterns are limited. Although the majority of research is conducted at the patch scale, an increasing number of studies are investigating fragmentation effects also at the landscape scale. Biodiversity responses to fragmentation are mostly studied at the local (habitat patch) level, and future research in Africa should also include other biodiversity components at multiple scales (i.e. landscape and regional level) so as to obtain a complete picture of fragmentation effects across diversity gradients to address these knowledge gaps (Olivier and Van Aarde, 2014).

2.6 Declarations

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Conflict of interest

The authors declare they have no conflict of interest.

Ethics approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate

Not applicable.

Consent for publication

All authors gave consent.

Data availability

The data belong to the University of KwaZulu-Natal and are stored there. They are available from the corresponding author upon reasonable request.

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CHAPTER 3

Using a multifaceted approach to reveal avian community responses to natural and anthropogenic effects in a fragmented Southern Mistbelt Forest system, South Africa

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Running header: Avian forest communities response to natural and anthropogenic effects

3.1 Abstract

Context Forest loss and fragmentation are major drivers of biodiversity decline globally. However, with the widely recognised notion that biodiversity is multifaceted, few studies have assessed the responses of different diversity metrics to forest landscape changes.

Objectives Here, we used a multifaceted approach to assess the effects of landscape composition, forest fragmentation (patch-level) and local habitat heterogeneity on avian alpha-diversity (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) of different ecological groups.

Methods We conducted fixed-radius point-count surveys across 32 Southern Mistbelt Forest fragments of southern KwaZulu-Natal and northern Eastern Cape, South Africa. Using linear mixed-effect models, we related multiple facets of bird diversity to landscape composition (i.e., matrix quality), habitat fragmentation (i.e., isolation distance and fragment-size) and local habitat heterogeneity (i.e., forest-structural complexity).

Results Matrix quality was a significant positive predictor of functional (FRic, sesFRic) and phylogenetic (sesPD) diversity of forest-dependent (forest specialist) species and functional diversity (FRic) of the whole community. Habitat fragmentation had significantly negative effects (i.e. increasing isolation distance and decreasing fragment size) on multiple diversity facets of all ecological groups, but non-forest-dependent (forest generalist) species showed no responses to isolation distance. Unexpectedly, diversity facets of forest-dependent species declined with increasing local vegetation complexity.

Conclusions Large and connected forest fragments are vital for maintaining avian diversity facets and promoting local vegetation complexity could contribute to the loss of forest-dependent species (forest specialists) in the naturally fragmented Southern Mistbelt Forests.

Keywords Phylogenetic clustering; Landscape composition; Community assemblage; Habitat heterogeneity; Matrix quality; Functional-Phylogenetic diversity

3.2 Introduction

Habitat loss and fragmentation are twin drivers associated with biodiversity declines, introducing potential detrimental impacts on ecosystem functioning in forested regions (Fahrig 2003; Haddad et al. 2015; Hanski 2015). Habitat loss (i.e., reduction of habitat amount by the conversion of habitat into different habitat types, c.f. Fahrig 2003) has a pervasively negative effect on biodiversity by increasing random extinction and reducing species population sizes (Fahrig 1997; Fahrig 2003; Wilson et al. 2016). Habitat fragmentation (i.e. subdivision of the original habitat into various fragments within a matrix different from the original habitat, c.f. Fahrig 2003) can have either positive or negative effects on biodiversity since the vulnerability to this process is generally species-specific (Debinski and Holt 2000; Ewers and Didham 2006; Fahrig 2017; Fletcher et al. 2018). In anthropogenic landscapes, habitat loss and fragmentation effects tend to act synergistically in influencing species persistence (Bartlett et al. 2016).

Effects of forest loss and the increasing separation between forest fragments drive changes in forest amount and diversity of local vegetation complexity, which reduces resource and niche availability within forest remnants (Laurance et al. 2011). Given these changes, dispersal and colonisation become gradually impeded between fragments, leading to declines in taxonomic diversity (species richness and abundance) and their associated functional traits (Filgueiras et al. 2021). Since the effects of fragmentation are typically species-specific, the vulnerability of species depends on their trophic level, dispersal ability, body size, niche-breadth and rarity (Ewers and Didham 2006; Ehlers Smith et al. 2015). For example, species with a more specialised diet, habitat structural fidelity and resource use are known to be more susceptible to forest fragmentation (Devictor et al. 2008; Matthews et al. 2014; Cooper et al. 2017; 2020). Consequently, with the absence or limitation of vulnerable traits in fragments, ecosystem function and resilience in forest remnants becomes jeopardised (Sekercioglu 2012;

Bregman et al. 2014). Conversely, non-specialised species (i.e., generalists) are known to thrive under fragmentation because of the increasing availability of different habitat types in the surrounding matrix introduced by habitat loss and fragmentation, to which they are tolerant (Matthews et al. 2014; Matuoka et al. 2020; Fahrig et al. 2019).

Forest fragments in terrestrial landscapes do not resemble oceanic islands, which are embedded within an inhospitable matrix (i.e. Island Biogeography Theory- IBT; MacArthur and Wilson 1967). The matrix surrounding habitat patches is widely recognised as an important factor influencing habitat connectedness, subsequently driving species distribution and persistence within habitat patches in terrestrial landscapes (Haila 2002; Prugh et al. 2008; Watling et al. 2011). Matrix effects can impact local community assemblages in habitat patches through variations in its permeability to inter-patch movement (Driscoll et al. 2013; Prevedello et al. 2016), provision of complementary or supplementary resources (Fahrig et al. 2011), and influencing within-patch habitat quality (via edge effects, vegetation structure, microclimate conditions, etc.) (Saunders et al. 1991; Ries et al. 2004; 2017). Thus, species diversity is expected to be maintained in matrices that are structurally similar to patch vegetation relative to high contrast matrix types (i.e. intensely utilised anthropogenic landscapes; Tscharntke et al. 2007; Boesing et al. 2018a). For instance, higher avian taxonomic diversity was found in heterogenous coffee plantations compared with homogenous pasture matrix (Boesing et al. 2018a). Also, avian taxonomic diversity was highest in forest patches embedded in a pine plantation matrix versus a grassland matrix, and these effects were strongest in smaller patches than in larger ones (Wethered and Lawes 2003; 2005). According to Athayde et al. (2015), avian taxonomic, functional and phylogenetic diversity were highest in native vegetation compared with an agricultural landscape matrix. Avian functional diversity increased with the proportion of secondary forest regeneration in the landscape matrix

(Farneda et al. 2018). Avian phylogenetic and functional diversity were lowest in oil palm plantations and highest in logged forests (Chapman et al. 2018).

Fragmentation effects lead to changes in habitat quality indirectly through edge effects which influence the local habitat heterogeneity (Franklin et al. 2002). Habitat heterogeneity is among the most important determinants of local avian community assemblages in habitat patches through landscape complementation (c.f. habitat heterogeneity hypothesis; MacArthur and Wilson 1967). This hypothesis assumes that structurally complex habitats should support greater species diversity by provisioning a diverse array of niches (MacArthur and MacArthur 1961; Müller et al. 2010; Vogeler et al. 2014). Despite the predicted positive relationship, some contradictory findings have also been reported (Reviewed in Tews et al. 2004; Kadmon and Allouche 2007; Tamme et al. 2010; Allouche et al. 2012; Laanisto et al. 2013). Empirical studies reveal contrasting responses of diversity facets to local heterogeneity. For example, Bae et al. (2018) found that habitat heterogeneity (NDVI; Normalised Difference Vegetation Index) had positive effects on taxonomic diversity, but negative effects on functional and phylogenetic diversity as explained by the more-individuals hypothesis, which posits that high resource availability (productivity) supports increased species abundance which utilises those resources (Srivastava and Lawton 1998). Rurangwa et al. (2021) revealed that local heterogeneity (soil moisture and vegetation height) had positive effects on taxonomic diversity, negative effects on phylogenetic diversity and no significant effects on functional diversity; these differences were linked to vegetation structure. Hanz et al. (2019) reported that functional diversity increased with heterogeneity driven by food resource availability, and phylogenetic diversity increased with heterogeneity driven by vegetation structure.

It is widely recognised that biodiversity is multidimensional and should incorporate, in addition to taxonomic diversity, species functional roles (functional diversity) and their evolutionary history (phylogenetic diversity), which reveal associations between biodiversity and the maintenance of ecosystem processes and functions (Diaz and Cabido 2001; Cadotte et al. 2013; Klingbeil and Willig 2016). Functional diversity represents the variation of species-specific ecological traits within communities (Tilman 2001; Cadotte et al. 2011). Functional diversity is a more valuable measure of biodiversity than taxonomic diversity, as it links species' ecological roles to ecosystem processes and functioning (Villéger et al. 2008; Naeem et al. 2012).

Phylogenetic diversity accounts for variation in total evolutionary history represented by a community (Faith 1992; 2008; Webb et al. 2002). Phylogenetic diversity has been used as a surrogate for functional diversity based on the phylogenetic niche conservatism hypothesis, which assumes that species traits represent shared evolutionary history; thus, their phylogeny reflects the diversity of hidden functional traits (Webb et al. 2002; Winter et al. 2013). Further, phylogenetic diversity may provide additional ecological information, given that functionally similar species may not be phylogenetically related (Losos 2008). Therefore, phylogenetic diversity may reveal either the capacity of a system to provide new evolutionary solutions to environmental change or the ability to persist regardless of those changes (Webb et al. 2002). According to Cianciaruso (2011), functional and phylogenetic diversity are complementary indices which provide an opportunity to explore underlying mechanisms of biodiversity-environment relationships. Recently, studies have recommended a combined approach of using functional and phylogenetic information to infer community assembly patterns (Cadotte et al. 2013; Lopez et al. 2016; Si et al. 2017). Such new approaches are beneficial in that they overcome the limitations of using either functional or phylogenetic metrics as separate measures (Cadotte et al. 2013). For instance, the limitations of using phylogenetic diversity as a surrogate for conserving functional diversity, i.e., functional traits may not be phylogenetically conserved (Losos 2008), or it may unreliably capture functional diversity (see.

Mazel et al. 2018). Moreover, the complexities of selecting ecologically informative trait attributes may limit the predictive power of functional diversity metrics (McGill et al. 2006).

The forest biome is the smallest in South Africa, comprising 0.6 % of the land surface, yet provisions the second-highest biodiversity behind the fynbos biome (Low and Rebelo 1996; von Maltitz et al. 2003; Berliner 2009). South African forests occur as an archipelago of natural fragments scattered along eastern and southern mountainous escarpments and coastal lowlands (Mucina and Geldenhuys 2006). The case of fragmentation is an interesting one for the indigenous forests of South Africa. Natural forest fragmentation occurred because of paleoclimatic changes, which drove historical fluctuations in forest extent (Eeley et al. 1999). Further historical anthropogenic fragmentation occurred during the colonial era, which caused forest extent and quality loss from extensive logging activities (Lawes et al. 2007a,b; Adie et al. 2013). Recent anthropogenic effects continue because of on-going land transformation (for agriculture and land development) and unsustainable harvesting of forest products in and around forest fragments (Adie et al. 2013; Olivier et al. 2013; Leaver et al. 2019). Consequently, these widespread changes have led to shifts in forest structure (Lawes et al. 2007a,b; Adie et al. 2013) and some loss of original fauna (Lawes et al. 2000; Lawes 2007a,b) following the increased structural heterogeneity associated with edge effects.

Here, we used a multifaceted approach to determine the responses of local avian diversity to the effects of landscape composition, natural forest fragmentation, and local habitat heterogeneity. We specifically assessed the effects of matrix quality (landscape composition), habitat fragmentation (isolation distance and fragment-size), and local habitat heterogeneity (forest-structural complexity) on various biodiversity facets (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) in Southern Mistbelt Forest systems which are characterised by both natural and anthropogenic forest fragmentation. We used the following diversity metrics in our approach: taxonomic diversity (species richness), functional diversity (functional richness), phylogenetic diversity (Faith's phylogenetic richness- PD, mean nearest taxon distance- MNTD), functional-phylogenetic diversity (FPD- an approach which combines both trait and phylogenetic information), and the standardised effect size (SES) of all diversity metrics (sesFRic, sesPD, sesMNTD, sesMFPD- Mean Functional-Phylogenetic Pairwise Distance).

In our study we tested the following hypotheses:

H_1. Matrix quality is a feature of landscape composition (Morante-Filho et al. 2020), which can affect species occurrence and persistence within forest remnants (Boesing et al. 2018a). Quality of the matrix can mitigate the effects of fragment isolation by facilitating dispersal among forest fragments (Ewers and Didham 2006). Thus, we predicted a positive influence of matrix quality on multifaceted avian diversity, particularly 1) given that specialist species have high habitat specificity and seldom cross the matrix, high matrix quality is expected to positively affect diversity facets of the forest-dependent (forest specialist) species assemblage (Newbold et al. 2014); 2) since generalist species tend to have similar ecological traits and are tolerant to the anthropic matrices, matrix quality is expected to show no effects on diversity facets of the non-forest-dependent (forest generalist) species assemblage (Pardini et al. 2010); thus 3) we expected diversity facets of the whole community bird assemblage to be maintained in a lower quality matrix because of changes in species composition driven by the turnover and proliferation of non-forest-dependent species replacing forest-dependent species (i.e. compensatory dynamics; Morante-Filho et al. 2015; 2018; Matuoka et al. 2020).

H_2. We hypothesised that habitat fragmentation would influence avian diversity and structure of communities by reducing habitat area and connectivity, thus limiting the dispersal of many species, particularly those with high forest affinity (Ehlers Smith et al. 2018a). Therefore, 1) we expected forest-dependent species to show a negative response since habitat fragmentation may reduce specialised niches by changing the internal forest structure and local habitat quality (Laurance et al. 2002; 2011); 2) generalist species are known to benefit from additional resources through landscape complementation (Farhrig 2003; 2017), thus we expected non-forest-dependent species assemblages to show positive or no responses to habitat fragmentation because of the lack of constraints to movementsand their behavioural flexibility (Ewers and Didham 2006); and 3) whole community diversity facets are expected to show positive or no effects to habitat fragmentation because of spillover of forest generalist species from the surrounding matrix, maintaining diversity especially in small and isolated fragments (Banks-Leite et al. 2012; Morante-Filho et al. 2015).

H_3. Forest structural complexity reveals the local availability of resources and niches at fine-scale habitat heterogeneity, a well-known driver of avian taxonomic and functional diversity (Ehlers Smith et al. 2018a; Maseko et al. 2019). Therefore, we predicted that high habitat heterogeneity would positively influence multifaceted avian diversity by providing diverse niches (Fahrig et al. 2011; Ehlers Smith et al. 2017; 2018a; Maseko et al. 2019). Particularly, 1) forest-dependent species were expected to be most affected by forest structural complexity, given their functional traits are associated with higher habitat specialisation and structural complexity (Morante-Filho et al. 2015); 2) non-forest-dependent species are not expected to respond to local habitat complexity because of their broad ecological requirements; thus 3) whole community diversity will show no response to habitat complexity and should be maintained even in focal fragments with lower habitat complexity by the forest generalist species assemblage proliferation.

3.3 Methods

3.3.1 Survey regions

Our study was conducted in Southern Mistbelt Forests (hereafter Mistbelt Forests) in three regions (Creighton - 29°58'24.43"S, 29°44'16.15"E; Ingeli-30°31'48.93"S, 133 29°41'13"E;

uMthatha- 31°25'1.58"S, 134 28°32'27"E) in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa (Fig. 3.1). These Mistbelt Forest regions are distributed in an agricultural matrix dominated by commercial exotic tree plantations covering ~41 % (Armstrong et al. 1998). Forest remnants in each region are surrounded by varying proportions of plantation (42.7 %- Creighton; 65.6 %- Ingeli; 39.1 %- Umthatha), indigenous forest (including contiguous dense bush) (18.3 %- Creighton; 20.8 %- Ingeli; 25.8 %- Umthatha) and natural grassland (25.6 %- Creighton; 11.2 %- Ingeli; 25.5 %- Umthatha) cover across the survey landscape. The distribution distance between survey regions was approx. 45 km (Creighton to Kokstad- KZN) and approx. 150 km (from Kokstad to Umthatha- between KZN and EC), respectively. Berliner (2009) reported that approximately 46%, and 29%, respectively, of the country's subtropical indigenous forest extent, are contained within KwaZulu-Natal and Eastern Cape provinces alone. Subtropical forests in South Africa are classified into two broad categories: Afrotemperate (within-which Mistbelt Forests are classified) and Indian Ocean Coastal Belt Forests (Mucina and Geldenhuys 2006). Mistbelt Forest fragments are naturally embedded within a natural grassland matrix; however, with the transformation of grasslands for agriculture, fragments are also surrounded by a matrix of commercial exotic timber plantations of pine *Pinus* spp. and gum *Eucalyptus* spp. (Adie et al. 2013). Mistbelt Forests occur at middle altitudes (850-1600 m asl), generally on steep south-facing slopes in fire-safe habitats (Mucina and Geldenhuys 2006). Mistbelt Forests experience seasonal changes in rainfall and temperature. Annual precipitation range is 724 - 1181 mm, concentrated within the summer months (> 75% rainfall from November to March) and low rainfall in the winter months (< 5% precipitation from May to August) (Schulze 2007). Annual temperature range is 0 - 29 ^{0}C (July is the coldest month, and January is the hottest month) (Schulze 2007).

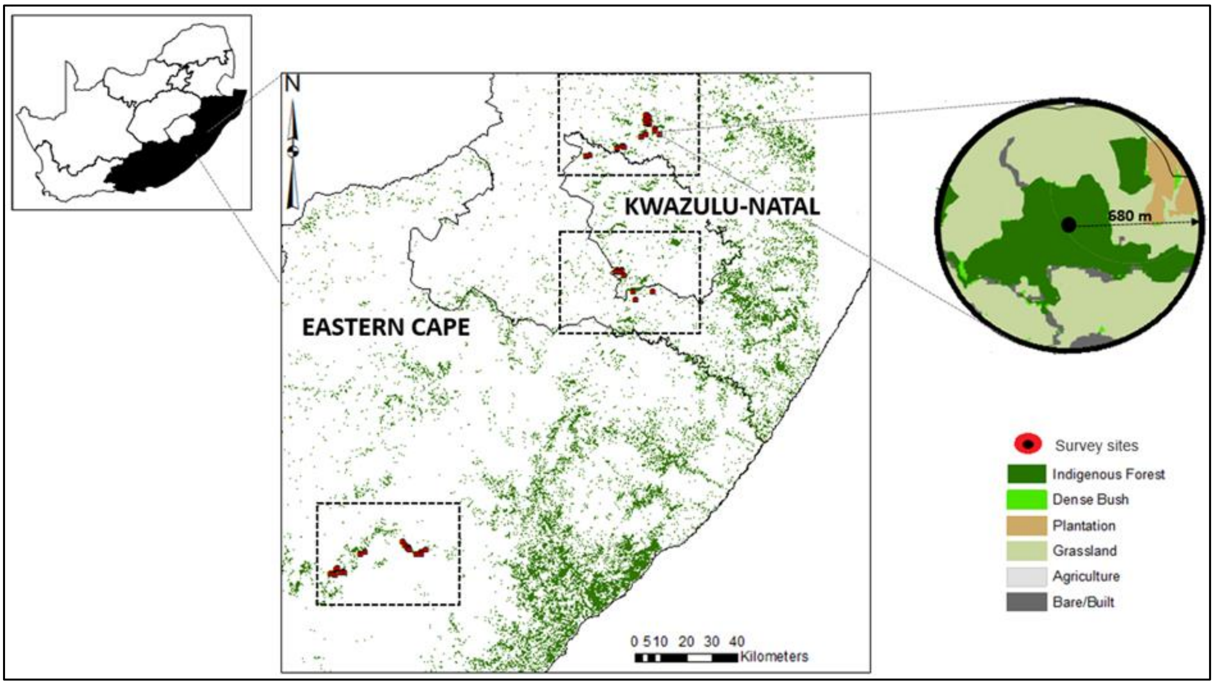

Fig. 3.1 Survey forest sites (highlighted in red) located in KwaZulu-Natal (KZN) and Eastern Cape (EC) provinces, South Africa (insert). We reveal landcover types of the surrounding matrix within a 680 m buffer radius of a selected mainland forest fragment. Survey regions highlighted in Creighton (top), Ingeli (middle) and uMthatha (bottom)

3.3.2 Survey design

We extracted layers of indigenous forest and dense-bush shapefiles after ground-truthing of survey sites (i.e. locations of individual forest fragments) revealed both vegetation types appeared as a contiguous habitat. Both were identified using the recent land-cover map layer (GeoTerra Image 2014) and were overlaid with a systematic 200 x 200 m grid in ArcGIS v 10.2 (Environmental Systems Research Institute 2011). Survey points (i.e. point-count locations within each forest fragment) were allocated at the intersection of each grid and projected onto a Global Positioning System (Garmin GPSMAP 64 Mapping Handheld GPS) for locating sites in the field. Due to geographic restrictions in the field, some points were not surveyed, and new points were created *ad-hoc* while ensuring a minimum distance of 200 m was maintained between survey points in all forest fragments (See Ehlers Smith et al. 2017;

2018a, b). Since indigenous forest in South Africa naturally resembles an archipelago-like distribution (von Maltitz et al. 2003), we applied the Island Biogeography Theory (MacArthur and Wilson 1967) and selected forest fragments representing mainland (largest patch - source) and satellite (surrounding) remnants varying in size (range: 0.03 – 732.42 ha) and isolation distance (range: 0 – 30.94 km) from the largest mainland patches in each region. Fragment size and isolation distance, respectively were thus in each region: Creighton (range: 0.03 – 494.36 ha; 0 – 15.71 km; n = 16); Ingeli (range: 11.97 – 732.42 ha; 0 – 0.87 km; n = 6); and uMthatha (range: 13.76 – 671.86 ha; 0 – 30.94 km; n = 10).

3.3.3 Bird surveys

We conducted fixed-radius point-count surveys (Bibby et al. 2000), totalling 747 (range: 4-195) survey points in 32 distinct forest fragments during the non-breeding (May-August) season and then repeated these in the breeding season (October-February) during 2018 and 2019. We recorded all bird species that were audible or visual within a 50 m distance-radius to determine the taxonomic diversity (abundance and number of species) at each survey point (Ehlers Smith et al. 2017). We conducted surveys from sunrise for 3 h, with counts lasting for l0 min at each sample point, thus only diurnal species were recorded (Appendix S3.1), and species were not recorded in cases of identification uncertainty (Bibby et al. 2000; See Ehlers Smith et al. 2017; 2018a, b).

3.3.4 Environmental predictors

Since bird response to landscape variables is scale-dependent (Smith et al. 2011; Skórka et al. 2016), we performed a multi-scalar analysis across a range of buffer sizes (200 m, 400 m, 600 m, 800 m, 1000 m, 1200 m) to determine the landscape size which adequately predicts bird community composition (c.f. Fahrig 2013). Additionally, we also included a 680 m buffer size following Olivier et al. (2013) methodology, which reveals the average inter-patch distances between indigenous and dense bush vegetation types since these occur in close proximity and appear structurally similar in South Africa. Thus, we determined the spatial scale which best predicts bird response (for each diversity facet analysed) to landscape predictors (i.e. matrix quality) at seven spatial scales (200 m, 400 m, 600 m, 680 m, 800 m, 1000 m, 1200 m) by using single factor General Linear Models (GLMs) with Poisson error variance (sensu Skórka et al. 2016). The best spatial scale was selected using the Akaike information criterion (AIC) and considered the spatial scale that best predicts bird response as having the lowest AIC value (Burnham and Anderson 2002). Using the best spatial scale (680 m; see Appendix S3.2), we determined the correlation with other spatial scales (Pearson correlation: $r > 0.70$; $N = 32$; Appendix S3.3). Thus, we selected the 680 m buffer radius to assess our explanatory variables. This ensured that spatial overlapping among forest fragment sites was avoided and that landscape characteristics would provide reliable inferences since bird response to landscape variables is scale-dependent (Peter et al. 2015; Skórka et al. 2016). We assessed the following explanatory variables: landscape composition (matrix quality), habitat fragmentation (fragment-size and isolation effect), and local habitat heterogeneity (forest-structural complexity) (Appendix S3.4).

To calculate fragment size, we merged both indigenous forest and dense bush layers (dissolving edge boundaries) and calculated area (ha) for all habitat fragments within our survey region (see Ehlers Smith et al. 2017; 2018a, b). We then assigned the largest fragment as the mainland fragment for each region (Maseko et al. 2019; 2020). Fragment isolation (hereafter isolation) was then calculated from the edge of the nearest mainland fragment to the edge of the survey sites as the Euclidean distance (in metres) (see Ehlers Smith et al. 2017; 2018a, b).

To calculate forest-structural complexity, we first recorded the vegetation structure and foliage profiles at each survey point in a 20 m radius (within individual quarters of the circular plots- totalling four habitat plots in each). Habitat covariates recorded were: percentage coverage of bare ground, leaf litter, grass cover, herbaceous cover, saplings and scrub/woody vegetation < 2 m, and percentage of scrub/woody vegetation and trees of 2–5, 6–10, 11–15 and 16– 20 m heights. Secondly, the mean heights of all vegetation classes were recorded using a telescopic pole equipped with a rule. Additionally, for each height class, the stem density of trees and that of all horizontal and vertical dead trees were recorded (Bibby et al. 2000; see Ehlers Smith et al. 2017; 2018a, b). We then used the Shannon-Weiner diversity index (SWDI) formula to convert mean height scores for each vegetation class thus:

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

where p*i* is the proportion of the total foliage which lies in the *i*th layer of the chosen horizontal layers (Bibby et al. 2000). Finally, we obtained the measure of FSC by using mean SWDI scores per survey point to create the average SWDI for each survey fragment.

Matrix quality from the perspective of forest bird species was estimated using an index that relates the quality of each land-cover type with its proportion (%) within the surrounding matrix (cf. Morante-Filho et al. 2021). This was accomplished by ranking land-cover types based on the vegetation structure from 1 (lowest quality) to 6 (highest quality) thus: 1 (water bodies, roads, human settlements), 2 (croplands), 3 (grassland), 4 (plantations), 5 (dense bush), 6 (indigenous forest). The index of matrix quality was calculated as: [(1 X % water, roads, human settlements) + (2 X % croplands) + (3 X % grassland) + (4 X % plantations) + (5 X % dense bush) + (6 X % indigenous forest)]/6 (see Morante-Filho et al. 2020). Additionally, since matrix quality is a species-specific measure (Fahrig et al. 2011), we considered matrix effect variation between the ecological groups (forest-dependent vs non-forest-dependent species). Specifically, matrix quality for forest-dependent species was categorised as 1 = non-forest land cover (including agriculture, grassland, and residential cover types, were categorised as 1); 3 = timber plantations (c.f. Cooper et al. 2017), and 6 = indigenous forest. According to Newbold et al. (2013), habitat generalists have a relatively similar probability of occurrence in undisturbed, lightly-used or intensively used land-use types. Thus, for the matrix quality of non-forest-dependent species, we categorised all land cover types as 3, as we considered the broad ecological tolerance of this ecological assemblage (Newbold et al. 2013; Bueno et al. 2018).

3.3.5 Multiple facets of avian diversity metrics

Bird diversity metrics calculated at the alpha (fragment) level (Whittaker 1972) for 1) whole community, 2) forest-dependent species, and 3) non-forest-dependent species were: Species richness (SR; taxonomic diversity), functional richness (FRic), Phylogenetic diversity metrics (Faith's PD- phylogenetic richness; and mean nearest taxon distance- MNTD; phylogenetic divergence), functional-phylogenetic diversity (FPD). Additionally, we calculated the standardised effect sizes (SES) of each diversity metric to control for effects of species richness (sesFric; sesPD; sesMNTD; sesMFPD).

3.3.6 Quantifying functional diversity

Our index of choice for the functional diversity metric was functional richness (FRic), which forms an aspect of several other most widely used functional diversity indices in ecological studies (i.e. functional dispersion (FDis), functional evenness (FEve), and functional divergence (FDiv). According to Mason et al. (2005), FRic is the amount of functional (niche) space filled by species in an assemblage. FRic uses the Gowers dissimilarity distance matrix (for both categorical and continuous variables) to measure this multidimensional space occupied by species within the community (Villéger et al. 2008). Since FRic is not dependent on abundances, the functional niche space may be occupied even with low abundances (Mason et al. 2005). Thus, we could also completely capture the functional diversity of even small fragment sizes regardless of low abundances using this index (but see Legras et al. 2018 for the advantages and drawbacks of FRic index). Low FRic scores indicate that available local resources may not be utilised; hence particular niches may not be occupied by the community (Mason et al. 2005). We calculated the FRic index using FD package ("dbFD" function) (Laliberté and Legendre 2010) in the statistical software R environment (R Core Team 2019). We also calculated standardised effect sizes (SES) of FRic since it is a measure that is highly correlated with species richness (see Appendix S3.5). We calculated this metric (sesFRic) as: (observed FRic values – mean of expected FRic values) / SD of expected FRic values, where positive SES values suggest low functional redundancy (e.g. driven by competitive exclusion) and negative SES values suggest high functional redundancy (e.g. driven by environmental filtering) (Petchey et al. 2007; Mouchet et al. 2010; Plass-Johnson et al. 2016).

A species trait matrix was created using carefully selected bird functional traits based on habitat use, resource acquisition and disturbance sensitivity: morphological (body mass, clutch size, wing length, tarsus length, culmen, tail length), diet (carnivory, folivory, frugivory, granivory, insectivory, nectarivory, scavenging, omnivory), foraging strata (ground, understorey, aerial, mid-high, canopy, mixed) and locomotion (altitudinal-migrant, breeding-migrant, nomadic, partial-migrant, sedentary). Traits of morphology, diet and locomotion were obtained from Hockey et al. 2005, and those of foraging strata were obtained from EltonTraits database (Wilman et al. 2014) (Appendix S3.6). Finally, bird species were classified according to their habitat specialisation (forest-dependent species and non-forest-dependent species) (Oatley 1989; Symes et al. 2002; Brown 2006). We defined forest dependence as those species with a high affinity to forest ecosystems for their ecological needs (Oatley 1989; Brown 2006). The main list of forest-dependent species was compiled from Oatley (1989) and supplemented with species from (Symes et al. 2002; Brown 2006), following concerns raised about the Oatley's list by Brown (2006) (Appendix S3.1).

