

Comparative Impacts of Fragmentation on Birds in Two Bioregions in a Biodiversity Hotspot, the Cape Floristic Region.

by

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Thesis presented in partial fulfilment of the requirements for the degree of Master of Science (Conservation Ecology).

at

Stellenbosch University



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Date: March 2009

DECLARATION

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ABSTRACT

Habitat loss and fragmentation are two of the most pressing threats to biodiversity. Avifaunal diversity and integrity is under immense pressure from these two processes. We have made major advances in our understanding of avifaunal responses to habitat fragmentation, but mostly focus on either fragment scale and/or landscape scale influences of fragmentation on birds. A more comprehensive approach to assessing the impacts of fragmentation was used in this study. The avifaunas of two different geographical regions and bioregions were surveyed and a multi-scale analysis of avifaunal responses to fragmentation was attempted. The study sites include the West Coast and East Coast Renosterveld Bioregions in the Cape Floristic Region, South Africa. Assemblage shifts, feeding guild compositional changes, species abundance variation and species persistence were examined at the three spatial scales. Time- and distance-restricted point counts were used to document birds that were directly dependent on the habitat fragments. Forty fragments were selected in each bioregion and a once-off snapshot of the avifaunal richness and diversity was obtained.

Results indicate that the avifauna of the two bioregions responded differently to habitat fragmentation. In the East Coast Renosterveld Bioregion, the assemblages, guild composition and species abundances were most accurately predicted by landscape configuration. An assemblage shift occurred at 20 ha fragment area, compared to the 50 ha fragment area threshold of the West Coast Renosterveld Bioregion's avifauna composition. In the West Coast Renosterveld Bioregion, fragment area was the better predictor of assemblage, guild composition and species abundances. However in both bioregions, the persistence of common species was equally sensitive to area and landscape scale effects.

If the influence of fragmentation is assessed from a multi-scale perspective, it becomes clear that its impacts on biodiversity and specifically avian diversity are complex. The conservation of large fragments is crucial to the conservation of avian integrity. However, a more even, homogenous distribution of fragments is no less important, as in the case of the East Coast Renosterveld Bioregion. Landscape configuration is essential in the persistence of metapopulations, as it facilitates dispersal of individuals, making more fragments accessible to

both sensitive and common species. Area effects become more prominent in landscapes that have less evenly arranged fragments.

Conservation of reserve networks, focussing on landscape scale conservation and incorporating stepping-stone fragment to connect larger fragments are indeed important to succeed in the effective protection of biodiversity. Future research, especially on avian integrity, should focus more on multi-scale approaches to reveal how patterns changes as landscape elements differ from region to region.

OPSOMMING

Habitat vernietiging en fragmentasie word tans as die twee grootste bedreigings tot biodiversiteit beskou. Voël-diversiteit en spesie-rykheid word spesifiek deur habitat vernietiging en fragmentasie bedreig. Die empiriese navorsing het uitmuntige vooruitgang gemaak in die begrip oor hoe fragmentasie voël-diversiteit benadeel. Daar is egter 'n gebrek in die literatuur – meeste studies fokus op die fragment- en/of landskap-vlak drywers. In dié betrokke studie word daar egter van 'n wyer benadering gebruik gemaak. Die effekte van fragmentasie op die voël-diversiteit van die Weskus Renosterveld en Ooskus Renosterveld Biostreke word geëvalueer op 'n fragment-, landskap- en biostreek vlak. Dié twee biostreke is egter geografies van mekaar geskei, en daarom fokus dié studie op drie ruimtelike-vlakke van fragmentasie. Die Weskus Renosterveld en Ooskus Renosterveld Biostreke vorm deel van die hoogs unieke Kaapse Floristiese Koningryk.

Binne die twee biostreke se voël-samestellings word vier aspekte bestudeer, i) algehele samestelling, ii) voedings-groep samestelling, iii) individuele spesie variasie in hoeveelhede en iv) die waarskynlikheid van spesie voortbestaan in die landskap. Veertig fragmente binne beide biostreke was geselekteer. Voël-data was bekom deur gebruik te maak van 'n enkele punt-telling in elke fragment. Dié punt-tellings was onderhewig aan 'n observasie afstand en tyd beperkinge. Slegs voëls (individue) wat direk afhanklik van die observasie-punt was, was in die studie gebruik.

Die resultate van die studie toon op aansienlike variasie tussen die twee betrokke biostreke. In die Ooskus Renosterveld Biostreek word landskap samestelling en konfigurasie as die mees beduidende faktor beskou in spesie-samestelling, voeding-groep samestelling en individuele spesie hoeveelheid variasie. 'n Samestelling-drempel van 20 ha in fragment grote was verkry vir dié biostreek, dit is kontrasterend met die 50 ha samestellings-drempel van die Weskus Renosterveld Biostreek. Die hoër samestelling-drempel van laasgenoemde word egter verklaar deur die sterk invloed van fragment grote in dié biostreek. Fragment grote was die mees beduidende faktor in spesie-samestelling, voeding-groep samestelling en individuele spesie hoeveelheid variasie. In die geval van waarskynlikheid van spesie voortbestaan in die landskap

word beide landskap konfigurasie en fragment grote as ewe belangrike indikators beskou in die twee bestudeerde biostreke.

Die veelvuldige ruimtelik-benadering wat in dié studie gevolg was het op uiterse belangrike verskille afgeloop in hoe die voël spesies en spesie-samestellings binne die twee biostreke verskil. Die Weskus Renosterveld Biostreek dui op die belang van die bewaring van groot habitat fragmente. Daarteenoor, dui die Ooskus Renosterveld Biostreek analise op die belang van landskap samestelling en konfigurasie. Die verskille word beter verstaan as die verskille in konfigurasie van die twee biostreke waargeneem word. Landskap konfigurasie is krities in die instandhouding van metapopulasies in gefragmenteerde landskappe. Konfigurasie kan die beweging van individue in en deur die landskap bevorder, of inhibeer. Laasgenoemde kan 'n groot rol speel in die voortbestaan van spesies in dié landskappe. Fragment grote word egter belangrik as die konfigurasie van die landskap nie beweging in die landskap kan fasiliteer nie. Bewaringsmaatreëls moet fokus op reservaat-netwerke wat beweging tussen groot fragmente bevorder. Daar word egter nog baie navorsing van 'n veelvoudige ruimtelike perspektief verlang ten einde dié patrone beter te verstaan.

The goal of life is living in agreement with nature.

-Diogenes Laertius -

**This thesis is a tribute to my sister, Carli Kieck
(05/09/1980 – 12/06/2004). You were a great
inspiration and are dearly missed. The memory of
you will remain alive in my heart for forever.**

ACKNOWLEDGEMENTS

I would like to thank my three supervisors, Dr. C.B. Krug, Professor M.J. Samways and Dr. P. Lloyd. Thank your for all your hard work that went into this project, your assistance, you patience, and above all, your faith in me. Without your guidance and help this project would not have been a possible.

I would like to thank the BIOTA (BMBF) Biolog: Southern Africa Project and the German Ministry of Research and Education for making this project possible both financially and logistically. My thanks also to the Ethel and Ernest Erikson Trust for giving additional funding for my studies; I truly appreciate your support. Thanks to the two academic institutions that provided me with ample, high standard resources, Stellenbosch University (SU) and the University of Cape Town (UCT). I would like to thank the Department of Conservation Ecology and Entomology at SU, in particular, for giving me this opportunity.

To other people who contributed to this success of this thesis – Dr. R. Krug and Prof. D. Nel (statistics), Ms O. Curtis (fieldwork assistance) and all the private landowners who allowed me to conduct my research on their property – many, many thanks. Especially to ms Christy Momberg, thank you for the proofreading of the entire thesis.

To my friends and family who stood by me during the tough times of these last two years, for believing in me and for encouraging me – thank you very much. It is because of you, who have carried me through these years that I owe my success to. Dave Pepler, my great friend and mentor, thank you for your invaluable wisdom and knowledge you have shared with me over last seven years and for believing in my abilities. To Anél, my fiancé, you were a pillar of strength through these two years for me; I appreciate every thing you have done.

Then lastly, but most importantly, I praise the Lord in heaven for giving me the intellect, the ability and the determination to accomplish this great feat.

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1. GENERAL INTRODUCTION

1.1. INTRODUCTION

Human modification of natural habitats through, for example, agriculture, urbanization and pollution, leads to extensive transformation of natural habitats. The resulting loss and fragmentation of natural habitats have serious repercussions on biodiversity (Andrén, 1994), and some authors now regard habitat transformation and fragmentation as some of the most pressing threat to biological systems (Tscharntke et al., 2002; Ewers and Didham, 2006).

The lowlands of the Cape Floristic Region (CFR) in South Africa have been, and still are, under severe pressure from human activities. Agricultural expansion, urban sprawl and alien invasive plants are three of the biggest drivers of habitat loss and fragmentation in this region and emerging threats such as climate change will only compound the conservation crisis (Rouget et al., 2003). The CFR is one of the smallest of the 34 designated biodiversity hotspots (87,892km²), but it boasts more than 9,000 plant species, of which 70% are endemic and 1,406 are listed in the International Union for Conservation of Nature (IUCN) Red Data Book. This is the highest concentration of rare plant species worldwide (Rouget et al., 2003; Giliomee, 2006). Furthermore, the CFR is recognised as one of WWF's "Global 200", a Terrestrial Ecoregion, of which there are 867 (Olson et al., 2001) with a critical/endangered global conservation status (Pressey et al., 2003). Renosterveld, a grassy shrubland with a high diversity of endemic geophytes (Winter et al., 2005), is the most threatened and severely fragmented habitat type within this region; only 6% of the original extent of 16,490 km² remains in roughly 18,000 fragments embedded in a predominantly agricultural landscape (von Hase et al., 2003; Winter et al., 2005). In addition, less than 1% of the remaining Renosterveld is currently under statutory protection.

Successful and efficient conservation and management of species in a fragmented landscape is a Herculean task, as the fragmentation process creates patches that can be too small and/or too isolated to enhance or conserve biodiversity in human-dominated landscapes (Tscharntke et al., 2005; Reed, 2004). Conservation planning therefore needs to be carefully conducted, and conservation beyond the borders of statutory reserves is becoming more and more important in mosaic landscapes (Dudley et al., 2005). For Renosterveld, there are now

various attempts to encourage private landowners to make fragments of their property available to nature conservation. Initiatives such as the Stewardship Programme of CapeNature, the provincial nature conservation administration of the Western Cape Province are a critically important in this context (Pressey et al., 2003; Winter et al., 2005).

Although habitat fragmentation per se is a simple process that entails the break-up of continuous habitat into small habitat fragments, or remnants, scattered across the landscape (Fahrig, 2003; Begon et al., 2003), its effects on biodiversity and ecological processes are immensely complex (Fahrig, 2003). Various taxa have been studied at community, population and species level to understand how they are influenced by fragmentation. Birds have received ample attention in the fragmentation literature. Although most bird studies have been conducted in the tropics (e.g. Baily, 2007; Ferraz et al., 2007; Antongiovanni and Metzger, 2005; Bortons et al., 2003; Cornelius et al., 2002; Boulinier et al., 2001; Catterall et al., 1998), results from other vegetation types (e.g. grasslands, Winter et al., 2006) have confirmed the patterns observed. Avian species richness and diversity increase with fragment size (Ferraz et al., 2007; Pavlacky and Anderson, 2007; Bender et al., 1998), while isolation effects are more prominent than area effects in determining species level pattern (Winter et al., 2006; Chace and Walsh, 2006). Edge effects lead to secondary threats such as increased nest predation and brood parasitism (Ewers and Didham, 2006). The persistence of many bird species is dependent on the conservation strategies implemented on a landscape scale, rather than a patch scale (Sinclair and Byrom, 2006; Marini and Garcia, 2005; Petit and Petit, 2003; Olson et al., 2002). Pimm et al. (2006) estimate that of the 2,821 bird species that are endemic to the original 25 global biodiversity hotspots, 1,250 may be lost by the year 2100, and that at the same year 6-14% of all historic species could be extinct and 7-25% functionally extinct (Şekercioğlu et al., 2004).

The conservation of bird species on a landscape scale is crucial, as birds fulfil a diverse range of ecological functions such as pollination, seed dispersal and predation (Şekercioğlu 2006; Gil-Tena et al., 2007). Birds are among the most successful and efficient mobile links in any ecosystem, transporting floral genetic material, via pollination or seed dispersal, between populations, while insectivores are crucial in managing insect populations and controlling crop pests (Şekercioğlu 2006; Gil-Tena et al., 2007; Kremen et al., 2007). Predation is another very important role, fulfilled by avian predators, to maintain healthy levels of rodent pests (Şekercioğlu 2006; Gil-Tena et al., 2007). However, those guilds that play some of the most important roles in ecosystem function, namely frugivores, herbivores, omnivores, piscivores and scavengers, are most vulnerable to extinction (Şekercioğlu et al.,

2004). Although insectivores, as a guild, are less susceptible to extinction, it is the guild with the highest proportion of extinction-prone species.

Considering the scale of habitat fragmentation in Renosterveld and the important role that birds play in ecosystem function, a thorough investigation of the effects of habitat fragmentation on bird communities in lowland Renosterveld is required. This study will focus on two highly fragmented and threatened vegetations, the shrublands of the West Coast Renosterveld Bioregion and the East Coast Renosterveld Bioregion (Mucina and Rutherford, 2006) (WCRB and ECRB, respectively), it aims to 1) identify the key factors underlying the responses to fragmentation of bird assemblages within the WCRB and the ECRB, 2) determine how individual species and feeding guilds respond to fragmentation effects and identify the underlying mechanisms, and 3) make suggestions for potential conservation strategies to maintain functionally important groups in a mosaic landscape. I should, however, point out that the study presented here will not be a mere replication of the latter work done by Cameron (1999) and Randrianasolo (2003). Both of these studies investigated fragmentation effects, but at a local scale, keeping their field surveys within the boundaries on a single bioregion. I will focus on Renosterveld in two different bioregions, hence making inferences to how fragmentation effects differ across vast regional scales.

1.2. THESIS OUTLINE

Chapter 1, above is a brief introduction to the topic of fragmentation effects on bird assemblages. I will be investigating the influence of fragmentation on the composition of avifaunal assemblages and on common species abundances. In this chapter, this topic is set against the framework of the literature, placing my work into context with the greater debate within conservation biology literature.

Chapter 2 reviews past and present literature regarding habitat fragmentation and its effects on biodiversity in general, and bird diversity specifically. Within this chapter, the predictions and hypotheses tested are presented.

Chapter 3, the first results chapter, concerns the effects of fragment and landscape scale pattern and influences on the avifaunal assemblages of the West- and East Coast Renosterveld Bioregions. This chapter takes a deeper look at how finer scale components within assemblages, e.g. feeding guilds, respond to area and landscape configuration effects, and makes comparisons at the gamma-diversity scale.

In *Chapter 4*, probability of occupancy of the generalist species within the WCRB and ECRB is examined, includes how common species abundances reacted to fragmentation and changes in habitat quality. The occupancy of these species is evaluated across fragment area and landscape configuration.

Chapter 5 integrates the essence of chapters 3 and 4 and puts the results in the context of the greater question of how to integrate research into conservation practice.

This thesis is written in scientific paper format, each results chapter follows the format of an individual paper, with an introduction, materials and methods, results and discussion section. References in this thesis follow the format of the journal *Biological Conservation*.

1.3. REFERENCES

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.
- Antongiovanni, M., Metzger, J.P., 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation* 122, 441-451.
- Baily, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238, 7-23.
- Begon, M., Harper, J.L., Townsend, C.R., 2003. *Ecology*. Blackwell Publishing. Oxford.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: meta-analysis of the patch size effect. *Ecology* 79, 517-533.
- Bestelmeyer, B.T., Weins, J.A., 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* 6, 1225-1240.
- Bortons, L., Mönkkönen, M., Martin, J.L., 2003. Are fragments islands? Landscape context and density-area relationships in Boreal forest birds. *The American Naturalist* 162, 343-357.
- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H., Pollock, K.H., 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 84, 1159-1169.
- Cameron, A., 1999. The effects of fragmentation of renosterveld vegetation on bird community composition. M.Sc. Thesis, University of Cape Town.
- Catterall, C.P., Kingston, M.B., Park, K., Sewell, S., 1998. Deforestation, urbanization and seasonality: interacting effects on a regional bird assemblage. *Biological Conservation* 84, 65-81.
- Chace, J.F., Walsh, J.J., 2006. Urban effect on native avifauna: a review. *Landscape and Urban Planning* 74, 46-69.
- Cornelius, C., Cofré, H., Marquet, P.A., 2002. Effects of habitat fragmentation on bird species in a relict forest in semiarid Chile. *Conservation Biology* 14, 534-543.
- Dudley, N., Baldock, D., Nasi, R., Stolton, S., 2005. Measuring biodiversity and sustainable management in forest and agricultural landscapes. *Philosophical Transactions of the Royal Society of London B* 360, 457-470.

- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117-142.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of the Ecology, Evolution and Systematics* 34, 487-515.
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard Jr., R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315, 238-241.
- Giliomee, J.H., 2006. Conserving and increasing biodiversity in the large-scale, intensive farming systems of the Western Cape, South Africa. *South African Journal of Science* 102, 375-378.
- Gil-Tena, A., Saura, S., Bortons, L., 2007. Effects of forest composition and structure on bird species richness in a Mediterranean context: implications for forest ecosystem management. *Forest Ecology and Management* 242, 470-476.
- Hanson, T.R., Newmark, W.D., Stanley, W.T., 2007. Forest fragmentation and predation on artificial nests in the Usambara Mountains, Tanzania. *African Journal of Ecology* 45, 499-507.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters* 10, 299-314.
- Marini, M.A., Garcia, F.I., 2005. Bird conservation in Brazil. *Conservation Biology* 19, 665-671.
- Mucina, L., Rutherford, C., Eds, 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial Ecoregions of the world: a new map of life on earth. *BioScience* 51, 933-938.
- Olson, D.M., Dinerstein, E., Powell, G.V.N., Wikramanayake, E.D., 2002. Conservation biology for the biodiversity crisis. *Conservation Biology* 16, 1-3.
- Pavlacky, D.C., Anderson, S.H., 2007. Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? *Animal Conservation* 10, 57-68.

- Petit, L.J., Petit, D.R., 2003. Evaluating the importance of human-modified lands for Neotropical bird conservation. *Conservation Biology* 17, 687-694.
- Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç.H., Ehrlich, P.R., 2006. Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 103, 10941-10946.
- Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* 112, 99-127.
- Randrianasolo, H., 2003. Birds in west coast renosterveld fragments: implications for a threatened habitat. M.Sc. Thesis, University of Cape Town.
- Reed, D.H., 2004. Extinction risk in fragmented habitats. *Animal Conservation* 7, 181-191.
- Rouget, M., Richardson, D.M., Cowling, R.M., 2003. The current configuration of protected areas in the Cape Floristic Region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biological Conservation* 112, 129-145.
- Şekercioğlu, C.H., 2006. Increasing awareness of avian ecological function. *Trends in Ecology and Evolution* 21, 464-397.
- Şekercioğlu, Ç.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystems consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* 103, 10941-10946.
- Sinclair, A.R.E., Burom, A.E., 2006. Understanding ecosystem dynamics for conservation of biota. *Journal of Animal Ecology* 75, 64-79.
- Tscharntke, T., Steffan-Dwenter, I., Kruess, A., Theis, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research* 17, 229-239.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dwenter, I., Theis, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8, 857-874.
- von Hase, A., Rouget, M., Maze, K., Helme, N., 2003. A fine-scale conservation plan for the Cape Lowlands Renosterveld: Technical Report. Cape Conservation Unit, Botanical Society, Cape Town.
- Winter, S.J., Esler, K.J., Kidd, M., 2005. An index to measure the conservation attitudes of landowners towards Overberg Coastal Renosterveld, a critically endangered vegetation type in the Cape Floristic Region, South Africa. *Biological Conservation* 126, 383-394.

Winter, M., Johnson, D.H., Shaffer, J.A., Donovan, T.M., Svedarsky, W.D., 2006. Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management* 70, 158-171.

2. LITERATURE REVIEW

2.1. BACKGROUND AND INTRODUCTION

Transformation of natural habitats and the resulting fragmentation of these habitats is an important topic in current conservation ecology. Habitat fragmentation from anthropogenic causes can be defined as the process whereby the loss of a natural habitat, through clearing for agricultural lands for example, breaks up the originally continuous habitat into fragments of differing size, shape and degree of isolation (Andrén, 1994; Bender et al., 1998; Walters et al., 1999; Flather and Bevers, 2002; Roslin, 2002; Begon et al., 2003; Fahrig, 2003). As the loss of natural habitat proceeds, the remaining fragments become initially more numerous, smaller in area, and more isolated from one another. Although habitat loss is still seen as the biggest threat to biodiversity, the size, shape and spatial arrangement of the remaining habitat fragments can have important additional effects on ecological processes that impact upon species persistence (Ewers and Didham, 2006). The fact that fragmentation creates small and isolated fragments compounds the problems that habitat loss per se imposes on biodiversity (Fahrig, 2003; Ewers and Didham, 2006). Fragmentation is a landscape-scale process. Thus, not only are fragment size and shape important when investigating the effects of fragmentation, but also fragment isolation and nearest-neighbour distance (Fahrig, 2003; Ewers and Didham, 2006; Watling and Donnelly, 2006). Isolation is not just a measure of habitat configuration, but can also be defined as the amount of habitat remaining in the landscape (Fahrig, 2003). Thus, if a fragment is more isolated, the landscape has less of the same habitat intact.

2.2. THE EFFECTS OF FRAGMENT SIZE AND ISOLATION ON AVIAN ASSEMBLAGES

Two features of habitat fragmentation are decreasing fragment size and increasing fragment isolation with increasing levels of fragmentation (Andr  n, 1994; Fahrig, 2003).

The importance of fragment area is first and foremost explained and understood by looking at the basic Species-Area Relationship (SAR) predictions. SAR indicates that species richness and area of habitat fragments is positively correlated (Ney-Nifle and Mangel, 2000). This tool has been widely deployed to assist modern ecological science to successfully predict extinctions in habitats that suffer area reductions through habitat loss (Ney-Nifle and Mangel, 2000). Studies that focus on the effects of fragment area and isolation often agree that decreasing fragment area is the most prominent role-player in decreasing species richness, diversity and abundances, thus affecting assemblage composition and structure (e.g. Bender et al., 1998; Cameron, 1999; Lee et al., 2002; Davis et al., 2006; Ferraz et al., 2007).

Several theories regarding the dominance of area effects in fragmented habitats exist. Firstly, smaller fragments often do not have sufficient resources, e.g. shelter, food and breeding habitat, to maintain the same levels of species richness as larger fragments. This often results in the loss of species with area requirements larger than the fragment (Davis, 2004; Watson et al., 2004). Secondly, smaller fragments have higher edge:area ratios, meaning that as fragment area decreases, there is a proportional increase in edge area. Edge habitats are often regarded as ecological traps (Helzer and Jelinski, 1999; Parker et al., 2005) because predation, nest predation and brood parasitism may be higher in fragment edges (Kaiser and Lindell, 2007). Thirdly, an individual bird is less likely to colonise a small habitat fragment than a large fragment (Parker et al., 2005).

It is important, however, to realize that area effects exerted on species richness, diversity and assemblage composition will be more than just the actual area of the habitat fragment, such as habitat condition, or health (Briggs et al., 2007). Briggs et al. (2007) documented a strong positive relationship between habitat condition and fragment size. Weinberg and Roth (1998), for example, found a strong negative effect of decreasing fragment size on the reproductive output of wood thrushes, which they concluded is the product of the inadequate representation of breeding habitat in small fragments.

However, area effects are not always this obvious and easy to predict or explain. Habitat fragments have long been thought to be ‘islands’ in a ‘sea’ of inhospitable habitats (Bortons et

al., 2003). However, the situation is not that simple. Habitat fragments are more accurately described as occurring in a matrix, and the quality of the matrix determines the ability of individuals of species to disperse from one fragment to another across the matrix. The quality of the matrix can have two effects on the more straightforward area effects described above: (i) effectively influence the movements and dispersal of individuals through the landscape and (ii) it can potentially supply species with additional resource not found within the fragment, thus having a complementary effect (Bortons et al., 2003). If the quality of the matrix is high and the contrast between the fragments' habitat and the matrix habitat low, the edge effects can be less severe and the edge:area ratio much smaller. Therefore, the variation in fragment area effects can be partly explained by the variation in quality and features of the surrounding landscape. Furthermore, area effects may well be influence by the life history traits of a species, i.e. whether it is a resident species or a migratory species.

Fragment isolation is the other great threat that habitat fragmentation imposes on the biodiversity of historically continuous habitats. As with area effects, the effects n species of fragment isolation is greatly influenced by the surrounding matrix. This can influence the ability of individuals to disperse between fragments and to colonize fragments in the landscape, affecting species occurrence as a whole. Indeed, the distance between fragments is the most important factor regarding the connectivity of habitat fragments in a fragmented landscape (Goodwin and Fahrig, 2002), but matrix quality can influence the maximum distance of dispersal. The amount of habitat in the landscape per se does not always have a significant effect on connectivity (Goodwin and Fahrig, 2002).

Species vary in their ability and resistance to cross gaps between habitat fragments (Shirley, 2006). Species that naturally require large home ranges or species that migrate are more likely to move between fragments in fragmented habitats (Grubb and Doherty, 1999; Shirley, 2006), but the negative effects of isolation are mostly less obvious than area effects (Ferraz et al., 2007). For the region considered in this study, Cameron (1999) and Randrianasolo (2003) showed that the effects of decreasing fragment area were more obvious than those of isolation or connectivity. Watson et al. (2004) also reported no relation between degree of isolation and avifaunal richness.

There are various reasons why species cross the matrix from one habitat fragment to another, e.g. (i) natal dispersal, (ii) finding and selecting mates, (iii) food availability, (iv) availability of shelter and adequate breeding habitat and (v) home-range gap-crossing (Grubb and Doherty, 1999; Shirley, 2006). It is important that individuals have enough resources to maintain themselves in the landscape. If the landscape is made up of a large number of small

fragments, finding and using these resources can pose a problem. Larger species are usually more capable of crossing gaps in the home range and to utilize resources found within fragments scattered across the landscape (Grubb and Doherty, 1999). This ability could potentially give large-bodied species the means to survive in landscapes where the individual component fragment areas are too small to sustain them. While some studies have recorded that species do cross gaps within their home range (Grubb and Doherty, 1999), others have found no such pattern (Watson et al., 2004). These differences might be based on habitat and matrix differences. A sharp contrast between the habitat fragment and the matrix could impair the ability of the species therein to utilize other habitat fragments in the landscape to expand their home range. Less sharp contrasts between habitat and matrix might be conducive to home ranges gap-crossing, allowing species to utilize more than one fragment. There are, however, several risks coupled with this method of utilizing the landscape, such as increased predation risk when crossing the matrix. There are also three factors to consider when birds need to leave one fragment for another, (i) moving away from the current fragment, (ii) deciding on a direction in which to move and (iii) arriving and stopping at the next suitable fragment (Grubb and Doherty, 1999). This implies another aspect of isolation; that an individual can only move to another fragment if it knows that of the existence and location of such fragments (Grubb and Doherty, 1999). Individuals will only use fragments that they can access. Should the distances between habitat fragments be too big, or the matrix not allow great distances of dispersal, individuals may not be able to utilize the number of fragments that could otherwise support and sustain it in the landscape.

As explained above, area, matrix and isolation effects can severely impair the state of the avifauna found within habitat fragments in the landscape. These effects influence species richness, diversity assemblage composition and can actually impair the critical ecological processes that are dependent on avian vectors (e.g. pollination, seed dispersal and predation). In a fragmented habitat, generalist and specialist species respond differently to reductions in fragment size, increasing isolation and the matrix surrounding the fragment. Species that are only found in the interior of habitat fragments are typically more sensitive to decreasing area than species with more general habitat requirements, with extreme habitat generalists having a mean area effect of close to zero (Bender et al., 1998).

Consistent with these area effects on specialist and generalist species, evidence shows that generalist species are more likely to disperse between habitat fragments and that the quality and structure of the matrix facilitate the movements through the landscape (Wethered and Lawes, 2003). The ability to exploit the matrix and the quality thereof allows species to

use a number of habitat fragments in the landscape (Goodwin and Fahrig, 2002), hence preventing subpopulation extinction as they colonize and re-colonize habitat fragments. Bortons et al. (2003) similarly argue that generalist species are usually much more resilient to the matrix and that they can successfully exploit its resources. Specialist species are often unable to use the surrounding matrix, so if the resources within the fragment are inadequate, they may suffer reduced breeding success, population declines and possible local extinction.

Besides the adverse effects that habitat fragmentation has on generalist and specialist species, it also affects overall avian richness, diversity and composition. A recent study in the central Amazon basin (Ferraz et al., 2007) confirms that local extinctions are much more probable in small fragments, and that species richness declines with decreasing fragment area. In the WCRB and the South Coast Renosterveld (recently classified as Western and Eastern Rûens Shale Renosterveld, Mucina and Rutherford 2006) the same pattern emerges (Cameron, 1999; Randrianasolo, 2003). In both of these vegetation types, fragment size was the key predictor of species richness, with isolation playing only a small part. The small fragments contained subsets of the avian assemblages found in the larger fragments. These subsets were made up of generalist species. Similarly, birds of USA grasslands exhibit this clear, positive correlation between area and species richness (e.g. Johnson and Igl, 2001). Grassland bird richness is also correlated with area effects (Johnson and Igl, 2001). In that study, some species exhibited strong area sensitivity while others did not. Typically, species do vary in their sensitivity to area effects. What makes these findings by Johnson and Igl (2001) interesting is that the same species show different degrees of area sensitivity in other studies conducted in different geographical regions. This is presumably because habitat attributes (e.g. resources, breeding habitat and landscape structure) may vary in the different regions, thus influencing area sensitivity (e.g. Davis, 2004). However, the latter study found that edge:area ratio was typically a better predictor of species richness. Again, isolation plays a seemingly small role in grassland assemblage composition and species richness.

It is important to realize, however, that there is a synergy between area and isolation effects. If there are enough large fragments available in the landscape to sustain populations, the need to disperse will be far less than if the total area of habitat is restricted to a large number of small fragments (Grubb and Doherty, 1999). If an individual must disperse from one fragment to another, and the location of the next small fragment is unknown, it must first locate the next fragment (Debinski et al., 2001). Thus the size of the fragment can affect, at any one time, the degree of isolation of habitat in the landscape. If the individual does not see the small fragment, it must disperse further into the matrix to locate the next one, which may

be out of reach. ‘Habitat sampling’ (Debinski et al., 2001) in this manner can be very risky for species not well adapted to disperse vast distances. By contrast, if there are enough small fragments in the landscape, arranged in an easily detected manner, they can “soften” the matrix (Fischer and Lindenmayer, 2002; Samways, 2005). These small fragments can act as stepping-stones between larger fragments meeting the species’ area, habitat and breeding requirement, thus supporting and facilitating its movement through the landscape (Fischer and Lindenmayer, 2002; Samways, 2005).

2.3. THE CONSISTENCY OF FRAGMENTATION EFFECTS ACROSS HABITATS AND VEGETATION TYPES

Habitat fragmentation clearly poses many threats to avian species richness and diversity. But are these effects, especially those of fragment area and isolation, consistent between various habitat or vegetation types? Most studies of fragmentation, and its effects on avifauna, are done in forest biomes (e.g. Telleria and Santos, 1995; Schmiegelow et al., 1997; Chan and Ranganathan, 2005; Pavlacky and Anderson, 2007). In this section, I investigate the consistency of fragmentation effects across habitat types, such as forests, woodlands and grasslands.

As mentioned earlier, one of the most obvious and threatening features of habitat fragmentation is that of decreasing fragment sizes. A Boreal forest study showed very strong positive relationships between species richness and fragment size (Schmiegelow et al., 1997). In this particular study, bird species were surveyed prior to fragmentation, and one and two years after fragmentation. In both of the post-fragmentation surveys, the smallest fragments were the least species-rich, except those well connected by corridors. Two years after fragmentation, resident species showed the greatest decrease in species richness, with migrants not severely affected. Parker et al. (2005) found that neotropical migrant songbirds preferred large fragments with plenty of good quality interior habitat. At the species level, it is also clear that species sensitive to certain areas and habitats either disappear from small fragments or show significant reductions in abundances (Schieck et al., 1995). For instance, wood thrush (*Hylocichla mustelina*), ovenbird (*Seiurus aurocappilla*) and red-eyed vireo (*Vireo olivacea*) abundances were positively correlated with fragment size (Chan and Ranganathan, 2005). The same pattern was found in the montane forests of Vancouver Island, Canada for habitat-sensitive species.

In the woodlands of southeastern Australia, area effects were also the most important factor contributing to species richness (Watson et al., 2005). Woodland fragments were sampled in agricultural, peri-urban and urban environments and fragment size showed strong and significant positive relationships with species richness consistently throughout the study area. Isolation effects, however, did not explain any reductions in species richness. This study shows that area effects can be detrimental for avian richness in a variety of matrix types.

Forests and woodlands, however, are structurally diverse. How would area effects impact on a more open and a less-structured, diverse habitat, such as grasslands? Herkert (1994) surveyed grassland communities in three grassland classes: native prairie, restored prairie and non-prairie. In all three classes, species richness showed a strong positive and significant relationship with fragment size. Another study, also conducted in the North American grasslands, found an even stronger positive relationship between area and species richness (Helzer and Jelinski, 1999). Both studies noted concern that grassland breeding species were most sensitive to area effects. This sensitivity may have serious repercussions for the persistence and survival of these species in small grassland fragments. Another observation that can have serious negative effects on the avifauna of grasslands is that nest survival and breeding success may well be negatively affected by decreasing fragment size (Davis, 2004; Davis et al., 2006). Across landscapes, however, area effects may shift in terms of severity. Johnson and Igl (2001) showed that species' sensitivity to area effects varied across landscapes. The only pattern they noted is that the rarest species avoided fragments smaller than 50 ha. This is consistent with results from other studies that indicate that specialist and rare species are much more likely to be affected by area effects than are generalist species (Bender et al., 1998). This pattern is true for many habitat types, ranging from forests to grasslands (Bender et al., 1998; Watson, 2003; Wilson et al., 2007).

Although isolation effects can be a very serious threat to biodiversity and avian richness in fragmented habitats, they are usually not as obvious or severe as area effects. Isolation does not have strong and apparent effect on species richness in woodland fragments, irrespective of matrix type (Watson et al., 2005). However, if we focus on the effects of isolation at the species-specific level, we may come to understand the concern about isolation effects on woodland avifauna. Studies have shown that individuals become isolated from other populations within the landscape (Bailey, 2007). This can, in effect, be critical for population persistence as it can reduce genetic flow across landscape fragments. Densities of

species may be severely altered if fragments become isolated from source habitats (Dunning et al., 1995).

In forests, the contrast between forest fragments and the matrix can affect the manner in which isolation effects manifest in avian assemblages and richness. Wethered and Lawes (2003), for instance, showed that isolation effects in montane forests can be significantly reduced if the matrix surrounding the fragments is structurally similar. Isolation effects alone have a weak relationship with species richness in forest fragments (Ferraz et al., 2007; Monteil et al., 2004). However, avian assemblage composition is greatly affected by isolation (Schmiegelow et al., 1997). In fact, isolation affects species turnover among forest habitat fragments.

It is, however, important to realize that to measure the true influence of any of these fragment components, i.e. area effects, isolation effect etc. one has to control for certain effects. For instance, to accurately measure the effect of fragment size on an assemblage, isolation effects must be controlled from within statistical procedures, and *visa versa*. Only by doing this will the true impact of fragment size be truly reflected.

In a recent study done in the Strandveld, Western Cape Province in South Africa, it was also found that assemblage composition and feeding-guild composition differed substantially in habitat fragments surveyed in golf estates (Fox and Hockey, 2007). In this particular study habitat fragments within a golf estate and in close proximity of a conservation area were surveyed. Even at this small and local scale did fragmentation play a major role in changing the face of native avifaunal diversity.

Are these effects, found in these variable habitat types, the same as found in the highly endemic and threatened Renosterveld of south-western South Africa? This vegetation type, part of the CFR, is dominated by shrubs and grasses. Area effects play by far, the greater role in the loss of species richness and shifts in assemblage composition (Cameron, 1999; Randrianasolo, 2003). Isolation did not show any significant relationship with species richness or diversity.

Fragmentation effects on birds seem fairly consistent across various vegetation types. Area effects are more prominent in determining species richness and diversity. However, isolation effects should not be disregarded as a threat. In terms of disruption of gene flow and ecological processes (e.g. pollination and predation), for instance, isolation must be considered as a great threat to biodiversity.

2.4. CONCLUSION

Research has provided conservation biologists and ecologists with convincing data to demonstrate the serious negative effects of habitat fragmentation on biodiversity. Birds illustrate this effect well. Area and isolation effects are widely recognized as two properties of habitat fragmentation that decrease species richness, diversity and abundance, with area effects the most prominent in this regard.

With area effects being more prominent in decreasing species richness and diversity, the importance of conserving large fragments becomes apparent. This clear and unambiguous guidance for conservation biologists and practitioners in setting conservation goals and refining conservation strategies.

Conservation biologists, ecologists, conservation agencies and landscape managers must embark on research to understand the requirements of bird species at the regional scale and to manage landscapes to reduce the rate of local and regional extinctions.

2.5. PREDICTIONS AND HYPOTHESES

From the literature, certain predictions can be made in terms of the present study.

2.5.1. Predictions

- (i) Species richness and diversity will decrease with decreasing area and more unfavourable landscape configuration.
- (ii) Assemblage composition will shift at a certain area threshold, seeing that the general structure and nature of the two bioregions are fairly similar I would predict that these thresholds will be at around the same fragment area.
- (iii) Individual species and feeding guilds will respond in quite different ways to area and configuration effects.

2.5.2. Hypotheses

- H₁:** Patterns identified in the two regions will not coincide with one another; different fragmentation effects will have variable influences on the avifauna of the two regions.
- H₀:** The WCRB and ECRB will show the same response to avifaunal fragmentation.

- H₁:** Feeding guilds will differ in their sensitivity and response to fragmentation, with insectivores and frugivores being most sensitive.
- H₀:** There will be no difference in the response to habitat fragmentation across different feeding guilds.

- H₁:** Species within assemblages will show different levels of sensitivity to the effects of habitat fragmentation.
- H₀:** All species are equally sensitive to fragmentation.

2.6. REFERENCES

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.
- Bailey, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 38, 7-23.
- Begon, M., Harper, J.L., Townsend, C.R., 2003. *Ecology*. Blackwell Publishing. Oxford.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: Meta-analysis of the patch size effect. *Ecology* 79, 517-533.
- Bortons, L., Mönkkönen, M., Martin, J.L., 2003. Are fragments islands? Landscape context and density-area relationships in Boreal forest birds. *The American Naturalist* 162, 343-357.
- Briggs, S.V., Seddon, J.A., Doyle, S.J., 2007. Structures of bird communities in woodland fragments in central New South Wales, Australia. *Australian Journal of Zoology* 55, 29-40.
- Cameron, A., 1999. The effects of fragmentation of renosterveld vegetation on bird community composition. M.Sc. Thesis, University of Cape Town.
- Chan, K.M.A., Ranganathan, J., 2005. Testing the importance of patch scale on forest birds. *Oikos* 111, 606-610.
- Crooks, K.R., Suarez, A.V., Bolger, D.T., M.E., Soulé, 2001. Extinction and colonization of birds on habitat islands. *Conservation Biology* 15, 159-172.
- Dardanelli, S., Nores, M.L., Nores, M., 2006. Minimum area requirements of breeding birds in fragmented woodland of Central Argentina. *Diversity and Distributions* 12, 687-693.
- Davis, S.K., 2004. Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in Southern Saskatchewan. *The Auk* 121, 1130-1145.
- Davis, S.K., Brigham, R.M., Shaffer, T.L., James, P.C., 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. *The Auk* 123, 807-821.
- Debinski, D.M., Ray, C., Saveraid, E.H., 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity. *Biological Conservation* 98, 179-190.
- Drinnan, I.N., 2005. The search for fragmentation in a southern Sydney suburb. *Biological Conservation* 124, 339-349.

- Dunning, Jr., J.B., Borgella, Jr., R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9, 542-550.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117-142.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of the Ecology, Evolution and Systematics* 34, 487-515.
- Fearer, T.M., Stauffer, D.F., 2003. Relationship of Ruffed Grouse (*Bonasa umbellus*) home range size to landscape characteristics. *The American Midland Naturalist* 150, 104-114.
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, Jr., R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315, 238-241.
- Fischer, J., Lindenmayer, D.B., 2002. Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. *Biological Conservation* 106, 129-136.
- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: The relative importance of habitat amount and arrangement. *The American Naturalist* 159, 40-56.
- Fox, S and Hockey, P.A.R., 2007. Impacts of a South African coastal golf estate on shrubland bird communities. *South African Journal of Science* 103, 27-34.
- Goodwin, B.J., Fahrig, L., 2002. How does landscape structure influence landscape connectivity. *Oikos* 99, 552-570.
- Grubb, Jr., T.C., Doherty, Jr., P.F., 1999. On home-range gap-crossing. *The Auk* 116, 618-628.
- Helzer, C.J., Jelinski, D.E., 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* 9, 1448-1458.
- Herkert, J.R., 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* 4, 461-471.
- Hinsley, S.A., 2000. The cost of multiple patch use by birds. *Landscape Ecology* 15, 765-775.
- Johnson D.H., Igl, L.D., 2001. Area requirements of grassland birds: A regional perspective. *The Auk* 118, 24-34.
- Kaiser, S.A., Lindell, C.A., 2007. Effects of distance to edge and edge type on nestling growth and nest survival in the wood thrush. *Condor* 109, 288-303.

- Lee, M., Fahrig, L., Freemark, K., Currie, D. J., 2002. Importance of patch scale vs. landscape scale selected forest birds. *Oikos* 96, 110-118.
- Monteil, C., Deconchat, M., Balent, G., 2004. Simple neural network reveals unexpected patterns of bird species richness in forest fragments. *Landscape Ecology* 20, 513-527.
- Mucina, L., Rutherford, C. (Eds), 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.
- Ney-Nifle, M., Mangel, M., 2000. Habitat loss and changes in the species-area relationship. *Conservation Biology* 14, 893-898.
- Parker, T.H., Stansberry, B.M., Becker, C.D., Gipson, P.S., 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology* 19, 1157-1167.
- Pavlacky, D.C., Anderson, S.H., 2007. Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? *Animal Conservation* 10, 57-68.
- Randrianasolo, H., 2003. Birds in west coast renosterveld fragments: implications for a threatened habitat. M.Sc. Thesis, University of Cape Town.
- Roslin, T., 2002. So near yet so far – habitat fragmentation and bird movement. *Trends in Ecology and Evolution* 17, 61.
- Samways, M.J., 2005. Insect diversity conservation. *Managing for insect diversity*, pp.226-231. Cambridge University Press, Cambridge.
- Schieck, J., Lertzman, K., Nyberg, B., Page, R., 1995. Effects of patch size on birds in old-growth montane forests. *Conservation Biology* 9, 1072-1081.
- Schmiegelow, F.K.A., Machatans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* 78, 1914-1932.
- Shirley, S.M., 2006. Movement of forest birds across river and clear-cut edges of varying riparian buffer strip widths. *Forest Ecology and Management* 223, 190-199.
- Shriver, W.G., Hodgman, T.P., Gibbs, J.P., Vickery, P.D., 2004. Landscape context influences salt marsh bird diversity and area requirements in New England. *Biological Conservation* 119, 545-553.
- Tellería, J.L., Santos, T., 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. *Biological Conservation* 71, 61-67.
- Vance, M.D., Fahrig, L., Flather, C.H., 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84, 2643-2653.
- van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langaton, R.H.W., Rose, R.J., 2001. Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role

- of vegetation type, habitat fragmentation and population size. *Biological Conservation* 101, 217-228.
- Walters, J.R., Ford, H.A., Cooper, C.B., 1999. The ecological basis of sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. *Biological Conservation* 90, 13-20.
- Watling, J.I., Donnelly, M.A., 2006. Fragments as islands: a synthesis of faunal responses to patchiness. *Conservation Biology* 20, 1016-1025.
- Watson, D.M., 2003. Long-term consequences of habitat fragmentation – highland birds in Oaxaca, Mexico. *Biological Conservation* 111, 283-303.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests on southeastern Madagascar. *Biological Conservation* 120, 311-327.
- Watson, J.E.M., Whittaker, R.J., Freudenberger, D., 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* 32, 1353-1370.
- Weinberg, H.J., Roth, R.R., 1998. Forest area and habitat quality for nesting wood thrushes. *The Auk* 115, 879-889.
- Wethered, R., Lawes, M.J., 2003. Matrix effect on bird assemblages in afromontane forests in South Africa. *Biological Conservation* 114, 327-340.
- Wilson, J.W., van Aarde, R.J., van Rensburg, B.J., 2007. Effects of habitat fragmentation on bird communities of sand forests in southern Mozambique. *Ostrich* 78, 37-42.
- With, K.A., King, A.W., 2001. Analysis of landscape sources and sinks: the effects of spatial pattern on avian demography. *Biological Conservation* 100, 75-88.

3. COMPARATIVE IMPACTS OF FRAGMENTATION ON BIRDS IN TWO BIOREGIONS

SUMMARY

Habitat fragmentation is known to have serious impacts on avian diversity. This study compares the adverse effects of fragmentation on the avifauna of two highly fragmented bioregions within a biodiversity hotspot, the Cape Floristic Region. The East- and West Coast Renosterveld Bioregions (ECRB and WCRB respectively) have been subjected to major habitat transformation and fragmentation. The landscapes of these two bioregions differ greatly in configuration.

Bird assemblages were surveyed and a snapshot of the avifaunal composition was recorded. Audio and visual identification and time- and distances-restricted point counts were the field methodologies adopted for the study. Multivariate techniques were used to analyse the data.