3.3.7 Quantifying phylogenetic diversity

We calculated four measures of phylogenetic diversity representing richness (Faith's PD, sesPD) and divergence (Mean Nearest Taxon Distance- MNTD, sesMNTD) (Faith 1992; Tucker et al. 2017) from the R "picante" package (Kembel et al. 2010). 1) Faith's PD accounts for the total amount of evolutionary history across species in a community in million years (Faith 1992). 2) We then calculated the standardised effect sizes (SES) of PD to correct for effects of species richness since the PD metric was highly correlated with species richness (Appendix S3.5). This was done by comparing observed values of PD to null PD values, while maintaining a constant species richness across the randomly selected gamma communities. 3) MNTD is a measure of divergence, which measures the mean pairwise distance to the closest non-conspecific relative (Morante-Filho et al. 2018). This metric measures the relatedness between taxa and has been incorporated into community ecology to understand assembly patterns structuring local communities (Webb et al. 2002; Tucker et al. 2017). 4) We also controlled for species richness by calculating the standardised effect sizes (SES) of MNTD relative to null models (999 randomisations), which measures the extent of phylogenetic clustering at the terminal ends of the phylogenetic tree. Positive values of SES.MNTD indicate clustering (closely related taxa occur more than expected), and negative values indicate phylogenetic evenness (closely related taxa occur less than expected).

A maximum-likelihood phylogeny in Garli 0.951 (Zwickl 2006) was constructed for our assemblage from the data in GenBank database. The phylogeny data matrices were constructed from mitochondrial genes (cytochrome oxidase I, COI, and NADH dehydrogenase 2, ND2) and nuclear markers (beta- fibrinogen, Bfib myoglobin (Mb) and transforming growth factor beta, TGFB). Where sequence data for species were missing, they were substituted with sequences from their congeneric representatives (within the genus or family). All individual functional traits were tested for a phylogenetic signal based on a Brownian motion model of trait evolution using the "phylosignal" function in ‘picante’ R package (Kembel et al. 2010). The K statistic estimates the probability of obtaining the observed trait signal relative to 1000 randomisation models (Blomberg et al. 2003). Bloomberg’s K statistic test for phylogenetic trait signal was less than 1 for most functional traits except for culmen and wing length, which were greater than 1 (Appendix S3.7: Table S3.7.1), meaning that most of our selected functional traits were not phylogenetically conserved.

3.3.8 Quantifying functional-phylogenetic diversity

We quantified functional-phylogenetic diversity as described by Cadotte et al. 2013, which incorporates trait distance (Gower distance) using ‘gowdis’ function in R “FD” package (Laliberte and Legendre 2010) and phylogenetic distance (patristic distance) using ‘cophenetic’ function in R “stats” package into a single distance matrix measure, the functional-phylogenetic distance (FPD) using funct.phylo.dist function in R “pez” package (Pearse et al. 2015). The created FPD matrix requires the use of a phylogenetic weighting parameter (a-value), which scales (0 to 1) the varying contribution of functional distance and phylogenetic distance to the created FPD matrix. For instance, if a = 0 only functional distance contributes to FPD matrix, and if a = 1 only phylogenetic distance contributes to the FPD matrix. Intermediate values of ‘a’ reflect that both functional distance and phylogenetic distance contribute to the created FPD matrix (Cadotte et al. 2013). We followed the description by Si et al. (2017) in selecting the best a-value as determined by the highest adjusted R^2 value from regressing a range of

SES.MFPD values, using increments of a = 0.1 (from 0 to 1). The maximum adjusted R^2 value was reached at 0.934 when a = 0, indicating that only functional distance contributed to the FPD matrix (Appendix S3.7: Fig. S3.7.1).

Thus, functional-phylogenetic diversity was calculated at the scale of a = 0, using the dbFD function in R "FD" package and replacing the original Gower distance as the created FPD matrix (Villéger et al. 2008; Cadotte et al. 2013). By combining both traits and phylogenies, we tried to overcome the limitations of approaches that exclusively use either diversity metric separately (Cadotte et al. 2013; Si et al. 2017). To reveal the assembly processes that structure our avian community (i.e., environmental filtering vs. competitive exclusion), we calculated standardised effect size of the mean functional–phylogenetic pairwise distance (SES.MFPD) using the 'ses.mpd' function in R package 'picante' (Kembel et al. 2010). The SES metric compares community structure randomness with null models: negative SES.MFPD values indicate clustering (i.e., competition) and positive SES.MFPD values indicate overdispersion (i.e., environmental filtering) (Webb et al. 2002). Significant community assembly processes were indicated by values greater than ± 1.96.

3.3.9 Statistical analyses

As a test for multicollinearity, we created a correlation matrix to test for significant correlations between our environmental covariates, and we selected a correlation threshold ≥ 0.7 (Dormann et al. 2013). We retained all environmental covariates since none exceeded our threshold (Appendix S3.8). We used logarithmically transformed values (log10) of all environmental covariates (landscape composition (matrix quality), habitat fragmentation (isolation distance and fragment-size), local habitat heterogeneity (forest-structural complexity) for a better model fit. We found all non-SES diversity metrics were highly correlated with species richness (Appendix S3.5). To determine the effects of our explanatory variables (matrix quality;

isolation distance and fragment-size; forest-structural complexity), we constructed linear mixed-effects models (lme) separately for response variables: taxonomic diversity, functional diversity, phylogenetic diversity, functional-phylogenetic diversity, and all SES metrics (sesFRic; sesPD; sesMNTD; sesMFPD) for each bird ecological grouping including (1) whole community, (2) forest-dependent species and (3) non-forest-dependent species, while retaining all explanatory covariates and including region (uMthatha, Ingeli, Creighton) as a random effect. We tested for spatial autocorrelation for all diversity indices (TD, FD, PD, MNTD, FPD) using the Global Moran’s Index in ArcGIS v10.4 (ESRI 2015). All diversity indices were not spatially autocorrelated ($p > 0.05$) (Appendix S3.9). We selected the model with the lowest AIC value as the best model. All analyses were performed using ‘lme4’ package (Bates et al. 2015) in R v4.1.0 (R Core Team 2019).

3.4 Results

Results show varying diversity responses of avian ecological groups to surrounding landscape composition (matrix quality), habitat fragmentation (isolation distance and fragment-size) and local habitat heterogeneity (forest-structural complexity) based on the lowest AIC values (Appendix S3.10-S3.11). Firstly, matrix quality was a positive influencing factor on a few diversity metrics of the whole community and forest-dependent species (Fig. 3.2). Functional diversity of community (FRic) and forest-dependent (FRic and sesFRic) assemblages, and the phylogenetic richness (sesPD) of forest-dependent species, significantly increased with matrix quality (Fig. 3.2). However, the non-forest-dependent species were not significantly influenced by matrix quality (Appendix S3.10). Secondly, habitat fragmentation (isolation distance and fragment-size) had a similar effect on multifaceted avian diversity of all evaluated bird ecological groups (Figs 3.3 – 3.4). In fact, we observed that the increase in isolation leads to decreases in diversity facets, but no diversity metric response was apparent for the non-forest-dependent species (Fig. 3.3). In contrast, we also detected an increase in diversity facets according to the increase in the size of forest fragments, except for phylogenetic divergence (MNTD) of the whole community and forest-dependent species, which decreased with increasing fragment area (Fig. 3.4). Thirdly, local habitat heterogeneity (forest-structural complexity) was the main influencing factor of forest-dependent bird species, which unexpectedly resulted in a decrease in functional (sesFRic) and phylogenetic diversity metrics (sesPD; MNTD and sesMNTD) with increasing vegetation complexity (Fig. 3.5). However, these relationships are likely driven by an outlier.

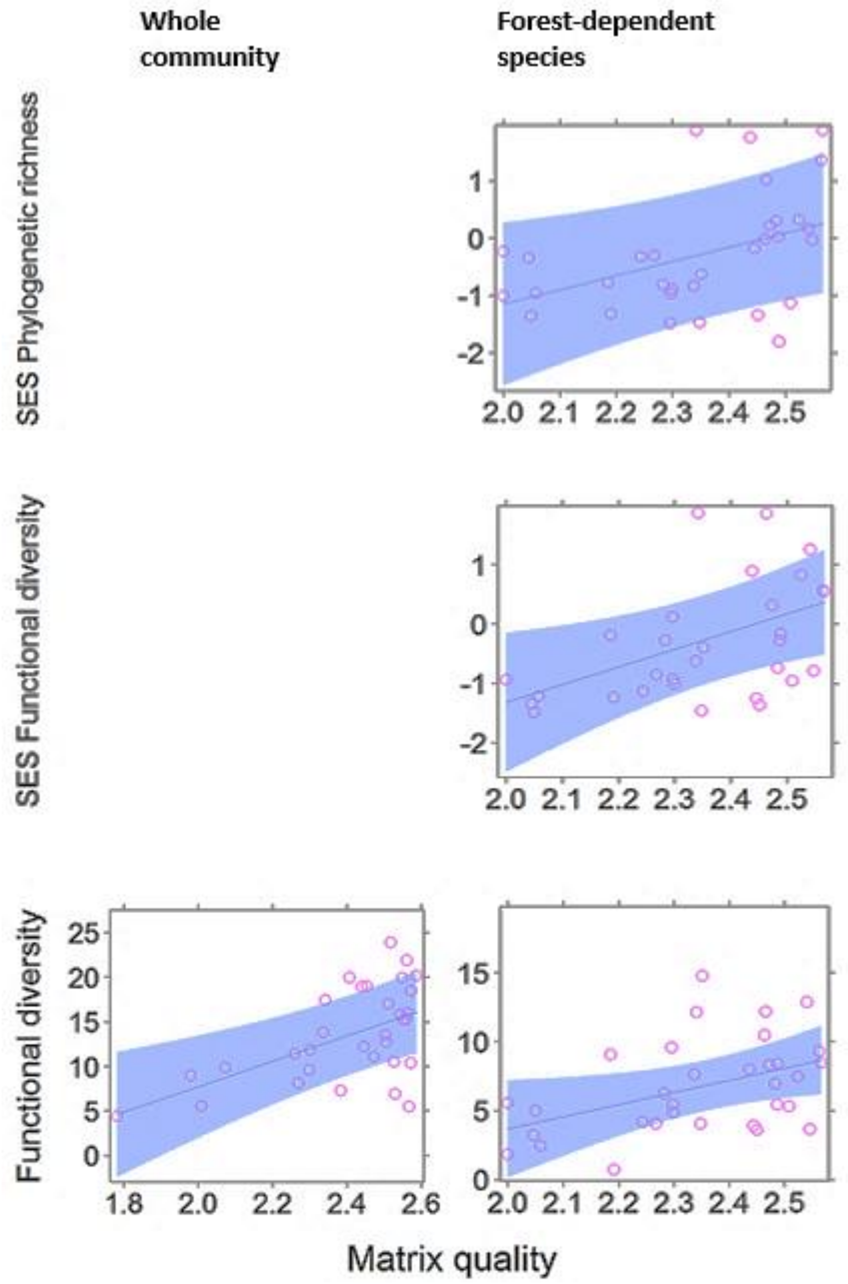

Fig. 3.2 Effect of logarithmized matrix quality on local avian multifaceted diversity indices in forest fragments located in Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa. We separately assessed the whole community, forest-dependent and non-forest-dependent bird species

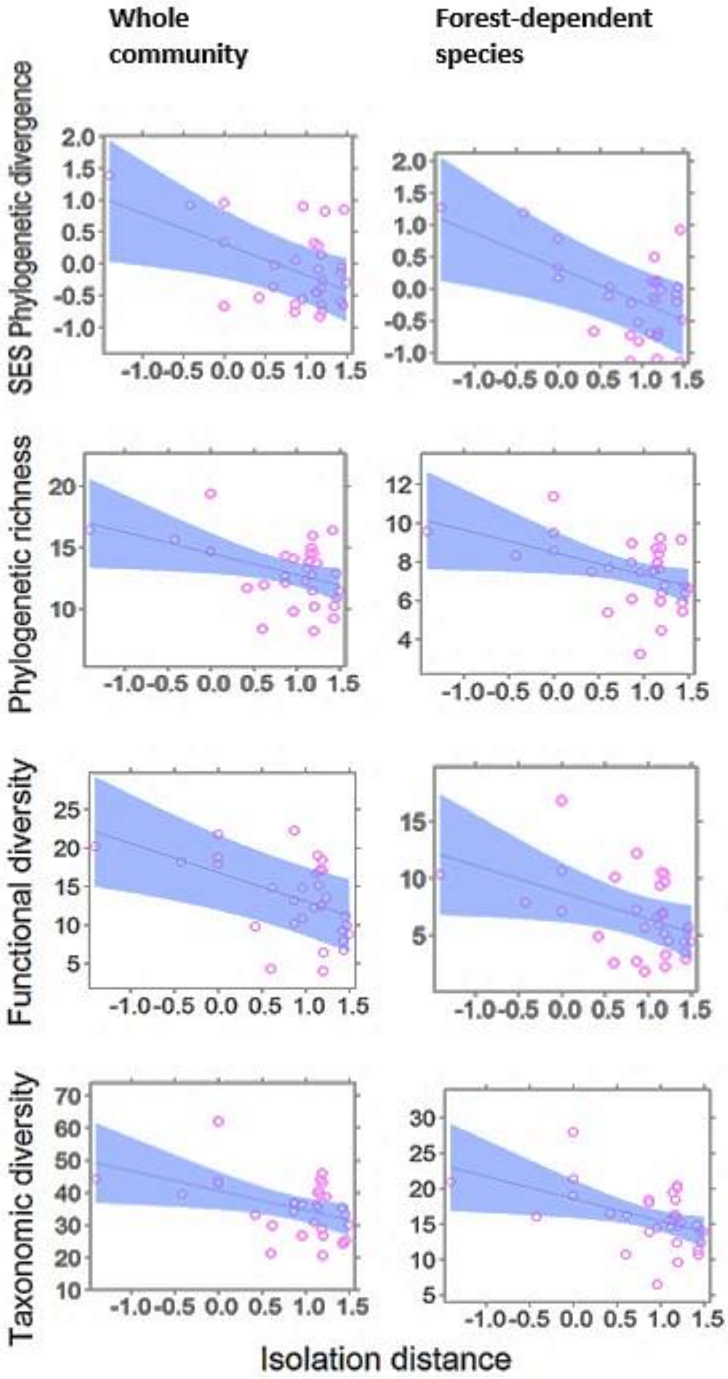

Fig. 3.3 Effect of logarithmized isolation distance on local avian multifaceted diversity indices in forest fragments located in Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

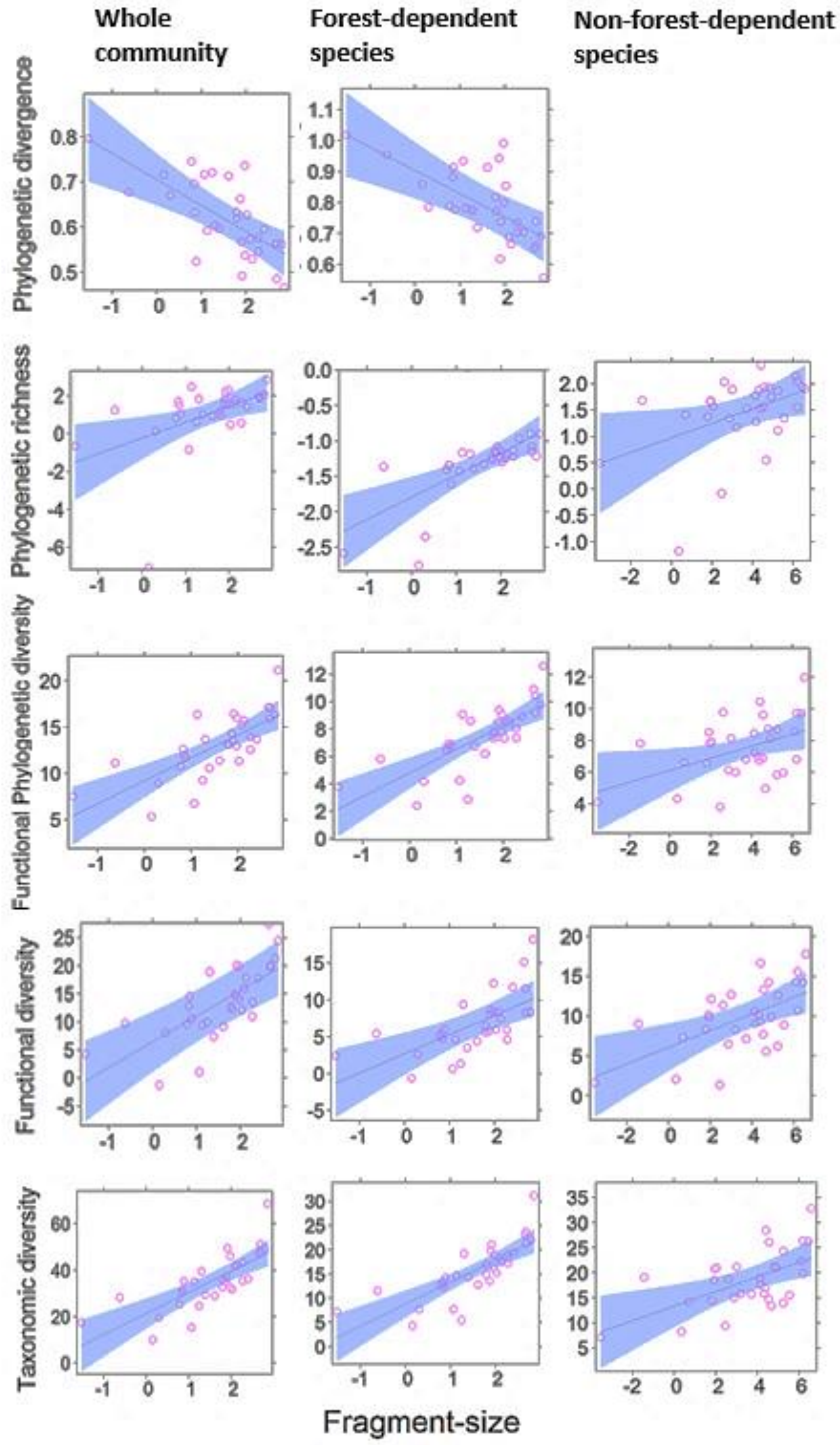

Fig. 3.4 Effect of logarithmized fragment-size on local avian multifaceted diversity indices in forest fragments located in Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

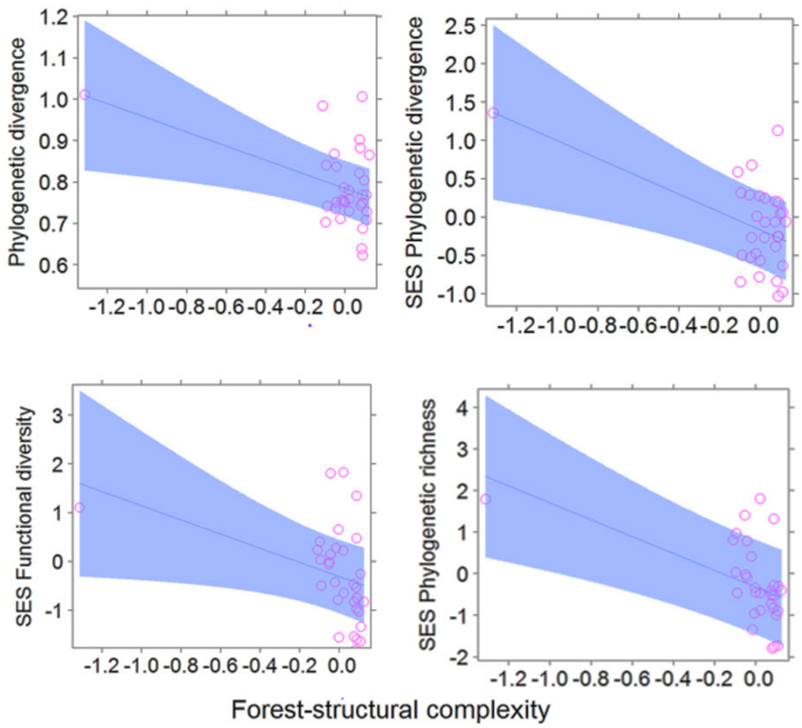

Fig. 3.5 Effect of logarithmized local habitat heterogeneity (Forest-Structural Complexity) on the forest-dependent bird species located in forest fragments located in Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa. SES functional diversity (Standardised Effect Sizes (SES) of functional richness; sesFRic), phylogenetic diversity metrics (include SES phylogenetic richness- SES of Faith's PD; sesPD and phylogenetic divergence- Mean Nearest Taxon Distance; MNTD and sesMNTD)

3.5 Discussion

Our study revealed that matrix quality was a significant positive predictor of functional (FRic and sesFRic) and phylogenetic (sesPD) diversity of forest-dependent (forest specialist) species and functional (FRic) diversity of the overall bird community. These findings support our predictions (H1), including that non-forest-dependent species, show no response to matrix quality in the surrounding landscape. Empirical studies reveal that generalist species show weak or no response to native vegetation structure in the landscape because they frequently move and travel relatively long distances across fragmented landscapes, thus benefitting from increased resource availability in edge habitats and matrices (Fahrig 2003; Pardini et al. 2010; Neuschulz et al. 2013; Carrara et al. 2015; Astudillo et al. 2019). Matrix quality and its effect on species diversity in remnant habitat patches can be explained by several mechanisms. Firstly, matrix composition imposes differential facilitation or hindrance of organismal movement between habitat patches (via landscape connectivity; Ricketts 2001; Watling et al. 2011; Driscoll et al. 2013). For example, matrices exhibiting higher structural contrast than habitat patches are predicted to strongly hinder movement among habitat patches; thereby influencing extinction and re-colonisation rates within habitat patches, hence population persistence especially in small and isolated habitat patches (Pfeifer et al. 2017; Boesing et al. 2018a; b). Secondly, matrix habitat can provide compensatory or supplemental resources (e.g. nesting and/or foraging sites; Ewers and Didham 2006; Fahrig et al. 2011), which also influences cross-habitat spillover between habitat patches and matrices (Estavillo et al. 2013; Montealegre-Talero et al. 2021). Thirdly, matrix composition can influence quality within habitat patches through modulating microclimate and vegetation dynamics in habitat edges (Saunders et al. 1991; Ries et al. 2004). Our findings appear to support the resource complementation in forest fragments inserted in landscapes composed by high quality matrix (Prevedello and Vieira 2010; Prevedello et al. 2016; Ruffell et al. 2017). The amount of native vegetation (e.g. forest, woodlands, etc.) cover in the matrix is an undeniable driver of forest bird diversity because of its direct influence on improving matrix quality (i.e. low contrast and more permeable) and landscape connectivity (Fahrig 2013; Fahrig et al. 2011; Villard and Metzger 2014; Häkkilä et al. 2017; Arroyo-Rodríguez et al. 2020). In addition, exotic timber plantations have also been shown to impact bird diversity in focal patches, but with contrasting (positive and negative) effects, depending on species-specific ecological characteristics (Pardini et al. 2009; Šálek et al. 2010; Biz et al. 2017; Ruffell et al. 2017). In our study system, the most dominant matrix type surrounding habitat patches are commercial exotic timber plantations, covering ~ 41 % of the Mistbelt Forest region (Armstrong et al. 1998). Cooper et al. (2017) reported that some forest-dependent species (e.g. birds of prey and species who inhabit tree plantations to buffer effects of forest loss) are positively influenced by tree plantation cover because of the provision of compensatory resources (e.g. foraging and nesting sites), especially in landscapes with low forest cover (Wethered and Lawes 2003; 2005).

Habitat fragmentation (isolation distance and fragment size) was the significantly negative predominant driver of the multifaceted diversity of avian assemblages in naturally fragmented Mistbelt Forest remnants. As expected, forest-dependent species were negatively affected by habitat fragmentation, a result obtained by numerous studies because of the narrow ecological specificity of this bird assemblage (Ewers and Didham 2006; Banks-Leite et al. 2012; Newbold et al. 2014; Morante-Filho et al. 2015; 2018). The non-forest-dependent species did not respond to isolation distance as expected (H2.2). Due to their broad ecological flexibility (high vagility, tolerance to matrix, high niche width), generalist species are known to respond positively to habitat fragmentation because they maximise benefits obtained from added resources in the anthropogenic matrix (Fahrig 2003; Banks-Leite et al. 2012). Thus, isolation distance may be weakly associated with non-forest dependent species, a trend supported by numerous empirical studies (Neuschulze et al. 2011; 2013; Carrara et al. 2015; Fahrig 2017). However, our findings do not support the hypothesis that species diversity would not suffer the effects of habitat fragmentation because of spillover of forest generalist birds from the surrounding landscape matrix (H2.3). Contrary, these findings support previous studies which reveal negative effects of habitat fragmentation (i.e. increasing isolation distance and decreasing fragment size), which reduces species movement and abundance into small and isolated fragments (Laurance et al. 2011; Haddad et al. 2015; Ehlers Smith et al. 2018a, b Maseko et al. 2019; 2020; Belcik et al. 2020). This is a cause for concern since most Mistbelt Forest fragments are under 10 ha in size and are patchily distributed throughout the indigenous forest landscape (von Maltitz et al. 2003; Mucina and Rutherford 2006). Therefore, although avifaunal assemblages in our system evolved under natural forest fragmentation (Lawes et al. 2007a), anthropogenic habitat fragmentation may pose a continual threat to avian diversity because of losses of specialist species. Habitat fragmentation causes rapid changes in species richness and abundance (taxonomic diversity), with consequent changes in species composition driven by fragment size effects (Luther et al. 2020). In large forest fragments, there is generally high structural complexity which provisions a diversity of ecological niches able to maintain a higher diversity of species, hence larger fragments tend to support more species richness and thus a variety of associated ecological traits (Maseko et al. 2019). Isolation effects negatively influence species movement (i.e., dispersal and colonisation) across remnant forest fragments in fragmented landscapes because of loss of habitat connectivity and increasing forest edge effects (Laurance et al. 2002). Well-connected forest fragments in the landscape support higher taxonomic diversity, facilitating the use of multiple patches and thus reducing the extent of negative effect of habitat fragmentation (Fahrig 2017; Fahrig et al. 2019).

Contrary to expectations, local habitat heterogeneity (forest-structural complexity) was a significant negative predictor of diversity metrics (sesFRic, sesPD, MNTD, sesMNTD) of the forest-dependent bird assemblage only, although this is likely driven by an outlier. These findings partially support our prediction that habitat heterogeneity was particularly important to the forest-dependent species group (H3.1). Although numerous studies reveal positive habitat heterogeneity- species diversity associations (reviewed in Tews et al. 2004; Sitters et al. 2016; Bae et al. 2018; Feng et al. 2020; Melo et al. 2020), negative relationships have also been reported (Kadmon and Allouche 2007; Lundholm 2009; Tamme et al. 2010; Allouche et al. 2012; Laanisto et al., 2013). Our findings can thus be explained by the Microfragmentation concept, a theory proposed as an alternative hypothesis that accounts for negative or neutral heterogeneity-diversity relationships, as suggested by Tamme et al. (2010). Accordingly, the microfragmentation concept posits that an increase in heterogeneity leads to small-scale patchy conditions caused by the isolation of required resources within the community (Tamme et al. 2010; Laanisto et al. 2013). Similar to landscape-scale habitat fragmentation, microfragmentation may increase the likelihood of species loss by reducing the probability for a species to reach suitable microhabitats at the community level. For example, an increase in habitat heterogeneity may cause a reduction in the amount of suitable area available, leading to loss of species diversity as a consequence of the isolation of suitable resources/conditions in local habitat (Laanisto et al. 2013). Specialist species are predicted to be especially vulnerable to micro fragmentation as they require specific conditions, and when critical resources become isolated, there is an expected loss of specialist species in very complex habitats (Tamme et al. 2010; Laanisto et al. 2013). Also, Tews et al. (2004) indicated that the increased heterogeneity may provide additional niches and may benefit some species while causing habitat fragmentation for other species.

The observed decrease in both functional (sesFRic) and phylogenetic diversity (richness- sesPD, divergence- MNTD, sesMNTD) of forest-dependent species with increasing habitat heterogeneity is an interesting and unexpected result obtained in our study. This may suggest that forest-dependent species with similar functional traits (i.e. ecologically redundant) and phylogenetically related lineages (lower lineage diversity) maintain diversity in structurally complex forests. Therefore, the loss of diversity facets with increasing local structural complexity in forest-dependent species may suggest the loss of ecological and evolutionary integrity in habitat patches with high structural complexity. Theoretically, we can infer that assembly processes structuring the community of forest-dependent species in highly complex forests were driven by environmental filtering, which selected functionally similar and phylogenetically clustered species than expected randomly as a mechanism to cope with some environmental conditions (e.g. climatic extinction filtering; Lawes et al. 2007a)

(Holdaway and Sparrow, 2006). Conversely, we suggest that ecologically distinct and phylogenetically distinct (greater lineage diversity) species inhabit forests with lower complexity. In this case, we can assume that the limiting similarity mechanism acts on separating species traits driven by intraspecific competition, which may exclude ecologically similar species and result in a forest-dependent community composed of functionally dissimilar and phylogenetically over-dispersed species than expected randomly (Holdaway and Sparrow, 2006; Calba et al., 2014).

3.5.1 Conclusions

Surrounding matrix quality was a significant positive predictor of forest-dependent (forest specialist) species (functional and phylogenetic diversity) and the whole community (functional diversity). These findings seem to support the resource complementation of high-quality matrix surrounding focal habitat fragments (Prevedello and Vieira 2010; Prevedello et al. 2016; Ruffell et al. 2017). Therefore, improving the matrix quality may help contribute to the conservation of ecological and evolutionary integrity of local forest-dependent species and whole community assemblages in the fragmented Mistbelt Forest system. Avian multifaceted diversity was negatively influenced by habitat fragmentation effects (i.e. declining with increasing isolation distance and increasing with fragment size). This highlighted the importance of large and connected forest fragments in conserving/ maintaining diversity facets of local avian assemblages in our system. Unexpectedly, the study shows that diversity facets of forest-dependent species assemblage decline with local vegetation complexity (habitat heterogeneity). Thus, these findings (although likely driven by an outlier) alternatively provide support for the Microfragmentation concept, which explains the negative relationship caused by small-scale patchiness isolating required resources/conditions with increasing local habitat heterogeneity (Tamme et al. 2010; Laanisto et al. 2013). These results demonstrate that promoting local structural complexity may contribute to the loss of forest-dependent species in the naturally fragmented Mistbelt Forests, where remnant faunal assemblages have adapted to climatic extinction events (Lawes et al. 2007a). However, we recommend that caution be enforced regarding this claim since our results were not very robust and further research may be required to support this finding.

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3.7 Declarations

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Conflict of interest

The authors declare they have no conflict of interest.

Ethics approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate

Not applicable.

Consent for publication

All authors gave consent.

Data availability

The data belong to the University of KwaZulu-Natal and are stored there. They are available from the corresponding author upon reasonable request.

Author contributions

SPN, CTD, DES and YES conceptualised the study. CTD sought funding. SPN, STG and MS collected the data. SPN analysed the data with assistance from DES. SPN wrote the draft manuscript. The other authors provided editorial input.

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3.9 Supplementary information

Appendix S3.1 Bird species recorded in selected Southern Mistbelt Forest patches of southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa

Coding	Scientific name	Common name	Habitat specialisation
SKBird1	*Accipiter melanoleucus*	Black Sparrowhawk	NFD
SKBird2	*Accipiter rufiventris*	Rufous-breasted Sparrowhawk	FD
SKBird3	*Accipiter tachiro*	African Goshawk	FD
SKBird4	*Amblyospiza albifrons*	Thick-billed Weaver	NFD
SKBird5	*Andropadus importunus*	Sombre Greenbul	NFD
SKBird6	*Apalis flavida*	Yellow-breasted Apalis	NFD
SKBird7	*Apalis thoracica*	Bar-throated Apalis	FD
SKBird8	*Apaloderma narina*	Narina Trogon	FD
SKBird9	*Columba larvata*	Lemon Dove	FD
SKBird10	*Batis capensis*	Cape Batis	FD
SKBird11	*Bostrychia hagedash*	Hadeda Ibis	NFD
SKBird12	*Bucorvus leadbeateri*	Southern Ground Hornbill	NFD
SKBird13	*Buteo trizonatus*	Forest Buzzard	FD
SKBird14	*Bycanistes bucanitor*	Trumpeter Hornbill	FD°
SKBird15	*Camaroptera brachyura*	Green-backed Camaroptera	FD
SKBird16	*Campephaga flava*	Black Cuckooshrike	NFD
SKBird17	*Cercotrichas leucophrys*	White-browed Scrub Robin	NFD
SKBird18	*Cercotrichas signata*	Brown Scrub Robin	NFD
SKBird19	*Chalcomitra amethystina*	Amethyst Sunbird	NFD
SKBird20	*Chlorophoneus olivaceus*	Olive Bushshrike	NFD
SKBird21	*Chrysococcyx caprius*	Diederik Cuckoo	NFD
SKBird22	*Chrysococcyx cupreus*	African Emerald Cuckoo	FD
SKBird23	*Chrysococcyx klaas*	Klaas's Cuckoo	NFD
SKBird24	*Cinnyris chalybeus*	Southern Double-collared Sunbird	NFD
SKBird25	*Cinnyris talatala*	White-bellied Sunbird	NFD
SKBird26	*Coccopygia melanotis*	Swee Waxbill	NFD
SKBird27	*Colius striatus*	Speckled Mousebird	NFD
SKBird28	*Columba arquatrix*	African Olive Pigeon	FD*
SKBird29	*Columba guinea*	Speckled Pigeon	NFD
SKBird30	*Coracina caesia*	Grey Cuckooshrike	FD
SKBird31	*Corvus albus*	Pied Crow	NFD
SKBird32	*Corvus capensis*	Cape Crow	NFD
SKBird33	*Cossypha caffra*	Cape Robin-chat	NFD
SKBird34	*Cossypha dichroa*	Chorister Robin-chat	FD
SKBird35	*Cossypha natalensis*	Red-capped Robin-chat	FD*
SKBird36	*Crithagra scotops*	Forest Canary	FD
SKBird37	*Cuculus clamosus*	Black Cuckoo	NFD
SKBird38	*Cuculus solitarius*	Red Chested Cuckoo	FD*
SKBird39	*Cyanomitra olivacea*	Olive Sunbird	FD
SKBird40	*Cyanomitra veroxii*	Grey Sunbird	NFD
SKBird41	*Dendropicus fuscescens*	Cardinal Woodpecker	NFD
SKBird42	*Dendropicus griseocephalus*	Olive Woodpecker	FD°

SKBird43	*Dicrurus adsimilis*	Fork-tailed Drongo	NFD
SKBird44	*Dryoscopus cubla*	Black-backed Puffback	NFD
SKBird45	*Euplectes orix*	Southern Red Bishop	NFD
SKBird46	*Francolinus afer*	Red-necked Spurfowl	NFD
SKBird47	*Hedydipna collaris*	Collared Sunbird	FD
SKBird48	*Indicator variegatus*	Scaly-throated Honeyguide	FD
SKBird49	*Lagonosticta rubricata*	African Firefinch	NFD
SKBird50	*Laniarius ferrugineus*	Southern Boubou	NFD
SKBird51	*Lanius collaris*	Common Fiscal	NFD
SKBird52	*Lophaetus occipitalis*	Long-crested Eagle	NFD
SKBird53	*Lybius torquatus*	Black-collared Barbet	NFD
SKBird54	*Malaconotus blanchoti*	Grey-headed Bushshrike	NFD
SKBird55	*Mandingoa nitidula*	Green Twinspot	FD
SKBird56	*Muscicapa adusta*	African Dusky flycatcher	NFD
SKBird57	*Muscicapa caerulescens*	Ashy Flycatcher	FD*
SKBird58	*Notopholia corruscus*	Black-bellied Starling	NFD
SKBird59	*Onychognathus morio*	Red-winged Starling	NFD
SKBird60	*Oriolus larvatus*	Black-headed Oriole	NFD
SKBird61	*Parus niger*	Southern Black Tit	NFD
SKBird62	*Phoeniculus purpureus*	Green Wood-hoopoe	NFD
SKBird63	*Phyllastrephus terrestris*	Terrestrial Brownbul	FD*
SKBird64	*Phylloscopus ruficapilla*	Yellow-throated Woodland Warbler	FD
SKBird65	*Ploceus bicolor*	Dark-backed Weaver	FD
SKBird66	*Pogoniulus bilineatus*	Yellow-rumped Tinkerbird	FD
SKBird67	*Pogoniulus pusillus*	Red-fronted Tinkerbird	NFD
SKBird68	*Pogonocichla stellata*	White-starred Robin	FD
SKBird69	*Poicephalus robustus*	Cape Parrot	FD
SKBird70	*Prinia hypoxantha*	Drakensberg Prinia	NFD
SKBird71	*Prinia subflava*	Tawny-flanked Prinia	NFD
SKBird72	*Pternistis natalensis*	Natal Spurfowl	NFD
SKBird73	*Pycnonotus tricolor*	Dark-capped Bulbul	NFD
SKBird74	*Stephanoaetus coronatus*	Crowned Eagle	FD
SKBird75	*Streptopelia capicola*	Cape Turtle Dove	NFD
SKBird76	*Streptopelia semitorquata*	Red-eyed Dove	NFD
SKBird78	*Sylvia nigricapillus*	Bush Blackcap	FD°
SKBird79	*Tauraco corythaix*	Knysna Turaco	FD
SKBird80	*Tauraco porphyreolophus*	Purple-crested Turaco	FD*
SKBird81	*Telophorus sulfureopectus*	Orange-breasted Bushshrike	FD*
SKBird82	*Telophorus zeylonus*	Bokmakierie	NFD
SKBird83	*Terpsiphone viridis*	African Paradise Flycatcher	NFD
SKBird84	*Tockus alboterminatus*	Crowned Hornbill	FD
SKBird85	*Trachyphonus vaillantii*	Crested Barbet	NFD
SKBird86	*Trochocercus cyanomelas*	Blue-mantled Crested Flycatcher	FD°
SKBird87	*Turdus olivaceus*	Olive Thrush	NFD
SKBird88	*Turtur tympanistria*	Tambourine Dove	FD
SKBird89	*Zoothera gurneyi*	Orange Ground Thrush	FD
SKBird90	*Zosterops virens*	Cape White-eye	NFD

Habitat specialisation categories: FD (forest dependent species) and NFD (non-forest dependent species). **FD** species list obtained from Oatley (1989), *° indicates supplementation of forest dependent species list by Oatley (1989) with * Brown (2006) and ° Symes et al. (2002), respectively.

Appendix S3.2 Akaike Information Criterion (AIC) values obtained from the various spatial scales tested for each diversity facet analyzed

Metric	**buff200m**	**buff400m**	**buff600m**	**buff680m**	**buff800m**	**buff1000m**	**buff1200m**
SR	318.31	317.85	317.74	300.74	317.61	317.37	316.91
Fric	210.6	210.65	210.6	209.06	210.61	210.65	210.75
PD	178.57	178.59	178.59	176.18	178.59	178.57	178.53
MNTD	64.06	63.44	63.429	66.32	63.403	63.391	63.384
FPD	441.81	441.81	441.82	440.94	441.82	441.82	441.81
MFPD	77.131	76.812	76.688	77.061	76.672	76.74	77.132
sesFric	95.454	95.691	95.585	95.453	95.505	95.464	95.589
sesPD	108.16	108.4	108.39	107.8	108.35	108.38	95.453
sesMNTD	68.241	69.723	69.652	71.636	69.81	69.749	69.766
sesMFPD	93.561	94.245	94.538	94.776	94.627	94.508	94.009

Metric = diversity facets analysed (response variables); Buff = buffer size (spatial scale); the lowest AIC values are highlighted in yellow; species richness (SR); functional richness (FRic); Faith's phylogenetic diversity (PD); Mean Nearest Taxon Distance (MNTD); Functional-phylogenetic diversity (FPD); Mean Functional-phylogenetic Distance (MFPD); ses = Standardized Effect Sizes

Appendix S3.3 Correlation of other spatial scales to the selected scale used in the current study from the matrix quality landscape scale metric

	buff200m	**buff400m**	**buff600m**	**buff680m**	**buff800m**	**buff1000m**	**buff1200m**
buff200m	*	0.864504	0.836034	0.6320395	0.817081	0.8011254	0.7919649
buff400m	0.864504	*	0.993067	0.7796995	0.984806	0.9758267	0.9660354
buff600m	0.836034	0.993067	*	0.7768147	0.997254	0.9917804	0.9802897
buff680m	0.632039	0.779699	0.776815	*	0.783438	0.7814747	0.7648343
buff800m	0.817081	0.984806	0.997254	0.7834376	*	0.9978102	0.9864966
buff1000m	0.801125	0.975827	0.99178	0.7814747	0.99781	*	0.9921828
buff1200m	0.791965	0.966035	0.98029	0.7648343	0.986497	0.9921828	*

Buff = buffer size (spatial scale); correlation threshold (≥ 0.70) highlighted in yellow revealing the high correlation of other spatial scales to the 680 m buffer radius chosen for the study

Appendix S3.4 Forest Characteristics of surveyed Southern Mistbelt Forest patches in southern KwaZulu-Natal and northern Eastern Cape Provinces, South Africa

Patch	**Latitude (S)**	**Longitude (E)**	**Region**	**Area (ha)**	**Isolation (m)**	**Matrix quality**	**Forest-structural complexity (FSC)**	**Species richness (n)**
X0	31°29'27.28"	28°24'32.76"	Mthatha	94.9	29266.24	432.9065	1.225344	30
X1	31°29'25.36"	28°23'51.27"	Mthatha	64.42	30941.92	402.495	0.048698	31
X2	31°29'16.78"	28°27'16.98"	Mthatha	13.76	26233.9	440.5315	1.292781	33
X3	31°29'11.65"	28°26'22.14"	Mthatha	41.54	27083.69	423.4686	1.192893	27
X4	31°28'27.51"	28°25'30.01"	Mthatha	124.38	28316.9	419.1864	1.288996	37
X5	31°28'17.91"	28°25'40.19"	Mthatha	107.65	26711.94	418.8423	1.337502	27
X6	31°25'38.67"	28°46'38.85"	Mthatha	634.66	0	412.0599	1.229115	55
X7	31°25'14.16"	28°32'52.44"	Mthatha	190.26	15872.81	420.5218	1.288908	33
X8	31°25'25.37"	28°31'34.67"	Mthatha	496.53	17174.25	432.5686	1.260993	48
X9	31°23'17.76"	28°41'58.04"	Mthatha	62.87	39.61965	360.09	1.187118	47
X10	30°33'40.52"	29°41'17.70"	Ngeli	25	2660.777	404.1035	1.233875	34
X11	30°32'10.16"	29°45'46.49"	Ngeli	11.97	3969.47	403.4738	1.196259	19
X12	30°31'52.17"	29°40'59.87"	Ngeli	732.42	0	451.3843	1.224544	74
X13	30°28'30.71"	29°38'50.58"	Ngeli	256.78	4141.849	439.2145	1.231512	39
X14	30°27'9.28"	29°38'19.39"	Ngeli	79.84	7261.737	425.6326	1.233298	39
X15	30°27'39.48"	29°36'49.57"	Ngeli	192.63	7394.097	417.8546	1.206599	44
X16	30°2'51.99"	29°30'17.57"	Creighton	139.9	9120.238	345.8567	0.954761	37
X17	30°2'42.15"	29°31'8.73"	Creighton	17.81	9170.021	385.2406	0.991781	20
X18	30°1'9.48"	29°39'39.77"	Creighton	75.52	381.6471	331.4595	0.777795	36
X19	30°1'29.62"	29°38'2.40"	Creighton	494.36	0	367.1179	0.910248	50
X20	29°59'7.44"	29°43'59.38"	Creighton	464.34	7439.02	425.1441	1.052419	48
X21	29°56'35.05"	29°45'49.48"	Creighton	7.16	13249.05	398.5087	0.886014	32
X22	29°56'19.52"	29°45'13.39"	Creighton	6.12	12557	379.0845	0.89937	26
X23	29°56'3.04"	29°46'2.45"	Creighton	6.89	14012.71	403.5192	0.808424	31
X24	29°55'30.95"	29°45'16.28"	Creighton	20.49	13791.63	302.7727	0.967599	38
X25	29°54'35.85"	29°45'31.68"	Creighton	42.6	42.63	407.5584	1.055337	14
X26	29°54'41.90"	29°45'36.30"	Creighton	83.1	14768.5	349.3605	1.060084	48
X27	29°54'29.93"	29°45'5.76"	Creighton	21.2	29.06	268.0578	0.816736	28
X28	29°58'56.25"	29°48'29.96"	Creighton	2.04	15289.58	397.9112	0.802192	20
X29	29°58'50.47"	29°48'31.82"	Creighton	1.45	15699.72	376.768	0	10
X30	29°58'46.65"	29°48'24.16"	Creighton	0.24	15430.78	398.8502	0.995364	29
X31	29°57'30.35"	29°47'15.83"	Creighton	97.38	14240.85	435.3281	0.910248	46

Isolation distance: mainland patches (i.e., largest patch within each survey region) are delimited by zero

Appendix S3.5 Results of correlation tests between avian species richness and other diversity metrics in the present study

Diversity metrics	**Correlation coefficient**	***p*-value**
TD – Functional richness (FRic)	0.87	0.02
TD – Phylogenetic richness (Faith's PD)	0.71	0.03
TD – Phylogenetic divergence (MNTD)	-0.78	0.02
TD – Functional-phylogenetic diversity (FPD)	0.72	0.04

TD- taxonomic diversity metric (species richness); functional diversity metric (FRic); Phylogenetic diversity metric (Faith's PD and Mean Nearest Taxon Distance- MNTD); Functional-phylogenetic diversity (FPD)

Appendix S3.6 Functional traits chosen for bird species recorded in selected Southern Mistbelt Forest patches of southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa

Trait type	**Data type**	**Variables**	**Functional significance**	**Trait references**
Morphology	Continuous	Mass (g), Clutch size (mean), Wing length (mm), Tarsus length (mm), Culmen (mm), Tail length (mm)	Traits related to reproductive capacity, metabolic rate, foraging behaviour, home range sizes, vulnerability to disturbances	Hockey et al. 2005
Diet	Categorical	Carnivory, Folivory, Frugivory, Granivory, Insectivory, Nectarivory, Scavenging, Omnivory	Traits related to food types consumed, which can be linked to ecosystem functioning (e.g., insect pest control, seed dispersal, pollination, etc.)	Hockey et al. 2006
Foraging stratum	Categorical	Ground, Understorey, Aerial, Mid-High, Canopy, Mixed	Traits related to niche variation in the vertical structure	Wilman et al. 2014
Locomotion	Categorical	Altitudinal-migrant, Breeding-migrant, Nomadic, Partial-migrant, Sedentary	Traits related to movement capacity	Hockey et al. 2006
Habitat specialisation	Categorical	forest-dependent (FD) species and non-forest dependent (NFD) species	Traits related to habitat and resource use affinity	Oatley 1989; Symes et al. 2002; Brown 2006

Appendix S3.7 Additional results for the mean functional–phylogenetic pairwise distance (MFPD) metric (including Table S3.7.1 and Fig. S3.7.1 below)

Table S3.7.1 Phylogenetic signal calculated from Bloomberg's K-statistic (with associated p-value) of various avian functional traits measured in our study

Ecological trait	**K-statistic**	**p-value**
Body mass	0.717	**0.005**
Clutch size	0.015	0.688
Wing length	1.190	**0.001**
Tarsus length	0.031	0.510
Culmen	1.472	**0.001**
Tail length	0.532	**0.001**
Altitudinal migrant	0.483	**0.003**
Breeding migrant	0.920	**0.001**
Nomadic	0.173	0.738
Partial migrant	0.004	0.919
Sedentary	0.019	0.366
Carnivory	0.717	**0.001**
Folivory	0.256	0.270
Frugivory	0.064	0.143
Granivory	0.189	0.087
Insectivory	0.215	**0.001**
Nectarivory	0.822	**0.001**
Scavenging	0.510	0.142
Ground	0.126	**0.035**
Understorey	0.029	0.298
Aerial	0.308	0.396
Mid High	0.060	0.067
Canopy	0.033	0.298

Significant p-values are highlighted in **bold**

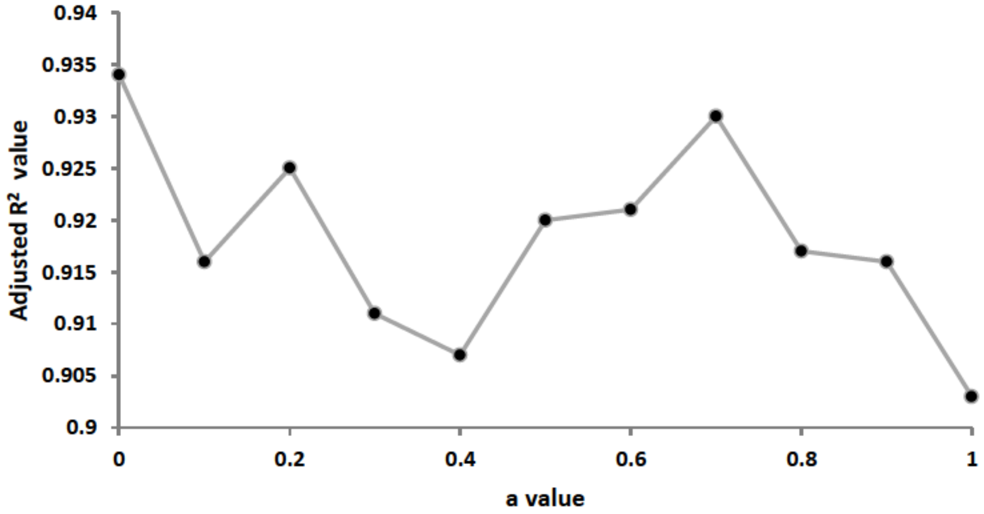

Fig. S3.7.1 Adjusted R^2 values of the regressions of standardised effect size (SES) of mean functional-phylogenetic pairwise distances (SES.MFPD) for best **a** value in the present study

Appendix S3.8 Results of multicollinearity tests obtained between environmental covariates in the present study

Environmental covariates	**Correlation coefficient**	***p*-value**
Log.Area - Log.Isolation	- 0.42	**0.02**
Log.Area - Log.FSC	0.07	0.71
Log.Area - Log.MatrixQ	0.21	0.28
Log.Isolation - Log.FSC	- 0.13	0.47
Log.Isolation - Log. MatrixQ	0.01	0.96

Log.Area (fragment-size); Log.Isolation (isolation distance from mainland patch); Log.FSC (forest-structural complexity); Log.MatrixQ (matrix quality of surrounding land use in the landscape); Log = log 10 transformation. Correlation threshold set at ≥ 0.7 (Dormann et al. 2013). Significant p-value highlighted in **bold**

Appendix S3.9 Spatial autocorrelation (Global Moran's I) test for avian multifaceted diversity metrics (significant p value depicts spatial autocorrelation between forest patches) Phylogenetic diversity metrics (Faith’s PD and Mean Nearest Taxon Distance- MNTD)

Moran I	**Observed**	**Expected**	**Z value**	***p*-value**
Species richness (TD)	0.128785	-0.034483	1.391450	0.164089
Functional richness (FD)	0.107489	-0.032258	0.725260	0.468293
Phylogenetic richness (Faith’s PD)	0.166864	-0.100841	0.644262	0.586649
Phylogenetic divergence (MNTD)	-0.230667	-0.125000	-0.299527	0.764538
Functional-phylogenetic diversity (FPD)	0.033851	-0.032258	0.718540	0.472424

Appendix S3.10 Response of multiple facets of avian diversity to natural forest fragmentation (isolation and fragment-size effect), forest-structural complexity and surrounding matrix quality in Southern Mistbelt Forests of KwaZulu-Natal and Eastern Cape, South Africa

Diversity Metric	Assemblage group	Log.Matrix Quality	Log.Isolation Distance (km)	Log.Fragment-size (ha)	Log.Forest-Structural Complexity
Taxonomic Diversity (species richness)	Whole Community	11.743 (7.928)	**-6.066 (2.494)***	**9.052 (1.620)*****	0.0424 (6.141)
	Forest-dependent	7.872 (4.783)	**-2.863 (1.332)***	**4.358 (0.768)*****	0.711 (3.028)
	Non-Forest-dependent	-27.555 (20.669)	-0.978 (0.589)	**1.131 (0.412)***	0.447 (1.466)
Functional Diversity (functional richness- FRic)	Whole Community	14.241 (4.021)	**-3.765 (1.211)****	**4.558 (0.845)*****	-4.453 (2.921)
	Forest-dependent	8.787 (4.018)	**-2.354 (1.076)***	**2.608 (0.649)****	-2.142 (2.351)
	Non-Forest-dependent	-22.639 (15.486)	-0.893 (0.442)	**1.042 (0.318)****	0.021 (1.095)
SES Functional Diversity (SES.FRic)	Whole Community	0.706 (0.991)	-0.034 (0.304)	-0.0539 (0.207)	-0.604 (0.741)
	Forest-dependent	**2.986 (1.175)***	-0.400 (0.308)	-0.040 (0.187)	**-1.451 (0.656)***
	Non-Forest-dependent	-3.723 (3.785)	0.0426 (0.104)	-0.029 (0.074)	-0.064 (0.515)

Phylogenetic richness (PD)	Whole Community	1.755 (1.012)	**-0.752 (0.322)***	**1.075 (0.204)*****	-0.259 (0.795)
	Forest-dependent	1.148 (1.778)	**-1.195 (0.557)***	**1.191 (0.365)****	0.165 (1.370)
	Non-Forest-dependent	-11.119 (8.11)	**-0.478 (0.231)***	**0.381 (0.162)***	0.018 (0.575)
SES Phylogenetic richness (SES.PD)	Whole Community	0.168 (0.489)	-0.25 (0.156)	-0.087 (0.097)	-0.730 (0.387)
	Forest-dependent	**2.480 (1.095)***	**-0.721 (0.282)***	0.165 (0.172)	**-2.026(0.591)****
	Non-Forest-dependent	-2.610 (5.066)		-0.159 (0.101)	-0.345 (0.359)
Phylogenetic divergence (MNTD)	Whole Community	-0.034 (0.0273)	-0.256 (0.144)	**-0.025 (0.006)****	-0.036 (0.021)
	Forest-dependent	0.060 (0.112)	-0.001 (0.008)	**-0.075 (0.018)*****	**-0.171 (0.063)***
	Non-Forest-dependent	-0.012 (0.337)	-0.011 (0.029)	-0.014 (0.007)	-0.029 (0.024)
SES Phylogenetic divergence (SES.MNTD)	Whole Community	-0.190 (0.261)	-0.006 (0.010)	-0.026 (0.055)	-0.336 (0.193)
	Forest-dependent	1.087 (0.694)	**-0.210 (0.080)***	0.012 (0.110)	**-1.165(0.383)****
	Non-Forest-dependent	-1.089 (3.591)	**-0.542 (0.181)****	-0.013 (0.0716)	-0.278 (0.255)
			-0.183 (0.102)		
Functional-Phylogenetic Diversity (FPD)	Whole Community	0.718 (0.620)	-0.372 (0.192)	**0.492 (0.128)*****	-0.198 (0.470)
	Forest-dependent	-0.207 (0.648)	-0.161 (0.205)	**0.361 (0.132)***	-0.083 (0.506)
	Non-Forest-dependent	-3.115 (2.998)	-0.076 (0.085)	**0.137 (0.061)***	-0.077 (0.212)

Mean Functional–Phylogenetic Pairwise Distance (MFPD)	Whole Community	0.003 (0.029)	-0.012 (0.009)	-0.001 (0.006)	-0.015 (0.023)
	Forest-dependent	0.013 (0.110)	-0.001 (0.0345)	0.023 (0.023)	0.007 (0.085)
	Non-Forest-dependent	0.399 (0.511)	-0.001 (0.015)	0.012 (0.010)	0.008 (0.036)
SES Mean Functional–Phylogenetic Pairwise Distance (SES.MFPD)	Whole Community	-0.279 (0.410)	-0.137 (0.131)	-0.119 (0.082)	-0.219 (0.324)
	Forest-dependent	0.109 (0.881)	0.091 (0.278)	0.293 (0.180)	-0.018 (0.685)
	Non-Forest-dependent	6.791 (3.952)	0.037 (0.113)	**0.171 (0.079)***	0.062 (0.280)

Landscape composition metric (log matrix quality); habitat fragmentation effect (log isolation distance and log fragment-size); local habitat heterogeneity (log Forest-structural complexity). LME estimates of slopes with standard errors (in brackets). Statistically significant effects are **emboldened**, with level of statistical significance indicating, ***P<0.001, **P<0.01, *P<0.05, ‘P<0.10. Standardized Effect Sizes (SES); Mean Nearest Taxon Distance (MNTD); Faith’s Phylogenetic richness (PD).

Appendix S3.11 Linear mixed-effects model (LME) summary of model selection based on the lowest AIC values for the responses of multiple facets of avian diversity (as separate covariates) to natural forest fragmentation (isolation and fragment-size effect), forest-structural complexity and surrounding matrix quality

Diversity metric	**Whole community**	**Forest-dependent species**	**Non-forest-dependent species**
SR	214.4374	173.0879	189.1941
Fric	177.5057	163.2397	169.2995
sesFric	101.3692	95.63312	89.9819
PD	155.4498	133.5623	133.8959
sesPD	116.477	91.92894	108.4723
MNTD	40.8472	31.17777	37.90414
sesMNTD	80.99878	67.01049	89.89381
FPD	127.9376	108.2893	80.40677
MFPD	36.27755	58.48534	16.76698
sesMFPD	106.9064	95.91982	93.73259

SR- taxonomic diversity metric (species richness); functional diversity metric (functional richness- FRic); Phylogenetic diversity metric (Faith’s PD and Mean Nearest Taxon Distance- MNTD); Functional-phylogenetic diversity metric (FPD and Mean Functional-phylogenetic Pairwise Distance- MFPD) and their Standardized Effect Sizes (ses). Avian Ecological groups separated as whole community; forest-dependent species (i.e. forest specialists) and non-forest-dependent species (i.e. forest generalists)

CHAPTER 4

Landscape drivers of bird taxonomic and functional diversity in selected South African Southern Mistbelt forests

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Running header: Landscape drivers of bird taxonomic and functional diversity

4.1 Abstract

Aim: Human landscape modifications are a predominant cause of global biodiversity declines. However, not all such modifications imply a decline in local biodiversity. Naturally, fragmented forest systems harbour resilient species, but these are presently experiencing increased anthropogenic pressures. This introduces novel challenges for diversity in remnant forests embedded within anthropogenic landscapes. Here, we investigated how key landscape features affected local bird diversity within naturally fragmented forests. We investigated the effects of habitat amount, compositional landscape heterogeneity and average isolation distance at the landscape level, particularly on forest bird species richness- (SR), functional richness (FRic) of avian community and forest-dependent (i.e. forest specialist) assemblages in 32 focal Mistbelt forest fragments.

Location: 32 Southern Mistbelt forest patches in KwaZulu-Natal and Eastern Cape Provinces, South Africa.

Taxon: Birds.

Methods: We extracted landscape metrics (habitat amount, average isolation distance and compositional landscape heterogeneity) surrounding 32 Mistbelt forest fragments (range 0.03 – 732.42 ha), on forest bird species richness and functional richness of the whole community and forest specialist assemblages. Using Linear mixed-effect models (lme), we revealed the importance of each landscape variable for each avian diversity index.

Results: Habitat amount in the landscape was the main significant positive predictor of local forest bird diversity for both the community and specialist assemblages in Mistbelt forest fragments. There was no significant influence of the average isolation distance and landscape heterogeneity on local avian diversity. Based on model Akaike’s weight, habitat amount was the most important landscape predictor, followed by landscape heterogeneity, then average isolation distance.