In the ECRB, which has more habitat scattered within the landscape, habitat configuration was key to the compositional changes of the avifauna found there. Area effects, however, were more important for the shaping of avifauna in the WCRB. This study highlights the importance of maintaining conservation networks within fragmented landscapes. Guild- and assemblage-level analyses in both these bioregions showed similar patterns in a bioregional context. Avian diversity is sensitive to landscape configuration, and once vast areas of habitat have been lost to transformation, conservation of remaining large habitat fragment becomes critical. However, as shown in this study, habitat quality is also of great importance, affecting guild composition and species diversity.

3.1. INTRODUCTION

Habitat fragmentation is one of the greatest threats to biodiversity (Schmiegelow et al., 1997; Smith and Hellmann, 2002; Davis et al., 2006; Bailey, 2007). Human activities, such as agricultural expansion and urbanization, have divided large and continuous tracts of natural habitat into an array of fragments scattered across the landscape, surrounded by new habitats that are unsuitable for many species (Davis et al., 2006). Three of the major effects governing biodiversity in fragmented landscapes are 1) area effects, 2) isolation effects and 3) edge effects (Andr  n, 1994; Fletcher et al., 2007). These effects are known to have important impacts on various taxa, including plants, invertebrates, birds and mammals (Fletcher et al., 2007). Many fragments in a highly fragmented landscape are either too small or too isolated from source habitats to sustain and maintain local populations. Smaller fragments are also subjected to large proportions of edge habitats that have negative effects on habitat-specific species (Davis et al., 2006; Ortega-Huerta, 2007).

Ecological processes and functionality are also greatly affected by the effects of fragmentation (Tscharntke and Brandl, 2004; Fletcher et al., 2007). For example, plant-insect interactions are increasingly placed under pressure as habitat fragments become more isolated (Tscharntke and Brandl, 2004), and pollination in fragmented habitats can be seriously impaired by size, edge and isolation effects, resulting in secondary effects such as reduced fruit and seedset, reducing plant reproductive success (Aguilar et al., 2006).

Birds are known to fulfil essential roles in ecosystems, such as predation, seed dispersal, pollination, and others (  kercio  lu, 2006; Gil-Tena et al., 2007; Kremen et al., 2007). Despite the fact that birds are essential in ecosystems, they are also one of the most threatened taxa. Estimates are that, of the 2,821 bird species that are endemic to the 25 global biodiversity hotspots, 1,250 may be lost by the year 2100, 6-14% of all historic bird species could be extinct and 7-25% functionally extinct by 2100 (  kercio  lu et al., 2004). Therefore, it is important to understand how habitat fragmentation influences avian diversity and assemblage integrity, as the persistence of many bird species could well depend on conservation strategies implemented at a landscape scale.

A decrease in patch size has serious repercussions for avifaunal richness, diversity, density and assemblage structure (Chan and Ranganathan, 2005), with species richness and diversity decreasing with a decrease in patch size (Parker et al., 2005). This reduction in species richness and abundance could be due to competition for limited resources in small and isolated fragments (Pearman, 2002; Brown and Sullivan, 2005). Furthermore, brood-

parasitism, nest predation and predation on adult birds all occur more frequently in small fragments (Weinberg and Roth, 1998; Batáry and Báldi, 2004; Johnson and Igl, 2004). As habitat fragmentation is the process whereby continuous habitat is transformed into a set of patches, differing in size and degree of isolation (Andrén, 1994; Bender et al., 1998; Fahrig, 2003; Flather and Bevers, 2002; Roslin, 2002; Walters et al., 1999), area effects exerted on species richness, diversity and assemblage composition may be more than just the actual area effect, but also include other factors, e.g. habitat condition, which are usually positively correlated with fragment size (Briggs et al., 2007). A decrease in habitat condition has serious implications for the forces that drive area effects on avian richness and diversity, as it changes interspecific competition and can reduce breeding success (Briggs et al., 2007).

Habitat heterogeneity and diversity are regarded as crucial parameters in avian ecology (Matlock and Edwards, 2006), as habitat variables, especially habitat structure and plant species composition, greatly influence avian diversity and assemblages (Lee and Rotenberry, 2005; Sallabanks et al., 2006; Shirley, 2006). Many studies have shown that avian diversity and assemblage composition can change drastically as habitat structure diminishes (Lee and Rotenberry, 2005; Matlock and Edwards, 2006; Shirley, 2004), yet, habitat generalists may show a small or negligible response to patch size and may even increase in abundance in disturbed or transformed landscapes (Bender et al., 1998; Wilson et al., 2007).

Another feature of fragmented landscapes that may affect avifaunal assemblages is the physical arrangement of habitat patches (habitat configuration; Goodwin and Fahrig, 2002; Bortons et al., 2003). Patch arrangement, as well as the quality or type of surrounding matrix, can increase the isolation of suitable habitats for species by restricting movement and preventing dispersal, thus influencing assemblage composition. While area effects have direct implications for local extinctions, isolation effects influence the colonization and re-colonization of habitat fragments, as this involves the movement of individuals between patches (Ferraz et al., 2007). There is, however, an interaction between isolation and area effects, as small fragments are generally harder to detect in the landscape, and the increased edge:area ratios of small fragments might also influence their detectability (Fischer and Lindenmayer, 2002; Goodwin and Fahrig, 2002). Isolation effects are dependent on the dispersing abilities of species (Hinsley et al., 1996; Bailey, 2007); habitat generalist species are more efficient at dispersing between patches. However, small patches can also soften the impact of the matrix if individuals can use these patches as 'stepping-stones' between larger and more favourable patches, allowing for habitat sampling (Debinski et al., 2001; Fischer and Lindenmayer, 2002; Samways, 2005). This patch connectivity can effectively reduce the

overall impact of isolation effects, e.g. through increased fledgling survival and territory establishment (Smith and Hellmann, 2002). Corridor establishment is one of the principal means to facilitate the movement of sensitive species through the landscape (Dunning et al., 1995; Shirley, 2006) and it is often regarded as a key management tool to soften the effects of fragmentation in landscapes.

Avian feeding guilds respond very differently to fragmentation because of their variability in behaviour and habitat use (Bishop and Myers, 2005). Two feeding guilds that are especially sensitive to habitat fragmentation are insectivorous and frugivorous species (Pearman, 2002; Watson et al., 2004; Gray et al., 2007). Insectivorous species are affected by both patch size and degree of isolation, and decrease in richness and mean abundance as fragmentation persists or increases in the landscape (Pearman, 2002; Watson et al., 2004), as they are usually very susceptible to microclimatic and microhabitat changes that affect food availability (Canaday, 1997; Ueze et al., 2005). The diversity and abundance of frugivorous species are impacted by changes in the abundance and spatial distribution of fruiting plants in a fragmented landscape (Githiru et al., 2002; Githiru et al., 2005). Granivorous species, by contrast, may benefit from fragmentation and disturbance, when fragmentation increases the availability of seed from weedy plants or grain crops in the altered habitats surrounding the fragments (Gray et al., 2007).

Renosterveld, an endemic vegetation type in the Cape Floristic Region (CFR) of South Africa, has been highly transformed and fragmented over the last two centuries (Krug and Krug, 2007). However, a restricted amount of information is available on how fragmentation of this vegetation type impacts on avian assemblages (Cameron, 1999; Randrianasolo, 2003). Even less information is available on the comparative effects of fragmentation across different vegetation types and bioregions. In this study, I will compare the effects of fragmentation on avifaunal composition in two different geographical regions, each characterised by different vegetation types, within a biodiversity hotspot, the Cape Floristic Region. This approach was chosen because of variable results obtained in the literature, as well as the limited knowledge of how fragmentation affects influence avian compositional integrity on a bioregional scale. I therefore aim to establish how fragmentation influences avian diversity and composition in the two bioregions. The two bioregions differ fundamentally with respect to the landscape configuration. Therefore I predict assemblages will be inclined to respond differently to fragment within these two bioregions

3.2. MATERIALS AND METHODS

3.2.1. Study sites

The study was conducted in the West- and East Coast Renosterveld Bioregions of the CFR (WCRB and ECRB, respectively; Mucina and Rutherford, 2006). The vegetation types within these bioregions are highly threatened and fragmented, and have been reduced to 12 % (WCRB) and 16.2 % (ECRB) of their former area. In addition, these vegetation types are very poorly represented in conservation areas (Table 3.1).

Table 3.1 - Original and present area proportions of the West Coast- and East Coast Renosterveld Bioregions (Mucina and Rutherford, 2006)

| Vegetation type | | Hectares |
|-----------------|-------------|----------|
| ECRB | Original | 59,732 |
| | Remaining | 9,678 |
| | % Remaining | 16.2 |
| | Conserved | 242 |
| | % Conserved | 0.4 |
| WCRB | Original | 60,555 |
| | Remaining | 7,267 |
| | % Remaining | 12 |
| | Conserved | 597.6 |
| | % Conserved | 0.9 |

The WCRB is located on the south-western coast of the Western Cape Province, South Africa. This region receives winter rainfall (highest in June-August) and has a mean annual precipitation (MAP) of 444 mm (Mucina and Rutherford, 2006). Mean annual temperature (MAT) is 17°C and mean daily temperature in summer months range between 15 and 28 30°C. Due to these high temperatures the WCRB has a mean annual potential evaporation (MAPE) of 2,230 mm (Mucina and Rutherford, 2006).

The vegetation in the WCRB is a shrubland mostly dominated by *Dicerotheramnus rhinocerotis* (commonly known as Renosterbos; Mucina and Rutherford, 2006). Other cupressoid-leaved, evergreen asteraceous shrubs form a strong component within this bioregion, but the vegetation also has a grass component. A unique feature of the WCRB is the high level of endemic geophytes. Currently, this vegetation type is threatened by anthropogenic habitat transformation and fragmentation through agricultural expansion, urban sprawl and alien invasive plants (Mucina and Rutherford, 2006).

The ECRB is found within the south-eastern regions of the Western Cape Province. The climate differs from that of the WCRB by a slightly lower MAP and MAT of 389 mm and 16.4°C respectively (Mucina and Rutherford, 2006). Rainfalls, although seasonal, is distributed more evenly over the year and mean daily temperature in the summer months range between 15 and 25°C (Mucina and Rutherford, 2006). Therefore the ECRB has a lower MAPE than that of the WCRB, of 1,948 mm (Mucina and Rutherford, 2006). The ECRB is therefore a moister region than the WCRB, despite its lower annual precipitation.

The vegetation in the ECRB is also dominated by *Dicerotheramnus rhinocerotis* and cupressoid-leaved, evergreen asteraceous shrubs, but has a higher grass component than the WCRB (Mucina and Rutherford, 2006). *Aloe ferox* and *Acacia karoo* are present in the western and eastern reaches of the bioregion, respectively. A mesotrophic asteraceous component is supported by calcrete deposits in the eastern reaches. Like the WCRB, the ECRB hosts a wide range of endemic geophytes. Major threats to the ECRB are agricultural expansion and grazing by domestic livestock.

I selected 80 fragments, 40 in each vegetation type, for this study (Fig. 3.1). Most of these fragments were located on private land, with the exception of three large fragments in the WCRB that were conservation areas (a list of actual fragments sizes is in Appendix 3.A). Fragments were firstly selected from the von Hase et al. (2003) GIS layers. These fragments were then visited, if the landowner has granted me access to the fragment. Thereafter a quick visual assessment determined whether the condition of the vegetation and structure was suitable for the purposes of the study. Furthermore, fragments were also selected, as far as possible, to ensure an even size-class distribution throughout the sample size of 40 fragments per bioregion.

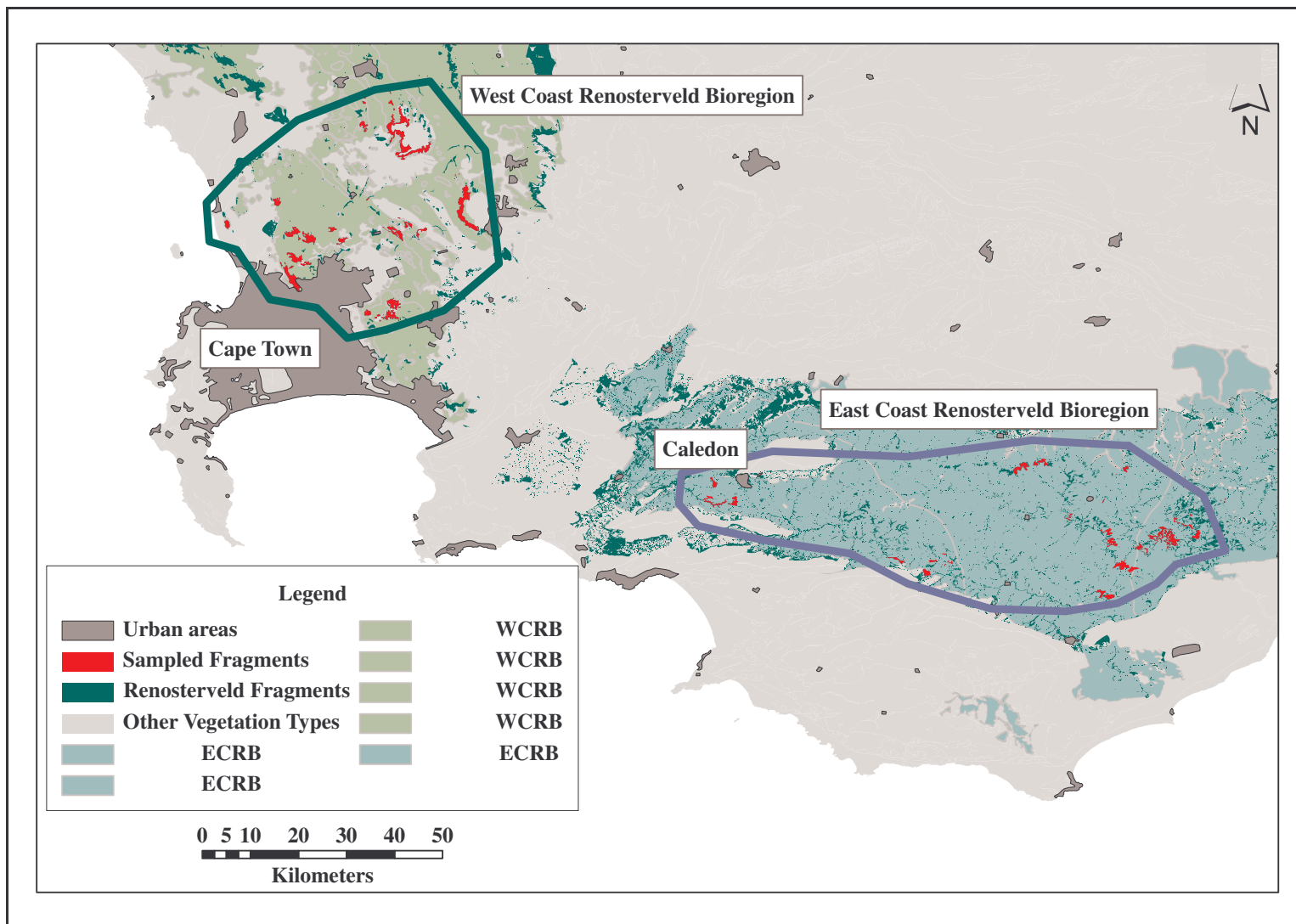


Figure 3.1 – Map indicating the two bioregions and fragments sampled

3.2.2. Bird Surveys

Bird surveys were conducted in May 2007 (WCRB) and May 2008 (ECRB). The cool month of May was selected as the ideal sampling periods as it allowed the observer to perform long periods of field surveys without tiredness and fatigue influencing his ability to accurately identify bird species. Surveys took place during the first four hours after sunrise and last four hours before sunset. Time-limited point counts (Dettmers et al., 1999; Royle and Nichols, 2003), with a single point count per fragment, were chosen. Each fragment had a single point count at the centre with an observation radius of 50 m, chosen because the smallest fragment in both vegetation types was 1 ha in size and thus only able to accommodate one count point, which ensured that all fragments were subject to the same sampling intensity. The centre of fragments were determined in ArcGIS v9.2 (ESRI, 2008), a geographic information systems package. Within the spatial management toolkit of ArcGIS there is a function, *feature points*, which allows the user to determine the point of gravity of any selected polygon. This is an accurate function that allows one to determine the centre of even irregular shaped polygons

The largest fragment in each of the bioregions (WCRB: 1,424 ha and ECRB: 630 ha) was used to determine the sampling duration within that particular bioregion's 40 fragments. It was sampled at a once off effort until species accumulation curves reached an asymptote (see Appendix 3.B). The sample time did differ between the bioregions, the WCRB fragments were sampled for three hours, while two hours were adequate for the ECRB. Using this sampling method ensured that all fragments were sampled to the same intensity. For the purposes of the study a snapshot of the avian assemblages were required, hence a once off sampling effort be adequate. By sampling once off allowed me to capture the species that were dependent on that particular fragment at that specific time. It also minimized the influence of dispersal between fragments during the study and between surveys. Species recorded in the fragment at the time of a second sample might have dispersed to surrounding fragments, thus not allowing me to gather information on its dependency on specific fragment surveyed

Visual and sound identification were used to identify the bird species, unidentified birds were not included in the surveys. Only individuals observed perched, foraging or roosting within the 50 m sampling radius were recorded and the abundances of each species were determined for each fragment. Because individuals were not marked, recounts may have occurred. However, this error is assumed to have been small and constant across all of the fragments. Complete species list for the ECRB and the WCRB are in Appendix 3.C and 3.D, respectively.

3.2.3. Habitat characteristics

Because habitat structure and condition have a strong influence on bird assemblages, certain habitat variables were measured in each fragment. Two perpendicular 100 m transects, crossing where the point count was situated, were used to measure the habitat variables at 2 m intervals: 1) the presence and/or absence of vegetation cover 2) plant life-form (e.g. grass, shrub, forb and restio) and 3) vegetation height. These data were then used to calculate average grass and shrub height as well as percentage cover of the plant life forms. All percentage data were arcsin-transformed prior to analyses.

3.2.4. Guild classification

All bird species surveyed were assigned to a feeding guild, as classified by Hockey et al. (2005). Species richness and abundance were calculated independently for each guild in every sample. In addition, the proportion each guild occupied in every assemblage was determined as a percentage of the total number of individuals in each assemblage. However, as pure abundance measures may have certain constraints, such as not including body size measures, I chose to include the previous measure, that of proportion each guild occupied in each assemblage, to put the abundances measure in perspective with general assemblage composition.

3.2.5. Data analyses

Spatial analyses for this study were carried out in ArcGIS v.9.2, GIS software package (ESRI, 2008). Information on fragment size (ha) and nearest neighbour distance of fragments was obtained from GIS layers produced by von Hase et al. (2003). Nearest neighbour distances (NND) were measured in metres and determined by measuring the shortest distance from the centre of each sampled fragment to the centre of the nearest neighbouring fragment. The rationale for this measurement of NND is based on the fact that I aimed to assess avian assemblages found within the core of every fragment, and not edge species or assemblages. Therefore, addressing the question of how far is core habitat from the next nearest core habitat, allowed me to truly assess core species richness, diversity and composition. To determine habitat arrangement in the landscape, a set of buffers were created around each sample point using the Buffer function in the Proximity analysis toolkit in ArcGIS v.9.2 (Fig. 3.2), which allows the user to create fixed bands around points. These buffers were 0 - 500 m, 0 - 1,000 m, 0 - 2,000 m, 0 - 4,000 m and 0 - 5,000 m (Tischendorf et al., 2003; Hamer et

al., 2006). The total area within each buffer and in between buffers was calculated. In addition to this, the average size of patches within each buffer and between buffers was calculated. A measure of edge:area ratio was also included in the analyses, calculated as: *compactness* (van Teefelen et al., 2006; GRASS Development Team 2008). The most compact shape is a circle, with a compactness value of 1:

$$Compactness = \frac{Perimeter}{2\sqrt{\pi \times area}}$$

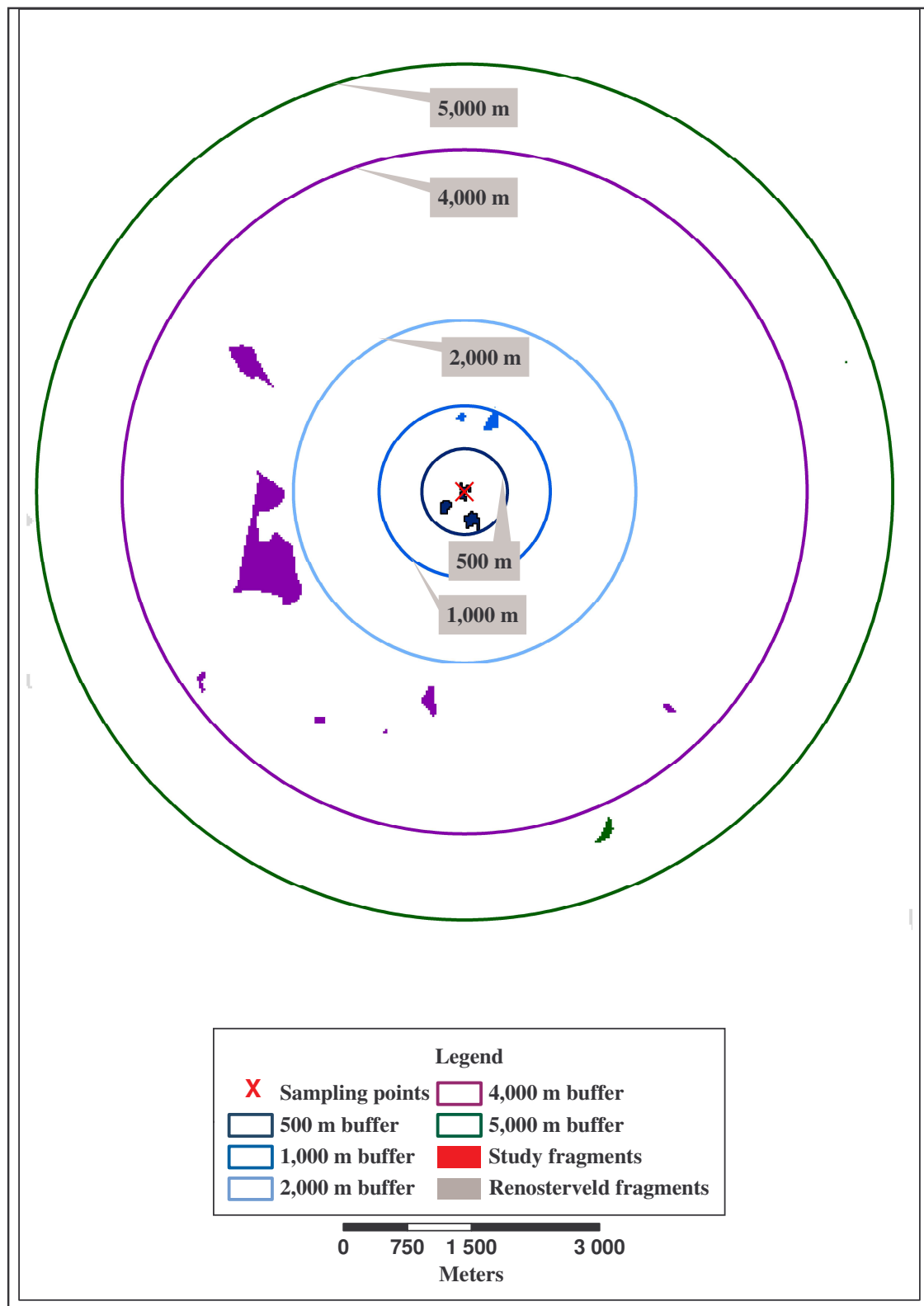


Figure 3.2. – Buffer-system used to determine habitat configuration within the landscapes.