Main conclusions: Habitat amount in the surrounding landscape was the most important predictor of local avian diversity in the naturally fragmented Southern Mistbelt forest fragments. Thus, we recommend the preservation and increase of forest cover to promote biodiversity persistence in other naturally fragmented ecosystems.

KEYWORDS: Biodiversity resilience, forest fragmentation, guild diversity, Habitat Amount Hypothesis, Island Biogeography Theory, landscape effects

4.2 Introduction

Anthropogenic landscape modification is recognised as one of the primary threats to biodiversity declines at local, regional and global scales (Foley et al., 2005; Newbold et al., 2015). Consequently, this has led to reductions in forest extent and the fragmentation of formerly large tracts of natural forests into smaller fragments surrounded by predominantly agricultural and urban land-use types (Haddad et al., 2015). The general effects of forest loss and/or fragmentation on biodiversity is a topic of ongoing contention (Miller-Rushing et al., 2019), particularly of the validity of fragmentation per se (i.e. breaking apart of habitat independent from habitat loss) as a cause for biodiversity declines (see Fahrig, 2013, 2017; Fahrig et al. 2019). These studies conclude that the effects of fragmentation per se are generally weak or positive (but these findings have been questioned – see Haddad et al., 2017; Fletcher Jr. et al., 2018). However, since habitat loss and fragmentation are processes that are linked and interdependent in real landscapes, some have argued that distinguishing between these processes may be conceptually flawed (Ruffell, Banks-Leite, & Didham, 2016; Fletcher Jr. et al., 2018) and dismissing the significance of fragmentation per se as a negative driver of species loss is considered premature and unsafe (Püttker et al., 2020).

Two contrasting theories have been proposed as predictors of biodiversity in habitat patches of fragmented landscapes, namely the island biogeography theory and the habitat amount hypothesis. In fragmented landscapes, patterns of local habitat colonisation have been directly attributed to habitat area and isolation alone, following the traditional island biogeography theory (MacArthur & Wilson, 1967; Cook, Lane, Foster, & Holt, 2002). This is based on the oceanic island view of habitat and matrix (i.e. hostile/unsuitable habitat surrounding focal habitat patches) and has largely been adopted in predicting biodiversity patterns in terrestrial systems. However, the matrix habitat is characterised as the area within-which focal habitat is embedded and is able to facilitate/impede species movement and dispersal patterns (Gascon et al., 1999; Lindenmayer & Franklin, 2002). Thus, in terrestrial systems, the matrix habitat is composed of structurally complex landscapes (unlike a homogenous oceanic matrix). Therefore, leading most to conclude that studies based on the island biogeography theory may not represent realistic (i.e. real-world) biodiversity patterns (Brodie, Mohd-Azlan, & Schnell, 2016). Such studies reveal that the surrounding matrix, particularly in heterogeneous landscapes, is fundamental in determining species occurrences in habitat patches because of their varying effects on connectivity and permeability to species dispersal among patches (Prugh, Hodges, Sinclair, & Brashares, 2008; Fahrig et al., 2011; Thompson, Rayfield, & Gonzalez, 2017). Thus, the habitat amount hypothesis has been put forward as an alternative to the island biogeography theory, which challenges the patch concept of habitat fragmentation as the predictor of species richness at the landscape level (c.f. Fahrig, 2013).

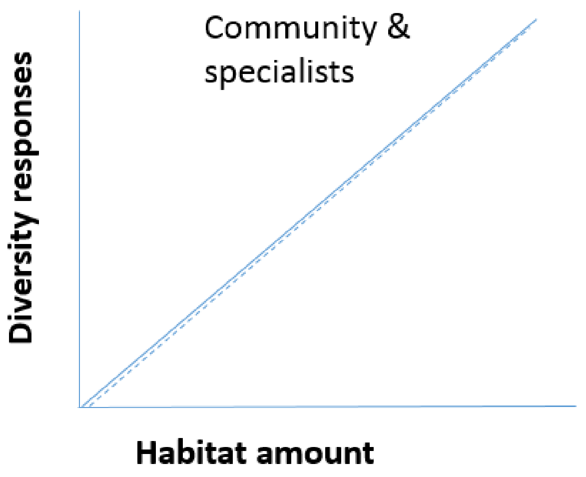
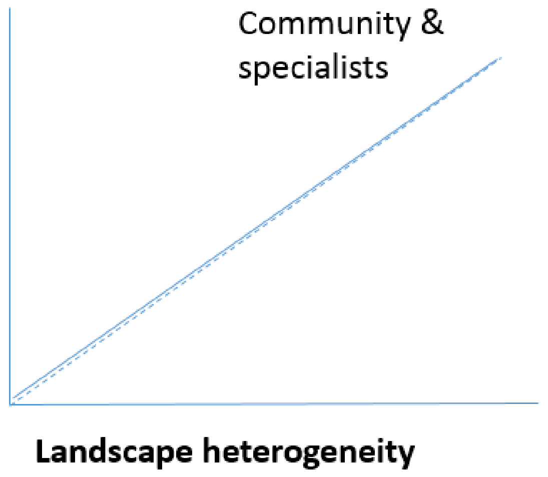
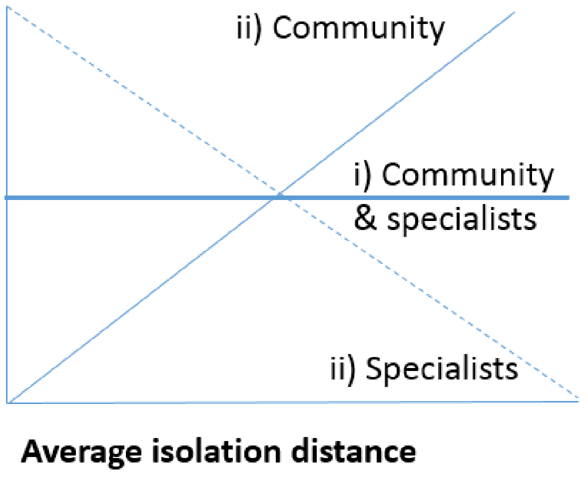
The habitat amount hypothesis posits that the surrounding habitat amount in the landscape is the better predictor of local species richness and that species persistence in small-isolated habitat patches is compensated by the larger available habitat amount in the landscape, thus making effects of habitat size and isolation negligible as both become the function of habitat amount at the landscape scale (Fahrig, 2013). However, there are major contentions in the literature regarding the habitat amount hypothesis, with some studies supporting (Martin,

2018) or disproving it (Haddad et al., 2017; Hanski, 2015; Vieira, Almeida-Gomes, Delciellos, Cerqueira, & Crouzeilles, 2018; Saura, 2021). Disparities in the proposed ways of testing and interpreting the habitat amount hypothesis; use of poor predictors of patch-isolation metrics; and the selection of landscape-scale effects that are biased toward the support of the habitat amount hypothesis (Vieira et al., 2018; Bueno & Peres, 2019; Saura, 2021). These are some of the criticisms cited against favouring the habitat amount hypothesis over the island biogeography theory.

Present research recognises the need to move beyond the traditional taxonomic perspective (i.e. species richness and/or species abundances- taxonomic diversity- TD), and incorporate trait-based diversity measures (i.e. functional diversity- FD) in determining species responses to environmental changes (Gagic et al., 2015). The shift from exclusively using TD may be because of its inability to relate the implications of biodiversity changes to species ecological functioning and the potential provisioning of ecosystem services (Jarzyna & Jetz, 2017). In contrast, ecosystem processes form an integral aspect of FD as it is created from species' ecological characteristics related to ecosystems' functioning and services (Petchey & Gaston, 2006). Also, compared with TD, findings from FD are assumed to provide more generalisable predictions across biological organisation and geographic scales (Shipley et al., 2016). Although, as an added benefit, the combined approach of using TD and FD may further the understanding of how different facets of diversity relates to ecological processes and environmental conditions (Mouchet, Villéger, Mason, & Mouillot, 2010).

Here, we aimed to reveal the effects of habitat amount, landscape heterogeneity (i.e. matrix compositional heterogeneity) and average isolation distance (i.e. distance effect of fragmentation per se) on forest bird alpha (α) taxonomic richness and functional richness of community and forest-dependent (i.e. forest specialist species) assemblages in selected

Southern Mistbelt forest fragments of KwaZulu-Natal (KZN) and Eastern Cape (EC) provinces. We proposed the following predictions:

		
1: Habitat amount would positively affect local avian diversity indices and especially forest specialists (Carrara, Arroyo-Rodríguez, Vega-Rivera, Schondube, de Freitas, & Fahrig, 2015) by providing additional resources and increasing habitat connectivity, favouring dispersal among habitat fragments and reducing dispersal resistance in the fragmented landscape (c.f. Fahrig, 2013).	**2:** Landscape heterogeneity would have a positive effect on local avian diversity indices through the provisioning of complementary resources and habitat, thus facilitating species persistence in forest fragments, particularly fragments embedded within landscapes of reduced forest cover (Fahrig et al., 2011; Neuschulz, Botzat, & Farwig, 2011; Neuschulz, Brown, & Farwig, 2013). Thus, community diversity would especially increase due to the proliferation of forest generalist species in the surrounding landscape (Morante-Filho, Arroyo-Rodríguez, de Andrade, Santos, Cazetta, & Faria, 2018). And, heterogeneous landscapes may provide valuable stepping stones for forest specialist movement across forest patches in the fragmented landscape (Neuschulz et al., 2013).	**3: i)** The distance effect of fragmentation per se (i.e. average isolation distance) would be of no influence in landscapes with sufficient habitat amount (Fahrig, 2003; 2013; 2017). Alternatively, in landscapes with low habitat amount, fragmentation per se would be a negative driver of local avian diversity indices by impeding dispersal and colonisation of isolated habitat fragments (MacArthur & Wilson, 1967; Cook et al., 2002), particularly for forest specialists which are known to decline with increasing patch isolation (Wethered & Lawes, 2005; Ehlers Smith et al., 2018b).

4.3 Methods

4.3.1 Study site description

Our study was conducted in the historically fragmented Southern Mistbelt forests (hereafter, Mistbelt forest) along KwaZulu-Natal (KZN; southern-most) and Eastern Cape (EC; northern-most) Provinces (Figure 4.1, Appendix S1); as they contain the highest combined proportion of forest cover (75 %) in South Africa (Berliner, 2009). The natural fragmentation of indigenous forests in South Africa resulted from climatic fluctuations during the Quaternary, which influenced the distribution and extent of forests (Partridge, 1997). Of the three broad classifications of South African forest types (i.e. Afrotemperate; Scarp, and Coastal forests), Afrotemperate forests (including Mistbelt forest subtype) are the oldest and most persistent because of their existence before the Last Glacial Maximum (LGM; Lawes, 1990; Eeley et al., 1999). Therefore, forest biotas within these forests have experienced the most events of climatic extinction filtering relative to Scarp (which were refugia for Afrotemperate forests during the LGM) and coastal forests (which established after the LGM; <8000 years) (Lawes, 1990; Eeley et al., 1999). Consequently, the naturally small and patchy nature of Afrotemperate forests likely contain extant forest fauna, which may be resilient to further events of disturbance (Lawes, Eeley, Findlay, & Forbes, 2007; Betts et al., 2019). Additionally, because of their mobility, forest avifauna provide the best pattern of dispersal after an extinction event relative to other vertebrate taxa such as mammals and amphibians, where extinction filtering tends to be strongest (Lawes et al., 2007).

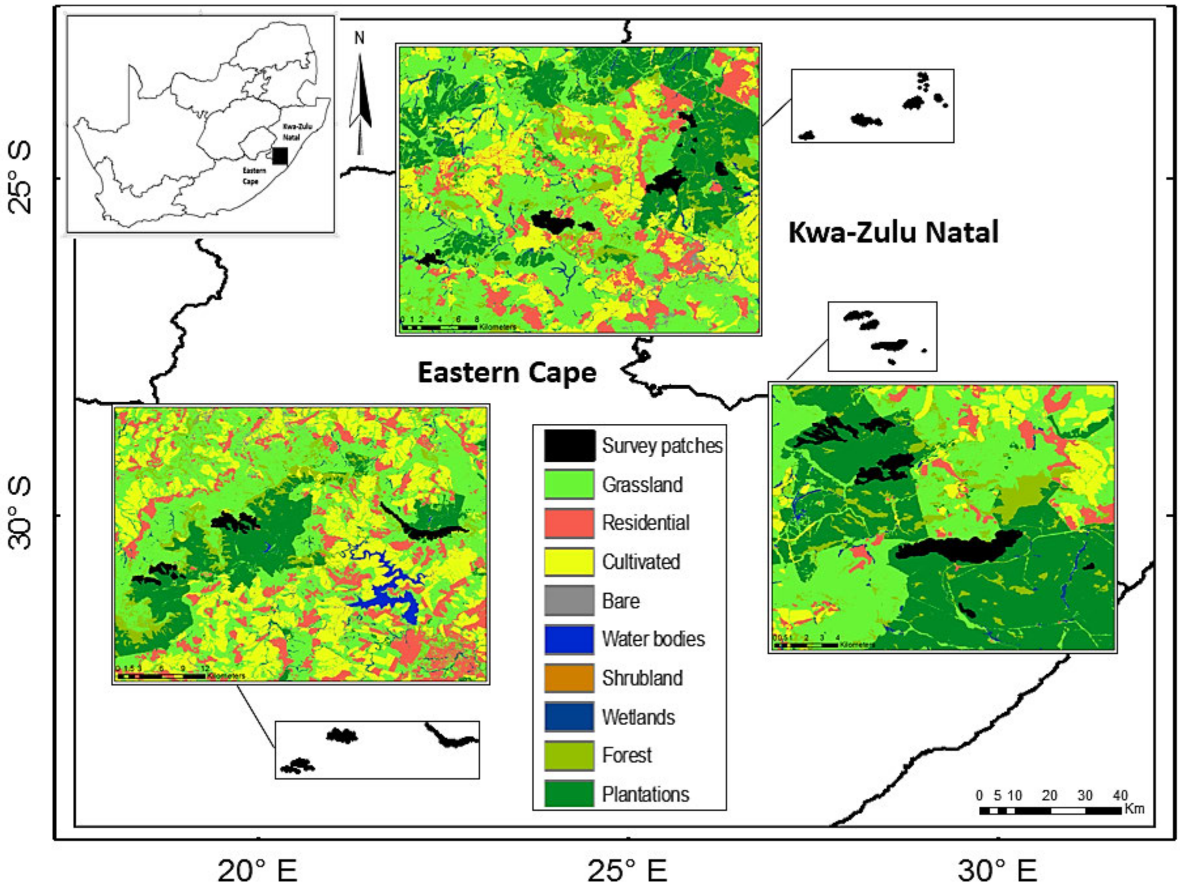


FIGURE 4.1 Location of study site in KwaZulu-Natal (KZN) and Eastern Cape (EC) provinces, South Africa (top left insert). Landcover surrounding selected Mistbelt forest patches in the three survey clusters; Creighton (top insert), Ingeli (middle insert) in KZN, and Mthatha (bottom insert) in EC

4.3.2 Study design and landscape covariates

We selected 32 Mistbelt forest patches/fragments varying in size (range: 0.03 – 732.42 ha, Appendix S1) in three regions/ clusters (Weza-Ingeli (hereafter Ingeli), Creighton, and Mthatha) using the 2014 landcover maps based on a 30 m Landsat 8 imagery (GeoTerra Image, 2015). We reclassified this landcover map before selecting our study sites into ten broad categories (of the original 72 landcover classes). Following Ehlers Smith et al. (2017; 2018a; b), a systematic grid (200 X 200 m) was overlaid on a merged indigenous forest and thicket/dense bush shapefile layer using ArcGIS v10.2 (Environmental Systems Research Institute- ESRI, 2011). This was done because both vegetation types appeared visually similar (> 75% canopy cover) and occurred in close proximity upon ground-truthing (South African National Land-Cover - SANLC, 2018; pers. obs.). Within each cluster, the largest forest fragment (Ingeli -732.42 ha; Creighton - 494.36 ha; Mthatha – 634.66 ha) was surveyed as well as the surrounding smaller fragments (i.e. satellite patches). We ensured a 200 m distance between survey point locations, with survey effort distributed evenly relative to fragment area (Bibby, Burgess, & Hill, 2000; Ehlers Smith et al., 2017; 2018a; b).

We quantified characteristics of landscape covariates surrounding focal Mistbelt forest fragments using the land-cover map described above in ArcGIS v10.2 (ESRI, 2011) (Appendix S1). To select an appropriate landscape buffer size, we used a multi-scalar approach across varying ranges of buffer sizes (200 m, 400 m, 600 m, 800 m, 1000 m, 1200 m). We also included a buffer size of 680 m based on the average inter-patch distance between patches of indigenous forest and thicket/dense bush (Olivier, van Aarde, & Lombard, 2013). Based on this approach, single factor General Linear Models (GLMs) with Poisson error variance were used to determine the best scale at which local species richness responded to landscape composition (sensu Skórka, Lenda, & Sutherland, 2016). We considered the best spatial scale as that with the lowest value Akaike information criterion (AIC; Burnham & Anderson, 2002). Thus, calculations for landscape predictors were determined at the 0.68 km buffer. Within this buffer; a) habitat amount was calculated as the amount of forest cover (including the area of habitat within the patch itself); b) average isolation distance was calculated as the mean distance between forest fragments surrounding the focal habitat patch; and c) landscape heterogeneity was calculated as the aggregated composition (%) of the 10 (forest, woodland, plantation, grassland, agriculture, human habitation, roads and rails, water bodies, wetlands, bare ground) land-cover types surrounding focal forest fragments. We then calculated the compositional landscape heterogeneity (Fahrig et al., 2011; referred here as 'landscape heterogeneity') using the Shannon-Weiner diversity index (SHDI):

$$\mathrm{SHDI} = -\sum_{i=1}^{m} P_i \ln P_i ,$$

Where the landcover type is represented by i, and pi is the proportion of the landcover, m indicates the number of landcover types. The SHDI determines diversity of the landscape and is a common index of landscape heterogeneity (Shannon, 1948; McGarigal, Cushman, Neel, & Ene, 2012). A landscape has less diversity when the SHDI value is low (i.e. landscape may be dominated by a few landcover types). Landscape heterogeneity increases when the number and/or proportion of landcover types increases. However, the main disadvantage of SHDI is that it can only express the total extent of each landcover and cannot represent the spatial distribution of the landcover category within a landscape (Dušek & Popelková, 2017).

4.3.3 Bird sampling and functional trait selection

Bird survey sampling was conducted during the breeding (October 2018 – February 2019) and non-breeding (May 2018 – July 2018) seasons by using the fixed-radius point count methodology. For each forest fragment, bird species richness (i.e. the number of species) was recorded at 200 m inter-point distance, during the first 3 h (in 10 min. durations) after sunrise and on windless/rainless days (to ensure avian detectability) (Bibby et al., 2000). Any identification uncertainty of a species was not recorded.

A functional trait matrix was constructed based on the morphology and ecology of each recorded species, including morphology (body mass, clutch size, wing length, tarsus length, culmen, tail length- Hockey, Dean, & Ryan, 2005), main diet (carnivory, folivory, frugivory, granivory, insectivory, nectarivory, scavenging, omnivory- Hockey et al. 2005), main foraging strata (ground, understorey, aerial, mid-high, canopy, mixed- Wilman et al., 2014), locomotion (altitudinal-migrant, breeding-migrant, nomadic, partial-migrant, sedentary- Hockey et al., 2005), and habitat specialisation (forest-dependent (i.e. forest specialist) species and non-forest dependent (i.e. forest generalist) species) (Oatley, 1989; Symes et al., 2002; Brown, 2006; Appendices S2, S3).

4.3.4 Data analyses

We determined local bird species richness (i.e. patch-level) based on the total number (i.e. pooled) recorded of species within each patch (i.e. per forest fragment). We calculated functional richness (FRic), which is a measure of functional diversity (FD) that describes the volume of functional (niche) space individual species occupy within the community (Mason, Mouillot, Lee, & Wilson, 2005). We calculated FRic using a Gower's distance matrix, which determines the pairwise distance scores of species' traits within a community and allows the combination of both categorical and continuous trait variables (Gower, 1966). We did this using the "FD" package (Laliberté & Legendre, 2010) in R v3.3.1 (R Core Team, 2019). FRic scores were then calculated using a principal coordinate analysis (PCoA) obtained from the species functional matrix described above. We retained the first three PCoA axes explaining 87 % of the total inertia. Lastly, FRic scores for each patch were calculated using the FRic index of the "FD" package. We also calculated FRic scores for forest specialist assemblage within each forest fragment in our survey region.

We tested for spatial autocorrelation using the Moran's index tool ('Global Moran's I') in ArcGIS (v10.2) for both SR and FRic scores based on the Euclidean distance to ensure that the assumption of independence was not violated. There was no spatial autocorrelation ($p > 0.05$ for both diversity measures; Appendix S4). Additionally, we checked for residual autocorrelation for each model using the 'plot' and 'qqPlot' functions from the "nlme" package (Pinheiro, Bates, DebRoy, & Sakar, 2012) and "carData" package (Fox, Weisberg, & Price, 2022), respectively. We created a correlation matrix between explanatory variables (habitat amount, average isolation distance and landscape heterogeneity) to avoid possible problems of multicollinearity using a threshold of $r \geq 0.7$ (Garden, McAlpine, & Possingham, 2010). All landscape covariates were retained since none exceeded this threshold (Appendix S4). However, an absence of high correlation may not indicate an absence of multicollinearity. Therefore, we also calculated an index for multicollinearity in each model using the Variance Inflation Factor (VIF) from the "performance" package (Lüdecke, Ben-Shachar, Patil, Waggoner, & Makowski, 2021). We constructed linear mixed-effects models (lme), with maximum likelihood (ML) in the "lme4" package (Bates, Machler, Bolker, & Walker, 2015) to test the effects of habitat amount, average isolation distance and landscape heterogeneity (i.e. explanatory variables) on local species richness (SR) and functional richness (FRic) for the whole community and forest specialist assemblages separately (i.e. response variables), with the region as the categorical fixed effect. We created various combinations of our explanatory variables for each model, including their interaction effects on the response variables independently (Table 4.1). For example, we created a ‘full’ model with each explanatory covariate and their interaction effects, and we also created models with each covariate independently. Information theoretic (IT) analysis was used to determine models of best fit based on the Akaike’s Information Criterion (AIC- Burnham & Anderson, 2002). Thus, we considered all models with Δ AIC < 2 as equally plausible in each model selection (Burnham & Anderson, 2002). We calculated the strength of variable importance using the function ‘‘AICctab’’ from the “bbmle” package (Bolker, 2020). We distinguished the relative importance of the predictors by summing the Akaike weights (ΣWi) of models containing the variable under consideration independently and their interactions (Burnham & Anderson, 2002; Bonfim, Dodonov, & Cazetta, 2021). We used model averaging from the “MuMIn” package (Barton, 2009) to determine the relative effect size of the environmental predictors with conditional averages. A one-way analysis of variance (ANOVA) was used to test for differences in the diversity metrics among survey regions, and no significant differences were observed. All analyses were performed in R version 3.5.3 (R Core Team 2019).

4.4 Results

We recorded 89 forest bird species (of which 37 were forest specialists) totalling 9,037 individual birds throughout our survey region across 747 surveys within 32 distinct forest fragments during the breeding and non-breeding survey cycles. Overall, our surveyed forest fragments equated to a mean α species richness (± SD) (hereafter SR) = 35.5 ± 12.8 (range 16 – 74) and a mean α functional richness (hereafter FRic) FRic score = 14.5 ± 6.0 (range 1.7 – 27.5) respectively. Local avian species richness (SR) and functional richness (FRic) were significantly correlated ($r^2 = 0.87$, $P < 0.0001$). Our summary of model selection indicated that habitat amount and landscape heterogeneity were important covariates (Δ AIC < 2) for species richness of both community and specialist assemblages (Table 4.1). For functional diversity, habitat amount was represented in the best approximating model (Δ AIC = 0) for both community and specialist assemblages (Table 4.1). Habitat amount was the only significant predictor of local avian diversity in Mistbelt forest fragments (Table 4.2). In terms of the relative importance of each landscape predictor on response variables: habitat amount was the most important for both measures of the diversity of community and specialist assemblages, followed by landscape heterogeneity for community (both) and specialist (species richness), then average isolation distance and lastly, interaction effects of the landscape predictors (Figure 4.2)

TABLE 4.1 Linear mixed-effect model (LME) summary revealing measures of habitat amount, landscape heterogeneity and average isolation distance surrounding survey forest fragments on species richness and functional richness of local forest bird community and forest specialist assemblages in the present study

Response	**Models**	**Df**	**AICc**	**Δ AIC**	**Weight (ωi)**	**logLik**
Community SR	**Hab**	**4**	**231.03**	**0.00**	**0.49**	**-110.77**
	Hab + Landhet	**5**	**232.09**	**1.06**	**0.29**	**-109.89**
	Hab + AvgIso	5	233.86	2.83	0.12	-110.77
	Hab + AvgIso + Landhet	6	235.11	4.08	0.06	-109.87
	Hab + AvgIso + Landhet + Hab*AvgIso	7	237.09	6.06	0.02	-109.21
	Full model	9	239.81	8.78	0.01	-106.81
	Hab + AvgIso + Landhet + Hab*AvgIso + Hab*Landhet	8	239.83	8.80	0.01	-108.79
	Landhet	4	256.08	25.05	0.00	-123.30
	AvgIso + Landhet	5	258.90	27.87	0.00	-123.29
	AvgIso	4	262.16	31.13	0.00	-126.34
Community FRic	**Hab**	**4**	**196.74**	**0.00**	**0.60**	**-93.63**
	Hab + Landhet	5	198.97	2.23	0.20	-93.33
	Hab + AvgIso	5	199.49	2.75	0.15	-93.59
	Hab + AvgIso + Landhet	6	201.98	5.23	0.04	-93.31
	Hab + AvgIso + Landhet + Hab*AvgIso	7	205.26	8.51	0.00	-93.30
	Hab + AvgIso + Landhet + Hab*AvgIso + Hab*Landhet	8	208.40	11.65	0.00	-93.07
	Landhet	4	210.51	13.77	0.00	-100.52
	Full model	9	211.84	15.10	0.00	-92.83
	AvgIso + Landhet	5	213.22	16.47	213.22	-100.46
	AvgIso	4	213.22	16.47	0.00	-100.46

Forest specialist SR	**Hab**	**4**	**190.79**	**0.00**	**0.53**	**-90.65**
	Hab + Landhet	**5**	**192.60**	**1.81**	**0.21**	**-90.15**
	Hab + AvgIso	5	193.09	2.30	0.17	-90.39
	Hab + AvgIso + Landhet	6	195.25	4.46	0.06	-89.95
	Hab + AvgIso + Landhet + Hab*AvgIso	7	197.30	6.51	0.02	-89.32
	Full model	9	199.72	8.93	0.01	-86.77
	Hab + AvgIso + Landhet + Hab*AvgIso + Hab*Landhet	8	199.80	9.01	0.01	-88.77
	Landhet	4	212.91	0.00	22.13	-101.72
	AvgIso + Landhet	5	215.45	0.00	24.66	-101.57
	AvgIso	4	217.43	0.00	26.64	-103.97
Forest specialist FRic	**Hab**	**4**	**171.22**	**0.00**	**0.64**	**-80.87**
	Hab + Landhet	5	174.03	2.80	0.16	-80.86
	Hab + AvgIso	5	174.04	2.82	0.16	-80.87
	Hab + AvgIso + Landhet	6	177.07	5.84	0.03	-80.85
	Hab + AvgIso + Landhet + Hab*AvgIso	7	179.15	7.92	0.01	-80.24
	Hab + AvgIso + Landhet + Hab*AvgIso + Hab*Landhet	8	181.71	10.49	0.00	-79.73
	Full model	9	185.13	13.90	0.00	-79.47
	Landhet	4	188.11	16.89	0.00	-89.32
	AvgIso	4	189.57	18.34	0.00	-90.04
	AvgIso + Landhet	5	190.86	19.63	0.00	-89.27

SR = species richness; FRic = functional richness; Hab = Habitat amount; Landhet = Landscape heterogeneity; AvgIso = Average isolation distance; * indicates an interaction effect between explanatory covariates (Hab*AvgIso; Hab*Landhet; AvgIso + Landhet). Models with Δ AIC <2arein**bold**

TABLE 4.2 Relative effect sizes of model averaged effects of habitat amount, landscape heterogeneity and average isolation distance surrounding forest fragments of Southern Mistbelt forests in KwaZulu-Natal (KZN) and Eastern Cape (EC)

Response	Coefficients	Estimate	Std. Error	z-value	p-value
Community SR	Intercept	24.007	6.359	3.682	
	Habitat amount	0.049	0.016	2.983	**0.003****
	Landscape heterogeneity	6.634	5.275	1.203	0.229
	Average isolation distance	0.397	7.027	0.118	0.906
Community FRic	Intercept	10.520	2.641	3.844	
	Habitat amount	0.019	0.005	3.408	**0.001****
	Landscape heterogeneity	2.239	3.046	0.702	0.483
	Average isolation distance	1.309	5.102	0.245	0.806
Forest specialist SR	Intercept	10.447	2.880	3.523	
	Habitat amount	0.024	0.009	2.672	**0.008****
	Landscape heterogeneity	2.688	2.875	0.895	0.371
	Average isolation distance	4.012	7.541	0.518	0.604
Forest specialist FRic	Intercept	4.734	1.469	3.080	
	Habitat amount	0.014	0.005	2.800	**0.005****
	Landscape heterogeneity	-0.289	2.074	0.133	0.894
	Average isolation distance	0.5117	3.563	0.137	0.891

SR= species richness; FRic = functional richness; P < 0.05; **P < 0.01; ***P < 0.001

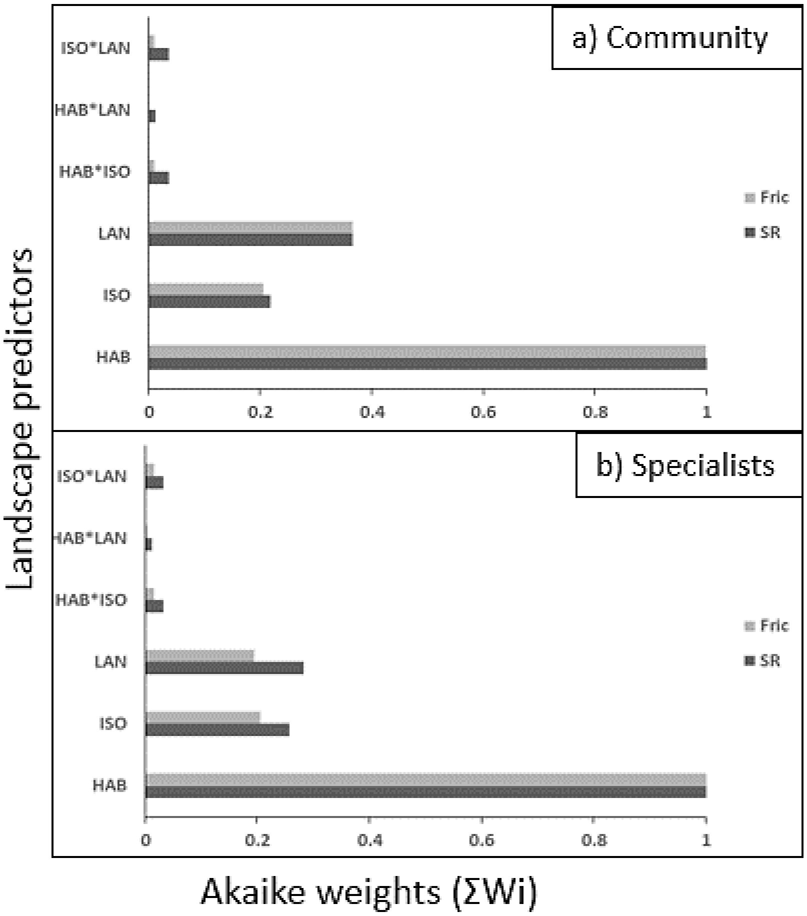


FIGURE 4.2 Landscape variable importance on species richness and functional richness of local a) community and b) forest specialist assemblages in Southern Mistbelt forest natural fragments in the present study. The sum of Akaike weights (ΣWi) indicates the relative importance of each landscape predictor on each response variable. (HAB = habitat amount; LAN = compositional landscape heterogeneity; ISO = average isolation distance; and * indicating their interaction effects)

4.5 Discussion

Our findings revealed that habitat amount was the sole significant landscape predictor, positively influencing the local forest bird community and specialist assemblages in the naturally fragmented Mistbelt forest system (Table 4.2; Figure 4.2). These findings were expected per our first prediction and are consistent with several previous studies (Fahrig et al., 2019; Watling et al., 2020; Morante-Filho et al., 2021). Moreover, our results potentially support the 'Habitat Amount Hypothesis' proposed by Fahrig (2013), which predicts that surrounding habitat amount in the landscape is the key determining driver of species persistence regardless of fragment area or isolation effects. This could be that habitat amount in the surrounding matrix improves landscape connectivity in fragmented landscapes, thereby facilitating dispersal and colonisation among habitat fragments (Lindenmayer et al., 2020). Therefore, our results highlight that the maintenance of forest habitat amount in the naturally fragmented landscape of the Mistbelt forest system is paramount for sustaining forest bird persistence and ecological processes. This is particularly crucial since the indigenous forest biome in South Africa covers less than 1 % of the land surface area (Low & Rebelo, 1996). In addition, these naturally fragmented forests are presently experiencing further anthropogenic modifications in the surrounding matrix (Adie et al., 2013), which introduces additional threats to extant forest biotas (Cooper, Wannenburgh, & Cherry, 2017; Cooper, Norris, & Cherry, 2020).

Landscape heterogeneity was not a significant predictor of local avian diversity in our study system (Table 4.2); however, model selection indicated the importance of this variable for species richness of both community and forest specialist assemblages (although this was non-significant- Table 4.1). Studies that investigate the effects of compositional landscape heterogeneity surrounding habitat patches reveal that this variable influences bird movement behaviour via providing vital stepping stones (i.e. short-distance movement of forest specialists) and feeding opportunities (i.e. long-distance movements of forest generalists) throughout the fragmented landscape (Neuschulz et al. 2011; 2013; Astudillo, Schabo, Siddons, & Farwig, 2019). However, the lack of effect of landscape heterogeneity may further verify that the amount of forest cover in the landscape is the strongest predictor of species biodiversity patterns in fragmented landscapes, as revealed by other previous studies (Fahrig, 2003; 2013; 2017; Matuoka, Benchimol, de Almeida-Rocha, & Morante-Filho, 2020; Morante-Filho et al., 2021).

We observed no significant effects of average isolation distance in our study (Table 4.2). These findings may indicate that the distance effect of fragmentation per se on local avian species richness may generally be weak or absent (Prugh et al., 2008; Martin, 2018; Morante-Filho et al., 2021). On the other hand, isolation metrics based solely on distance (such as those used in the present study) fare poorly in predicting local species occurrence since they only measure the presence of habitat patches and do not account for habitat amount in the surrounding landscape (Fahrig, 2013; Vieira et al., 2018; Brodie & Newmark, 2019). But then again, forest avifauna are revealed to be resilient to forest fragmentation because of the naturally patchy nature of indigenous forest distribution across the South African landscape. These findings are also consistent with previous studies in other forest types of South Africa (Neuschulz et al., 2013- Scarp forest; Ehlers Smith et al., 2018- Coastal forest). This has been attributed to the historical climatic (i.e. during the Quaternary) and anthropogenic (i.e. logging during the colonial era) events driving the present distribution and extent of forest remnants (Eeley et al., 1999; Adie et al., 2013). Moreover, in regions with high historical disturbance rates, the proportion of species that are sensitive to fragmentation tends to be low because of extinction-filtering of more resilient species (Betts et al., 2019). Therefore, Mistbelt forest avifauna may be resilient to fragmentation effects because of being shaped by evolutionary adaption to the patchy nature of indigenous forests in South Africa.

4.6 Conclusions

This study adds evidence to the ongoing debate on the contrasting effects of habitat amount and fragmentation per se on biodiversity within the perspective of naturally fragmented habitats. Habitat amount was the most important landscape driver influencing local forest bird communities in these fragmented forest landscapes, providing potential support for the habitat amount hypothesis (Fahrig, 2013). However, we caution that these findings were obtained from a single fragmentation variable and should we have selected another, our findings might have been different. Nevertheless, we highlight the importance of preserving forest cover in the landscape for maintaining forest bird diversity within forest fragments, especially since forest cover in the South African landscape is less than 1 % (Low & Rebelo, 1996). The wider implication for other naturally fragmented ecosystems (characteristic of our study system) may suggest that the positive effects resulting from forest cover in the landscape may promote the resilience of local biodiversity as long as habitat amount is preserved or increased in fragmented forest landscapes. Therefore, conservation efforts should aim to promote landscape forest cover if conservation goals are to maintain biodiversity in forest remnants of fragmented landscapes.

4.7 Declarations

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Conflict of interest

The authors declare they have no conflict of interest.

Data availability

The data belong to the University of KwaZulu-Natal and are stored there. They are available from the corresponding author upon reasonable request.

Biosketch

The research group, under South African Research Chair Prof Colleen T. Downs, investigates ecosystem health and functionality across a range of taxa and biomes in the Eastern Cape and KwaZulu-Natal Provinces of South Africa. It is concerned with species distributions, persistence and anthropogenic threats and producing recommendations for conservation and landscape managers on how best to preserve ecosystem functionality based on sound ecological research. Samukelisiwe P. Ngcobo is a PhD candidate at the School of Life Sciences (Center for Functional Biodiversity; CFB) - University of KwaZulu-Natal (UKZN) in South Africa. Her main research interests lie in biodiversity conservation, particularly responses of the multifaceted biodiversity to anthropogenic landscape transformations.

Author contributions

SPN, CTD, DES and YES conceptualised the study. CTD sought funding. SPN, STG and MS collected the data. SPN analysed the data with assistance from DES. SPN wrote the draft manuscript. The other authors provided editorial input.

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4.9 Supplementary information

Appendix S4.1. Landscape covariates and local forest bird diversity (Species and Functional richness) of the surveyed Mistbelt Forest fragments in KwaZulu-Natal and Eastern Cape Provinces, South Africa

Patch	Latitude (S)	Longitude (E)	Cluster	Patch size (ha)	Habitat amount (ha)	Average isolation distance	Landscape heterogeneity	Species Richness (n)	Functional Richness (FRic score)
X0	31°29'27.28"	28°24'32.76"	Mthatha	94.9	123.3	0.003	1.436355	30	12.75516
X1	31°29'25.36"	28°23'51.27"	Mthatha	64.42	92.12	0.005	1.500172	31	15.38472
X2	31°29'16.78"	28°27'16.98"	Mthatha	13.76	40.26	0.277	1.05867	33	9.471168
X3	31°29'11.65"	28°26'22.14"	Mthatha	41.54	63.04	0.51	1.400488	27	8.707298
X4	31°28'27.51"	28°25'30.01"	Mthatha	124.38	158.38	0.178	1.637277	37	12.45387
X5	31°28'17.91"	28°25'40.19"	Mthatha	107.65	142.95	0.3	1.68462	27	8.709478
X6	31°25'38.67"	28°46'38.85"	Mthatha	634.66	671.86	0.406	1.729068	55	23.92871
X7	31°25'14.16"	28°32'52.44"	Mthatha	190.26	221.06	0.276	1.532487	33	8.931108
X8	31°25'25.37"	28°31'34.67"	Mthatha	496.53	533.23	0.184	1.518007	48	16.96653
X9	31°23'17.76"	28°41'58.04"	Mthatha	62.87	95.37	0.34	1.509568	47	21.3545
X10	30°33'40.52"	29°41'17.70"	Ngeli	25	36	0.358	1.354271	34	11.20923
X11	30°32'10.16"	29°45'46.49"	Ngeli	11.97	21.97	0.364	0.969814	19	4.708129
X12	30°31'52.17"	29°40'59.87"	Ngeli	732.42	771.52	0.273	1.465634	74	26.41688
X13	30°28'30.71"	29°38'50.58"	Ngeli	256.78	284.58	0.3	1.419492	39	19.17038
X14	30°27'9.28"	29°38'19.39"	Ngeli	79.84	101.24	0.478	1.309052	39	16.13501
X15	30°27'39.48"	29°36'49.57"	Ngeli	192.63	212.83	0.269	1.43619	44	13.61395
X16	30°2'51.99"	29°30'17.57"	Creighton	139.9	164.2	0.233	1.369627	37	13.78544
X17	30°2'42.15"	29°31'8.73"	Creighton	17.81	41.01	0.142	1.12568	20	7.271353
X18	30°1'9.48"	29°39'39.77"	Creighton	75.52	99.72	0.29	1.288646	36	14.63979
X19	30°1'29.62"	29°38'2.40"	Creighton	494.36	534.26	0.34	1.505657	50	19.29795
X20	29°59'7.44"	29°43'59.38"	Creighton	464.34	499.54	0.315	1.651108	48	27.54629
X21	29°56'35.05"	29°45'49.48"	Creighton	7.16	12.16	0.442	1.078194	32	17.30413
X22	29°56'19.52"	29°45'13.39"	Creighton	6.12	12.42	0.519	1.388095	26	12.32719
X23	29°56'3.04"	29°46'2.45"	Creighton	6.89	13.59	0.44	1.102102	31	15.78685
X24	29°55'30.95"	29°45'16.28"	Creighton	20.49	31.89	0.427	1.66479	38	19.26976

X25	29°54'35.85"	29°45'31.68"	Creighton	0.03	42.63	0.504	1.808381	14	7.841494
X26	29°54'41.90"	29°45'36.30"	Creighton	83.1	102.3	0.01	1.923287	48	19.57236
X27	29°54'29.93"	29°45'5.76"	Creighton	7.86	29.06	0	1.848033	28	10.31975
X28	29°58'56.25"	29°48'29.96"	Creighton	2.04	11.94	0	0.734632	20	11.59666
X29	29°58'50.47"	29°48'31.82"	Creighton	1.45	11.45	0	1.050952	10	1.725209
X30	29°58'46.65"	29°48'24.16"	Creighton	0.24	8.84	0	0.651301	29	14.13845
X31	29°57'30.35"	29°47'15.83"	Creighton	97.38	126.28	0	1.436132	46	20.68775

Average isolation distance: patches = zero, indicate that there were no forest fragments within the delimited 0.68 km buffer of those focal patches

Appendix S4.2. Bird species occurrence records and selected functional traits in focal Mistbelt Forest fragments of KwaZulu-Natal and Eastern Cape Provinces, South Africa

Scientific name	Mass (g)	Clutch size (cm)	Wing length (cm)	Tarsus length (cm)	Culmen (cm)	Tail length (cm)	Primary diet	Foraging Strata	Locomotion ability	Habitat Specialisation
Accipiter melanoleucus	698.99	2.77	316	84.25	31.28	234	Carnivory	Mixed	Sed	NFD
Accipiter rufiventris	198	3	217.5	54	20.75	346	Carnivory	Mixed	Sed	FD
Accipiter tachiro	381	2.2	228.5	66	23.75	187.25	Carnivory	Mixed	Sed	FD
Amblyospiza albifrons	41.59	3.1	92.25	23.5	21.05	67.75	Omnivory	Mid-High	Sed	NFD
Andropadus importunus	27.4	2.02	90.4	23.2	19.4	89.6	Frugivory	Canopy	Sed	NFD
Apalis flavida	8.19	2.9	49.9	19.1	13.6	47	Insectivory	Canopy	Alt	NFD
Apalis thoracica	11.08	2.7	54.05	21.25	14.65	52.35	Insectivory	Mixed	Alt	FD
Apaloderma narina	67.69	2.6	132	16.5	19.25	159.5	Insectivory	Mid-High	Alt	FD
Columba larvata	155	1.89	150.6	26.9	21.3	102.9	Frugivory	Ground	Sed	FD
Batis capensis	11.74	2.1	61.05	20.6	16.35	44.7	Insectivory	Mixed	Sed	FD
Bostrychia hagedash	1238	2.4	248.5	72	123	154.5	Insectivory	Ground	Sed	NFD
Bucorvus leadbeateri	3750	1.85	544	139	199.5	279	Carnivory	Ground	Sed	NFD
Buteo trizonatus	615	2	350.5	67.5	21.6	181	Carnivory	Canopy	Part	FD
Bycanistes bucanitor	642.5	3	275.5	42	124	207	Frugivory	Canopy	Part	FD
Camaroptera brachyura	9.74	2.9	52	19.2	13.5	35.1	Insectivory	Mixed	Sed	FD
Campephaga flava	32.3	1.9	129.25	23.5	19.5	112.5	Insectivory	Ground	Breed	NFD
Cercotrichas leucophrys	20	2.7	69.3	24.4	17.9	64.6	Insectivory	Ground	Sed	NFD
Cercotrichas signata	35	2.8	83.3	26.5	22.4	75.55	Insectivory	Understorey	Sed	NFD
Chalcomitra amethystina	15	1.8	70.55	18	30.8	48	Nectarivory	Mixed	Sed	NFD
Chlorophoneus olivaceus	34	1.6	83.1	25.3	21.75	79.6	Insectivory	Canopy	Alt	NFD
Chrysococcyx caprius	32.79	4	118.9	18.3	17.05	88	Insectivory	Canopy	Breed	NFD
Chrysococcyx cupreus	37.7	3.5	110.25	79	17	91	Insectivory	Canopy	Breed	FD
Chrysococcyx klaas	27.37	3.5	99.2	14.4	16.4	74.7	Insectivory	Mixed	Breed	NFD
Cinnyris chalybeus	8	2.2	52.4	14.75	21.1	43.55	Nectarivory	Mixed	Sed	NFD
Cinnyris talatala	7	2	53.85	16.05	21.55	36	Nectarivory	Mid-High	Nom	NFD
Coccopygia melanotis	7.75	4.7	47.75	13.55	8.6	36.95	Granivory	Ground	Alt	NFD
Colius striatus	51.1	3	92.8	21.6	12.95	207.5	Frugivory	Mid-High	Alt	NFD
Columba arquatrix	400	1.5	223.2	26	24.1	138	Frugivory	Mid-High	Nom	FD

Columba guinea	350	2	229.5	27	22.5	113.5	Granivory	Ground	Sed	NFD
Coracina caesia	65	1.5	129.25	23.5	19.5	112.5	Insectivory	Mixed	Alt	FD
Corvus albus	524	4.1	356	58	57.3	187.5	Omnivory	Ground	Sed	NFD
Corvus capensis	553	3.5	325.5	66	58.5	181.5	Omnivory	Ground	Sed	NFD
Cossypha caffra	28.5	2.4	85.7	30.2	15.7	74.2	Insectivory	Ground	Alt	NFD
Cossypha dichroa	45.81	2.9	98	30.55	20.5	84.4	Insectivory	Mixed	Sed	FD
Cossypha natalensis	34.1	2.9	89.3	27.8	16.8	72.7	Insectivory	Ground	Part	FD
Crithagra scotops	15	3.4	67.6	16.15	10.2	51	Granivory	Mid-High	Sed	FD
Cuculus clamosus	78.8	4.5	176	20.45	22.75	154.5	Insectivory	Mixed	Breed	NFD
Cuculus solitarius	76.73	1	170.5	19.45	20.45	143.75	Insectivory	Ground	Breed	FD
Cyanomitra olivacea	11.5	2	63.5	17.55	26.85	54.9	Omnivory	Mixed	Sed	FD
Cyanomitra veroxii	12	2.2	63.6	18.1	29.2	49.4	Nectarivory	Mid-High	Nom	NFD
Dendropicus fuscescens	26	1.9	92.5	16	12.5	47.5	Insectivory	Mixed	Sed	NFD
Dendropicus griseocephalus	50	2.5	108	18.5	28.5	65.5	Insectivory	Mid-High	Sed	FD
Dicrurus adsimilis	45	2.8	137	22.5	21	120.5	Insectivory	Mixed	Sed	NFD
Dryoscopus cubla	26.23	2.7	80.3	22.5	19.25	66.7	Insectivory	Mixed	Sed	NFD
Euplectes orix	22.97	3	68	20.5	14.95	38	Omnivory	Canopy	Sed	NFD
Francolinus afer	454.81	5.1	193.4	57.05	21.45	96	Herbivory	Ground	Sed	NFD
Hedydipna collaris	8	2.2	50.8	16.15	14.25	35.65	Insectivory	Mixed	Sed	FD
Indicator variegatus	48.76	1	107.5	15.75	12.2	68.35	Nectarivory	Mixed	Sed	FD
Lagonosticta rubricata	10.16	3.7	48.35	15.4	11.3	42.15	Granivory	Ground	Sed	NFD
Laniarius ferrugineus	46.8	2.5	95.95	35.85	24.25	94.8	Insectivory	Mixed	Sed	NFD
Lanius collaris	36.44	3.5	98.9	27.5	20.5	106.5	Insectivory	Ground	Sed	NFD
Lophaetus occipitalis	1067	1.6	389.5	96.3	38.4	209.5	Carnivory	Ground	Sed	NFD
Lybius torquatus	51.7	3.3	91.3	22.3	22.7	55.7	Frugivory	Mid-High	Sed	NFD
Malaconotus blanchoti	78.7	2.9	114	32	28.5	111.5	Carnivory	Mixed	Sed	NFD
Mandingoa nitidula	9.6	5	50	14.5	9.5	31	Granivory	Mixed	Sed	FD
Muscicapa adusta	10.4	2.8	67.7	15.5	14.85	53.9	Insectivory	Mixed	Alt	NFD
Muscicapa caerulescens	17.6	2.8	74.75	16.25	11.5	53.8	Insectivory	Mid-High	Part	FD
Notopholia corruscus	56.07	2.9	108	25.8	21.75	80.5	Frugivory	Mixed	Sed	NFD
Onychognathus morio	132.9	3	146.5	33.65	32.75	130.5	Omnivory	Mixed	Alt	NFD

Oriolus larvatus	66.1	2.4	138.15	22.5	30.6	92.5	Omnivory	Mixed	Alt	NFD
Parus niger	21.5	3.6	82.75	19	11	71.1	Insectivory	Mid-High	Sed	NFD
Phoeniculus purpureus	73.21	3.8	140.5	30.6	49.8	212.1	Insectivory	Mid-High	Sed	NFD
Phyllastrephus terrestris	31.08	2.1	82.7	22.9	21.95	86.6	Omnivory	Mixed	Sed	FD
Phylloscopus ruficapilla	7.7	2.7	53.25	20.1	10.8	42.1	Insectivory	Mixed	Sed	FD
Ploceus bicolor	34.54	3	86.5	23.4	21.85	60	Insectivory	Ground	Sed	FD
Pogoniulus bilineatus	13.1	3.5	56.8	16.5	12.9	30.8	Frugivory	Mid-High	Sed	FD
Pogoniulus pusillus	9.6	2.8	60.1	15.85	12.55	34.25	Frugivory	Mid-High	Sed	NFD
Pogonocichla stellata	18.6	3	84.85	26.4	16.4	69.25	Insectivory	Various	Alt	FD
Poicephalus robustus	343.01	3.5	214.4	21.6	39.55	92.05	Frugivory	Mid-High	Sed	FD
Prinia hypoxantha	10.5	3.1	52.8	22.9	12.9	61.8	Insectivory	Understorey	Alt	NFD
Prinia subflava	8.64	3.1	49.5	20.7	11.7	60.65	Insectivory	Mixed	Alt	NFD
Pternistis natalensis	445	3.9	165.9	47.7	19.9	96	Herbivory	Understorey	Sed	NFD
Pycnonotus tricolor	37.5	2.7	95.4	21.7	19.15	85.05	Frugivory	Mid-High	Sed	NFD
Stephanoaetus coronatus	3640	1.6	499	99.5	48.75	326	Carnivory	Mixed	Sed	FD
Streptopelia capicola	142	1.9	161.75	21.4	15.7	105.6	Omnivory	Ground	Sed	NFD
Streptopelia semitorquata	176	1.8	189	24.6	21.8	125	Omnivory	Ground	Sed	NFD
Sylvia nigricapillus	29.64	2	82.1	24	15.3	83.2	Frugivory	Various	Alt	FD
Tauraco corythaix	308	1.7	185	41.8	23.5	214	Frugivory	Mid-High	Sed	FD
Tauraco porphyreolophus	259	2.3	180.5	40	24.9	197	Frugivory	Mid-High	Sed	FD
Telophorus sulfureopectus	27.1	2	90.7	17	18	90.1	Insectivory	Mid-High	Sed	FD
Telophorus zeylonus	65.02	3.1	98.25	34	26.55	95.65	Insectivory	Mixed	Sed	NFD
Terpsiphone viridis	13.23	2.7	80.7	16	14.8	154.05	Insectivory	Canopy	Breed	NFD
Tockus alboterminatus	223.65	3.5	244.5	33.5	88.5	224.5	Omnivory	Canopy	Sed	FD
Trachyphonus vaillantii	69.4	3.5	101.45	28.45	24.15	85.6	Omnivory	Ground	Sed	NFD
Trochocercus cyanomelas	10.2	2.2	68	17.5	14.4	78.5	Insectivory	Mixed	Alt	FD
Turdus olivaceus	67.29	2.9	113.7	30.4	22.2	83.55	Insectivory	Ground	Alt	NFD
Turtur tympanistria	70.58	1.85	114.85	19.8	15.6	88.25	Granivory	Ground	Sed	FD
Zoothera gurneyi	57.85	1.9	111.8	34.1	23.1	86.9	Insectivory	Ground	Sed	FD
Zosterops virens	13.5	3	62.6	17.9	13.6	47.05	Omnivory	Mixed	Sed	NFD

Locomotion ability categories: Sed (Sedentary), Alt (Altitudinal migrant), Part (Partial migrant), Breed (Breeding migrant), Nom (Nomadic). Habitat specialisation categories: FD (forest dependent species- forest specialists) and NFD (non-forest dependent species- forest generalists)

Appendix S4.3. Functional traits chosen for bird species recorded in selected Mistbelt Forest fragments of KwaZulu-Natal and Eastern Cape Provinces, South Africa

Trait type	Data type	Variables	Functional significance	Trait references
Morphology	Continuous	Mass (g), Clutch size (mean), Wing length (mm), Tarsus length (mm), Culmen (mm), Tail length (mm)	Traits related to reproductive capacity, metabolic rate, foraging behaviour, home range sizes, vulnerability to disturbances	Hockey et al. 2005
Diet	Categorical	Carnivory, Folivory, Frugivory, Granivory, Insectivory, Nectarivory, Scavenging, Omnivory	Traits related to food types consumed, which can be linked to ecosystem functioning (e.g. insect pest control, seed dispersal, pollination, etc.)	Hockey et al. 2005
Foraging stratum	Categorical	Ground, Understorey, Aerial, Mid-High, Canopy, Mixed	Traits related to niche variation in the vertical structure	Wilman et al. 2014
Locomotion	Categorical	Altitudinal-migrant, Breeding-migrant, Nomadic, Partial-migrant, Sedentary	Traits related to movement capacity	Hockey et al. 2005
Habitat specialization	Categorical	forest-dependent (FD) species and non-forest dependent (NFD) species	Traits related to habitat and resource use affinity	Oatley (1989), Symes et al. (2002), Brown (2006)

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Appendix S4.4. Spatial autocorrelation (Global Moran's I) test for avian multifaceted diversity metrics (significant p value depicts spatial autocorrelation between forest patches)in the present study

Moran I	**Observed**	**Expected**	**Z value**	***p* value**
Species richness (TD)	0.128785	-0.034483	1.391450	0.164089
Functional richness (FD)	0.107489	-0.032258	0.725260	0.468293

Appendix S4.5. Multiple correlation of landscape covariates in the present study

	Habitat amount (ha)	**Fragment area (ha)**	**Average isolation distance (km)**	**Landscape heterogeneity**
Habitat amount (ha)	*			
Fragment area (ha)	0.999129	*		
Average isolation distance (km)	0.097895	0.100651	*	
Landscape heterogeneity	0.365696	0.345158	0.131993	*

* Landscape covariate threshold was r ≥ 0.7; only fragment area was excluded from further analysis since it exceeded this threshold.

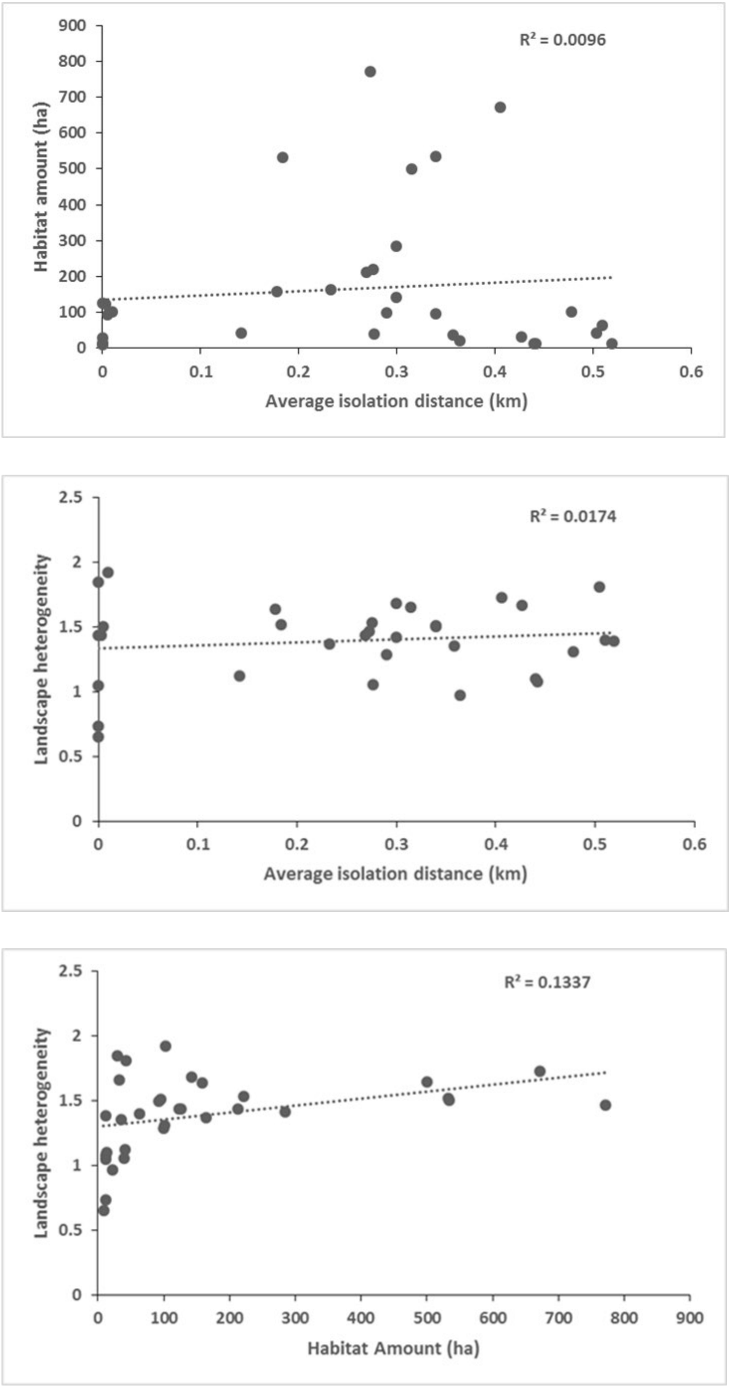

Figure S4.4 Relationships between the landscape predictor variables in the present study

CHAPTER 5

Evaluating habitat connectivity based on the requirements of a most sedentary forest-specialised bird species (*Aplopelia larvata*) in focal Southern Mistbelt Forests within human-altered landscapes in KwaZulu-Natal and Eastern Cape, South Africa

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Running header: Identifying habitat connectivity of focal Southern Mistbelt Forests

5.1 Abstract

Species persistence in fragmented forest systems, intensified by increasing anthropogenic practices surrounding forest remnants in human-altered landscapes, poses threats of local extinctions when habitat fragments become further isolated and species movement becomes impeded. However, sufficient forest cover in the landscape can favour habitat connectivity, promoting biodiversity by facilitating species ecological movements among habitat patches across the fragmented landscape, thus mitigating the negative effects of fragmentation. Therefore, the naturally fragmented Southern Mistbelt Forest, confined within the increasingly anthropogenic land-use matrix, provides an opportunity to assess potential ecological connectivity. Thus, we mapped connectivity of core Southern Mistbelt Forest patches provisioning the highest (≥ 50 %) avian phylogenetic diversity to identify landscape features that promote or impede habitat connectivity in southern KwaZulu-Natal and northern Eastern Cape, South Africa. We based our connectivity approach on a hybrid of least-cost pathway and ecological circuit theory, modelling habitat suitability guided by a surrogate forest-specialised and dispersal-limited bird species (Lemon dove - *Aplopelia larvata*) to assess features that improve habitat connectivity and allow biodiversity persistence in the fragmented Southern Mistbelt Forest mosaic landscape. Our findings highlight that Southern Mistbelt Forest fragments are connected in areas with indigenous forest cover (i.e. low resistance/permeable habitat) and have low connectivity in regions of other habitat types with higher resistance (exotic timber plantations, grassland, agriculture, and residential land-cover). Thus, we reveal the importance of indigenous forest cover in the landscape for promoting habitat connectivity among core forest patches of fragmented Southern Mistbelt Forest in southern KwaZulu-Natal and northern Eastern Cape. Therefore, we recommend the conservation of indigenous forests as it provides high-quality habitat for the maintenance of forest biodiversity in the fragmented mosaic landscape. However, since indigenous forest cover in South Africa is less than one percent, we recommend the conservation of thicket/dense bush (regenerating forest), which is more abundant, shares similar tree species composition (~77 %) and occurs in close proximity to indigenous forest. Therefore, conserving this vegetation type will improve habitat connectivity among fragmented forest remnants. In areas with low connectivity, we suggest improving matrix quality surrounding habitat patches by increasing vegetation (tree) cover to decrease matrix contrast, thereby encouraging the use of the matrix by forest species and thus ensuring the long-term survival of forest species in these fragmented mosaic landscapes.