Species richness used in the analyses for both species and guild data were observed number of species. Species diversity, life-form diversity and guild diversity were calculated using the Shannon Diversity Index (Colwell, 2005) provided in the community ecology package “vegan” (Oksanen et al., 2007) for R (R Development Core Team, 2007):

$$H' = -\sum_{i=1}^s p_i \ln p_i .$$

Where n_i is the number of individuals in each species, s is number of species, N is the total number of individuals, p_i is the relative abundance of each species which is calculated as the proportion of individuals of a given species to the total number of individuals in the assemblage: $\frac{n_i}{N}$.

Before any analyses were carried out, all predictor variables were tested for colinearity. Predictors were entered into a Spearman Rank Correlation matrix to determine whether they were correlated or not. These results were subsequently verified in a factor analysis using the statistical software package STATISTICA 8 (StatSoft, inc., 2007). Only independent predictor variables were used in all of the following analyses. The model presented five factors that have various degrees of colinearity. Within each of these factors, the variable with the strongest factor score was selected for further analysis (Table 3.2; entire summary of factor analysis is in Appendix 3.E). These predictor variables were subsequently used in all statistical models and techniques used in this study. Because the landscape and geographical regions differed in configuration, predictor variables in resulting models were not similar throughout. Throughout this study, a confidence level of 95% was the benchmark for rejecting null hypotheses.

Table 3.2 - Factor scores of selected independent predictor variables

| Bioregion | Selected Predictor | Factor Score |
|-----------|---|--------------|
| ECRB | Compactness | -0.752 |
| | Total Area in 1,000 m (ha) | 0.946 |
| | Total Area in 5,000 m (ha) | 0.985 |
| | Vegetation Life-form Diversity | -0.759 |
| | Percentage Shrub Cover | 0.805 |
| WCRB | Area (ha) | 0.800 |
| | Total Area in 1,000 m (ha) | 0.937 |
| | Total Area between 2,000 – 4,000 m (ha) | 0.919 |
| | Average Area between 4,000 – 5,000 m (ha) | 0.804 |
| | Percentage Bare Ground | -0.870 |

In the statistical software package STATISTICA 8 (StatSoft, inc., 2007), regression analyses were used to determine the influence of fragment area, nearest neighbour distance and the most relevant landscape configuration parameter for the particular region (predictor variables) on species richness and species diversity (dependent variables). Three dimensional graphs were constructed to show detailed interrelationships between the predictor variables and species richness and diversity, with response variables fitted to a distance-weighted least squares model.

Other statistical tools used were canonical ordinations, i.e. canonical correspondence analyses (CCA). The statistical software package CANOCO 4.5 (ter Braak and Šmilauer, 2002) was used for these analyses. The scaling focus of the CCA analyses fell on the inter-response variable distances. The data remained untransformed during these analyses. The technique was used to investigate the influence of the predictor variables on the feeding guild composition of the two bioregions.

Non-metric multi-dimensional scaling (MDS) was conducted in CANOCO 4.5. (ter Braak and Šmilauer, 2002) to determine the area threshold at which assemblage composition shifts. Through a process of elimination, samples were separated according to size categories until a definite split in composition was identified.

Best subset general linear models (GLM) in STATISTICA 8 (StatSoft, inc., 2007) were used to determine the effect of various independent predictor variables on selected response variables (species richness, species diversity and the habitat variables).

Best subset general linear models allow for the building of linear models for data consisting of continuous and independent predictor variables. Best subset general linear models request the subset of multiple independent variables that best predict a given dependent variable by multiple linear regressions. To obtain the final model, all possible combinations of the variables will be tested and those with the highest coefficient selected, which is an indication of the strength of the relationship between response and predictor variables (Sokal and Rohlf, 2003). Best subset general linear models are thus ideal to use on large data sets making it easier to interpret the data and making the confidence bands narrower, therefore making the results of the regression model more precise (Zuur et al., 2007).

3.3. RESULTS

3.3.1. Independent predictor variable effects on habitat characteristics

Models obtained from the GLM procedure relating habitat variables to independent predictors showed that in the ECRB, the percentage of bare ground and compactness of fragments were inversely related (model coefficient = - 0.05, $p = 0.002$; Table 3.3). In the WCRB, vegetation life form diversity was positively correlated to increasing fragment area (model coefficient = 0.003, $p = 0.0001$).

Table 3.3 - Summary of best subset general linear model indicating key predictors of change in habitat characteristics

| Bioregion | Habitat variable | Whole Model Prediction | | | Best Subset Model Prediction | | | | |
|-----------|------------------------|------------------------|-------------|----------|-------------------------------------|-------------|---------|-------------|----------|
| | | Adj. R ² | F-statistic | P-value | Predictor | Coefficient | SE | t-statistic | p-value |
| ECRB | Percentage Bare Ground | 0.329 | 6.552 | 0.001 | Compactness | -0.050 | 0.015 | -3.360 | 0.002 |
| WCRB | Life Form Diversity | 0.502 | 10.814 | < 0.0001 | Area (ha) | 0.003 | 0.001 | 4.335 | < 0.0001 |
| | Percentage Shrub Cover | 0.257 | 4.376 | 0.006 | Average Area between 0-5,000 m (ha) | -0.0001 | 0.00003 | -3.315 | 0.002 |

3.3.2. Species Richness, Species Diversity and Guild Diversity

A total of 2,677 individual birds from 48 species were recorded during sampling at the 40 fragments visited in the ECRB. Observed species richness ranged from 7 to 20 and species diversity from 1.748 to 2.813 (Appendix 3.E). For the WCRB, 69 species comprising 5,165 individuals were recorded during sampling. Species richness ranged from 9 to 39 and Shannon Diversity Index from 1.576 to 3.329 (Appendix 3.F). Differences between the richness and diversity of these two bioregions are shown in Table 3.4.

Table 3.4 - Descriptive statistics indicating differences in species richness and diversity of the two studied bioregions

| Bioregion | | Mean | Std. Dev. | Minimum | Maximum |
|-----------|-------------------|--------|-----------|---------|---------|
| ECRB | Species Richness | 13.550 | 3.186 | 7 | 20 |
| | Species Diversity | 2.368 | 0.256 | 1.748 | 2.813 |
| WCRB | Species Richness | 18.775 | 6.116 | 9 | 39 |
| | Species Diversity | 2.540 | 0.323 | 1.576 | 3.329 |

Species richness – observed, Species diversity – Shannon Diversity Index (also see Appendix 3.F)

Fragments of similar areas in both regions were compared in terms of species richness and diversity. The ECRB was found to have similar species richness levels at the lower scale of fragment areas (Fig. 3.3.a). However, within larger fragments, the WCRB was more species-rich than the ECRB. Species diversity overall did not differ significantly between the regions (Fig. 3.3.b).

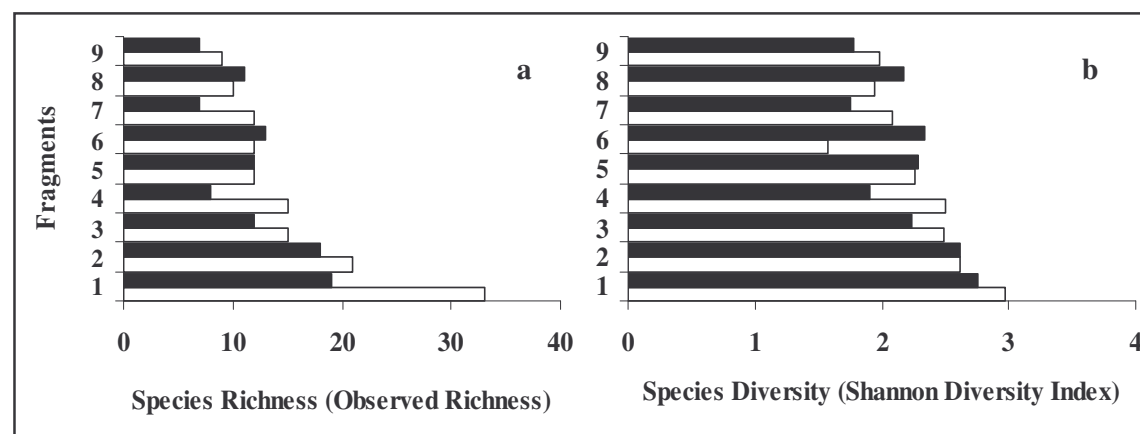


Figure 3.3 – Frequency distribution of species richness and diversity in similarly sized fragments in the two bioregions. Solid black bars are ECRB fragments; white bars are WCRB fragments.

General linear models revealed a significant relationship between species richness of the ECRB and the total area of habitat within 1,000 m from the sampling points (model coefficient = 0.033, $p = 0.01$; Table 3.5). In the WCRB, species richness was positively influenced by an increase in fragment area (model coefficient = 0.01, $p < 0.0001$), the total area of habitat within 1,000 m from the sampling points (model coefficient = 0.054, $p < 0.0001$), and, was negatively influenced by an increase in the average area of habitat at the buffer between 2,000 - 4,000 m from the sampling points (model coefficient = -0.006, $p = 0.033$).

Species diversity in the WCRB was positively influenced by an increase in the average area of habitat at the buffer between 2,000 - 4,000 m from the sampling points (model coefficient = 0.003, $p < 0.0001$) and negatively by an increase in the amount of bare ground within the fragments (model coefficient = -7.371, $p = 0.024$).

The regression analyses showed that in the ECRB species richness was positively correlated with fragment area ($R^2 = 0.182$, $p = 0.011$), and total area of habitat within 1,000 m from the sampling point ($R^2 = 0.21$, $p = 0.006$). Species diversity was significantly correlated with fragment area ($R^2 = 0.193$, $p = 0.008$) and the total area of habitat with 1,000 m from the sampling points ($R^2 = 0.231$, $p = 0.003$).

In the WCRB, species richness was significantly positively correlated with fragment area ($R^2 = 0.564$, $p < 0.0001$), and total area of habitat within 1,000 m of the sampling points ($R^2 = 0.639$, $p < 0.0001$). Diversity was positively correlated with fragment area ($R^2 = 0.296$, $p = 0.0003$), and total area of habitat 1,000 m from the sampling points ($R^2 = 0.486$, $p < 0.0001$).

Table 3.5 - Summary of best subset general linear model indication key predictors of species richness, species diversity.

| Bioregion | | Whole Model Prediction | | | Best Subset Model Prediction | | | | |
|-----------|-------------------|------------------------|-------------|----------|--------------------------------|-------------|-------|-------------|----------|
| | | Adj. R ² | F-statistic | P-value | Predictor | Coefficient | SE | t-statistic | p-value |
| ECRB | Species Richness | 0.310 | 4.062 | 0.006 | Total Area in 1,000 m (ha) | 0.033 | 0.012 | 2.764 | 0.01 |
| WCRB | Species Richness | 0.768 | 26.825 | < 0.0001 | Area (ha) | 0.010 | 0.002 | 4.679 | < 0.0001 |
| | | | | | Total Area in 1,000 m (ha) | 0.054 | 0.009 | 6.165 | < 0.0001 |
| | | | | | Area between 2,000-4,000m (ha) | -0.006 | 0.003 | -2.217 | 0.033 |
| | Species Diversity | 0.560 | 10.911 | < 0.0001 | Area between 2,000-4,000m (ha) | 0.003 | 0.001 | 4.601 | < 0.0001 |
| | | | | | Percentage Bare Ground | -7.371 | 3.113 | -2.367 | 0.024 |

The three-dimensional graphs emphasised the influence of area effects on both species richness and diversity in ECRB. Species richness is influenced more by fragment area than connectivity as expressed by nearest neighbour distance (Fig 3.4.a). However, when the total area of habitat 1,000 m from the sampling points was added to the equation, the slope of the species richness-area relationship evened out slightly, indicating the influence of the amount of habitat in the landscape (Fig 3.4.b). Species diversity was influenced in a similar way (Fig 3.4.c and d).

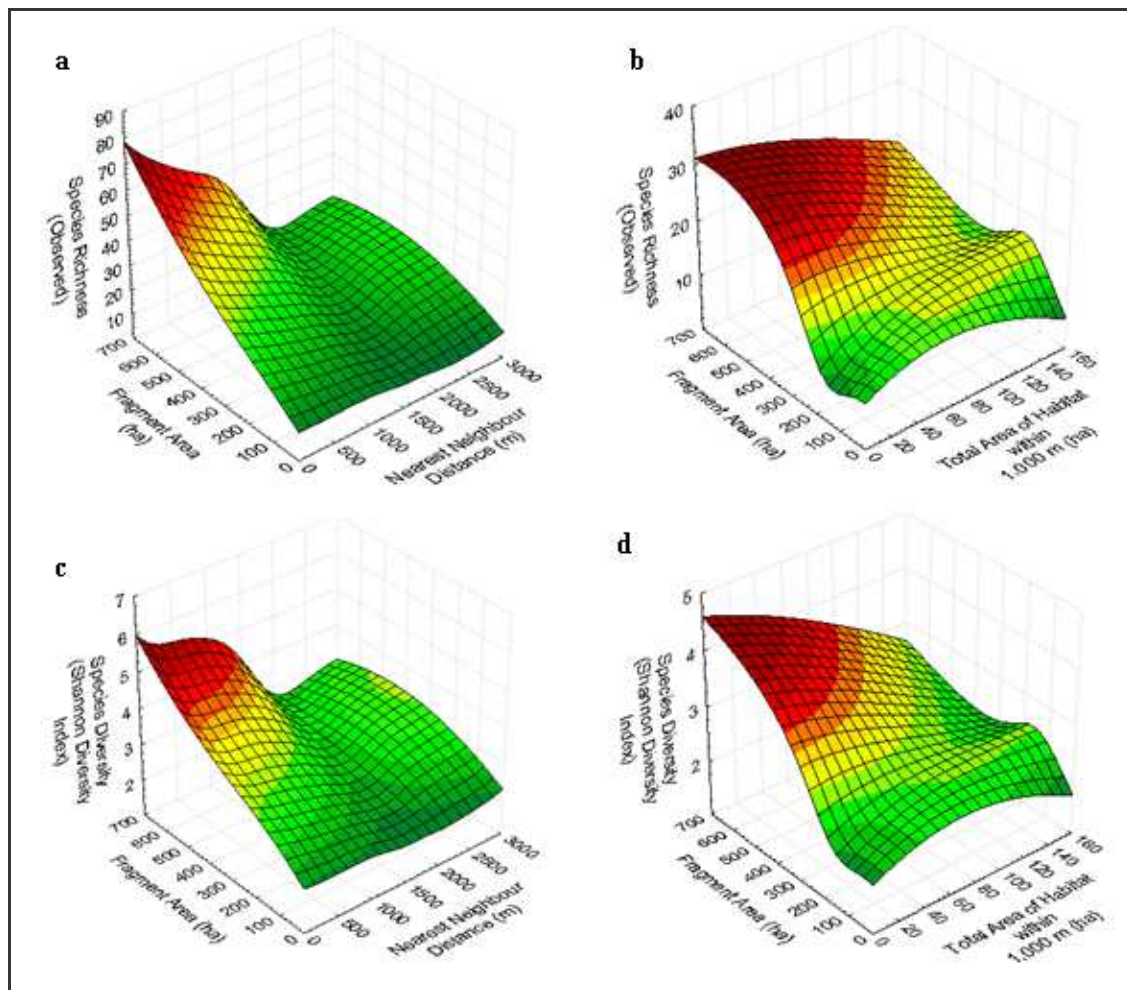


Figure 3.4 - Three-dimensional graphs indicating the influence of fragment area, nearest neighbour distances, and landscape configuration on species richness and diversity in the East Coast Renosterveld Bioregion. Graphs consist of 40 data points per axis.

For the WCRB, the three-dimensional graphs showed interesting patterns of species richness and diversity. Species richness was highest at intermediate fragment sizes and increased as nearest neighbour distance increased (Fig 3.5.a). It does seem, however, that the amount of habitat within 1,000 m from the sampling point does have little effect on species richness (Fig 3.5.b). A similar pattern was observed for species diversity. However, two peaks were identified with nearest neighbour distance on the x-axis. Species diversity was greatest in intermediately sized fragments with little habitat remaining in the landscape (Fig 3.5.c). Diversity was high at intermediate to larger fragments close to other fragments, and again at fragments of the same size class further afield (Fig 3.5.d).

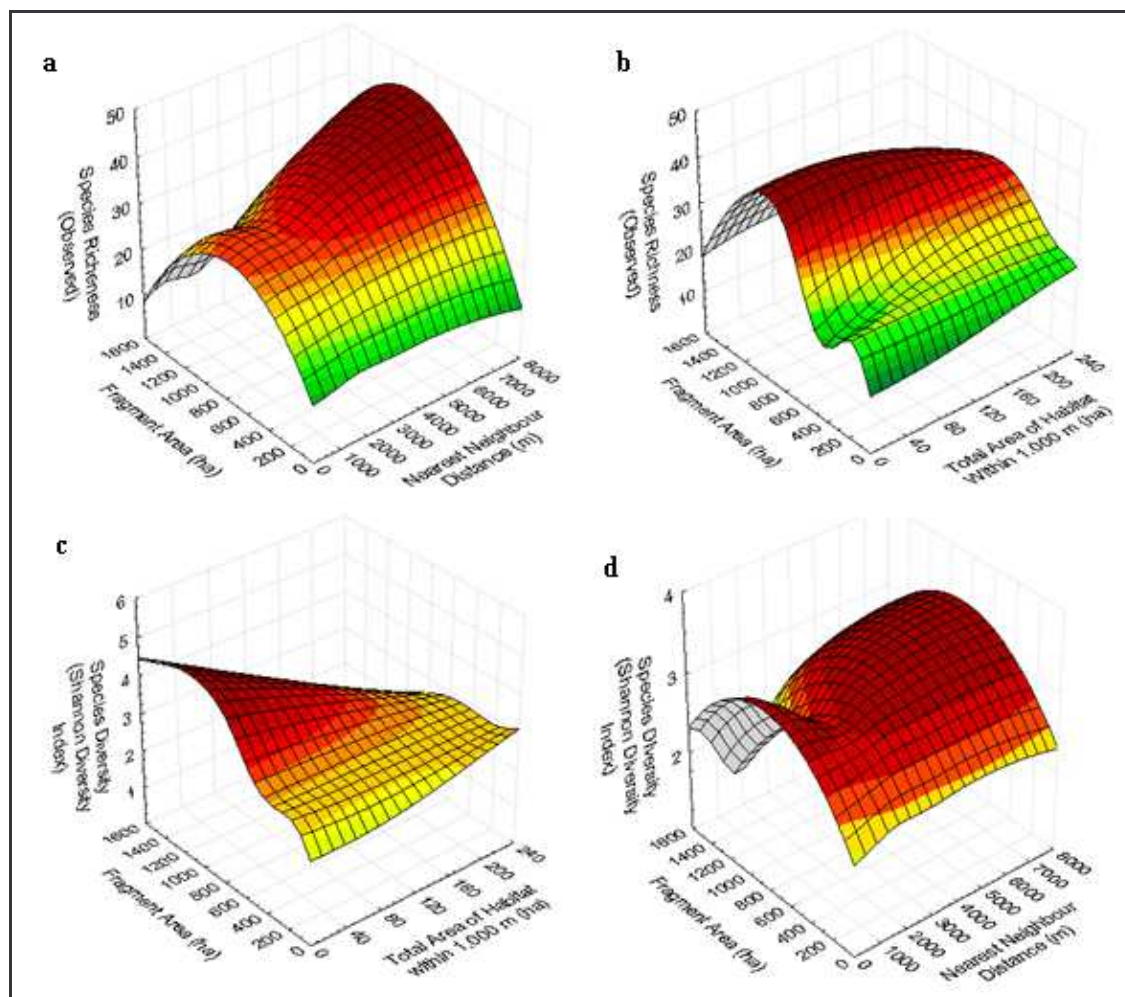


Figure 3.5 - Three-dimensional graphs indicating the influence of fragment area, nearest neighbour distances, and landscape configuration on species richness and diversity in the West Coast Renosterveld Bioregion. Graphs consist of 40 data points per axis.

3.3.3. Assemblage composition

MDS scaling (Fig 3.6) indicated a shift in assemblage composition at two very different area thresholds for the two regions. The ECRB assemblage compositions underwent a major shift at 20 ha fragment size. Assemblage composition in fragments smaller than 20 ha did differ from those in fragments greater than 20 ha. In the WRCB, this shift occurred at 50 ha fragment size (Fig 3.7).

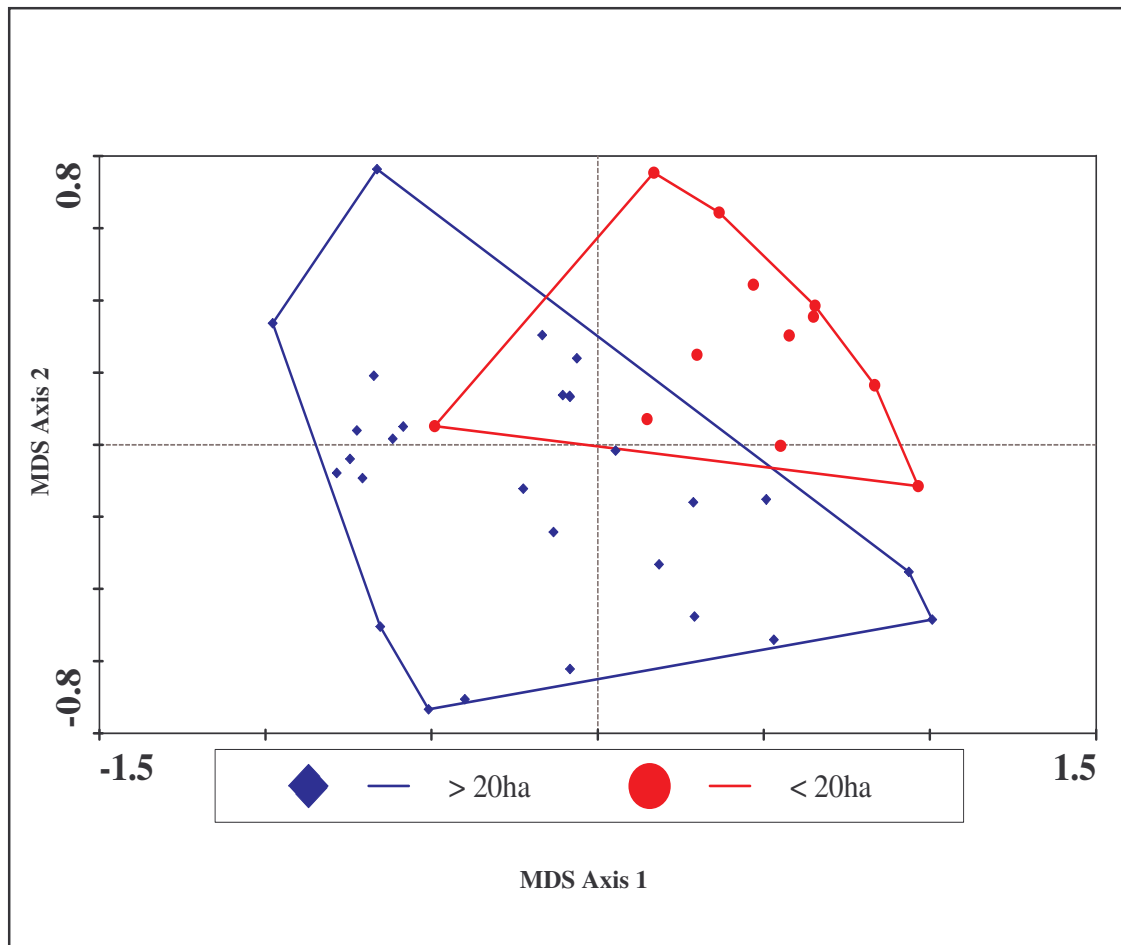


Figure 3.6 – Non-metric Multi-Dimensional Scaling of East Coast Renosterveld Bioregion samples, indicating a clear shift in composition at 20 ha. Eigenvalues: 0.306 (Axis 1) and 0.135 (Axis 2); cumulative percentage variance: 30.6 (Axis 1) and 44.1 (Axis 2).