Keywords: Avian community, Ecological corridors, Forest fragmentation, Functional connectivity, Habitat resistance, Land use, Landscape connectivity

5.2 Introduction

Land transformation driven by a growing human population has caused the loss and degradation of natural ecosystems and is a significant biodiversity threat worldwide (Foley et al., 2005; Newbold et al., 2015; Tilman et al., 2017). Particularly, conversions of forest habitats for agriculture and urbanising land-uses are causally related to forest loss, degradation and fragmentation, with detrimental consequences to forest biotas (DeFries et al., 2004; Seto et al., 2013; Curtis et al., 2018). Forest loss and fragmentation are inter-related processes involving loss of total habitat area, patch size reduction, increased density (number) of patches and increased inter-patch distances, which are processes collectively termed ‘fragmentation’ (Wilcove et al., 1986; Didham et al., 2012). However, this definition of forest fragmentation reflects that fragmentation effects are considered while controlling for those of habitat loss (see Fahrig, 1997; Villard and Metzger, 2014).

Although both processes occur simultaneously (Didham et al., 2012), it has been stressed by some that these two phenomena should be separated since the effects of habitat loss far exceed those of fragmentation (Fahrig, 1997; 2003; Smith et al., 2011). While others argue that both processes are important because the effects of fragmentation strengthen those of habitat loss in the landscape as the amount of habitat decreases (Ewers and Didham, 2006; Didham et al., 2012; Rybicki and Hanski, 2013). Also, the existence of non-linear relationships between habitat loss and species richness indicates the presence of a threshold whereby fragmentation effects have an influence at either low to intermediate levels (0-30 %) of habitat loss (Andrén, 1994; Pardini et al., 2010; Villard and Metzger, 2014). Thus, the interaction between the arrangement of habitat and matrix influences landscape permeability (Cooper et al., 2011; Aben et al., 2012).

In fragmented landscapes, forest fragments are surrounded by varying levels of anthropogenic land-use intensities, which may further isolate and inhibit animal movement among habitat patches in a matrix of increasingly unsuitable habitat (Fischer and Lindenmayer, 2006; Pardini et al., 2010; Driscoll et al., 2013). Therefore, there is increasing interest in maintaining and improving landscape connectivity to facilitate movement among habitat patches and biodiversity persistence in fragmented landscapes (Hanski, 1999; Schooley and Branch, 2011; Lindenmayer et al., 2020). Promoting landscape connectivity by creating permeable habitats in suitable locations could provide links and stepping stones among isolated populations, thus reducing or even reversing the detrimental effects of fragmentation on biodiversity (Watts and Handley, 2010; Mueller et al., 2014).

Landscape connectivity is defined as the magnitude to which movement among resource and habitat patches is facilitated or hindered by the landscape (Taylor et al., 1993), which varies depending on the dispersal ability of a given species. Two main concepts are included in this definition of landscape connectivity; namely, i) structural connectivity: spatial relationships of landscape elements, independent of species-specific ecological characteristics (Tischendorf and Fahrig, 2000; Crooks and Sanjayan, 2006); and ii) functional/habitat connectivity (adopted here): species behavioural response to the landscape structure (Tischendorf and Fahrig, 2000; Fischer and Lindenmayer, 2007; Mühlner et al., 2010). Landscape elements vary in their permeability to movements, whereby optimal habitat patches (those with greater likelihood of provisioning species' needs) are located in more suitable (permeable versus impermeable) areas (Gao et al., 2017).

Habitat connectivity is fundamental in promoting biodiversity persistence in fragmented landscapes by aiding the movement of individuals (Auffret et al., 2015), colonisation of disjunct patches (Hatfield et al., 2018), and facilitating healthy gene flow (Amos et al., 2014; Klinga et al., 2019), thus reducing local extinction risks (Donald et al., 2019) and improving ecosystem functionality (Emer et al., 2018). Therefore, a landscape is considered connected when it facilitates species movement among habitat patches, but this is dependent on species behaviour and dispersal capability (Taylor et al., 1993; Tischendorf and Fahrig, 2000). Consequently, species with highly specialised habitat requirements and/or low dispersal ability would be most vulnerable to habitat reduction and isolation exacerbated by matrix transformation in the surrounding landscape (Banks-Leite et al., 2014; Barlow et al., 2016). Thus, it is important that conservation planning identifies the need to maintain connectivity and link ecological processes to conserve biodiversity in fragmented landscapes.

Phylogenetic diversity accounts for the total amount of evolutionary history across species in a community (Faith, 1992). In the last decade, phylogenetic diversity has increasingly been recognised as an important value for conservation since it provides additional information beyond that captured by taxonomic diversity (Devictor et al., 2010; Davies and Buckley, 2011; Cardoso et al., 2014; Jetz et al., 2014; Miller et al., 2017; Tucker et al., 2017; Faith, 2018). Changes in phylogenetic diversity can also incorporate genetic, behavioural or morphological variations (Faith, 1992; Mace and Baillie, 2007; Tucker et al., 2017). For instance, phylogenetic diversity has been proposed as a surrogate for functional diversity, although the relationship between these two metrics has been variable and complex (Faith, 1992; Winter et al., 2013; Mazel et al., 2017; 2018; Tucker et al., 2018). Assuming that related species share similar traits and distinct species vary in their trait representation, then maintaining high phylogenetic diversity would potentially also conserve functional diversity, hence the maintenance of ecological processes (i.e. ecosystem functioning; Forest et al., 2007; Srivastava et al., 2012; Winter et al., 2013). In fact, conserving phylogenetic diversity may inevitably protect unique/unknown functional trait features (Faith, 1992; Owen et al., 2019), improving the functionality and stability of ecosystems (Cadotte et al., 2012; Srivastava et al., 2012; Cadotte, 2013). Moreover, if a community has high phylogenetic diversity, there is greater evolutionary potential and adaptability to future environmental changes (Faith, 1992; Lavergne et al., 2010). Also, there is greater intrinsic value in conserving phylogenetically diverse assemblages, which are likely to contain evolutionary lineages of rare or distinct taxa (Mi et al., 2012; Winter et al., 2013; Jetz et al., 2014). Given the plethora of significant research conducted on phylogenetic diversity in the recent decade, seldom have these results been applied to conservation practices in actuality (Winter et al., 2013; Veron et al., 2017).

Species persistence in the naturally fragmented Southern Mistbelt Forests consists of endemic fauna and flora, which are evolutionarily adapted to the archipelago-like distribution of forest remnants (Lawes, 1990; Lawes et al., 2000; 2007). However, the accumulative effects of increasing anthropogenic practices (land conversions for agriculture and land development) surrounding forest remnants further isolate habitat fragments and impedes species movements, presenting threats of local extinctions when conditions become unfavourable (Adie et al., 2013; Olivier et al., 2013; Leaver et al., 2019a). On the other hand, if there is sufficient habitat connectivity in the landscape, small forest patches distributed near larger patches can act as corridors to facilitate animal movement across the fragmented landscape (c.f. Fahrig, 2013). Therefore, our present study aimed to assess potential habitat connectivity of core Southern Mistbelt Forest patches provisioning ≥ 50 % avian phylogenetic diversity along southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa. We based our connectivity approach on a hybrid of least-cost pathway and ecological circuit theory (Keitt et al., 1997; Adriaensen et al., 2003; McRae and Kavanagh, 2011). This hybrid approach provides an advantage over these methods alone in that it simultaneously identifies multiple connectivity routes which may facilitate or impede movement and estimates the most likely corridors to be utilised by focal individuals as they move between habitat patches (Cushman et al., 2013; McRae et al., 2008). This method has been used by several previous studies in other forest systems in South Africa (Ehlers Smith et al., 2019; Alexander et al., 2019; Colyn et al., 2020).

5.3 Methods

5.3.1 Survey sites

Our study was conducted in Southern Mistbelt Forests in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa (Fig. 5.1). We selected 32 Southern Mistbelt Forest fragments varying in size (0.03 – 732.42 ha range) in three survey regions (Kokstad (Weza-Ingeli)- 30°31'48.93"S, 133 29°41'13"E; Creighton- 29°58'24.43"S, 29°44'16.15"E; and uMthatha-

31°25'1.58"S, 134 28°32'27"E) (Fig. 5.1). The distribution distance between survey regions was ~45 km (Creighton to Kokstad- KZN) and ~150 km (from Kokstad to Umthatha), respectively. The survey regions occur in a subtropical climate, with an annual precipitation range of 481-1481 mm (Mucina et al., 2021). The surrounding land-cover matrix in all regions is dominated by exotic tree plantations (49 %), followed by indigenous forest (21.6 %) and natural grassland (20.8 %) (Fig. 5.1; Adie et al., 2013). The other land-cover classes contribute approximately 8.6 % of the landscape in the survey regions but vary in proportion within each region (Fig. 5.1).

Southern Mistbelt Forests are patch-like throughout their distribution (Mucina and Rutherford, 2011) and have been naturally fragmented because of historical climate change and biogeographic influences since the Last Glacial Maximum (LGM; ca.18,000 years Before Present-BP) (Eeley et al., 1999), conditions which remnant biota evolved and are presently distributed (Lawes et al., 2007). However, present anthropogenic disturbances in the landscape matrix further fragments forest remnants, presenting additional challenges to forest diversity (Adie et al., 2013; Olivier et al., 2013; Leaver et al., 2019a;b; 2020; 2021). For instance, in the surrounding landscape of Southern Mistbelt Forests, the most dominant anthropogenic conversion impact are commercial exotic timber plantations of *Pinus* spp. and *Eucalyptus* spp., and the selected logging of indigenous yellowwood trees (*Afrocarpus* spp. and *Podocarpus* spp.), which threaten to change forest composition, structure, extent, and carbon sequestration capacity (Symes and Woodborne, 2010; Adie et al., 2013).

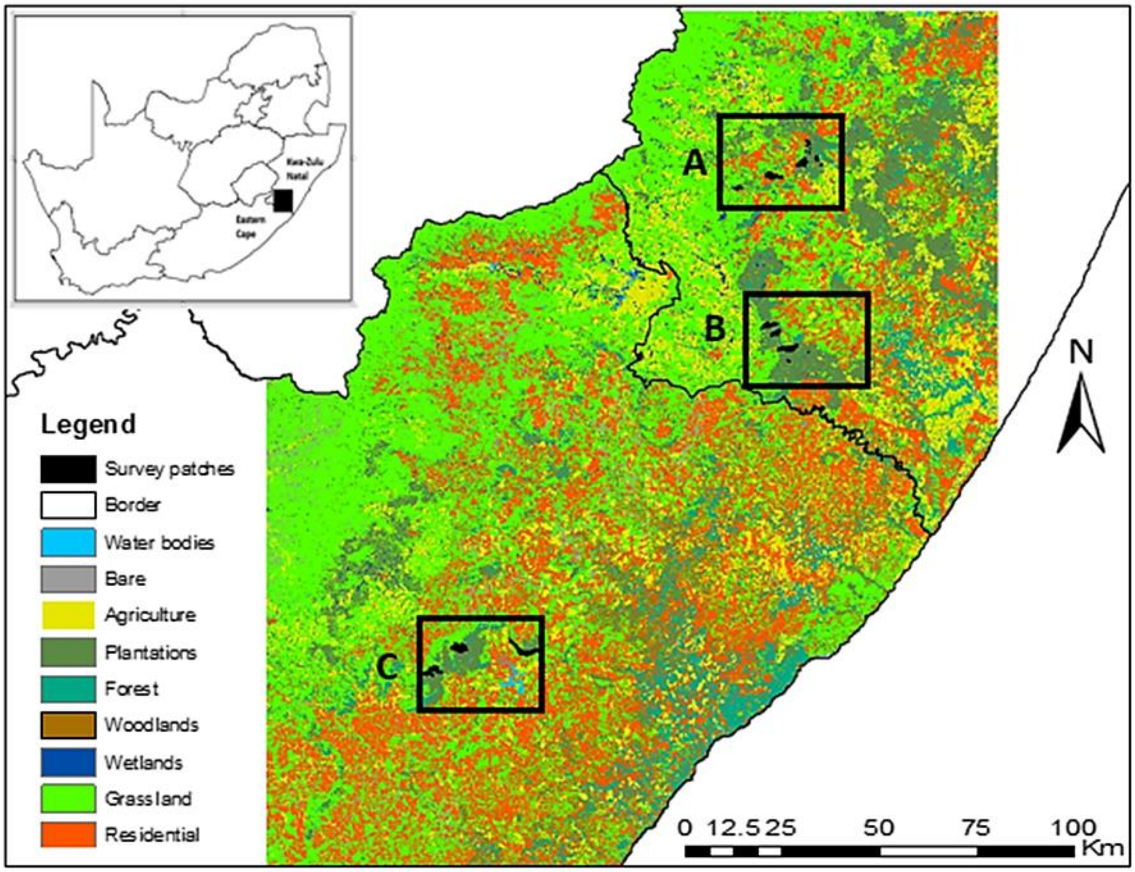

Fig. 5.1 Study area highlighting the three sample regions (A. Creighton; B. Kokstad (Ingeli-Weza); C. Umthatha) of Southern Mistbelt Forest fragments situated along southern KwaZulu-Natal and Eastern Cape, South Africa, with the surrounding land-cover types shown.

5.3.2 Survey design

Using the latest land-cover GIS (Geographic Information System) layers (GeoTerra Image, 2014, based on 30 m resolution), we identified polygons of indigenous and contiguous dense forest cover (hereafter, forest) within the three survey regions in ArcGIS v10.2 (Environmental Systems Research Institute- ESRI, 2011). We made area calculations for each forest-patch polygon, and following a stratified survey design, a 200m X 200m fishnet grid was overlaid to assign survey points at forest-patch location sites (Ehlers Smith et al., 2017a, 2018a, 2018b). Each survey point was allocated at the intersection of the gridline, and the sampling effort was proportional to the size of each forest patch (Bibby et al., 2000; Ehlers Smith et al., 2017a). Then, the created survey points at each forest patch location were uploaded onto a Global Positioning System (GPS, Garmin GPS map 62; Garmin USA) and identified in the field, wherein we maintained a minimum of 200 m distance per survey point.

5.3.3 Bird surveys

During the southern African breeding (October 2018- February 2019) and non-breeding (May-August 2019) seasons, bird surveys were conducted using fixed-radius point-counts within a 50 m distance-radius and recorded all visual or audible bird species to determine the taxonomic diversity (species richness and abundance) at each survey point (Bibby et al., 2000, See Ehlers Smith et al. 2017; 2018a, b). Field surveys began at dawn +3 h, and a duration of 10 min was allocated for each survey point at each forest patch location site. Thus, only diurnal species were surveyed and recorded because of our survey timing. Records of species and individual abundance estimates were pooled per forest patch site, and any identification uncertainties were discarded. In total, we completed 374 surveys and recorded 89 bird species in 32 distinct forest patches (Appendices 5.1-5.2).

5.3.4 Phylogenetic diversity

Using the available data from GenBank database, a maximum likelihood phylogeny was constructed for our Southern Mistbelt Forest avian assemblages (Fig. 5.2; see Ehlers Smith et al., 2021 for further description). The following data matrices were used for the constructed phylogeny: cytochrome oxidase I (COI); NADH dehydrogenase 2 (ND2); betafibrinogen (Bfib);

myoglobin (Mb), and transforming growth factor beta (TGFB), where COI and ND2 are mitochondrial genes, and Bfib, Mb and TGFB are nuclear markers. In cases of missing data sequences for species, we obtained sequences from other available species within the genus or family to reduce missing data in the phylogenetic supermatrix analysis. A community assemblage of 82 of the 89 recorded bird species was used in the constructed phylogeny. The maximum likelihood method was used to calculate branch lengths in Garli 0.951 (Zwickl 2006). Then, a partitioned maximum likelihood analysis was conducted to infer the phylogeny. We used the Akaike information criterion (AIC) in jModelTest 2.1.7 to determine the optimal substitution model for each estimated gene region (Darriba et al. 2012). Finally, the penalised likelihood method in the package 'ape' (Paradis and Schliep 2019) was used to convert the maximum likelihood phylogeny into an ultrametric rooted phylogeny in R v3.3.1 (R Core Team, 2019). Using the created phylogenetic tree, we then calculated Faith's phylogenetic diversity (Faith 1992) of our bird community using the 'picante' package (Kembel et al. 2010) in R v3.6.1 (R Core Team, 2019). Faith's phylogenetic diversity is the most popular metric of phylogenetic diversity, which accounts for the total evolutionary history connecting all species of a given assemblage and is proportional to divergence time (i.e. million years) (Faith 1992). However, it is considered as a phylogenetic generalisation of taxonomic diversity (i.e. species richness) (Chao et al. 2010).

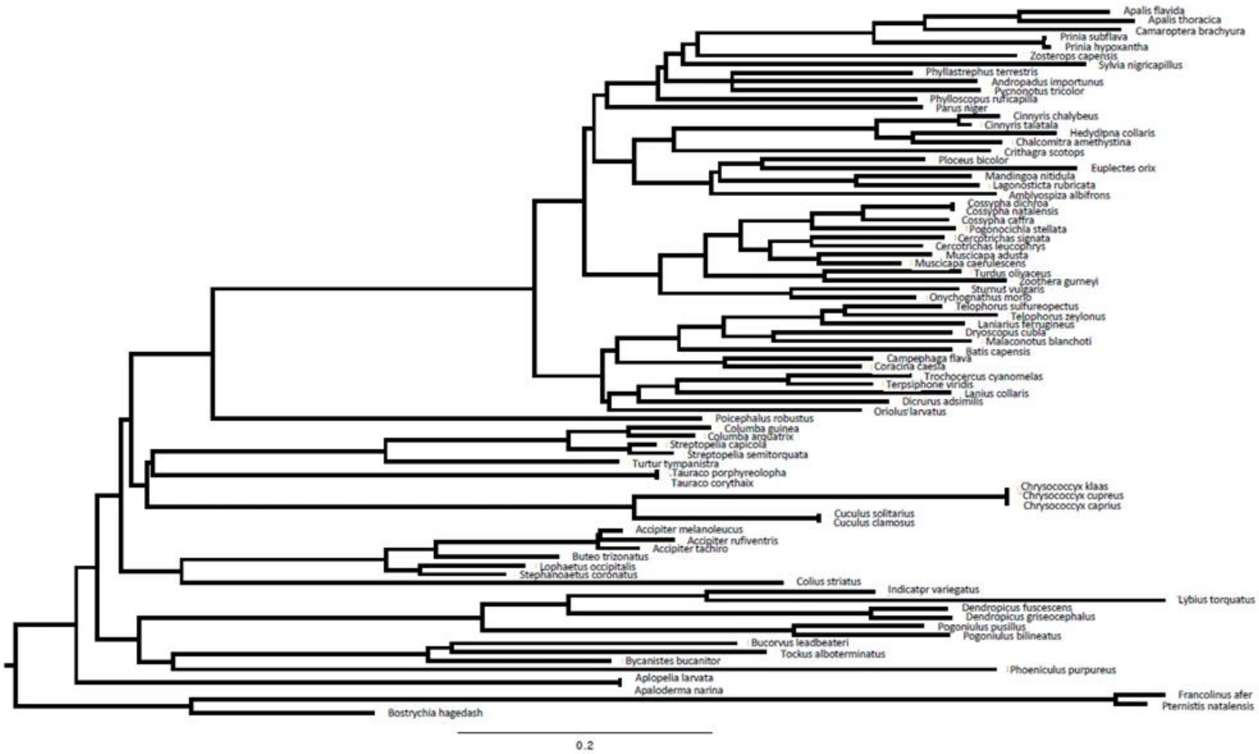

Fig. 5.2. Phylogenetic tree of bird assemblage recorded in the Southern Mistbelt Forest fragments of southern KwaZulu-Natal and northern Eastern Cape, South Africa (See Appendix 5.1).

5.3.5 Habitat connectivity mapping

5.3.5.1 Identifying core forest fragments and ideal surrogate species

We identified core forest fragments of selected Southern Mistbelt Forest fragments in our three regions of southern KwaZulu-Natal and northern Eastern Cape as those provisioning ≥ 50 % total avian phylogenetic diversity. This was done by ranking phylogenetic diversity scores of each forest fragment within our study regions and keeping only those fragments providing ≥ 50 % avian phylogenetic diversity (i.e. 22 of 32 forest fragments; see Ehlers Smith et al., 2019; Appendix 5.2). We selected the lemon dove (*Aplopelia larvata*) as an ideal surrogate species to assess habitat suitability and guide the connectivity mapping as we assumed that connecting core habitats required for this particular species would also incorporate the minimum requirements of all other species in our community (Alexander et al., 2019; Ehlers Smith et al., 2019). The lemon dove is the most sedentary forest specialist with a low dispersal capability (~500m maximum dispersal; Ehlers Smith et al., 2017a) and was considered an effective surrogate for potentially providing the most conservative estimate of landscape connectivity, particularly for other sedentary species recorded in our regions (> 60 % sedentary species; Appendix 5.1).

5.3.5.2 Habitat mapping and landscape resistance

We used the Gnarly Landscape Utilities Package v0.1.0 (Shirk and McRae, 2013), a plug-in toolbox for ArcGIS v10.4, to create maps of habitat suitability (from the 'Habitat Mapper' tool) and landscape resistance (from the 'Resistance' tool) based on the ecological requirements of the lemon dove (Appendix 5.3). Scores of habitat suitability and resistance were informed by the landscape and microhabitat covariates shown to positively or negatively affect local patch habitat occupancy and detection probability of the lemon dove (Ehlers Smith et al., 2017a; Gumede et al., 2020). For habitat suitability, we used a continuous scale of suitability scores ranging from 0 (unsuitable) to 1 (most suitable); and set the habitat suitability method of calculation to 'maximum'. The most ideal habitat types being the contiguous (indigenous) forest (1); contiguous low forest & thicket (0.8), and dense forest & woodland (0.7) (Appendix 5.3; Ehlers Smith et al. 2017a,b). For resistance, a continuous scale of resistance scores ranging from 1 (no resistance) to 100 (maximal resistance) were used; and setting the resistance calculation method to the recommended "sum+1" (Appendix 5.3; McRae et al., 2013; Ehlers Smith et al., 2019). These scores were thus created based on the assumption that different landscape features have varying effects on a species' habitat requirements and avoidances (McRae et al., 2013).

5.3.5.3 Corridor mapping

We used a plug-in toolbox of Linkage Mapper v2.0 (McRae and Kavanagh, 2011) in ArcGIS v10.4, to perform corridor and connectivity analyses. From the Linkage Mapper Toolkit, we used the Linkage Pathways Tool to build network and map linkages to create the least-cost pathways. For our model inputs, we added our core habitat patches and the resistance raster created from Gnarly landscape utilities toolbox. We then accepted all default processing steps (excluding step 4) and selected the Cost-weighted and Euclidean options as the network adjacency method to finalise analyses. Then, we used Pinchpoint Mapper v2.0 (McRae, 2012a), applying the same inputs as Linkage Mapper and including least-cost pathways created above to identify pinch-points (critical pathways) within the least-cost corridors. Additionally, we set the cost-weighted distance cut-off (corridor width cutoff) to 12 km, checked all boxes (except ‘square resistance values’ option), and the calculation for raster centrality was the pairwise method. Finally, we used Barrier Mapper v2.0 (McRae, 2012b), to identify regions of resistance/ barriers to connectivity, using the same inputs as Linkage Mapper and including the created CWD output raster maps from Linkage Mapper. For additional settings, we set the minimum and maximum detection radii at 500 m and 2,000 m, with a 500 m step-up radius (Ehlers Smith et al., 2019; Colyn et al., 2020). The above were conservative estimates whereby a strip of land could be rehabilitated (McRae, 2012b; Colyn et al. 2020). We then calculated both maximum and sum as the method of combining multiple core area pairs.

5.4 Results

Regions of low habitat suitability (0) corresponded with regions of high habitat resistance (101) and the opposite effect for high habitat suitability (1) and low habitat resistance (1) (Fig. 5.4 A-B). Habitat suitability corresponded with the distribution of indigenous forest cover, and areas of low habitat suitability were observed in regions with exotic tree plantation cover, grassland, agricultural (cultivated commercial/subsistence), and residential (rural and urban habitations) (Fig. 5.1 and Fig. 5.3-5.4). Cost-weighted distances indicated a scale of connectivity ranging from 0 (maximal connectivity) to 11844010 (no connectivity) between core Southern Mistbelt Forest patches provisioning ≥ 50 % avian phylogenetic diversity (Fig. 5.5). Connectivity appeared to be maintained along with the distribution of Southern Mistbelt Forest fragments in our study region for the surrogate taxon (Fig. 5.5). Pinch-point Mapper highlighted regions of maximised connectivity (103,546) and no connectivity (0) between the three study regions; most connectivity was observed within each region relative to between regions (Fig. 5.6). The Kokstad (Ingeli-Weza) region had the greatest connectivity (Fig. 5.5b) followed by Creighton (Fig. 5.6a), then Umthatha region (Fig. 5.6c). Barrier Mapper highlighted regions of maximal (97,36) and lowest barriers/resistance (0) between the three survey regions (Fig. 5.7). Creighton had the most barriers (highest connectivity resistance) (Fig. 5.7a) than the Kokstad (Ingeli-Weza) and Umthatha regions which had the lowest connectivity resistance (Fig. 5.7b-c).

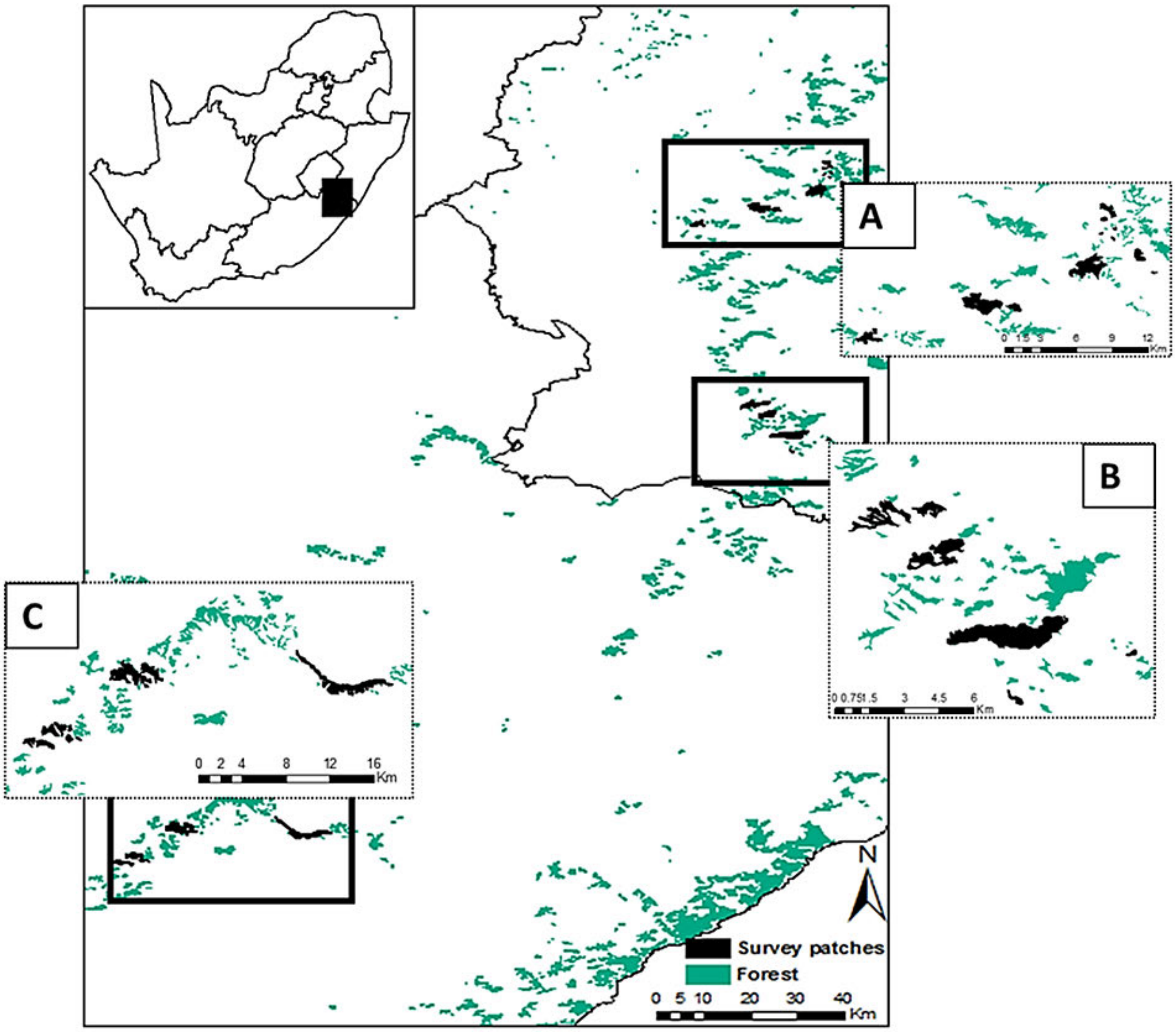

Fig. 5.3 Study area highlighting the three sample regions (A. Creighton; B. Kokstad (Ingeli-Weza); C. Umthatha) of Southern Mistbelt Forest fragments situated in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa, with the distribution of indigenous forest cover shown in green.