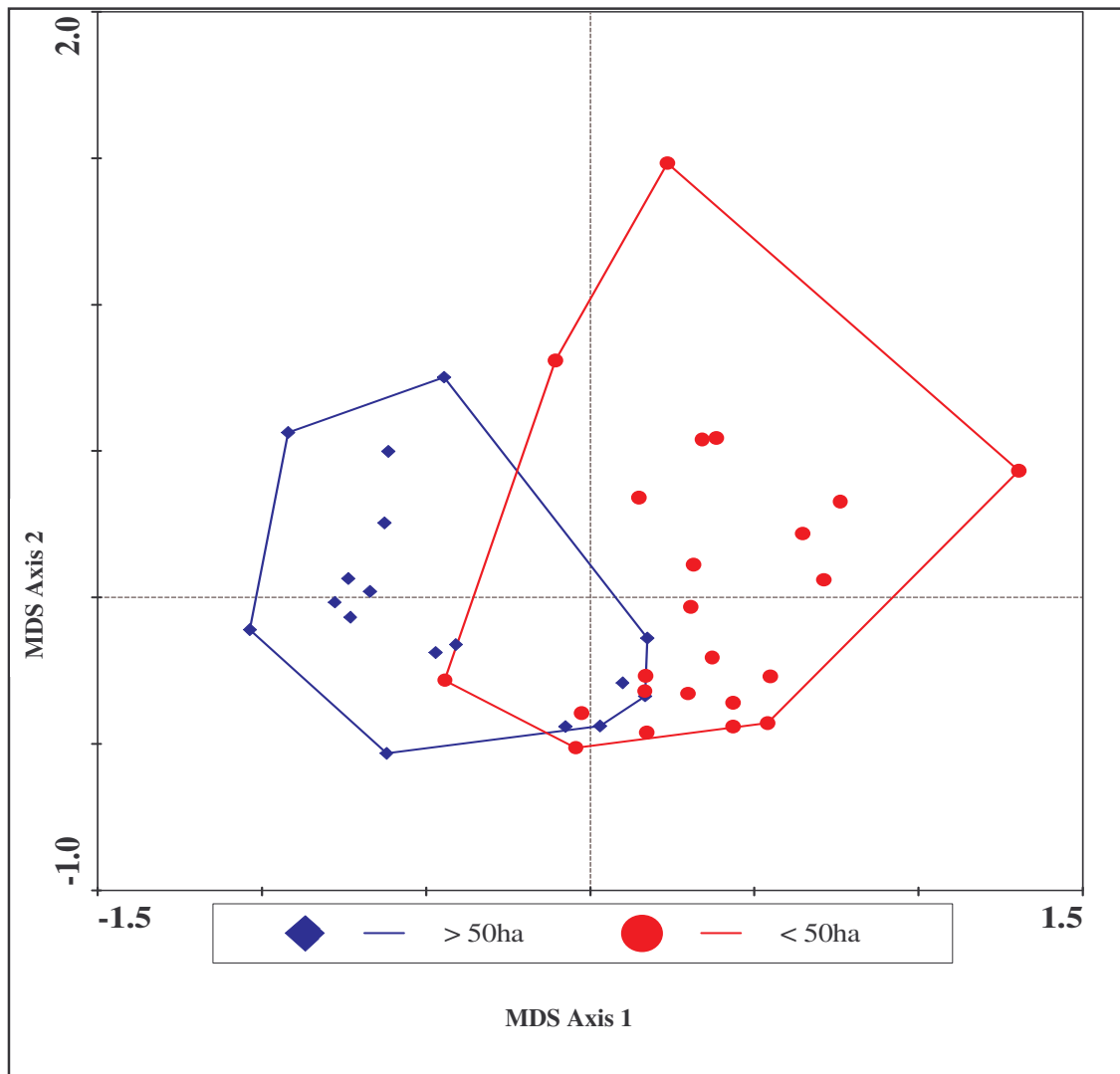


Figure 3.7 – Non-metric Multi-Dimensional Scaling of West Coast Renosterveld Bioregion samples, indicating a shift in composition at 50ha. Eigenvalues: 0.278 (Axis 1) and 0.193 (Axis 2); cumulative percentage variance: 27.8 (Axis 1) and 47 (Axis 2).

3.3.4. Guild-level analyses

Observed guild composition varied between the two bioregions, but not by much (Fig. 3.8). The greatest difference was the percentage of insectivores and granivores in the assemblages. The ECRB had a greater component of insectivorous species than the WCRB, while the WCRB had a larger component of granivorous species.

Table 3.6 - Percentage on each guild within each bioregion's assemblage.

| Guild | Percentage within each Bioregion | |
|--------------|----------------------------------|---------|
| | WCRB | ECRB |
| Carnivores | 0.00 % | 2.08 % |
| Raptors | 7.25 % | 4.17 % |
| Insectivores | 49.28 % | 58.33 % |
| Granivores | 20.29 % | 14.58 % |
| Nectarivores | 4.35 % | 4.17 % |
| Frugivores | 7.25 % | 8.33 % |
| Omnivores | 11.59 % | 8.33 % |

Species labeled as carnivores are species feeding on prey, but that are not referred to as insectivores and raptors, e.g. herons.

Inter-guild variation was tested with CCA. For the ECRB (Fig. 3.9), frugivore composition was best predicted by the total area of habitat within 5,000 m from the sampling points. Nectarivore abundances were associated with percentage shrub cover, however, the proportion of nectarivores and nectarivore richness were influenced by the total area of habitat within 5,000 m of the sampling points. Omnivore abundance was influenced by the total area of habitat within 1,000 m from the sampling points. Insectivore composition, as well as omnivore richness and proportions were sensitive to fragment compactness and vegetation life form diversity. Granivore abundance showed a weak relationship with shrub cover and the total area of habitat within 5,000 m from the sampling points.

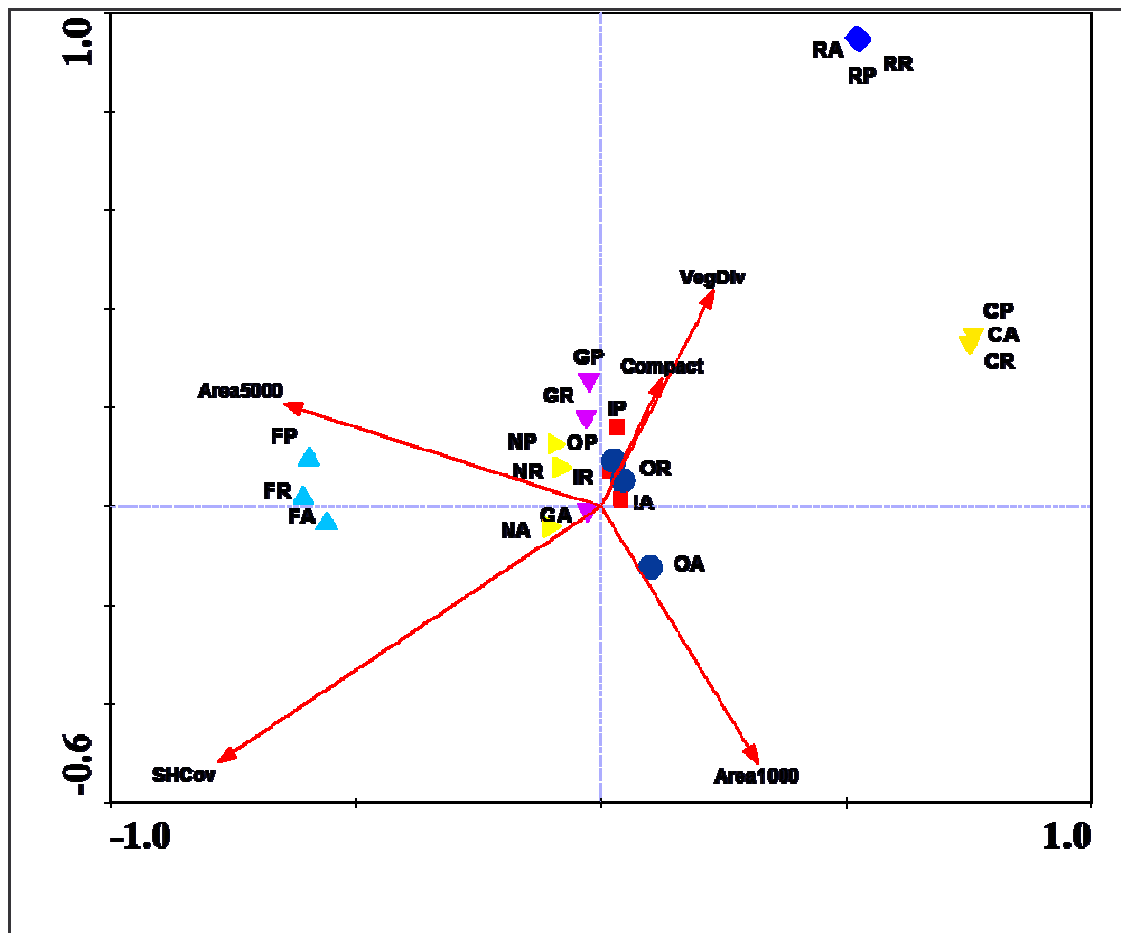


Figure 3.9 – CCA indicating the responses of feeding guilds to the fragmentation effect in the East Coast Renosterveld Bioregion. Eigenvalues: 0.034 (Axis 1) and 0.009 (Axis 2); cumulative percentage variance: 59.5 (Axis 1) and 76.1 (Axis 2).

Compact – compactness, Area5000– total area of habitat within 5,000 m from sampling point, Area1000 – total area of habitat within 1,000 m from sampling point, SHCov – percentage shrub cover, VegDiv – Vegetation life form diversity.

First letter: C – Carnivores; R – Raptors; O – Omnivores; G – Granivores; F – Frugivores; N – Nectarivores; I – Insectivores. Second letter: R – Species richness in guild; A – relative abundance in guild; P – Proportion of guild in assemblage.

In the WCRB, different relationships became apparent (Fig. 3.10). The proportion of frugivores and frugivore species richness showed a strong relationship with fragment area. Frugivore abundances, on the other hand, showed a strong relationship with the total area of habitat within 1,000 m from the sampling points. Percentage bare ground in the fragments influenced the abundances of two guilds, omnivores and granivores. Raptor composition was strongly affected by the average area of fragments within 5,000 m from the sampling points.

Within guild compositions of the WCRB, a cluster of feeding guilds occurred in close proximity of the base of fragment area, indicating the importance of area effects in this bioregion. Within this cluster are insectivore abundances, nectarivore abundances, granivore richness and nectarivore- and insectivore richness.

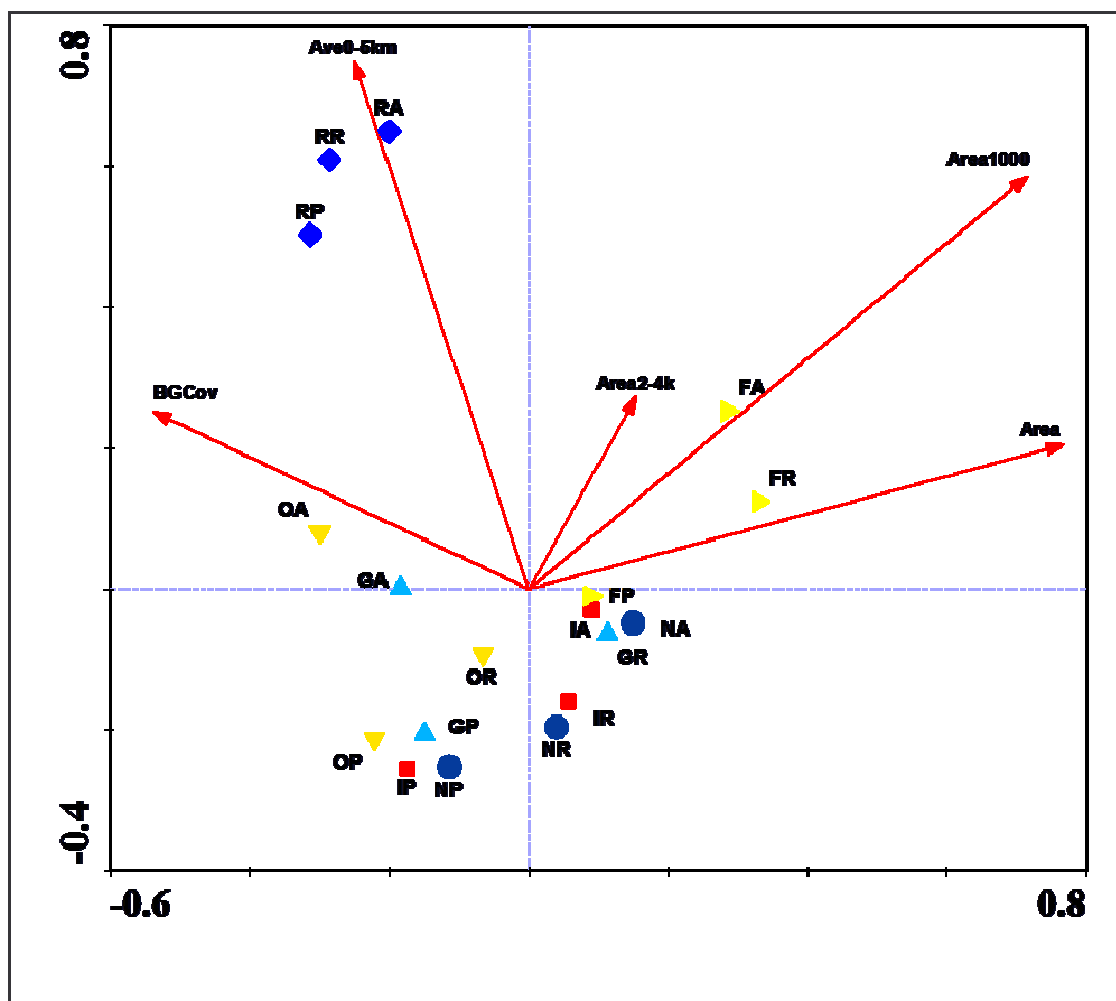


Figure 3.10 – CCA indicating the responses of feeding guilds to the fragmentation effect in the West Coast Renosterveld Bioregion. Eigenvalues: 0.03 (Axis 1) and 0.01 (Axis 2); cumulative percentage variance: 62.5 (Axis 1) and 84 (Axis 2).

Compact – compactness, Area5000– total area of habitat within 5,000 m from sampling point, Area1000 – total area of habitat within 1,000 m from sampling point, SHCov – percentage shrub cover, VegDiv – Vegetation life form diversity.

First letter: C – Carnivores; R – Raptors; O – Omnivores; G – Granivores; F – Frugivores; N – Nectarivores; I – Insectivores. Second letter: R – Species richness in guild; A – relative abundance in guild; P – Proportion of guild in assemblage.

3.4. DISCUSSION

Assemblage composition is known to shift as fragments become smaller and landscapes more fragmented (Lindenmayer et al., 2002; Santos et al., 2002; Castelletta et al., 2005; Drinnan, 2005; Watson et al., 2005; Yeoman and MacNally, 2005; Watling and Donnelly, 2006; Ferraz et al., 2007; Gil-Tena et al., 2007). What is less obvious is the consistency of these effects on biodiversity on a greater geographical scale. In both the bioregions studied, landscape configuration seems to be accountable for shifts in species richness. However, in the WCRB, the more fragmented of the two bioregions, the influence of fragment area was more important. What is also interesting in the WCRB is the strong influence that bare ground cover had on species diversity.

The ECRB has much more habitat, albeit in smaller fragments, scattered across the landscape than the WCRB, where there are fewer fragments spaced further apart. Therefore, in the ECRB, individuals can potentially disperse through the landscape with more ease than in the WCRB. The small fragments that are scattered in the ECRB may act as stepping-stones, making it more likely for species to move through the landscape and occupy more fragments (Fischer and Lindenmayer, 2002; Şekercioğlu et al., 2007). In the WCRB, there are more large fragments within this bioregion, but fewer habitat fragments dispersed among them, thus dispersal between fragments is potentially restricted.

Coppedge et al. (2001) argued that landscape configuration in landscapes is more important than area effects per se in grassland avifauna in both highly and minimally fragmented landscapes. Landscape configuration was indeed the most important factor in the ECRB, where there are still many habitat fragments scattered across the landscape. In the WCRB, however, where the landscape is highly fragmented, fewer habitat fragments are available to be used as stepping-stones, and thus area effects also became a key predictor in certain elements of the avian assemblages found within the remaining fragments.

The amount of habitat and the landscape arrangement thereof in the ECRB can also be linked to the small fragment size at which compositional shifts occurred. In the WCRB, the individuals may be more dependent on the fragment they occupy. A decrease in dispersal may thus result between fragments possibly explaining the 50 ha threshold that was obtained. However, in the ECRB, the more continuous arrangement of the fragments can facilitate the dispersal of individuals. They gain access to more fragments and thus matrix sensitive species are able to occupy smaller fragments. The latter is well illustrated in Opdam et al. (2002). Habitat fragments in the landscape act as a network, and the cohesion of this network

determines the ecological integrity of habitat fragments and the landscape. The WCRB may have a greater total area of habitat, but the ECRB has habitat spread in such a manner that it should facilitate emigration and immigration between patches, maintaining greater ecosystem integrity and function.

The habitat configuration of the WCRB relates to the greater importance of nearest neighbour distance (or connectivity). Here, the larger- and intermediate-sized fragments were more isolated, and therefore, species cannot easily disperse to surrounding fragments, as they are not well connected by stepping-stone habitat fragments. In the ECRB, connectivity was important, but as a measure of habitat arrangement, especially the amount of habitat within 1,000 m from the sampling points. The ECRB has more habitat fragments within this 1,000 m zone, allowing species to use multiple fragments. This can ultimately influence bird species richness and abundance in the patches. Those species that were common in both regions were generally more abundant in the WCRB.

It is important to consider the changes in assemblage composition from a functional point of view, as reflections of biological integrity (Bishop and Myers, 2005). Guild-level results were very different for the two bioregions. Guilds represented in the ECRB were mostly influenced by the shape, or compactness of the fragments and the diversity of the plant life forms, however, the amount of habitat within 5,000 m of the sampling points also affected some of the guilds. Frugivores and nectarivores, for instance, are adapted to feeding on patchy distributed resources, and would therefore be predicted to be influenced more by landscape configuration (Sarraco et al., 2004). Insectivores are sensitive to change in microclimatic and microhabitat conditions (Canaday, 1997; Ueze et al., 2005), therefore they are likely to be affected by fragment shape, and thus compactness. Fragments with a more compact shape are better protected against the elements of the matrix, therefore allowing the habitat within the fragments to be more intact and suitable to species sensitive to habitat changes, such as insectivores.

In the WCRB, however, where the landscape is much more fragmented than in the ECRB, the importance of fragment area outweighs the other predictors. Only frugivore abundance and raptor composition were sensitive to some measures of landscape configuration. The overall greater importance of fragment size in the WCRB is consistent with a recent study done in another highly fragmented shrubland type in the Western Cape Province, South Africa. Fox and Hockey (2007) also found that species richness was positively correlated to fragment size. They also found that frugivorous species richness, consistent with my findings, was positively correlated to fragment size.

As indicated by the findings in this study, landscape patterns can influence ecological processes (Lawler and Schumaker, 2004). Landscape pattern influences ecological processes through its effect on dispersal behaviour of species (Cooper et al., 2002). Frugivores, nectarivores and granivores are essential in the dispersion of floral genetic material (Şekercioğlu, 2006; Gil-Tena et al., 2007). Their responses to fragmentation in this study have been linked to area effects and the arrangement of habitat within the landscape. This highlights once more the importance of network cohesion (Opdam et al., 2003). In a highly fragmented landscape, these mobile links are of utmost importance. The conservation of one component, e.g. avian diversity and avian functional integrity, can have major repercussions on another component in the ecosystem, such as maintaining floral gene flow at healthy levels.

The final element that was identified as influential in the present study was the quality of the habitat within the fragments. Avian assemblages are known to be highly influenced by habitat structure and quality (Briggs et al. 2007). This is supported by the strong negative relationship recorded between species diversity and the absence of vegetation cover. The reduced cover creates a situation where individuals must forage, roost and/or nest where less cover, and hence protection, is available (Virgós, 2001; Santos et al., 2008).

3.5. CONCLUSION

Differences in landscape configuration of these two bioregions resulted in two very different patterns of avian assemblages. In the WCRB, the more fragmented of the two bioregions, area effects were a prominent predictor of species richness. This is consistent with many fragmentation studies that refer to area effects being a great threat to avian diversity (Santos et al., 2002; Castelletta et al., 2005; Watson et al., 2005). However, in the ECRB the situation was different. Area effects were not potentially important and landscape configuration was the most influential predictor of richness at most levels with the assemblages. At the landscape scale, however, it was the amount of habitat within 1,000 m of fragments that had the greatest influence on the avian integrity of both these bioregions. The fact that there was more habitat within this radius of the sampling points in the ECRB may aid dispersal of individuals, allowing them to more easily colonise surrounding fragments.

This study, therefore, contrasts with the findings of Coppedge et al. (2001), that landscape pattern is more important in highly- and minimally-fragmented habitats. In the

highly fragmented landscapes of the WCRB, area effects were of greater importance than in the less fragmented ECRB. However, in the landscapes with more habitat fragments, area effects become less important. This emphasises the importance of conserving large portions of habitat within the landscape, even small fragments, as they will act as corridors and stepping stones, facilitating dispersal. This study supports a previous study done in the WCRB, in that area effects are prevalent and important in shaping avian assemblages (Randrianasolo, 2003). Research done in the ECRB also found area effects to be the most influential factor to avian assemblages (Cameron, 1999). However, I have shown that landscape configuration may well be the most important factor in altering avian assemblages in the latter.