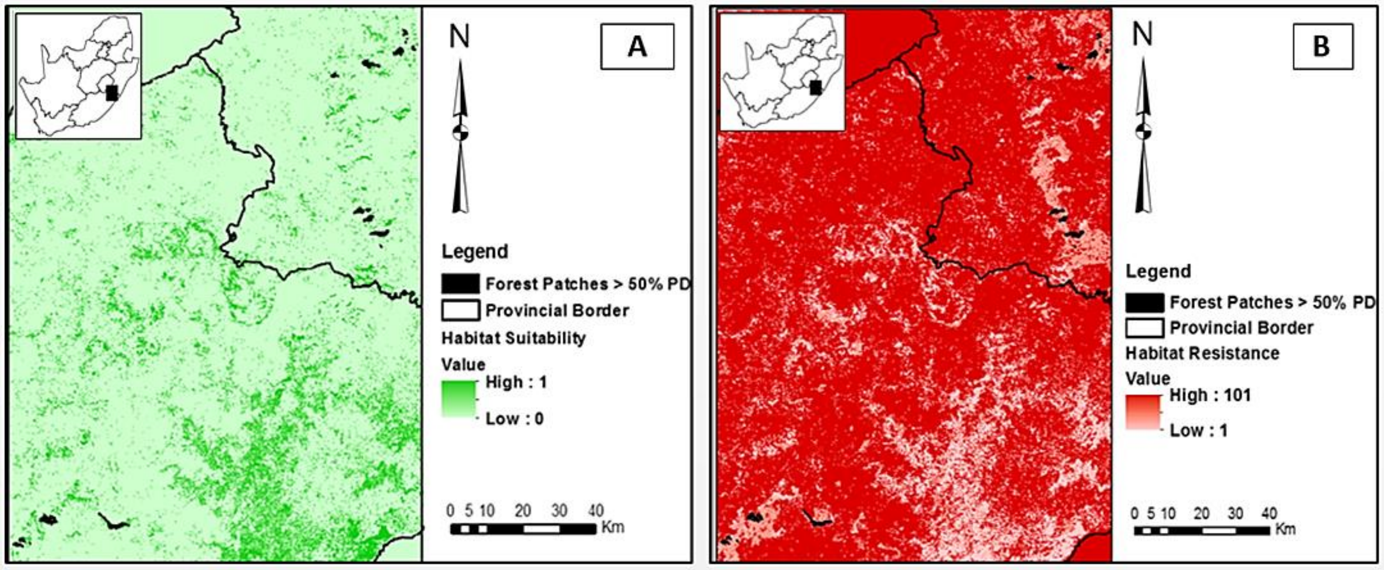

Fig. 5.4 Maps of habitat suitability (A) and habitat resistance (B) calculated using ecological requirements and dispersal capacity of the lemon dove (*Aplopelia larvata*) in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa. Gnarly Landscape Utilities was used for calculations of habitat suitability and resistance scores (McRae et al., 2013).

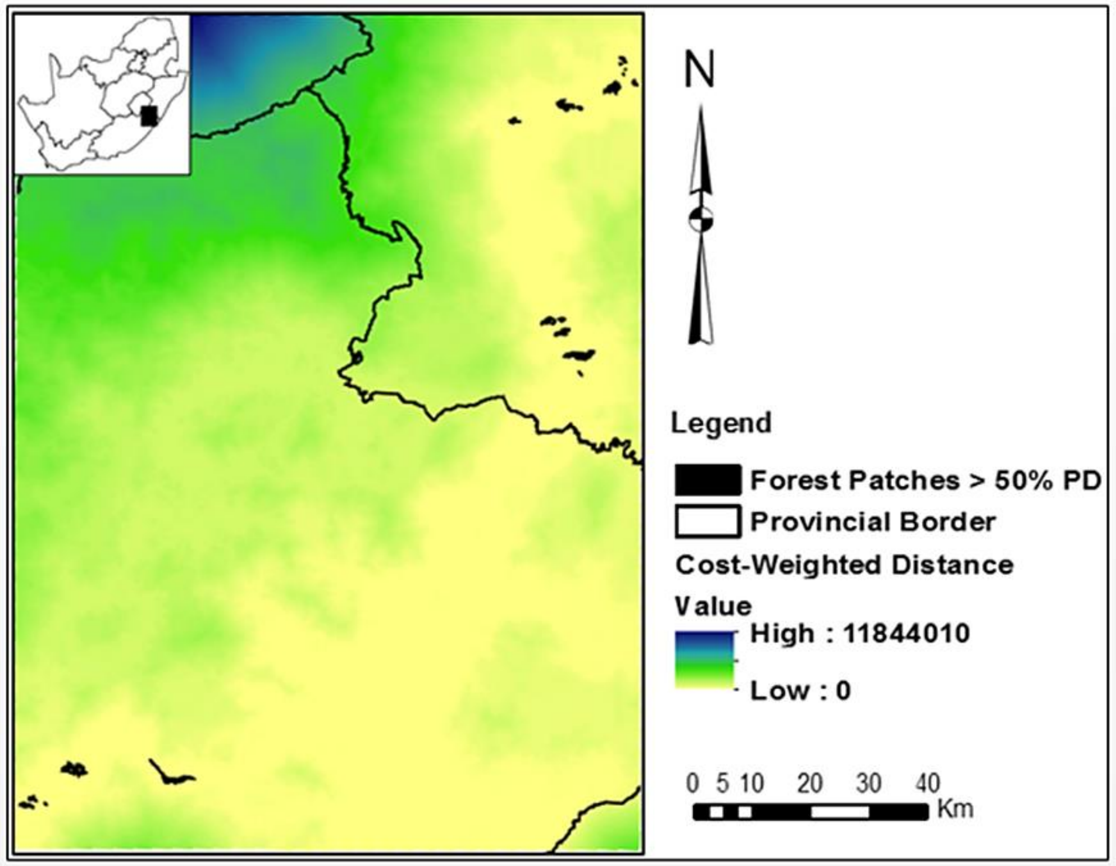

Fig. 5.5 Cost-weighted distances calculated between core Southern Mistbelt Forest patches containing ≥ 50% avian phylogenetic diversity in southern KwaZulu-Natal and northern Eastern Cape, South Africa. Highlighted here are regions of perfect connectivity (0) and no connectivity (11844010) based on habitat suitability and resistance maps, as calculated using Linkage Mapper (McRae and Kavanagh, 2011).

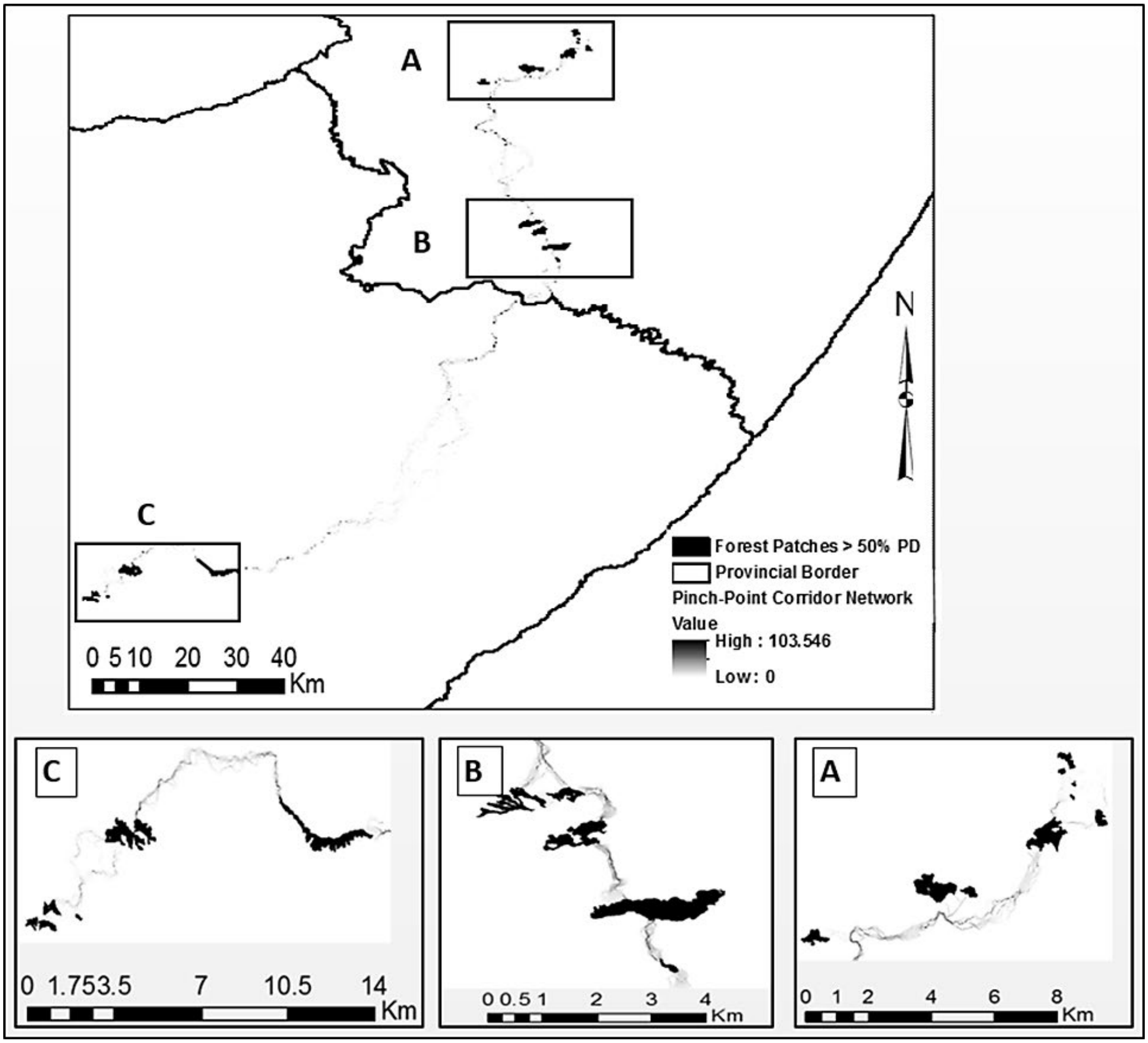

Fig. 5.6 Pinch-point connectivity between core Southern Mistbelt Forest patches containing ≥ 50% avian phylogenetic diversity in three survey regions (A. Creighton; B. Kokstad (Ingeli-Weza); C. Umthatha) situated in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa. Pinch-point revealed corridors that were most constrained, showing areas of maximal (103,546) and no connectivity (0) based on calculations from Pinchpoint Mapper (McRae, 2012a).

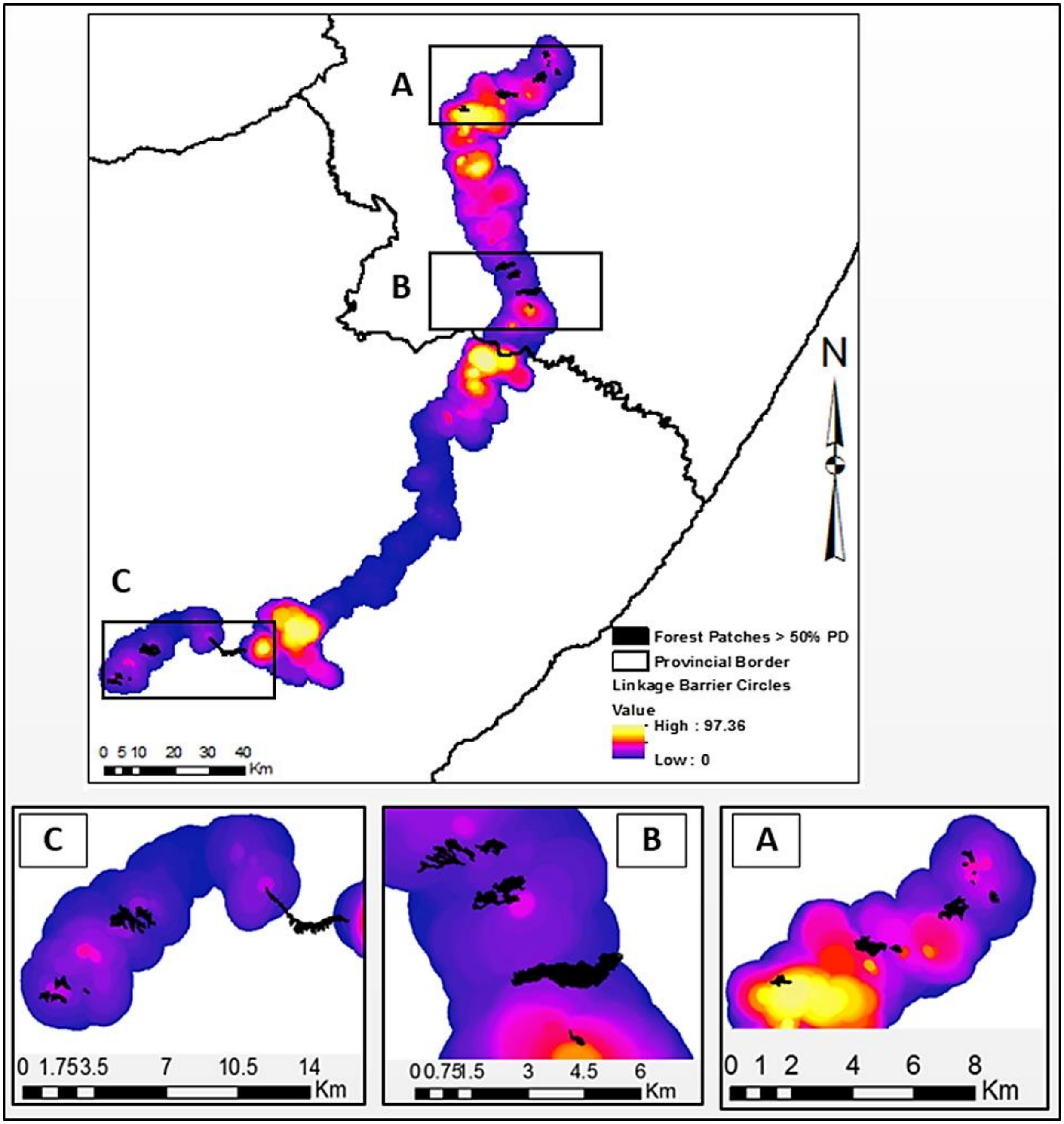

Fig. 5.7 Linkage barrier corridor connectivity between core Southern Mistbelt Forest patches containing ≥ 50% avian phylogenetic diversity in three survey regions (A. Creighton; B. Kokstad (Ingeli-Weza); C. Umthatha) situated in southern KwaZulu-Natal and northern Eastern Cape provinces, South Africa. Barrier circles show the lowest (0) and maximal resistance (97,36), where

areas of high resistance would benefit most from rehabilitation, as calculated using Barrier Mapper (McRae et al., 2012).

5.5 Discussion

We highlight potential habitat connectivity of focal forest fragments provisioning ≥ 50 % avian phylogenetic diversity in core Southern Mistbelt Forest fragments in southern KwaZulu-Natal and northern Eastern Cape provinces. Our findings highlight that Southern Mistbelt Forest fragments are connected in areas of suitable habitat, where there is natural indigenous forest (including contiguous dense forest) cover and have low connectivity in regions of unsuitable surrounding habitat for the surrogate species (i.e. exotic timber plantations, grassland, agriculture, residential land-cover). The importance of matrix features to forest diversity is highly dependent upon its 1) permeability and quality (Prevedello and Vieira, 2010; Vergara, 2011); 2) habitat amount in the landscape (Fahrig, 2013; Salgueiro et al., 2021), and 3) species-specific ecological traits (Rubio and Saura, 2012). For instance, high-quality matrix (i.e. structurally similar to focal habitat) is known to reduce extinction thresholds, especially when native vegetation (forest) is of sufficient cover in the landscape (Swift and Hannon, 2010; Fahrig, 2013; Boesing et al., 2018). Moreover, movement distances tend to be longer, and crossing an inhospitable matrix increases proportionally in fragmented landscapes (Aben et al., 2012). Generally, the surrounding matrix has a greater effect on dispersal-limited species because of their sensitivity to changes in matrix permeability (Castellón and Sieving, 2006; Breckheimer et al., 2014).

The most dominant matrix surrounding Southern Mistbelt Forest fragments in our study regions are commercial exotic timber plantations (Fig. 5.1; Adie et al., 2013). This land-cover type, although categorised as unsuitable for the surrogate species (lemon dove; *Aplopelia larvata*), can have negative or positive effects on forest species, depending on species-specific characteristics (Ewers and Didham, 2006; Cooper et al., 2017). Lemon dove occupancy and extinction probability showed no responses to plantation cover (John and Kabigumila, 2011; Cooper et al., 2017). However, Malan (2014) reported that in forests bordering plantations, our species was found 15-60 m into plantations, driven by seasonal changes (Autumn and not Spring). This was attributed to the feeding behaviour of the species, although it is unknown whether the species forages or nests in plantations (Malan, 2014). Exotic tree plantations can act as connecting corridors among forest patches, thus facilitating the dispersal of some species, and can also improve the diversity of tolerant species when forest cover is reduced in the landscape (Wethered and Lawes, 2005; Aben et al., 2012; Ruffell et al., 2017). Contrary, exotic tree plantations can inhibit the distribution of indigenous forests and restrict the movement of some forest species between habitat patches (Wethered and Lawes, 2003; Pliscoff et al., 2020).

Higher network connectivity was most apparent in the Kokstad region because of the close proximity of core forest fragments which appeared to improve corridor network connection in the landscape. There were lower connectivity corridors in Creighton and Umthatha regions because core patches were more isolated across the landscape, thus limiting the network connection of core patches. Areas with high habitat connectivity promote the movement of individuals, which allows species to use numerous functionally connected habitat patches (Martensen et al., 2012). This is especially true for highly mobile species with a capacity to cross the surrounding matrix of anthropogenic land use (Lees and Peres, 2009; Neuschulz et al., 2013; Vélez et al., 2015; Ramos et al., 2020). Therefore, it is pivotal to promote habitat connectivity as this may minimise the negative influences of habitat loss and fragmentation, especially in fragmented human-altered landscapes (Bregman et al., 2014; Haddad et al., 2015).

Furthermore, this may guarantee the maintenance of phylogenetic diversity (Monteiro et al., 2021), which can safeguard key ecological processes provided by these avian communities. It is well-known that phylogenetic diversity (with or without functional diversity) is an important predictor of biodiversity and is related to ecosystem functioning and stability (Srivastava et al., 2012; Tucker et al., 2017; Faith, 2018).

Contrary, areas of low habitat connectivity can impact the movement of individuals, gene flow and/or survival, subsequently causing loss or changes in ecosystem functionality (Şekercioḡlu et al., 2002; Wilson et al., 2016; Liu et al., 2018). In these areas, effects of habitat fragmentation would intensify, increasing connectivity resistance and severity of pinch-points and barriers, subsequently disrupting individual movement and thus genetic diversity (impacting population integrity) with reduced connectivity (McRae and Kavanagh, 2011; Redford et al., 2011). Also, in less connected habitats, we would expect low species diversity because less connectivity may hinder species from moving freely in the landscape and filtering of barrier sensitive species which are unable to cross unsuitable surrounding matrices (Banks-Leite et al., 2014; Barlow et al., 2016), and a reduced community composition which would mainly consist of a nested subset of the regional species pool (Brown and Sullivan, 2005; Bovo et al., 2018; Luther et al., 2020).

In our survey regions, Kokstad and Umthatha had the lowest connectivity resistance (i.e. barriers). This indicated that the movement of individuals between habitat patches may not be hindered in these regions and is most likely facilitated by indigenous forest cover in the landscape, which may remedy the effects of the impermeable matrix surrounding core forest patches (Heinrichs et al., 2016; Fahrig, 2017; Bueno and Peres, 2019). While the most connectivity resistance was more evident in the Creighton region, we observed that those core patches occurred in areas with low indigenous forest cover and were mostly surrounded by grassland, exotic tree plantations, agriculture and residential land-cover types. It is known that responses to matrix effects are species-specific and tend to favour generalist traits (Ewers and Didham, 2006; Prevedello and Vieira, 2010), as these species have wider diets breadths (Katayama et al., 2014), higher perpetual abilities (Rubio and Saura, 2012), and higher behavioural flexibility (i.e. can cross matrix, travel faster and longer in open habitats, etc.) (Awade and Metzger, 2008; Neuschulz et al., 2013; Ramos et al., 2020). Contrary, species with specialist requirements tend to have high site fidelity and/or low dispersal ability, and these are particularly vulnerable to local extinctions since they will seldom traverse outside forest into the surrounding matrix (Gillies et al., 2011; Bregman et al., 2014; Halstead et al., 2019). As a consequence, this region could lose species and thus phylogenetic diversity, which may negatively affect ecological resilience and ecosystem recovery capacity (Hughes et al., 2020; Monteiro et al., 2021). However, those regions of high connectivity resistance would benefit the most from rehabilitation (McRae et al., 2012).

5.5.1 Conclusions and recommendations

This study used a dispersal restricted, highly specialised forest species as a surrogate to direct habitat connectivity modelling (Alexander et al., 2019; Ehlers Smith et al., 2019). The use of a focal species as a representative for conserving an entire community is an approach that numerous other studies have adopted (Lambeck, 1997; Roberge et al., 2008; Humphrey et al., 2009; Alexander et al., 2019; Ehlers Smith et al., 2019; Colyn et al., 2020). These are generally under the assumption that enforcing connectivity for the most connectivity-demanding focal species will simultaneously ensure the conservation of multiple other species sharing that space (Lambeck, 1997; Breckheimer et al., 2014). This approach has been recommended by some studies (Epps et al., 2011; Rubio and Saura, 2012; Braaker et al., 2014; Ehlers Smith et al., 2019; Lõhmus et al., 2020). We do acknowledge that functional connectivity is a species-specific measure, and using a focal species may not favour others (Koen et al., 2014; Meurant et al., 2018). However, a) unlike the majority of our species pool, there is detailed ecological information available for our surrogate species (*Aplopelia larvata*) (Ehlers Smith et al., 2017a; Gumede et al., 2020); and b) this focal species is the most sedentary and is assumed to be an efficient proxy for other sedentary species of which > 60 % in our community are sedentary (Appendix 5.1). Therefore, we consider our focal species as a potential representative for > 60 % of the species in our community, and meeting the connectivity requirements for this species, may guarantee that others would sufficiently also fulfil their ecological needs in the landscape mosaic of Southern Mistbelt Forest fragments. However, we suggested that these results be implemented with caution since we used a single surrogate species. These findings could change if multiple surrogate species with varying ecological requirements were selected.

Our findings reveal the importance of indigenous forest cover in the landscape for promoting habitat connectivity among core forest patches of fragmented Southern Mistbelt Forest in southern KwaZulu-Natal and northern Eastern Cape provinces. Therefore, we recommend the conservation of indigenous forest as it provides high-quality habitat for the maintenance of forest biodiversity in the fragmented mosaic landscape (c.f. Fahrig, 2013). However, because the natural forest is the smallest biome and only covers a land surface of approx. 7,177 km2 (0.56 %) in South Africa (Low and Rebelo, 1996); we additionally recommend the conservation of thicket/dense bush cover because it is structurally similar, it occurs in close proximity to natural forest, and it is most abundant across the forested landscape of South Africa (Mucina and Rutherford, 2011; Ehlers Smith et al., 2017b). According to Ehlers Smith et al. (2017b), this vegetation type in coastal KwaZulu-Natal contains similar tree species composition (approx. 77 %) to the natural coastal forests (i.e. Indian Ocean Coastal Belt Forest) and is considered a regenerating forest. Moreover, by conserving this vegetation type, habitat connectivity among fragmented forest remnants can be promoted and biodiversity maintained in the landscape (Alexander et al., 2019).

Also, we highlight regions that could greatly benefit from rehabilitation initiatives and improve habitat connectivity in the landscape, particularly those occurring in areas of low indigenous forest cover and are surrounded by increased cover of grassland, exotic tree plantations, agriculture and residential land-cover types. In these areas, we suggest improving matrix quality surrounding habitat patches by increasing vegetation (tree) cover to decrease matrix contrast, thereby encouraging the use of the matrix by forest species and thus ensuring the long-term survival of forest species in fragmented mosaic landscapes (Fahrig, 2001; Swift and Hannon, 2010; Reider et al., 2018).

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5.8 Supplementary information

Appendix 5.1

Bird species occurrence records and selected functional traits in focal Mistbelt Forest fragments of KwaZulu-Natal and Eastern Cape Provinces, South Africa

Scientific name	**Mass (g)**	**Clutch size (cm)**	**Wing length (cm)**	**Tarsus length (cm)**	**Culmen (cm)**	**Tail length (cm)**	**Primary diet**	**Foraging Strata**	**Locomotion ability**	**Habitat Specialisation**
Accipiter melanoleucus	698.99	2.77	316	84.25	31.28	234	Carnivory	Mixed	Sed	NFD
Accipiter rufiventris	198	3	217.5	54	20.75	346	Carnivory	Mixed	Sed	FD
Accipiter tachiro	381	2.2	228.5	66	23.75	187.25	Carnivory	Mixed	Sed	FD
Amblyospiza albifrons	41.59	3.1	92.25	23.5	21.05	67.75	Omnivory	Mid-High	Sed	NFD
Andropadus importunus	27.4	2.02	90.4	23.2	19.4	89.6	Frugivory	Canopy	Sed	NFD
Apalis flavida	8.19	2.9	49.9	19.1	13.6	47	Insectivory	Canopy	Alt	NFD
Apalis thoracica	11.08	2.7	54.05	21.25	14.65	52.35	Insectivory	Mixed	Alt	FD
Apaloderma narina	67.69	2.6	132	16.5	19.25	159.5	Insectivory	Mid-High	Alt	FD
Columba larvata	155	1.89	150.6	26.9	21.3	102.9	Frugivory	Ground	Sed	FD
Batis capensis	11.74	2.1	61.05	20.6	16.35	44.7	Insectivory	Mixed	Sed	FD
Bostrychia hagedash	1238	2.4	248.5	72	123	154.5	Insectivory	Ground	Sed	NFD
Bucorvus leadbeateri	3750	1.85	544	139	199.5	279	Carnivory	Ground	Sed	NFD
Buteo trizonatus	615	2	350.5	67.5	21.6	181	Carnivory	Canopy	Part	FD
Bycanistes bucanitor	642.5	3	275.5	42	124	207	Frugivory	Canopy	Part	FD
Camaroptera brachyura	9.74	2.9	52	19.2	13.5	35.1	Insectivory	Mixed	Sed	FD
Campephaga flava	32.3	1.9	129.25	23.5	19.5	112.5	Insectivory	Ground	Breed	NFD
Cercotrichas leucophrys	20	2.7	69.3	24.4	17.9	64.6	Insectivory	Ground	Sed	NFD
Cercotrichas signata	35	2.8	83.3	26.5	22.4	75.55	Insectivory	Understorey	Sed	NFD
Chalcomitra amethystina	15	1.8	70.55	18	30.8	48	Nectarivory	Mixed	Sed	NFD
Chlorophoneus olivaceus	34	1.6	83.1	25.3	21.75	79.6	Insectivory	Canopy	Alt	NFD
Chrysococcyx caprius	32.79	4	118.9	18.3	17.05	88	Insectivory	Canopy	Breed	NFD
Chrysococcyx cupreus	37.7	3.5	110.25	79	17	91	Insectivory	Canopy	Breed	FD
Chrysococcyx klaas	27.37	3.5	99.2	14.4	16.4	74.7	Insectivory	Mixed	Breed	NFD