Many fragmentation studies have focused on how fragment scale influences biodiversity. The value of the present study is its comparative approach across bioregions which highlighted the importance of network cohesion and how this affects avian diversity and integrity at different levels.

Investigating species richness, diversity and guild composition proved to be useful for assessing how fragmentation affects assemblages at multiple levels. In some cases, different patterns emerged within each of the levels used in the analyses. A prime example of this emergence is the overwhelming importance of the presence and/or absence of vegetation cover for species abundances. However, within each bioregion, certain patterns and predictors remained universal within the three levels within the assessed assemblages, which should be investigated further.

A further recommendation for research is to also to investigate the similarities in life-history traits of species that repeatedly show a high level of sensitivity to fragmentation, area effect and landscape configuration (Okes et al., 2008).

3.5.1. Conservation recommendations

Based on the results of this study, I make the following recommendations for conservation strategies and practices for maintaining intact avian assemblages:

- Conservation should look beyond the approach of protecting only large fragments. Small fragments play an essential role on stepping stones in rapidly changing ecosystems. Also, habitat quality must remain a pivotal criterion in the selection of fragments adequate for conservation;
- The conservation of landscape- or network-cohesion is as important as conserving large fragments. Strategic conservation plans that are based on a landscape-scale approach, and

that give recognition to conservation networks, will undoubtedly be the most effective means for conserving avifaunal integrity;

- Guilds that display measurable levels of sensitivity to area and landscape configuration effects should be used as surrogates to monitor the condition of avifaunal integrity;
- This research showed that the best practice for avifauna conservation is to conserve large, well-connected fragments, using smaller fragments as stepping-stones and corridors.

3.6. REFERENCES

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9, 968–980.
- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.
- ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, California. Copyright © 1999-2008 ESRI.
- Baily, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management* 238, 7-23.
- Batáry, P., Báldi, A., 2004. Evidence of the edge effects on avian nest success. *Conservation Biology* 18, 389-400.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: Meta-analysis of the patch size effect. *Ecology* 79, 517-533.
- Bishop, J.A., Myers, W.L., 2005. Associations between avian functional guild response and regional landscape properties for conservation planning. *Ecological Indicators* 5, 33-48.
- Briggs, S.V., Seddon, J.A., Doyle, S.J., 2007. Structures of birds communities in woodland remnants in central New South Wales, Australia. *Australian Journal Of Zoology* 55, 29-40.
- Brown, W. P., Sullivan, P. J., 2005. Avian community composition in isolated fragments: a conceptual revision. *Oikos* 111, 1-8.
- Bortons, L., Mönkkönen, M., Martin, J.L., 2003. Are fragments islands? Landscape context and density-area relationships in Boreal forest birds. *The American Naturalist* 162, 343-357.
- Cameron, A., 1999. The effects of fragmentation of renosterveld vegetation on bird community composition. M.Sc. Thesis, University of Cape Town.
- Canaday, C., 1997. Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation* 77, 63-77.
- Castelletta, M., Thiollay, J., Sodhi, N.S., 2005. The extreme forest fragmentation on the bird community of Singapore Island. *Biological Conservation* 121, 135-155.
- Chan, K.M.A., Ranganathan, J., 2005. Testing the importance of patch scale on forest birds. *Oikos* 111, 606-610.

- Colwell, R.K., 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Cooper, C.C., Walters, J.R., Priddy, J., 2002. Landscape patterns and dispersal success: simulated population dynamics in the brow treecreeper. *Ecologica Applications* 12, 1576-1587.
- Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2001. Avian responses to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications* 11, 47-59.
- Davis, S.K., Brigham, R.M., Shaffer, T.L., James, P.C., 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. *The Auk* 123, 807-821.
- Debinski, D.M., Ray, C., Saveraid, E.H., 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity. *Biological Conservation* 98, 179-190.
- Dettmers, R., Buehler, D.A., Bartlett, J.G., Klaus, N.A., 1999. Influence of point count length and repeated visits on habitat model performance. *Journal of Wildlife Management* 63, 815-823.
- Drinnan, I.N., 2005. The search for fragmentation in a southern Sydney suburb. *Biological Conservation* 124, 339-349.
- Donner, D.M., Probst, J.R., Ribic, C.A., 2008. Influence of habitat amount, arrangement, and use on population trends estimates of male Kirkland's warblers. *Landscape Ecology* 23, 467-480.
- Dunning, Jr., J.B., Borgella, Jr., R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9, 542-550.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of the Ecology, Evolution and Systematics* 34, 487-515.
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, Jr., R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315, 238-241.
- Fischer, J., Lindenmayer, D.B., 2002. Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. *Biological Conservation* 106, 129-136.

- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: The relative importance of habitat amount and arrangement. *The American Naturalist* 159, 40-56.
- Fletcher, Jr., R.J., Ries, L., Battin, J., Chalfoun, A.D., 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology* 85, 1017–1030.
- Fox, S and Hockey, P.A.R., 2007. Impacts of a South African coastal golf estate on shrubland bird communities. *South African Journal of Science* 103, 27-34.
- Gil-Tena, A., Saura, S., Bortons, L., 2007. Effects of forest composition and structure on bird species richness in a Mediterranean context: implications for forest ecosystem management. *Forest ecology and Management* 242, 470-476.
- Githiru, M., Lens, L., Bennur, L.A., Ogol, C.P.K.O., 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96, 320-330.
- Githiru, M., Bennur, L.A., Lens, L., Ogol, C.P.K.O., 2005. Spatial and temporal variation in fruit and fruit-eating birds in the Taita Hills, south-east Kenya. *Ostrich* 76, 37-44.
- Goodwin, B.J., Fahrig, L., 2002. How does landscape structure influence landscape connectivity. *Oikos* 99, 552-570.
- GRASS Development Team, 2008. Geographic Resources Analysis Support System (GRASS GIS) Software, Open Source Geospatial Foundation.
- Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* 21, 133-141.
- Hamer, T.L., Flather, C.H., Noon, B.R., 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landscape Ecology* 21, 569-583.
- Hinsley, S.A., Pakeman, R., Bellamy, P.E., Newton, I., 1996. Influence of habitat fragmentation on bird species distribution and regional population sizes. *Proceedings of the Royal Society of London: Biological Sciences* 263, 307-313.
- Hockey, P.A.R., Dean, W.R.J., Ryan, P.G., 2005. *Roberts Birds of Southern Africa*. 7th Edn. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Johnson, D.H., Igl, L.D., 2001. Area requirements of grassland birds: A regional perspective. *The Auk* 118, 24-34.

- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10, 299-314.
- Krug, C.B., Krug, R.M., 2007. Restoration of old fields in renosterveld: a case study in a Mediterranean shrubland of South Africa. In Cramer V.A., Hobbs R.J. (eds) *Old fields: Dynamics and restoration of abandoned farmland*. Island Press / Society for Ecological Restoration.
- Lawler, J.J., Schumaker, N.H., 2004. Evaluating habitat as a surrogate for population viability using a spatially explicit population model. *Environmental Monitoring and Assessment* 94: 85–100, 2004.
- Lee, P., Rotenberry, J.T., 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. *Journal of Biogeography* 32, 1139-1150.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H., Lindenmayer, B.D., 2002. Effects of forest fragmentation on bird assemblages in a novel landscape context. *Ecological Monographs* 72, 1-18.
- Matlock, R.B., Edwards, P.J., 2006. The influence of habitat variables on bird communities in forest remnants in Costa Rica. *Biodiversity and Conservation* 15, 2987-3016.
- Mucina, L., Rutherford, C., (Eds), 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria.
- Okes, N.C., Hockey, P.A.R., Cumming G.S., 2008. Habitat use and life history as predictors of bird responses to habitat change. *Conservation Biology* 22, 151-162.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B., 2007. *Vegan: Community ecology package version 1.8-6*. <http://cran.r-project.org>.
- Opdam, P., Verboom, J., Pouwels, R., 2003. Landscape cohesion: an index for the conservation potential of landscape for biodiversity. *Landscape Ecology* 18, 113-126.
- Ortega-Huerta, M.A., 2007. Fragmentation patterns and implications for biodiversity conservation in three biosphere reserves and surrounding regional environments, north-eastern Mexico. *Biological Conservation* 134, 83-95.
- Parker, T.H., Stansberry, B.M., Becker, C.D., Gipson P.S., 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology* 19, 1157-1167.

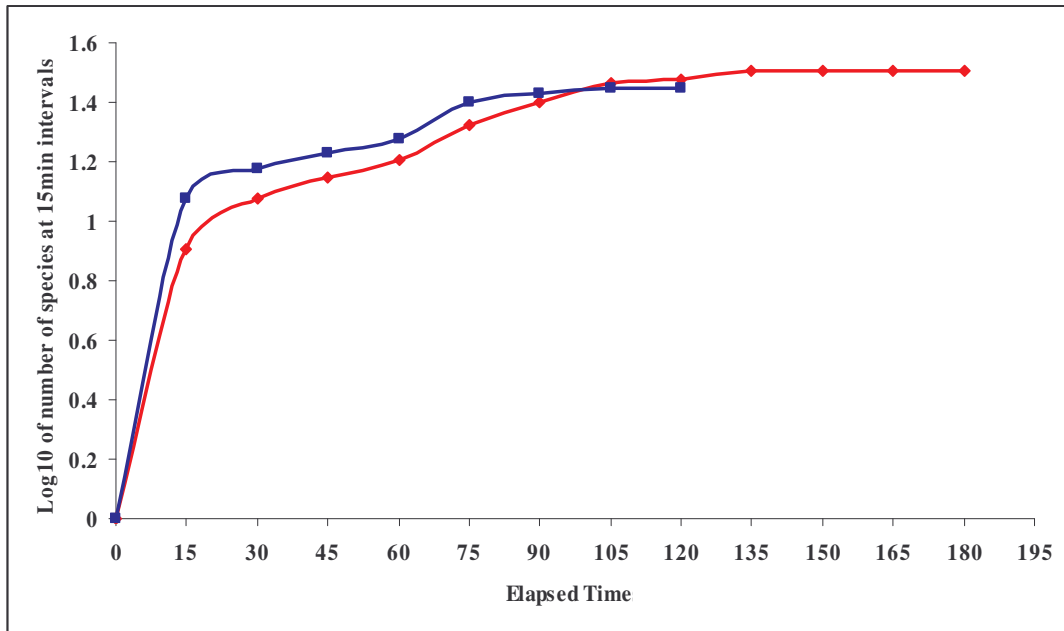
- Pearman, P.B., 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understorey. *Ecological Monographs* 72, 19-39.
- Randrianasolo, H., 2003. Birds in west coast renosterveld fragments: implications for a threatened habitat. M.Sc. Thesis, University of Cape Town.
- R Development Core Team, 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Roslin, T., 2002. So near yet so far – habitat fragmentation and bird movement. *Trends in Ecology and Evolution* 17, 61.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777-790.
- Sallabanks, R., Riggs, R.A., Cobb, L.E., Dodson, S.W., 2006. Bird-habitat relationships in Grand Fir forest of the Blue Mountains, Oregon. *Forest Science* 52, 489-502.
- Samways, M. J., 2005. *Insect Diversity Conservation*. Cambridge Press. Cambridge.
- Santos, T., Díaz, J.A., Pérez-Tris, J., Carbonell, R., Tellería, J.L., 2008. Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. *Animal Conservation* 11, 46–56.
- Santos, T., Tellería, J.L., Carbonell, R., 2002. Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation. *Biological Conservation* 105, 113-15.
- Saracco, J.F., Collazo, J.A., Groom, M.J., 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139, 235-245.
- Schmiegelow, F.K.A., Machtans, G.S., Hannon, S.J., 1997. Are Boreal birds resilient to forest fragmentation? An experimental study of the short-term community responses. *Ecology* 78, 1914-1932.
- Şekercioğlu, Ç.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R.F., 2007. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* 99, 263-267.
- Şekercioğlu, Ç.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystems consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* 103, 10941-10946.
- Şekercioğlu, C.H., 2006. Increasing awareness of avian ecological function. *Trends in Ecology and Evolution* 21, 464-397.

- Shirley, S.M., 2006. Movement of forest birds across river and clearcut edges of varying riparian buffer strip widths. *Forest Ecology and Management* 2006, 190-199.
- Smith, J.N.M., Hellmann, J.J., 2002. Population persistence in fragmented landscapes. *Trends in Ecology and Evolution* 17, 397-399.
- Sokal, R.R., Rohlf, F.J., 2003. *Biometry: the principles and practice of statistics in biological research*, 3rd Edition. W.H. Freeman, New York.
- StatSoft, Inc., 2007. STATISTICA (data analysis software system), version 8. www.statsoft.com.
- ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 4.5). Microcomputer Power (Ithaca, NY, USA), p35-37, 64,65.
- Tischendorf, L., Bender, D.J., Fahrig, L., 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18, 41-50.
- Tscharntke, T., Brandl, R., 2004. Plant-insect interactions in fragmented landscapes. *Annual Reviews of Entomology* 49, 405-30.
- Ueze, A., Metzger, J.P., Vielliard, J.M.E., 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic forest bird species. *Biological Conservation* 123, 507-519.
- van Teeffelen, A.J.A., Cabeza, M., Moilanen, A., 2006. Connectivity, probabilities and persistence: comparing reserve selection strategies. *Biodiversity and Conservation* 15, 899-919.
- von Hase, A., Rouget, M., Maze, K., Helme, N., 2003. A fine-scale conservation plan for the Cape Lowlands Renosterveld: Technical Report. Cape Conservation Unit, Botanical Society, Cape Town.
- Virgós, E., 2001. Role of isolation and habitat quality in shaping species abundance: a test with badgers (*Meles meles* L.) in a gradient of forest fragmentation. *Journal of Biogeography* 28, 381-389.
- Walters, J.R., Ford, H.A., Cooper, C.B., 1999. The ecological basis of sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. *Biological Conservation* 90, 13-20.
- Watling, J.I., Donnelly, M.A., 2006. Fragments as islands: a synthesis of faunal responses to patchiness. *Conservation Biology* 20, 1016-1025.

- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31, 1791-1807.
- Watson, J.E.M., Whittaker, R.J., Freudenberger, D., 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* 32, 1353-1370.
- Weinberg, H.J., Roth, R.R., 1998. Forest area and habitat quality for nesting wood thrushes. *The Auk* 115, 879-889.
- Wethered, R., Lawes, M.J., 2003. Matrix effect on bird assemblages in afromontane forests in South Africa. *Biological Conservation* 114, 327-340.
- Wilson, J.W., van Aarde, R.J., van Rensburg, B.J., 2007. Effects of habitat fragmentation on bird Communities of sand forests in southern Mozambique. *Ostrich* 78, 37-42.
- Yeoman, F., Mac Nally, R., 2005. The avifaunas of some fragmented, periurban, coastal woodlands in south-eastern Australia. *Landscape and Urban Planning* 72, 297-312.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer, New York

Appendix 3.A - Size (ha) of fragments included in the study for both bioregions

| no. | ECRB | WCRB | no. | ECRB | WCRB |
|-----|------|------|-----|------|------|
| 1 | 630 | 1425 | 21 | 48 | 28 |
| 2 | 243 | 882 | 22 | 38 | 23 |
| 3 | 153 | 596 | 23 | 33 | 13 |
| 4 | 139 | 299 | 24 | 33 | 22 |
| 5 | 132 | 282 | 25 | 25 | 21 |
| 6 | 130 | 266 | 26 | 23 | 18 |
| 7 | 127 | 266 | 27 | 19 | 16 |
| 8 | 123 | 254 | 28 | 18 | 16 |
| 9 | 123 | 249 | 29 | 15 | 14 |
| 10 | 120 | 142 | 30 | 14 | 13 |
| 11 | 111 | 115 | 31 | 12 | 12 |
| 12 | 109 | 100 | 32 | 10 | 11 |
| 13 | 104 | 100 | 33 | 10 | 7 |
| 14 | 103 | 97 | 34 | 10 | 8 |
| 15 | 100 | 92 | 35 | 6 | 7 |
| 16 | 88 | 79 | 36 | 5 | 6 |
| 17 | 88 | 78 | 37 | 5 | 6 |
| 18 | 70 | 50 | 38 | 4 | 3 |
| 19 | 58 | 45 | 39 | 2 | 2 |
| 20 | 49 | 44 | 40 | 1 | 1 |



Appendix 3.B – Species accumulation curves for the ECRB (blue) and WCRB (red).

Appendix 3.C - Species list from ECRB field surveys

| Common Name | Scientific Name | Common Name | Scientific Name |
|--------------------------|----------------------------------|---------------------------------|---------------------------------|
| Black-Headed Heron | <i>Ardea melanocephala</i> | Capped Wheatear | <i>Oenanthe pileata</i> |
| Black-shouldered Kite | <i>Elanus caeruleus</i> | Cape Grassbird | <i>Sphenoeacus afer</i> |
| Black Harrier | <i>Circus maurus</i> | Grey-backed Cisticola | <i>Cisticola subruficapilla</i> |
| Grey-winged Francolin | <i>Scleroptila africanus</i> | Cloud Cisticola | <i>Cisticola textrix</i> |
| Cape Turtle Dove | <i>Streptopelia capicola</i> | Bar-throated Apalis | <i>Apalis thoracica</i> |
| Laughing Dove | <i>Streptopelia senegalensis</i> | Karoo Prinia | <i>Prinia maculosa</i> |
| Speckled Mousebird | <i>Colius striatus</i> | Yellow-bellied Eremomela | <i>Eremomela icteropygialis</i> |
| Redfaced Mousebird | <i>Urocolius indicus</i> | Long-billed Crombec | <i>Sylvietta rufescens</i> |
| Acacia Pied Barbet | <i>Tricholaema leucomelas</i> | Fiscal Flycatcher | <i>Sigelus silens</i> |
| Cape Clapper Lark | <i>Mirafrapiata</i> | Cape Batis | <i>Batis capensis</i> |
| Agulhas Clapper Lark | <i>Miraframarjorriae</i> | Common Fiscal | <i>Lanius collaris</i> |
| Large-Billed Lark | <i>Galerida magnirostris</i> | Southern Tchagra | <i>Tchagra tchagra</i> |
| Agulhas Long-billed Lark | <i>Certhilauda brevirostris</i> | Bokmakierie | <i>Telophorus zeylonus</i> |
| Red-Capped Lark | <i>Calandrella cinerea</i> | African Pied Starling | <i>Spreo bicolor</i> |
| Cape Wagtail | <i>Motacilla capensis</i> | Malachite Sunbird | <i>Nectarinia famosa</i> |
| Cape Longclaw | <i>Marconyx capensis</i> | Southern Double-collard Sunbird | <i>Cinnyris chalybeus</i> |
| African Pipit | <i>Anthus cinnamomeus</i> | Cape White Eye | <i>Zosterops capensis</i> |
| Cape Penduline-tit | <i>Anhoscopus minutus</i> | Cape Sparrow | <i>Passer meuslanur</i> |
| Cape Bulbul | <i>Pycnonotus capensis</i> | Cape Weaver | <i>Ploceus capensis</i> |
| Grey Tit | <i>Parus afer</i> | Yellow Bishop | <i>Euplectes capensis</i> |
| Cape Robin-chat | <i>Cossypha caffra</i> | Common Waxbill | <i>Estrilda astrild</i> |
| Karoo Scrub-robin | <i>Cercotrichas coryphaeus</i> | Yellow Canary | <i>Serinus flaviventris</i> |
| African Stonechat | <i>Saxicola torquatus</i> | White-throated Canary | <i>Serinus albogularis</i> |
| Familiar Chat | <i>Cercomela familiaris</i> | Cape Bunting | <i>Emberiza capensis</i> |

Appendix 3.D - Species list from WCRB field surveys

| Common Name | Scientific Name | Common Name | Scientific Name |
|------------------------|----------------------------------|---------------------------------|---------------------------------|
| Black-shouldered Kite | <i>Elanus caeruleus</i> | Chestnut-vented Tit-babbler | <i>Parisoma subcaeruleum</i> |
| Rufous-chetsed | | | |
| Sparrowhawk | <i>Accipiter rufiventris</i> | Neddicky | <i>Cisticola fulvicapilla</i> |
| Jackal Buzzard | <i>Buteo rufofuscus</i> | Grey-backed Cisticola | <i>Cisticola subruficapilla</i> |
| Rock Kestrel | <i>Falco rupicolus</i> | Levaillant's Cisticola | <i>Cisticola tinniens</i> |
| Peregrine Falcon | <i>Falco peregrinus</i> | Zitting Cisticola | <i>Cisticola juncidis</i> |
| Helmeted Guineafowl | <i>Numida meleagris</i> | Cloud Cisticola | <i>Cisticola textrix</i> |
| Grey-winged Francolin | <i>Scleroptila africanus</i> | Bar-throated Apalis | <i>Apalis thoracica</i> |
| Cape Spurfowl | <i>Pternistes capensis</i> | Karoo Prinia | <i>Prinia maculosa</i> |
| Southern Black Korhaan | <i>Eupodotis afra</i> | Long-billed Crombec | <i>Sylvietta rufescens</i> |
| Spotted Thick-knee | <i>Burhinus capensis</i> | Fiscal Flycatcher | <i>Sigelus silens</i> |
| Speckled Pigeon | <i>Columba guinea</i> | Fairy Flycatcher | <i>Stenostira scita</i> |
| Red-eyed Dove | <i>Streptopelia semitorquata</i> | Cape Batis | <i>Batis capensis</i> |
| Cape Turtle Dove | <i>Streptopelia capicola</i> | Common Fiscal | <i>Lanius collaris</i> |
| Laughing Dove | <i>Streptopelia senegalensis</i> | Southern Boubou | <i>Laniarius turatii</i> |
| Speckled Mousebird | <i>Colius striatus</i> | Bokmakierie | <i>Telophorus zeylonus</i> |
| Redfaced Mousebird | <i>Urocolius indicus</i> | African Pied Starling | <i>Spreo bicolor</i> |
| African Hoopoe | <i>Upupa africana</i> | Redwinged Starling | <i>Onychognathus morio</i> |
| Acacia Pied Barbet | <i>Tricholaema leucomelas</i> | Orange-breasted Sunbird | <i>Anthobaphes violacea</i> |
| Lesser Honeyguide | <i>Indicator minor</i> | Malachite Sunbird | <i>Nectarinia famosa</i> |
| Cape Clapper Lark | <i>Mirafra apiata</i> | Southern Double-collard Sunbird | <i>Cinnyris chalybeus</i> |
| Cape Longclaw | <i>Marconyx capensis</i> | Cape White Eye | <i>Zosterops capensis</i> |
| Pied Crow | <i>Corvus albus</i> | Cape Sparrow | <i>Passer meusanur</i> |
| White-necked Raven | <i>Corvus albicollis</i> | Cape Weaver | <i>Ploceus capensis</i> |
| Cape Penduline-tit | <i>Anhoscopus minutus</i> | Southern Masked Weaver | <i>Ploceus velatus</i> |
| Cape Bulbul | <i>Pycnonotus capensis</i> | Southern Red Bishop | <i>Euplectes orix</i> |
| Grey Tit | <i>Parus afer</i> | Yellow Bishop | <i>Euplectes capensis</i> |
| Sentinel Rock-thrush | <i>Monticola explorator</i> | Sweet Waxbill | <i>Coccygia melanotis</i> |
| Olive Thrush | <i>Turdus olivaceus</i> | Common Waxbill | <i>Estrilda astrild</i> |