Cinnyris chalybeus	8	2.2	52.4	14.75	21.1	43.55	Nectarivory	Mixed	Sed	NFD
Cinnyris talatala	7	2	53.85	16.05	21.55	36	Nectarivory	Mid-High	Nom	NFD
Coccopygia melanotis	7.75	4.7	47.75	13.55	8.6	36.95	Granivory	Ground	Alt	NFD
Colius striatus	51.1	3	92.8	21.6	12.95	207.5	Frugivory	Mid-High	Alt	NFD
Columba arquatrix	400	1.5	223.2	26	24.1	138	Frugivory	Mid-High	Nom	FD
Columba guinea	350	2	229.5	27	22.5	113.5	Granivory	Ground	Sed	NFD
Coracina caesia	65	1.5	129.25	23.5	19.5	112.5	Insectivory	Mixed	Alt	FD
Corvus albus	524	4.1	356	58	57.3	187.5	Omnivory	Ground	Sed	NFD
Corvus capensis	553	3.5	325.5	66	58.5	181.5	Omnivory	Ground	Sed	NFD
Cossypha caffra	28.5	2.4	85.7	30.2	15.7	74.2	Insectivory	Ground	Alt	NFD
Cossypha dichroa	45.81	2.9	98	30.55	20.5	84.4	Insectivory	Mixed	Sed	FD
Cossypha natalensis	34.1	2.9	89.3	27.8	16.8	72.7	Insectivory	Ground	Part	FD
Crithagra scotops	15	3.4	67.6	16.15	10.2	51	Granivory	Mid-High	Sed	FD
Cuculus clamosus	78.8	4.5	176	20.45	22.75	154.5	Insectivory	Mixed	Breed	NFD
Cuculus solitarius	76.73	1	170.5	19.45	20.45	143.75	Insectivory	Ground	Breed	FD
Cyanomitra olivacea	11.5	2	63.5	17.55	26.85	54.9	Omnivory	Mixed	Sed	FD
Cyanomitra veroxii	12	2.2	63.6	18.1	29.2	49.4	Nectarivory	Mid-High	Nom	NFD
Dendropicus fuscescens	26	1.9	92.5	16	12.5	47.5	Insectivory	Mixed	Sed	NFD
Dendropicus griseocephalus	50	2.5	108	18.5	28.5	65.5	Insectivory	Mid-High	Sed	FD
Dicrurus adsimilis	45	2.8	137	22.5	21	120.5	Insectivory	Mixed	Sed	NFD
Dryoscopus cubla	26.23	2.7	80.3	22.5	19.25	66.7	Insectivory	Mixed	Sed	NFD
Euplectes orix	22.97	3	68	20.5	14.95	38	Omnivory	Canopy	Sed	NFD
Francolinus afer	454.81	5.1	193.4	57.05	21.45	96	Herbivory	Ground	Sed	NFD
Hedydipna collaris	8	2.2	50.8	16.15	14.25	35.65	Insectivory	Mixed	Sed	FD
Indicator variegatus	48.76	1	107.5	15.75	12.2	68.35	Nectarivory	Mixed	Sed	FD
Lagonosticta rubricata	10.16	3.7	48.35	15.4	11.3	42.15	Granivory	Ground	Sed	NFD
Laniarius ferrugineus	46.8	2.5	95.95	35.85	24.25	94.8	Insectivory	Mixed	Sed	NFD
Lanius collaris	36.44	3.5	98.9	27.5	20.5	106.5	Insectivory	Ground	Sed	NFD
Lophaetus occipitalis	1067	1.6	389.5	96.3	38.4	209.5	Carnivory	Ground	Sed	NFD
Lybius torquatus	51.7	3.3	91.3	22.3	22.7	55.7	Frugivory	Mid-High	Sed	NFD

Malaconotus blanchoti	78.7	2.9	114	32	28.5	111.5	Carnivory	Mixed	Sed	NFD
Mandingoa nitidula	9.6	5	50	14.5	9.5	31	Granivory	Mixed	Sed	FD
Muscicapa adusta	10.4	2.8	67.7	15.5	14.85	53.9	Insectivory	Mixed	Alt	NFD
Muscicapa caerulescens	17.6	2.8	74.75	16.25	11.5	53.8	Insectivory	Mid-High	Part	FD
Notopholia corruscus	56.07	2.9	108	25.8	21.75	80.5	Frugivory	Mixed	Sed	NFD
Onychognathus morio	132.9	3	146.5	33.65	32.75	130.5	Omnivory	Mixed	Alt	NFD
Oriolus larvatus	66.1	2.4	138.15	22.5	30.6	92.5	Omnivory	Mixed	Alt	NFD
Parus niger	21.5	3.6	82.75	19	11	71.1	Insectivory	Mid-High	Sed	NFD
Phoeniculus purpureus	73.21	3.8	140.5	30.6	49.8	212.1	Insectivory	Mid-High	Sed	NFD
Phyllastrephus terrestris	31.08	2.1	82.7	22.9	21.95	86.6	Omnivory	Mixed	Sed	FD
Phylloscopus ruficapilla	7.7	2.7	53.25	20.1	10.8	42.1	Insectivory	Mixed	Sed	FD
Ploceus bicolor	34.54	3	86.5	23.4	21.85	60	Insectivory	Ground	Sed	FD
Pogoniulus bilineatus	13.1	3.5	56.8	16.5	12.9	30.8	Frugivory	Mid-High	Sed	FD
Pogoniulus pusillus	9.6	2.8	60.1	15.85	12.55	34.25	Frugivory	Mid-High	Sed	NFD
Pogonocichla stellata	18.6	3	84.85	26.4	16.4	69.25	Insectivory	Various	Alt	FD
Poicephalus robustus	343.01	3.5	214.4	21.6	39.55	92.05	Frugivory	Mid-High	Sed	FD
Prinia hypoxantha	10.5	3.1	52.8	22.9	12.9	61.8	Insectivory	Understorey	Alt	NFD
Prinia subflava	8.64	3.1	49.5	20.7	11.7	60.65	Insectivory	Mixed	Alt	NFD
Pternistis natalensis	445	3.9	165.9	47.7	19.9	96	Herbivory	Understorey	Sed	NFD
Pycnonotus tricolor	37.5	2.7	95.4	21.7	19.15	85.05	Frugivory	Mid-High	Sed	NFD
Stephanoaetus coronatus	3640	1.6	499	99.5	48.75	326	Carnivory	Mixed	Sed	FD
Streptopelia capicola	142	1.9	161.75	21.4	15.7	105.6	Omnivory	Ground	Sed	NFD
Streptopelia semitorquata	176	1.8	189	24.6	21.8	125	Omnivory	Ground	Sed	NFD
Sylvia nigricapillus	29.64	2	82.1	24	15.3	83.2	Frugivory	Various	Alt	FD
Tauraco corythaix	308	1.7	185	41.8	23.5	214	Frugivory	Mid-High	Sed	FD
Tauraco porphyreolophus	259	2.3	180.5	40	24.9	197	Frugivory	Mid-High	Sed	FD
Telophorus sulfureopectus	27.1	2	90.7	17	18	90.1	Insectivory	Mid-High	Sed	FD
Telophorus zeylonus	65.02	3.1	98.25	34	26.55	95.65	Insectivory	Mixed	Sed	NFD
Terpsiphone viridis	13.23	2.7	80.7	16	14.8	154.05	Insectivory	Canopy	Breed	NFD
Tockus alboterminatus	223.65	3.5	244.5	33.5	88.5	224.5	Omnivory	Canopy	Sed	FD
Trachyphonus vaillantii	69.4	3.5	101.45	28.45	24.15	85.6	Omnivory	Ground	Sed	NFD

Trochocercus cyanomelas	10.2	2.2	68	17.5	14.4	78.5	Insectivory	Mixed	Alt	FD
Turdus olivaceus	67.29	2.9	113.7	30.4	22.2	83.55	Insectivory	Ground	Alt	NFD
Turtur tympanistria	70.58	1.85	114.85	19.8	15.6	88.25	Granivory	Ground	Sed	FD
Zoothera gurneyi	57.85	1.9	111.8	34.1	23.1	86.9	Insectivory	Ground	Sed	FD
Zosterops virens	13.5	3	62.6	17.9	13.6	47.05	Omnivory	Mixed	Sed	NFD

Locomotion ability categories: Sed (Sedentary), Alt (Altitudinal migrant), Part (Partial migrant), Breed (Breeding migrant), Nom (Nomadic).
Habitat specialisation categories: FD (forest dependent species- forest specialists) and NFD (non-forest dependent species- forest generalists)

Appendix 5.2

Forest Characteristics of surveyed Mistbelt Forest patches in southern KwaZulu-Natal and northern Eastern Cape Provinces, South Africa

Patch	Latitude (S)	Longitude (E)	Region	Area (ha)	Isolation (km)	Phylogenetic diversity (PD)
X0	31°29'27.28"	28°24'32.76"	Mthatha	94.9	29.26624	12.275
X1	31°29'25.36"	28°23'51.27"	Mthatha	64.42	30.94192	12.435
X2	31°29'16.78"	28°27'16.98"	Mthatha	13.76	26.2339	15.755
X3	31°29'11.65"	28°26'22.14"	Mthatha	41.54	27.08369	10.813
X4	31°28'27.51"	28°25'30.01"	Mthatha	124.38	28.3169	13.729
X5	31°28'17.91"	28°25'40.19"	Mthatha	107.65	26.71194	9.8030
X6	31°25'38.67"	28°46'38.85"	Mthatha	634.66	0	18.092
X7	31°25'14.16"	28°32'52.44"	Mthatha	190.26	15.87281	11.795
X8	31°25'25.37"	28°31'34.67"	Mthatha	496.53	17.17425	16.170
X9	31°23'17.76"	28°41'58.04"	Mthatha	62.87	0.03961965	17.133
X10	30°33'40.52"	29°41'17.70"	Ngeli	25	2.660777	11.945
X11	30°32'10.16"	29°45'46.49"	Ngeli	11.97	3.96947	7.7776
X12	30°31'52.17"	29°40'59.87"	Ngeli	732.42	0	22.702
X13	30°28'30.71"	29°38'50.58"	Ngeli	256.78	4.141849	14.541
X14	30°27'9.28"	29°38'19.39"	Ngeli	79.84	7.261737	14.038
X15	30°27'39.48"	29°36'49.57"	Ngeli	192.63	7.394097	14.139
X16	30°2'51.99"	29°30'17.57"	Creighton	139.9	9.120238	13.890
X17	30°2'42.15"	29°31'8.73"	Creighton	17.81	9.170021	7.5079
X18	30°1'9.48"	29°39'39.77"	Creighton	75.52	0.3816471	14.121
X19	30°1'29.62"	29°38'2.40"	Creighton	494.36	0	16.145
X20	29°59'7.44"	29°43'59.38"	Creighton	464.34	7.43902	17.475
X21	29°56'35.05"	29°45'49.48"	Creighton	7.16	13.24905	12.287
X22	29°56'19.52"	29°45'13.39"	Creighton	6.12	12.557	11.035
X23	29°56'3.04"	29°46'2.45"	Creighton	6.89	14.01271	12.906
X24	29°55'30.95"	29°45'16.28"	Creighton	20.49	13.79163	13.248
X25	29°54'35.85"	29°45'31.68"	Creighton	42.6	0.04263	6.8006
X26	29°54'41.90"	29°45'36.30"	Creighton	83.1	14.7685	16.056
X27	29°54'29.93"	29°45'5.76"	Creighton	21.2	0.02906	10.678
X28	29°58'56.25"	29°48'29.96"	Creighton	2.04	15.28958	9.1630
X29	29°58'50.47"	29°48'31.82"	Creighton	1.45	15.69972	5.3005
X30	29°58'46.65"	29°48'24.16"	Creighton	0.24	15.43078	11.307
X31	29°57'30.35"	29°47'15.83"	Creighton	97.38	14.24085	16.132

Isolation distance: mainland patches (i.e., largest patch within each survey region) are delimited by zero; **bold** 'Patch' numbers are the core patches provisioning ≥ 50 % phylogenetic diversity (PD)

Appendix 5.3

Scores of habitat suitability and landscape resistance based on the ecological requirements of the lemon dove for creating maps of habitat and resistance using the Gnarly Landscape Utilities Package

Class ID	Class Description	Habitat value	Resistance value
0		0	100
1	contiguous (indigenous) forest	1	0
2	contiguous low forest & thicket	0.8	0
3	dense forest & woodland	0.7	0
4	open woodland	0	70
5	contiguous & dense plantation forest	0.1	30
6	open & sparse plantation forest	0	90
7	temporary unplanted (clear-felled) plantation forest	0	100
8	low shrubland (other)	0	90
12	sparsely wooded grassland	0	90
13	natural grassland	0	90
14	natural rivers	0	60
15	natural estuaries & lagoons	0	80
16	natural ocean & coastal	0	100
18	natural pans (flooded @ observation times)	0	80
19	artificial dams (including canals)	0	90
20	artificial sewage ponds	0	100
21	artificial flooded mine pits	0	100
22	herbaceous wetlands (currently mapped)	0	100
23	herbaceous wetlands (previously mapped)	0	100
24	mangrove wetlands	0	100
25	natural rock surfaces	0	100
26	dry pans	0	100
27	eroded lands	0	100
29	coastal sand & dunes	0	100
30	bare riverbed material	0	100
31	other bare	0	100
32	cultivated commercial permanent orchards	0	90
34	cultivated commercial sugarcane pivot irrigated	0	100
36	cultivated commercial sugarcane non-pivot	0	100
37	cultivated emerging farmer sugarcane non-pivot	0	100
38	commercial annual crops pivot irrigated	0	100
39	commercial annual crops non-pivot irrigated	0	100
40	commercial annual crops rain-fed / dryland	0	100
41	subsistence / small-scale annual crops	0	100
42	fallow land & old fields (trees)	0.4	20
43	fallow land & old fields (bush)	0	80
44	fallow land & old fields (grass)	0	100
45	fallow land & old fields (bare)	0	100
47	residential formal (tree)	0.6	10

48	residential formal (bush)	0	80
49	residential formal (low veg / grass)	0	100
50	residential formal (bare)	0	100
51	residential informal (tree)	0.6	10
52	residential informal (bush)	0	80
53	residential informal (low veg / grass)	0	100
54	residential informal (bare)	0	100
55	village scattered (bare & low veg/ grss combo)	0	100
56	village dense (bare & low veg / grss combo)	0	100
57	smallholdings (tree)	0.6	10
58	smallholdings (bush)	0	80
59	smallholdings (low veg / grass)	0	100
60	smallholdings (bare)	0	100
61	urban recreational fields (tree)	0.7	0
62	urban recreational fields (bush)	0	70
63	urban recreational fields (grass)	0	100
64	urban recreational fields (bare)	0	100
65	commercial	0	100
66	industrial	0	100
67	roads & rails (major linear)	0	100
68	mines: surface infrastructure	0	100
69	mines: extraction pits, quarries	0	100
71	mine: tailings and resource dumps	0	100
72	land-fills	0	100
73	fallow land & old fields (wetlands)	0	80

CHAPTER 6

Conclusions

6.1 Overview

Forest loss and fragmentation per se are processes that are collectively termed 'fragmentation' since they involve both the loss/reduction and the breaking apart of habitat into other habitat types, which also become embedded in an altered matrix (c.f. Fahrig, 2003). In the past decades, contention has arisen in questioning the extent to which fragmentation per se (i.e. just the breaking apart of the habitat) drives species declines (see Fahrig, 2017; Fletcher Jr et al., 2018; Miller-Rushing et al., 2019). Although effects of forest loss are pervasively negative, those of fragmentation per se are highly variable and tend to be context-dependent (Debinski and Holt, 2000; Ewers and Didham, 2006). According to Fahrig (2017), species responses to fragmentation per se are either weak or significantly positive, but these findings have fiercely been questioned by other studies (Haddad et al., 2017; Fletcher Jr. et al., 2018; Püttker et al., 2020). For example, research authored by Fahrig advocates viewing the effects of habitat loss and habitat fragmentation per se independently, arguing that this will lead to the correct interpretation of fragmentation effects (Fahrig, 2003; 2017; Fahrig et al., 2019). However, this has been criticized based on the collinearity of both processes in real-world landscapes (Ruffell et al., 2016; Fletcher Jr et al. 2018) and the non-linear interaction of habitat fragmentation effects at low (0-30%; Andrén, 1994) to intermediate levels (30-60%; Püttker et al., 2020) of habitat amount gradient (see Villard and Metzger, 2014). Also, dismissing the negative effects of habitat fragmentation per se (c.f. Fahrig, 2017, 2019; Fahrig et al., 2019) has been considered premature and unsafe (Püttker et al., 2020).In fragmented terrestrial landscapes, biodiversity patterns within habitat patches are predicted to conform to two contrasting theories: the traditional island biogeography theory (MacArthur and

Wilson, 1967; Cook et al., 2002) or the habitat amount hypothesis (c.f. Fahrig, 2013). These theories differ based on their recognition of the importance of the surrounding matrix in influencing species persistence in habitat patches. The former theory views the matrix as hostile/inhospitable (similar to oceanic islands), while the latter identifies the surrounding matrix as a determining factor that variably affects species dispersal among habitat patches depending on the degree of matrix permeability (Prugh et al., 2008; Fahrig et al., 2011; Thompson et al., 2017). The habitat amount hypothesis challenges the patch-level concept (i.e. patch-size and patch isolation distance) of the traditional theory, arguing that local biodiversity patterns are only influenced by the surrounding habitat amount (and not habitat configuration). That is, species occupying small and isolated habitat patches would still persist based on habitat amount in the surrounding landscape. Therefore, there is a growing recognition that the persistence of species in fragmented landscapes will largely depend upon the degree of landscape connectivity to aid species movement and colonisation of disjunct patches (Schnell et al., 2013; Auffret et al., 2015; Hatfield et al., 2018; Donald et al., 2019). This is particularly because fragment communities are finding themselves having to persist in forest remnants increasingly isolated by the surrounding anthropogenic matrix in fragmented landscapes.

The indigenous forest biome in South Africa offers a unique opportunity to study the effects of forest fragmentation, landscape habitat amount and connectivity because of the naturally fragmented characteristic of these forests. Forest fragmentation occurred as early as the Quaternary and was driven by paleoclimatic fluctuations during the Last Glacial Maximum (approx.18 000 years ago) which determined the distribution and extent of forests in the region (Lawes, 1990; Partridge, 1997; Eeley et al., 1999). Further historical fragmentation occurred during the Colonial era and was driven by pervasive logging practices throughout the forested region (Adie et al., 2013). Presently, increasing anthropogenic activities in the surrounding landscape of forest remnants continues to isolate forest fragments. Therefore, this research aimed to reveal local and landscape predictors of avian community diversity facets in the naturally fragmented Southern Mistbelt forests of KwaZulu-Natal and Eastern Cape, South Africa.

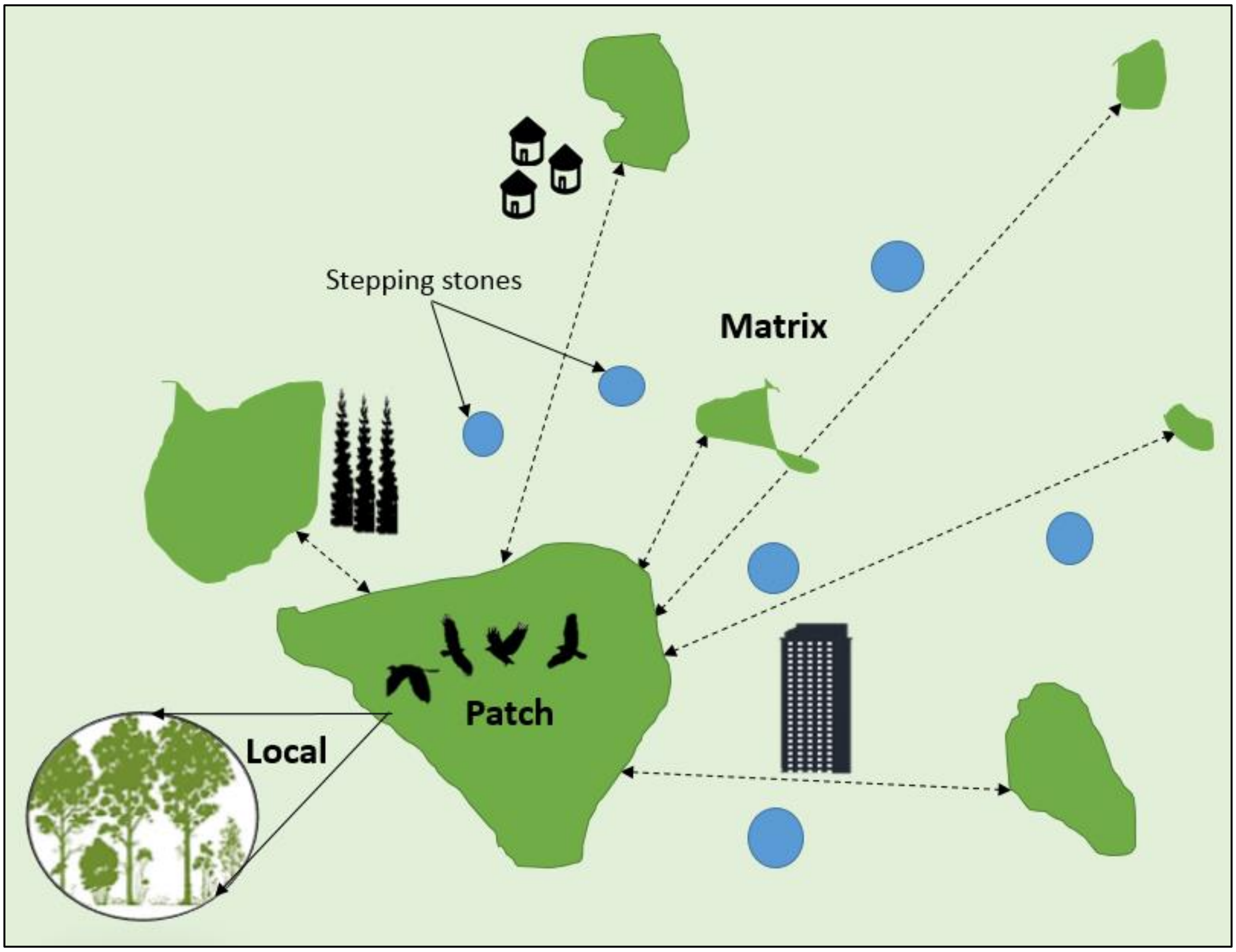

Fig. 6.1 A graphical summary abstract of the Chapter 3 study that aimed to determine responses of local avian multifaceted (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) diversity to the effects of landscape composition (matrix quality), habitat fragmentation (decreasing fragment size and increasing isolation distance), and local habitat heterogeneity (forest-structural complexity) in the naturally fragmented Southern Mistbelt forest fragments.

6.2 Research findings

The Chapter 3 study aimed to determine responses of local avian multifaceted (taxonomic, functional, phylogenetic and functional-phylogenetic diversity) diversity to the effects of landscape composition (matrix quality), habitat fragmentation (decreasing fragment size and increasing isolation distance), and local habitat heterogeneity (forest-structural complexity) in the naturally fragmented Southern Mistbelt forest fragments (Fig. 6.1) It was found that the surrounding matrix quality had significantly positive effects on functional and phylogenetic diversity; habitat fragmentation had a significantly negative influence on the multiple diversity facets; and local vegetation complexity unexpectedly caused a decline in the diversity facets of forest specialist assemblages (Chapter 3).

The Chapter 4 study aimed to reveal the effects of landscape drivers (habitat amount, landscape (matrix) heterogeneity and average isolation distance) on forest bird (α) taxonomic richness and functional richness of community and forest specialist assemblages (Fig. 6.2). The findings revealed that habitat amount in the landscape was the main significant positive predictor of local forest bird diversity for both assemblages (Chapter 4). Additionally, habitat amount was the most important landscape predictor based on model Akaike's weight. However, no significant influences of the average isolation distance and landscape heterogeneity on local avian diversity were found (Chapter 4).

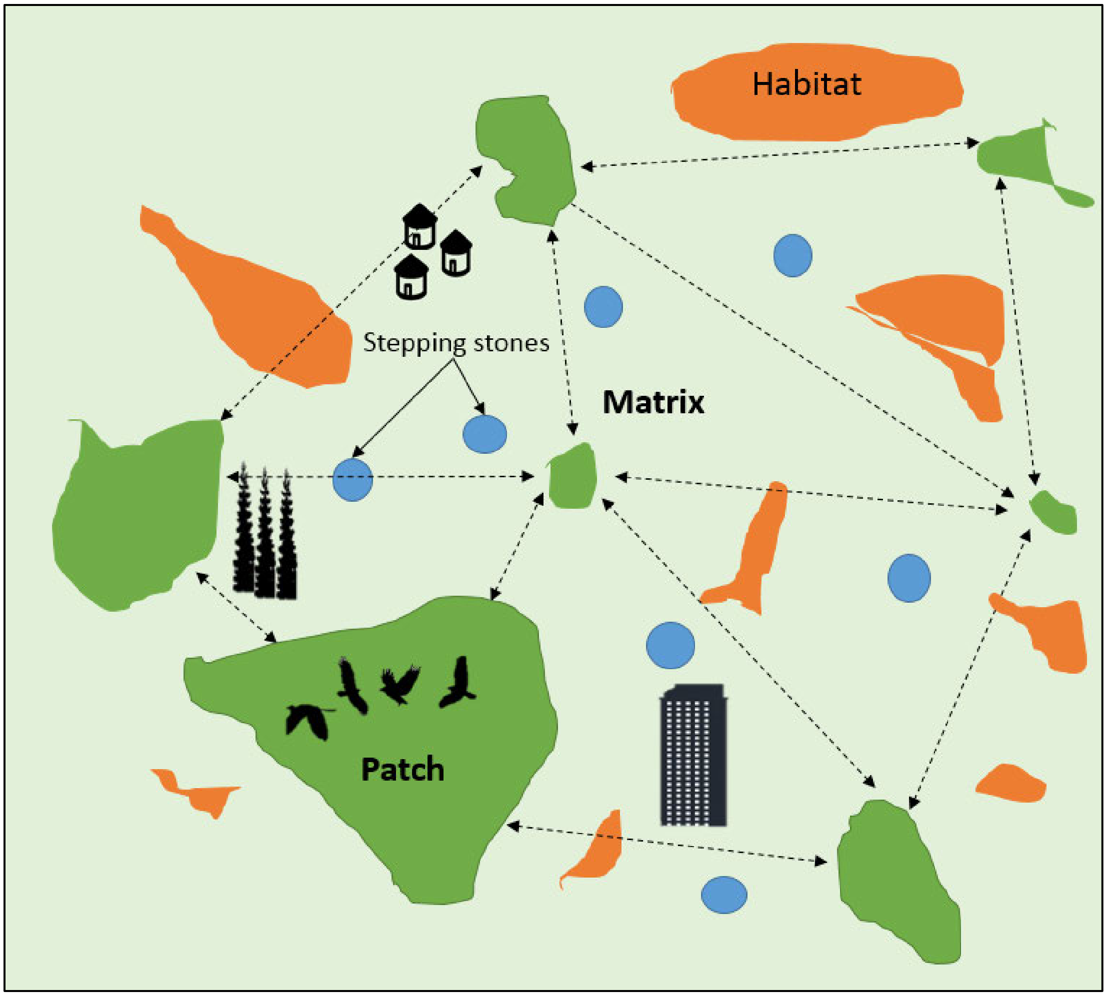

Fig. 6.2 A graphical summary abstract of the Chapter 4 study that aimed to reveal the effects of landscape drivers (habitat amount, landscape (matrix) heterogeneity and average isolation distance) on forest bird (α) taxonomic richness and functional richness of community and forest specialist assemblages.

The Chapter 5 study aimed to assess the potential habitat connectivity of core Southern Mistbelt Forest patches provisioning ≥ 50 % avian phylogenetic diversity using a hybrid of least-cost pathway and ecological circuit theory for the connectivity approach (Fig. 6.3). The findings revealed the importance of indigenous forest cover in the landscape for promoting habitat connectivity among core forest patches of fragmented Southern Mistbelt Forests because regions of connectivity corresponded with areas of indigenous forest cover (suitable habitat) and regions of low connectivity we observed habitat cover types that were unsuitable (i.e. exotic timber plantations, grassland, agriculture, and residential land-cover) (Chapter 5).

Fig. 6.3: A graphical summary abstract of the Chapter 5 study that aimed to assess the potential habitat connectivity of core Southern Mistbelt Forest patches provisioning ≥ 50 % avian phylogenetic diversity using a hybrid of least-cost pathway and ecological circuit theory for the connectivity approach; where 'low-high' represents resistance to movement.

6.3 Conclusions and recommendations

The present research results expand the results of previous studies by addressing the multi-faceted nature of species diversity, in contrast to using a single or just a few measures of community diversity to quantify the fragmentation-diversity relationship (Chapter 3). Patch-level fragmentation effects (i.e. decreasing fragment size and increasing isolation distance) indicate the importance of large and connected forest fragments in conserving/ maintaining diversity facets of local avian assemblages in the Southern Mistbelt forest system. However, it also highlighted the importance of the surrounding matrix quality in mediating the negative effects of habitat fragmentation (i.e. decreasing fragment size and increasing isolation distance) on local forest bird diversity (c.f. Fahrig, 2003; 2013; 2017). Therefore, improving the quality of the surrounding matrix may conserve the ecological and evolutionary integrity of local forest specialist species and whole community assemblages in the fragmented Southern Mistbelt Forest system.

The results provide a relevant contribution to understanding how landscape configuration affects biodiversity and important insights into naturally fragmented ecosystems (Chapter 4). They provide evidence supporting the habitat amount hypothesis (Fahrig, 2013) in the naturally fragmented study system. Thus, the results highlight the need to preserve or increase landscape habitat if the positive effects of forest cover are to be maintained to conserve local avian diversity in naturally fragmented forest landscapes.

Regarding habitat connectivity (Chapter 5), it is recommended that indigenous forest be conserved as it provides high-quality habitat and connectivity of focal habitat patches to maintain forest biodiversity in the fragmented mosaic landscape (c.f. Fahrig, 2013). However, because of the low amount of forest cover in South Africa (< 1 %; Low and Rebelo, 1996), it is also recommended that there is conservation of the structurally similar thicket/dense bush cover as it is more abundant (approx. 77 %) and it occurs in close proximity to natural forest (Mucina and Rutherford, 2011; Ehlers Smith et al., 2017). Regions that could benefit most from rehabilitation were identified, specifically those regions with low forest cover. Thus, the need to improve matrix quality in surrounding regions by decreasing matrix contrasts with increasing vegetation (tree) cover is highlighted, which could encourage some forest species to use the matrix and thus ensure the survival and persistence of forest species in fragmented mosaic landscapes (Fahrig, 2001; Swift and Hannon, 2010; Reider et al., 2018).

The protection of biodiversity is the main theme that links sustainable development goals and has an undeniable role in the pursuit of sustainable development worldwide (CBD Secretariat, 2014). Moreover, the Convention on Biological Diversity (CBD) highlights the need to reduce direct causes of species declines and safeguard species diversity as a means of improving biodiversity and achieving the Aichi Biodiversity goals (i.e. Target 5: reducing habitat loss and fragmentation). As an option to policy-makers, we recommend preserving and increasing forest cover in the landscape, particularly where most forest cover has been lost, to improve matrix quality and habitat connectivity. This will ensure that the increasing vulnerability of these fragmented forest landscapes will be reduced and ultimately lead us towards progress in attaining targets of biodiversity and sustainable development (CBD Secretariat, 2014).

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