Appendix 3.D – Continued

| Common Name | Scientific Name | Common Name | Scientific Name |
|----------------------|--------------------------------|-----------------------|-----------------------------|
| Cape Robin-chat | <i>Cossypha caffra</i> | Pin-tailed Whydah | <i>Vidua macroura</i> |
| Karoo Scrub-robin | <i>Cercotrichas coryphaeus</i> | Yellow Canary | <i>Serinus flaviventris</i> |
| African Stonechat | <i>Saxicola torquatus</i> | Cape Canary | <i>Serinus canicollis</i> |
| Familiar Chat | <i>Cercomela familiaris</i> | White-throated Canary | <i>Serinus albogularis</i> |
| Sickle-winged Chat | <i>Cercomela sinuata</i> | Protea Seed-eater | <i>Serinus leucopterus</i> |
| Cape Grassbird | <i>Sphenoeacus afer</i> | Cape Bunting | <i>Emberiza capensis</i> |
| Layard's Tit-babbler | <i>Parisoma layardi</i> | | |

Appendix 3.E – Factor analysis results.

| | ECRB | | | | | WCRB | | | | |
|---------------------------------------|---------------------|---------------------|---------------------|----------------------|----------------------|---------------------|---------------------|---------------------|---------------------|----------------------|
| | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 | Factor 1 | Factor 2 | Factor 3 | Factor 4 | Factor 5 |
| Area (ha) | -0.155 | 0.726 | -0.078 | -0.428 | 0.247 | 0.467 | 0.152 | <u>0.800</u> | 0.025 | 0.072 |
| Compactness | -0.138 | 0.096 | -0.006 | <u>-0.752</u> | 0.017 | 0.344 | 0.209 | 0.717 | 0.009 | 0.091 |
| Average Area between 4000-5000 m (ha) | 0.897 | -0.128 | 0.071 | 0.093 | 0.038 | 0.120 | 0.071 | -0.088 | <u>0.804</u> | -0.083 |
| Total Area between 2000-4000m (ha) | 0.957 | -0.079 | 0.125 | 0.093 | -0.009 | 0.087 | <u>0.919</u> | 0.025 | 0.225 | 0.107 |
| Total Area in 1000 m (ha) | 0.120 | <u>0.946</u> | -0.077 | -0.144 | 0.055 | <u>0.937</u> | 0.227 | 0.116 | -0.038 | 0.063 |
| Total Area in 5000 m (ha) | <u>0.985</u> | 0.021 | 0.060 | 0.088 | 0.033 | 0.248 | 0.756 | 0.270 | 0.371 | 0.195 |
| Vegetation Life-form Diversity | -0.031 | -0.023 | -0.180 | -0.105 | <u>-0.759</u> | 0.695 | -0.021 | 0.296 | -0.132 | 0.407 |
| Shrub Cover | 0.315 | 0.170 | <u>0.805</u> | 0.005 | 0.201 | 0.215 | 0.023 | 0.222 | -0.517 | 0.720 |
| Bare Ground Cover | 0.316 | -0.076 | 0.056 | 0.625 | 0.388 | -0.042 | -0.079 | -0.086 | -0.230 | <u>-0.870</u> |

Appendix 3.F - Species richness and Shannon Diversity indices of all fragments surveyed.

| Fragment | ECRB | | WCRB | |
|----------|------------------|-------------------|------------------|-------------------|
| | Species Richness | Species Diversity | Species Richness | Species Diversity |
| 1 | 19 | 2.755 | 28 | 2.802 |
| 2 | 14 | 2.405 | 39 | 3.329 |
| 3 | 13 | 2.296 | 33 | 2.975 |
| 4 | 18 | 2.755 | 24 | 2.749 |
| 5 | 18 | 2.628 | 25 | 2.893 |
| 6 | 17 | 2.579 | 21 | 2.755 |
| 7 | 16 | 2.550 | 26 | 3.034 |
| 8 | 15 | 2.550 | 24 | 2.745 |
| 9 | 18 | 2.711 | 24 | 2.747 |
| 10 | 15 | 2.572 | 21 | 2.691 |
| 11 | 18 | 2.615 | 21 | 2.613 |
| 12 | 16 | 2.525 | 23 | 2.838 |
| 13 | 15 | 2.575 | 22 | 2.738 |
| 14 | 9 | 2.018 | 21 | 2.806 |
| 15 | 12 | 2.248 | 18 | 2.388 |
| 16 | 14 | 2.432 | 20 | 2.592 |
| 17 | 10 | 2.231 | 20 | 2.740 |
| 18 | 13 | 2.314 | 19 | 2.579 |
| 19 | 12 | 2.350 | 18 | 2.578 |
| 20 | 12 | 2.213 | 21 | 2.791 |
| 21 | 17 | 2.611 | 16 | 2.389 |
| 22 | 15 | 2.431 | 17 | 2.452 |
| 23 | 15 | 2.519 | 16 | 2.256 |
| 24 | 11 | 2.099 | 14 | 2.394 |
| 25 | 15 | 2.548 | 15 | 2.339 |
| 26 | 12 | 2.236 | 15 | 2.488 |
| 27 | 8 | 1.907 | 15 | 2.502 |
| 28 | 20 | 2.813 | 14 | 2.266 |
| 29 | 11 | 2.266 | 15 | 2.526 |
| 30 | 14 | 2.470 | 19 | 2.687 |
| 31 | 13 | 2.455 | 14 | 2.386 |
| 32 | 12 | 2.257 | 15 | 2.353 |
| 33 | 12 | 2.134 | 14 | 2.356 |
| 34 | 11 | 2.077 | 16 | 2.645 |
| 35 | 12 | 2.261 | 13 | 2.346 |
| 36 | 12 | 2.291 | 12 | 2.265 |
| 37 | 13 | 2.336 | 12 | 1.576 |
| 38 | 7 | 1.748 | 12 | 2.078 |
| 39 | 11 | 2.166 | 10 | 1.945 |
| 40 | 7 | 1.777 | 9 | 1.986 |

4. THE INFLUENCE OF HABITAT FRAGMENTATION AND HABITAT SUITABILITY ON THE ABUNDANCE AND OCCUPANCY OF COMMON SPECIES IN TWO ENDANGERED BIOREGIONS

SUMMARY

Fragmentation of natural habitats has changed biotic communities and assemblages in many parts of the world. Many studies focus on how fragment area, isolation and landscape configuration affect the organisms in these fragmented habitats. However, these studies mostly focus on habitat specific and sensitive species. In this study, I focus on those species that are most common in two highly fragmented and endangered bioregions in the Cape Floristic Region. Ecological processes, such as pollination and seed dispersal, may well depend on common species, as these species have a higher likelihood of persisting in fragmented landscapes.

Forty fragments in the East- and West Coast Renosterveld Bioregions were sampled, using single, time and distance restricted point counts. Data such as species abundances and habitat characteristics were collected. Multivariate techniques were used to analyse both abundance and occupancy data, including generalised linear models and zero-inflated Poisson models.

Three major findings arose from this study. Firstly, the common bird species in the two bioregions do not respond to the same predictors, with area effects being more prominent in the West Coast Renosterveld Bioregion and the amount of habitat more prominent in the landscape in the East Coast Renosterveld Bioregion. Secondly, as a whole, fragment area was consistently the best predictor of both species abundances and occupancy if results were not compared in the bioregional scale. Thirdly, fragment specific predictors, i.e. area and habitat suitability, were stronger in most models than landscape effects.

4.1. INTRODUCTION

Biodiversity is currently under immense pressure from disturbances such as agricultural and urban expansion, and the introduction of exotic species, leading to large-scale habitat loss and fragmentation (Stockwell et al., 2003). Habitat loss and fragmentation, together with alien invasive species and climate change are widely accepted as the major drivers in the accelerating levels of species extinctions, population crashes and the loss in ecological function (Cushman and McGarigal, 2003; Castellón and Sieving, 2006; Ewers and Didham, 2006).

Habitat fragmentation is defined as the process where focal habitat is subdivided into a discontinuous array of habitat fragments scattered across the landscape, and which are surrounded by novel and potentially hostile environments (Villard et al., 1999; Fahrig, 2003; Ewers and Didham, 2006). Habitat fragmentation effects on birds have been well studied, and our understanding of these adverse effects on local and regional avifauna has improved greatly.

There is widespread evidence for the negative effects of fragmentation on biodiversity. Area, isolation and edge effects have been cited as three of the major threats to local and regional biodiversity in fragmented landscapes (Cushman and McGarigal, 2003; Radford and Bennet, 2004; Wiegand et al., 2005; Ewers and Didham, 2006; Ewers and Didham, 2007b). Species richness and diversity are usually positively correlated with fragment area (Mitchell et al., 2006), and negatively with isolation (Ford et al., 2001). Furthermore, higher edge to core ratios have also been identified as a major threat to habitat sensitive species (Miller and Cale, 2000; Tschardt et al., 2008).

However, fragmentation can also be measured at the landscape scale, i.e. the arrangement of fragments within the landscape (Fahrig, 2003). Once the adverse effects of fragmentation effects are measured at this scale, the impact of the effects on biodiversity becomes evident. The arrangement of fragments within the landscape influences the immigration to and emigration from fragments within the landscape (Cale, 2003; Ewers and Didham, 2007b). Population persistence within fragmented landscapes is a function of metapopulation dynamics, and where individuals are unable to colonize fragments local extinction in these fragments may occur (Foppen et al., 2000; Fahrig, 2002; Fitzgibbon et al., 2007).

The importance of population persistence has been investigated in various habitat types and landscapes differing in configuration and extent of fragmentation (Villard et al., 1999;

Urban and Keitt, 2001; Vance et al., 2003). Most of these studies show consistent results, indicating that species occupancy of landscape decreases as habitats become more fragmented (Trzcinski et al., 1999; Urban and Keitt, 2001). Bird species that are sensitive to fragmentation are usually the most sensitive to the demise of intact landscapes because the matrix presents dispersal barriers (Donovan and Flather, 2002; Ims and Andreassen, 2005; Betts et al., 2007; Ferraz et al., 2007). As a result, these species are lost from fragments within the greater landscape when the arrangements of the fragments are inadequate. The probability of occupancy by bird species is crucial for maintaining avifaunal diversity within the landscape. However, many landscapes are so excessively fragmented, with such low levels of habitat cover remaining, that habitat-sensitive species are restricted to large fragments, thus reducing the chances of individuals colonizing other fragments (Lindenmayer et al., 2002; Ewers and Didham, 2006). These occupancy thresholds are generally thought to become apparent at extreme levels of habitat fragmentation (Guénette and Villard, 2005). When less than 20% of habitat remains across the landscape, fragment occupancy and population persistence may decline (Ford et al., 2001; Fahrig, 2002; Fahrig, 2003; Ewers and Didham, 2006).

However, few studies have investigated the effects of fragmentation at both the landscape and fragment scale, and on both generalist and fairly common species (e.g. Villard et al., 1999). Fragmentation studies have generally focused on habitat specialist species (Ewers and Didham, 2006; Didham et al., 2007; Donner et al., 2008). This bias towards specialist species may well be a shortcoming within empirical and ecological research. Habitat generalist and common species may become increasingly important in highly transformed and fragment landscapes. These species are often less affected by habitat fragmentation (Ewers and Didham, 2006), and can therefore perform ecological roles within these fragmented landscapes that the specialists would otherwise have performed (Mennechez and Clergeau, 2006). It remains important to keep generalists to buffer ecosystems against major functional collapse. These species are thought to be more resilient to unfavourable landscape configuration and should therefore be more likely to occupy fragments. In Chapter 3, the loss of sensitive species was documented, which suggests that generalist, or common species might be necessary to maintain ecological function.

Birds are, however, highly influenced by the habitat characteristic of fragments. Many studies have found profound effects of habitat suitability on bird species in fragmented landscapes, influencing both their occupancy and their abundances (Diefenbach et al., 2007). Species tend to only occupy and utilise fragments that have the appropriate habitat

characteristics to accommodate their specific needs (Betts et al., 2007). However, some studies have shown that, despite the habitat within a fragment being suitable, species may not necessarily use these fragments (Dunning et al., 1995). This can be mainly due to fragments being inaccessible due to small sizes or being too isolated. Nonetheless, the importance of habitat characteristics is a crucial aspect in researching bird species occupancies and abundances.

This study uses a multi-scale approach to investigate the effects of fragmentation on the occupancy and relative abundance of common bird species in natural habitats. Three scales are considered, the fragment scale (fragment area), landscape scale (landscape configuration or habitat cover) and a bioregional scale (two different vegetation types, geographically separated from each other). These bioregions are endemic shrublands (collectively known as Renosterveld) within a biodiversity hotspot, the Cape Floristic Region (Mucina and Rutherford, 2006). Both these bioregions have been subjected to major transformation (von Hase et al., 2003), with less than 20% of habitat cover remaining within the landscape. I predict that species that are shared between the bioregions will respond the same to area- and landscape-scale effects. As the sensitivity of common species and a multi-scale approach have not received much attention in the literature, I aim to determine the effects of fragmentation at these three scales (fragment, landscape and bioregional) on common bird species in each of two critically endangered bioregions.

4.2. METHODS AND MATERIALS

4.2.1. Study Area

80 fragments, 40 in each of the two geographically distinct bioregions, were sampled in the West Coast- and East Coast Renosterveld Bioregions (WCRB and ECRB, respectively; Mucina and Rutherford, 2006). Both of these are in Western Cape province, South Africa (Chapter 3, Fig. 3.1). These are regions that have been heavily transformed through anthropogenic practices, mainly agricultural expansion. They are characterised by major habitat fragmentation and have fragments scattered across each region's extent. The WCRB has been reduced to 12.0% of its original extent and the ECRB to 16.2% (Mucina and Rutherford, 2006). The ECRB has more habitat fragments scattered across the region than the WCRB.

The vegetation type found within these regions is collectively known as Renosterveld, a shrubland vegetation type that is dominated by *Dicerotheramnus rhinocerotis*, commonly known as Renosterbos. A large component of other cupressoid-leaved, evergreen asteraceous shrubs is also present, as well as a great diversity of local endemic geophytes (Mucina and Rutherford, 2006). A major difference between the WCRB and the ECRB is the more dominant grass component in the latter. Additionally, the ECRB also supports *Aloe ferox* and *Acacia karoo*, two features absent from the WCRB. For a more detailed description of the study sites and bioregions, see Chapter 3.

4.2.2. Sampling Design and Surveys

The two regions were sampled in two successive years, May 2007 for the WCRB and May 2008 for the ECRB. In the WCRB, the surveys were done for three hours in each fragment, for the ECRB two hours were adequate. These times were determined by species accumulation curves from pilot studies in the largest fragment in each region. More detail on the bird surveys is found in Chapter 3.

Time and distance restricted (50 m radius) point counts were used as sampling method (Dettmers et al., 1999; Royle and Nichols, 2003). The smallest of the fragments was 1 ha in size. Based on this, each fragment was allocated one point count. This was done to ensure a constant sampling effort across the entire set of fragments to make the data comparable. Sampling was conducted during the first four hours after sunrise and four hours before sunset. Bird species were recorded visually and using sound identification.

4.2.3. Habitat characteristics

Because habitat structure and condition have a strong influence on bird assemblages, some measures were taken at each fragment. Two perpendicular 100 m transects, crossing where the point count was situated, were used to measure the habitat variables at 2 m intervals: 1) plant life-form (e.g. grass, shrub, forb and restio), 2) vegetation height and 3) the presence and/or absence of vegetation cover. These data were then used to average grass and shrub height and percentage cover of these plant life forms. All percentage data were arcsin transformed prior to analyses.

4.2.4. Spatial Analysis

Maps created by von Hase et al. (2003) were used to determine fragment sizes, nearest neighbour distances and landscape configuration. Fragment size, or area, is measured in hectares (ha) for the purposes of this study. Nearest neighbour distances are given in meters (m). In order to define landscape configuration, a buffer approach was adopted (Tischendorf et al., 2003; Hamer et al., 2006; Chapter 3, Fig. 3.2). A buffer, or concentric band with a radius of 5,000 m was created around each sampling point using the *buffer tool* in ArcGIS v9.2's *toolbox* (ESRI, 2008). Afterwards the amount of habitat, i.e. the sum of all remaining fragments' area, was determined in ArcGIS v9.2.

4.2.5. Statistical Analyses

For the purposes of this study, the most common species in each bioregion were selected for analysis. The selected species were those that had been recorded in 10 or more fragments in either one or both bioregions (species list for analyses in Appendix 4.A). Each species in each bioregion was treated on an individual basis in the analysis, which examined the influence of various predictor variables on bird species abundance using a generalized linear modelling (GLM) approach. GLM models were fitted using the software R 2.4.1 (Ihaka and Gentleman, 1996), following the methods of Crawley (2002). Model simplification using backward-elimination of non-significant explanatory variables and interaction terms was adopted. Terms were systematically removed from the model and only added again if their removal resulted in a significant loss of model explanatory power, determined by comparing the log-likelihood of the full model to the log-likelihood of the reduced model using a Wald χ^2 -test with one degree of freedom (Quinn and Keough, 2002). The significance of each explanatory variable was similarly determined by comparing the log-likelihood of the full minimal model including the variable of interest to the log-likelihood of the reduced model with this same variable excluded. Residual plots and normal probability plots were used to check for deviations from normality in the final model. In instances where there was an over-dispersion of zeros in the dataset, a zero-inflated Poisson (ZIP) modelling approach was used (Welsh et al., 1996). A ZIP model involves: (1) modelling factors associated with species occupancy using a GLM with a logit link and binomial error; and (2) modelling factors associated with abundance in cases where the species was present, using a GLM with a log link and truncated Poisson error. ZIP models were fitted using the `zeroinfl()` function in R (Jackman et al., 2008). The output of the ZIP model has two components. The first is a model based on the count, or abundance data, which indicates the best predictors, like the

GLM, that influence the variation in species abundances. The second is a model that indicates factors associated with the presence/absence of the species. In the count model component, a positive coefficient indicates a positive relationship whereas in the occupancy model component, a positive coefficient indicates a negative relationship.

For each species, several variables were selected as potential predictor variables. These were fragment size, nearest neighbour distance, the amount of natural habitat within 5,000 m of the sampling point, and several variables that characterised habitat structure, namely shrub cover, grass cover, ground cover, average shrub height and average grass height. The selection of specific habitat structure variables for each species was based on knowledge of the species' habitat preferences (see Table 4.1).

The minimal model, i.e. the model that incorporated only significant predictors with the lowest AIC value for each analysis, is presented in the results tables. The significance and strength of each predictor was calculated with a Wald test with a χ^2 -function in the lmttest package (Hothorn et al., 2008), written for R. Only data that were accurately predicted at the 95% confidence interval were included in this study.

Basic descriptive statistics were conducted for the predictors for both bioregions, which gave a concise overview of the differences within predictor variables selected for the two bioregions. Means, standard deviations, minimums and maximum values for each of the variables were calculated (Table 4.2). This was carried out in SPSS for Windows (SPSS for Windows, 2007).

Table 4.2 - Species specific predictors for general linear and zero-inflated Poisson models.

| Scientific Name | Common Name | Species-specific Predictors |
|---------------------------------|----------------------------------|---|
| <i>Saxicola torquatus</i> | African Stonechat | Grasscover |
| <i>Ploceus capensis</i> | Cape Weaver | Grasscover |
| <i>Mirafrja marjorriae</i> | Agulhas Clapper Lark | Grasscover + Groundcover |
| <i>Apalis thoracica</i> | Bar-throated Apalis | Shrubheight + Shrubcover |
| <i>Telophorus zeylonus</i> | Bokmakierie | Shrubheight + Shrubcover |
| <i>Pycnonotus capensis</i> | Cape Bulbul | Shrubheight + Shrubcover |
| <i>Cossypha caffra</i> | Cape Robin-chat | Shrubheight + Shrubcover |
| <i>Zosterops capensis</i> | Cape White-eye | Shrubheight + Shrubcover |
| <i>Parisoma subcaeruleum</i> | Chestnut-vented Tit-babbler | Shrubheight + Shrubcover |
| <i>Prinia maculosa</i> | Karoo Prinia | Shrubheight + Shrubcover |
| <i>Sylvietta rufescens</i> | Long-billed Crombec | Shrubheight + Shrubcover |
| <i>Nectarinia famosa</i> | Malachite Sunbird | Shrubheight + Shrubcover |
| <i>Cinnyris chalybeus</i> | Southern Double-collared Sunbird | Shrubheight + Shrubcover |
| <i>Colius striatus</i> | Speckled Mousebird | Shrubheight + Shrubcover |
| <i>Emberiza capensis</i> | Cape Bunting | Groundcover + Shrubcover |
| <i>Pternistes capensis</i> | Cape Spurfowl | Groundcover + Shrubcover |
| <i>Sphenoeacus afer</i> | Cape Grassbird | Grassheight + Grasscover + Restiocovert |
| Cape Longclaw | Cape Longclaw | Grasscover + Grassheight |
| <i>Cisticola textrix</i> | Cloud Cisticola | Grasscover + Grassheight |
| <i>Euplectes capensis</i> | Yellow Bishop | Grasscover + Grassheight |
| <i>Passer meuslanur</i> | Cape Sparrow | Groundcover + Grasscover + Grassheight |
| <i>Streptopelia capicola</i> | Cape Turtle Dove | Groundcover + Grasscover + Grassheight |
| <i>Estrilda astrild</i> | Common Waxbill | Groundcover + Grasscover + Grassheight |
| <i>Lanius collaris</i> | Common Fiscal | Shrubcover + Shrubheight + Groundcover |
| <i>Sigelus silens</i> | Fiscal Flycatcher | Shrubcover + Shrubheight + Groundcover |
| <i>Cisticola subruficapilla</i> | Grey-backed Cisticola | Shrubcover + Shrubheight + Groundcover |
| <i>Cisticola fulvicapilla</i> | Neddicky | Shrubcover + Shrubheight + Groundcover |
| <i>Cercotrichas coryphaeus</i> | Karoo Scrub-robin | Shrubcover + Shrubheight + Groundcover |
| <i>Serinus flaviventris</i> | Yellow Canary | Grasscover + Grassheight + Shrubcover |

Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

Table 4.3 - Summary statistics of landscape configuration in the ECRB and WCRB.

| | Bioregion | Minimum | Maximum | Mean | SD |
|---------------------------------------|-----------|---------|----------|----------|----------|
| Fragment Size (ha) | ECRB | 1.000 | 630.000 | 78.275 | 106.124 |
| Amount of habitat within 5,000 m (ha) | ECRB | 251.312 | 2230.331 | 884.103 | 543.430 |
| Nearest Neighbour Distance (m) | ECRB | 215.000 | 2723.000 | 961.150 | 612.220 |
| Shrub Cover (%) | ECRB | 4.00 | 70.70 | 42.30 | 16.20 |
| Ground Cover (%) | ECRB | 12.00 | 41.00 | 26.00 | 7.30 |
| Grass Cover (%) | ECRB | 1.30 | 65.00 | 28.10 | 17.00 |
| Average Shrub Height (cm) | ECRB | 10.000 | 109.313 | 51.302 | 24.045 |
| Average Grass Height (cm) | ECRB | 5.200 | 71.000 | 27.716 | 13.822 |
| Fragment Size (ha) | WCRB | 2.000 | 1424.000 | 142.650 | 271.402 |
| Amount of habitat within 5,000 m (ha) | WCRB | 86.181 | 1247.762 | 680.240 | 280.246 |
| Nearest Neighbour Distance (m) | WCRB | 625.000 | 6805.000 | 1808.500 | 1238.662 |
| Shrub Cover (%) | WCRB | 49.00 | 96.00 | 78.50 | 10.20 |
| Ground Cover (%) | WCRB | 1.00 | 37.00 | 13.70 | 8.30 |
| Grass Cover (%) | WCRB | 0.00 | 24.00 | 4.20 | 6.20 |
| Average Shrub Height (cm) | WCRB | 10.000 | 109.313 | 51.302 | 24.045 |
| Average Grass Height (cm) | WCRB | 5.200 | 71.000 | 27.716 | 13.822 |

4.3. RESULTS

4.3.1 Variation in Species Abundances in Fragments

Selected predictors served to explain variation in many species' abundances. However, there is little consistency among the predictors for the same species between the two bioregions (Table 4.3). Fragment size (*size*) was a significant predictor for only four of the species in the ECRB. These are the Karoo Prinia (*Prinia maculosa*; $\chi^2 = 12.881$, $p < 0.001$), Bokmakierie (*Telophorus zeylonus*; $\chi^2 = 10.780$, $p = 0.001$), Yellow Canary (*Serinus flaviventris*; $\chi^2 = 55.446$, $p < 0.001$) and the Grey-backed Cisticola (*Cisticola subruficapilla*; $\chi^2 = 4.443$, $p = 0.0035$). All these relationship were positive, thus, abundance increased with size. Nearest neighbour distance (*isolation*) was only a significant predictor for the Cloud Cisticola (*C. textrix*; $\chi^2 = 15.668$, $p < 0.001$) and Cape Sparrow (*Passer meuslanur*; $\chi^2 = 4.726$, $p = 0.030$) in the ECRB. The amount of habitat within 5,000 m from the sampling points (*landscape*) significantly explained the variation in abundances for the cloud cisticola ($\chi^2 = 6.179$, $p = 0.013$) and the African Stonechat (*Saxicola torquatus*; $\chi^2 = 5.060$, $p < 0.024$). These two species were favoured by the matrix as these two relationships were both positive in the ECRB, including the positive relationship of cloud cisticola abundance and increasing isolation. Analysis revealed the strong influence of species-specific habitat preferences. Shrub cover had positive relationships with Cape Robin-chat (*Cossypha caffra*; $\chi^2 = 9.367$, p

= 0.002), Karoo Prinia ($\chi^2 = 29.206$, $p < 0.001$) and Southern Double-collared Sunbird (*Cinnyris chalybeus*; $\chi^2 = 5.553$, $p = 0.018$) abundances, with average shrub height (*shrubheight*) affecting Speckled Mousebird abundances (*Colius striatus*, $\chi^2 = 4.875$, $p = 0.027$), also positively. Grass cover had a strong positive effect on Cloud Cisticola abundances ($\chi^2 = 11.540$, $p = 0.001$), with average grass height (*grassheight*) having a positive effect on Yellow Canary abundances ($\chi^2 = 6.983$, $p = 0.008$).

In the WCRB, fragment size was a more frequent predictor of species abundances. The abundances of Cape Robin-chat ($\chi^2 = 44.642$, $p < 0.001$), Karoo Prinia ($\chi^2 = 112.220$, $p < 0.001$), Bokmakierie ($\chi^2 = 24.958$, $p < 0.001$), Southern Double-collared Sunbird ($\chi^2 = 42.694$, $p < 0.001$), Bar-throated Apalis (*Apalis thoracica*; $\chi^2 = 9.068$, $p = 0.003$), Karoo Scrub-robin (*Cercotrichas coryphaeus*; $\chi^2 = 25.501$, $p < 0.001$), Cape Bulbul (*Pycnonotus capensis*; $\chi^2 = 22.017$, $p < 0.001$), Cape White-eye (*Zosterops capensis*; $\chi^2 = 21.447$, $p < 0.001$) and Neddicky (*Cisticola fulvicapilla*; $\chi^2 = 3.865$, $p = 0.049$) were all positively related to fragment size. Again, isolation explained the variation in Cloud Cisticola abundance ($\chi^2 = 5.805$, $p = 0.016$), however in contrast to the ECRB, the relationship was negative for the WCRB. Cape Bulbul abundances in the WCRB were also influenced by isolation ($\chi^2 = 23.908$, $p < 0.001$). The amount of habitat within the landscape only effected Cape White-eye ($\chi^2 = 11.785$, $p < 0.001$) abundances in this study. Shrub cover only favoured Grey-backed Cisticola ($\chi^2 = 12.881$, $p < 0.001$) abundances in the WCBR, with grass cover having positive relationships with Cloud Cisticola ($\chi^2 = 44.015$, $p < 0.001$) and Yellow Canary ($\chi^2 = 4.149$, $p = 0.048$) abundances. Karoo Scrub-robin was the only species to be favoured by the amount of bare ground within fragments (*groundcover*; $\chi^2 = 18.041$, $p < 0.001$). Average grass height also influenced Yellow Canary abundances ($\chi^2 = 4.149$, $p < 0.042$).

By summarising these results (Table 4.4), the differences between the two bioregions are highlighted. Fragment size did not only appear to be a more frequent predictor of abundance variance in the WCRB dataset, but in two cases (the Cape White-eye and Karoo Scrub-robin), the strongest predictor. Furthermore, the species' abundances in both bioregions were predicted by a mixture of landscape, isolation and habitat preferences.

Table 4.3 - Summary of count model predictions for individual species in both the ECRB and WCRB

| | ECRB | | | | WCRB | | | |
|----------------------------------|--------------------|----------|--------|----------------------|--------------------|----------|---------|----------------------|
| | Predictor | χ^2 | p | Effect size \pm SE | Predictor | χ^2 | p | Effect size \pm SE |
| Cape Robin-chat | Constant | | | -0.548 \pm 0.610 | Constant | | | 1.398 \pm 0.144 |
| | <i>Shrubcover</i> | 9.367 | 0.002 | 2.342 \pm 0.765 | Size | 44.642 | < 0.001 | 0.482 \pm 0.072 |
| Cloud Cisticola | Constant | | | -0.748 \pm 1.463 | Constant | | | 1.147 \pm 0.158 |
| | Isolation | 15.668 | <0.001 | 1.477 \pm 0.373 | Isolation | 5.805 | 0.016 | -7.097 \pm 2.946 |
| | <i>Grasscover</i> | 11.540 | 0.001 | 1.687 \pm 0.497 | <i>Grasscover</i> | 44.015 | < 0.001 | 3.281 \pm 0.495 |
| | Landscape | 6.179 | 0.013 | -1.173 \pm 0.472 | | | | |
| Karoo Prinia | Constant | | | -0.539 \pm 0.399 | Constant | | | 2.199 \pm 0.095 |
| | Size | 12.881 | <0.001 | 0.405 \pm 0.113 | Size | 112.22 | < 0.001 | 0.502 \pm 0.047 |
| | <i>Shrubcover</i> | 29.206 | <0.001 | 2.361 \pm 0.437 | | | | |
| Bokmakierie | Constant | | | -0.236 \pm 0.358 | Constant | | | 0.164 \pm 0.246 |
| | Size | 10.780 | 0.001 | 0.633 \pm 0.193 | Size | 24.958 | < 0.001 | 0.601 \pm 0.120 |
| Southern Double-collared Sunbird | Constant | | | -0.644 \pm 0.575 | Constant | | | 0.647 \pm 0.192 |
| | <i>Shrubcover</i> | 5.553 | 0.018 | 1.774 \pm 0.753 | Size | 42.694 | < 0.001 | 0.611 \pm 0.094 |
| Yellow Canary | Constant | | | 0.711 \pm 0.234 | Constant | | | 2.199 \pm 0.100 |
| | <i>Grassheight</i> | 6.983 | 0.008 | 0.010 \pm 0.004 | <i>Grassheight</i> | 39.712 | < 0.001 | 0.017 \pm 0.003 |
| | Size | 55.446 | <0.001 | 0.735 \pm 0.099 | <i>Grasscover</i> | 4.149 | 0.042 | -0.595 \pm 0.293 |
| Grey-backed Cisticola | Constant | | | 1.444 \pm 0.249 | Constant | | | -0.240 \pm 0.677 |
| | Size | 4.443 | 0.035 | 0.285 \pm 0.135 | <i>Shrubcover</i> | 10.157 | 0.001 | 1.881 \pm 0.590 |
| African Stonechat | Constant | | | 11.105 \pm 4.509 | NONE | | | |
| | Landscape | 5.060 | 0.024 | -3.612 \pm 1.606 | | | | |
| Cape Sparrow | Constant | | | 10.277 \pm 4.258 | N/A | | | |
| | Isolation | 4.726 | 0.030 | -2.330 \pm 1.072 | | | | |
| Speckled Mousebird | Constant | | | 0.872 \pm 0.410 | NONE | | | |
| | <i>Shrubheight</i> | 4.875 | 0.027 | 0.011 \pm 0.005 | | | | |
| Bar-throated Apalis | NONE | | | | Constant | | | 1.213 \pm 0.280 |
| | | | | | Size | 9.068 | 0.003 | 0.381 \pm 0.126 |

NONE - species that did not have variation in abundance explained by any of the predictors; N/A - species not applicable for particular bioregion as they were not recorded in the particular bioregion. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

Table 4.3 Continued

| | Predictor | ECRB | | | Predictor | WCRB | | |
|-----------------------------|-----------|----------|---|----------------------|-------------|----------|---------|----------------------|
| | | χ^2 | p | Effect size \pm SE | | χ^2 | p | Effect size \pm SE |
| Karoo Scrub-robin | NONE | | | | Constant | | | 1.195 \pm 0.219 |
| | | | | | Size | 25.501 | < 0.001 | 0.338 \pm 0.067 |
| | | | | | Groundcover | 18.041 | < 0.001 | 1.707 \pm 0.402 |
| Cape Bulbul | NONE | | | | Constant | | | 6.017 \pm 0.804 |
| | | | | | Size | 22.017 | < 0.001 | 0.532 \pm 0.113 |
| | | | | | Isolation | 23.908 | < 0.001 | -1.399 \pm 0.286 |
| Cape White-eye | N/A | | | | Constant | | | -2.333 \pm 1.045 |
| | | | | | Size | 21.447 | < 0.001 | 0.466 \pm 0.101 |
| | | | | | Landscape | 11.785 | < 0.001 | 1.355 \pm 0.395 |
| Neddicky | N/A | | | | Constant | | | 1.003 \pm 0.451 |
| | | | | | Size | 3.865 | 0.049 | 0.397 \pm 0.202 |
| Common Fiscal | NONE | | | | NONE | | | |
| Yellow Bishop | NONE | | | | NONE | | | |
| Common Waxbill | NONE | | | | NONE | | | |
| Cape Grassbird | NONE | | | | NONE | | | |
| Malachite Sunbird | NONE | | | | NONE | | | |
| Cape Spurfowl | N/A | | | | NONE | | | |
| Chestnut-vented Tit-babbler | N/A | | | | NONE | | | |
| Long-billed Crombec | N/A | | | | NONE | | | |
| Cape Turtle Dove | N/A | | | | NONE | | | |
| Fiscal Flycatcher | N/A | | | | NONE | | | |
| Cape Weaver | N/A | | | | NONE | | | |
| Cape Bunting | NONE | | | | N/A | | | |
| Agulhas Clapper Lark | NONE | | | | N/A | | | |
| Cape Longclaw | NONE | | | | N/A | | | |

NONE - species that did not have variation in abundance explained by any of the predictors; N/A - species not applicable for particular bioregion because they were not recorded in 10 or more fragments. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

Table 4.4 - Summary of model terms and predictors for Table 4.3

| Species | Size | Isolation | Landscape | Groundcover | Grasscover | Shrubcover | Grassheight | Shrubheight | Restiocover |
|----------------------------------|--------|-----------|-----------|-------------|------------|------------|-------------|-------------|-------------|
| African Stonechat | - / - | - / - | # / - | - / - | - / - | N/A | N/A | N/A | N/A |
| Agulhas Clapper Lark | - / - | - / - | - / - | - / - | - / - | N/A | N/A | N/A | N/A |
| Bar-throated Apalis | - / # | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Bokmakierie | # / # | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cape Bulbul | - / ** | - / * | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cape Bunting | - / - | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A |
| Cape Grassbird | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | - / - |
| Cape Longclaw | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Cape Robin-chat | - / # | - / - | - / - | N/A | N/A | # / - | N/A | - / - | N/A |
| Cape Sparrow | - / - | # / * | - / - | - / - | - / - | N/A | - / - | N/A | N/A |
| Cape Spurfowl | - / - | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A |
| Cape Turtle Dove | - / - | - / - | - / - | - / - | - / - | N/A | - / - | N/A | N/A |
| Cape Weaver | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A | N/A |
| Cape White-eye | - / * | - / - | - / ** | N/A | N/A | - / - | N/A | - / - | N/A |
| Chestnut-vented Tit-babbler | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cloud Cisticola | - / - | * / ** | *** / - | N/A | ** / * | N/A | - / - | N/A | N/A |
| Common Fiscal | - / - | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A |
| Common Waxbill | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Fiscal Flycatcher | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Grey-backed Cisticola | # / - | - / - | - / - | - / - | N/A | - / # | N/A | - / - | N/A |
| Karoo Prinia | ** / # | - / - | - / - | N/A | N/A | * / - | N/A | - / - | N/A |
| Karoo Scrub-robin | - / * | - / - | - / - | - / ** | N/A | - / - | N/A | - / - | N/A |
| Long-billed Crombec | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Malachite Sunbird | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Neddicky | - / # | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A |
| Southern Double-collared Sunbird | - / # | - / - | - / - | N/A | N/A | # / - | N/A | - / - | N/A |
| Speckled Mousebird | - / - | - / - | - / - | N/A | N/A | - / - | N/A | # / - | N/A |
| Yellow Bishop | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Yellow Canary | * / - | - / - | - / - | N/A | - / ** | - / - | ** / * | N/A | N/A |

ECRB/WCRB; Only predictor: #; Predictor null effect: -; Strength: 1st - *, 2nd - **, 3rd - ***. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grass height and Shrub height - Average (cm)

4.3.2 Variation in Species Occupancy in Fragments

The probability of a species occupying a fragment is analysed in the ZIP models (Table 4.5). Fragment size significantly influenced the probability of occupancy of only two species in the ECRB, the Cape Grassbird (*Sphenoeacus afer*; $\chi^2 = 4.077$, $p = 0.043$) and Cape Bunting (*Emberiza capensis*; $\chi^2 = 6.363$, $p = 0.012$). Both of these relationships were positive. Isolation had a negative effect on Malachite Sunbird occupancy (*Nectarinia famosa*; $\chi^2 = 4.060$, $p = 0.044$) and the amount of habitat within the landscape had a positive effect on Speckled Mousebird ($\chi^2 = 6.595$, $p = 0.010$) and Bar-throated Apalis ($\chi^2 = 6.179$, $p = 0.013$) occupancies. The availability of preferred habitat also played an important role in the occupancies of certain species. Shrub cover affected Cape Bulbul ($\chi^2 = 6.630$, $p = 0.010$) and Karoo Scrub-robin ($\chi^2 = 6.933$, $p = 0.008$) occupancies, with average shrub height being influential for Speckled Mousebird ($\chi^2 = 8.100$, $p = 0.004$) and Bar-throated Apalis ($\chi^2 = 8.517$, $p = 0.004$).

In the WCRB, fragment size was the only significant predictor for the occupancy probabilities of six species: Speckled Mousebird ($\chi^2 = 5.042$, $p = 0.025$), Cape Bulbul ($\chi^2 = 8.238$, $p = 0.004$), Cape Grassbird ($\chi^2 = 6.335$, $p = 0.012$), Bar-throated Apalis ($\chi^2 = 9.787$, $p = 0.002$), Cape White-eye ($\chi^2 = 4.206$, $p = 0.040$) and Cape Spurfowl (*Pternistes capensis*; $\chi^2 = 4.621$, $p = 0.032$). All these relationships were positive. Isolation had a notable effect on the occupancy of African Stonechat ($\chi^2 = 4.216$, $p = 0.040$), with ground cover having a strong negative effect on Grey-backed Cisticola occupancy ($\chi^2 = 5.407$, $p = 0.020$).

In summary (Table 4.6), fragment size was a more important predictor of species occupancy in the WCRB than in the ECRB. The amount of habitat in the landscape was more important in the ECRB, however, and habitat preferences still played in role as species occupancies were influenced by these measures.

Combining the abundance and occupancy summaries (Tables 4.4 and 4.6) fragment size was the most important factor influencing occupancy and abundance within the common species.

Table 4.5 - Summary of occupancy model predictions for individual species in both the ECRB and WCRB

| | ECRB | | | | WCRB | | | |
|-----------------------|--------------------|----------|-------|----------------------|--------------------|----------|-------|----------------------|
| | Predictor | χ^2 | p | Effect size \pm SE | Predictor | χ^2 | p | Effect size \pm SE |
| Speckled Mousebird | Constant | | | 39.562 \pm 14.499 | Constant | | | 3.299 \pm 1.171 |
| | <i>Shrubheight</i> | 8.100 | 0.004 | -0.124 \pm 0.043 | Size | 5.042 | 0.025 | -1.334 \pm 0.594 |
| | Landscape | 6.595 | 0.010 | -10.927 \pm 4.255 | | | | |
| Cape Bulbul | Constant | | | 14.219 \pm 5.453 | Constant | | | 2.518 \pm 1.039 |
| | <i>Shrubcover</i> | 6.630 | 0.010 | -17.652 \pm 6.855 | Size | 8.238 | 0.004 | -1.931 \pm 0.673 |
| Cape Grassbird | Constant | | | 2.705 \pm 1.222 | Constant | | | 7.163 \pm 2.687 |
| | Size | 4.077 | 0.043 | -1.400 \pm 0.693 | Size | 6.335 | 0.012 | -3.970 \pm 1.577 |
| Bar-throated Apalis | Constant | | | 31.011 11.379 | Constant | | | 3.433 \pm 1.211 |
| | Landscape | 6.179 | 0.013 | -8.244 \pm 3.316 | Size | 9.787 | 0.002 | -2.464 \pm 0.788 |
| | <i>Shrubheight</i> | 8.517 | 0.004 | -0.117 \pm 0.040 | | | | |
| Malachite Sunbird | Constant | | | -11.337 \pm 5.804 | NONE | | | |
| | Isolation | 4.060 | 0.044 | 3.916 \pm 1.944 | | | | |
| Karoo Scrub-robin | Constant | | | 4.526 \pm 1.933 | NONE | | | |
| | <i>Shrubcover</i> | 6.933 | 0.008 | -7.090 \pm 2.693 | | | | |
| Cape Bunting | Constant | | | 2.922 \pm 1.223 | N/A | | | |
| | Size | 6.363 | 0.012 | -1.808 \pm 0.717 | | | | |
| Cape White-eye | N/A | | | | Constant | | | 1.483 \pm 0.882 |
| | | | | | Size | 4.206 | 0.040 | -1.073 \pm 0.523 |
| Grey-backed Cisticola | NONE | | | | Constant | | | 16.135 \pm 8.033 |
| | | | | | <i>Groundcover</i> | 5.407 | 0.020 | 12.185 \pm 5.240 |
| African Stonechat | NONE | | | | Constant | | | 12.241 \pm 5.636 |
| | | | | | Isolation | 4.216 | 0.040 | -3.573 \pm 1.740 |
| Cape Spurfowl | N/A | | | | Constant | | | 3.010 \pm 1.259 |
| | | | | | Size | 4.621 | 0.032 | -1.616 \pm 0.752 |

NONE - species that did not have variation in abundance explained by any of the predictors; N/A - species not applicable for particular bioregion as they were not recorded in the particular bioregion. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

Table 4.5 Continued

| | ECRB | | | | WCRB | | | |
|----------------------------------|-----------|----------|---|----------------------|-----------|----------|---|----------------------|
| | Predictor | χ^2 | p | Effect size \pm SE | Predictor | χ^2 | p | Effect size \pm SE |
| Common Fiscal | NONE | | | | NONE | | | |
| Yellow Bishop | NONE | | | | NONE | | | |
| Common Waxbill | NONE | | | | NONE | | | |
| Cape Robin-chat | NONE | | | | NONE | | | |
| Cloud Cisticola | NONE | | | | NONE | | | |
| Karoo Prinia | NONE | | | | NONE | | | |
| Bokmakierie | NONE | | | | NONE | | | |
| Southern Double-collared Sunbird | NONE | | | | NONE | | | |
| Yellow Canary | NONE | | | | NONE | | | |
| Neddicky | N/A | | | | NONE | | | |
| Chestnut-vented Tit-babbler | N/A | | | | NONE | | | |
| Long-billed Crombec | N/A | | | | NONE | | | |
| Cape Turtle Dove | N/A | | | | NONE | | | |
| Fiscal Flycatcher | N/A | | | | NONE | | | |
| Cape Weaver | N/A | | | | NONE | | | |
| Cape Sparrow | NONE | | | | N/A | | | |
| Agulhas Clapper Lark | NONE | | | | N/A | | | |
| Cape Longclaw | NONE | | | | N/A | | | |

NONE - species that did not have variation in abundance explained by any of the predictors; N/A - species not applicable for particular bioregion because they were not recorded. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

Table 4.6 - Summary of model terms and predictors for Table 4.5

| Species | Size | Isolation | Landscape | Groundcover | Grasscover | Shrubcover | Grassheight | Shrubheight | Restiocovert |
|----------------------------------|--------------|--------------|---------------|--------------|------------|--------------|-------------|--------------|--------------|
| African Stonechat | - / - | <u>- / #</u> | - / - | - / - | - / - | N/A | N/A | N/A | N/A |
| Agulhas Clapper Lark | - / - | - / - | - / - | - / - | - / - | N/A | N/A | N/A | N/A |
| Bar-throated Apalis | <u>- / #</u> | - / - | <u>** / -</u> | N/A | N/A | - / - | N/A | <u>* / -</u> | N/A |
| Bokmakierie | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cape Bulbul | <u>- / #</u> | - / - | - / - | N/A | N/A | <u># / -</u> | N/A | - / - | N/A |
| Cape Bunting | <u># / -</u> | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A |
| Cape Grassbird | <u># / #</u> | - / - | - / - | N/A | - / - | N/A | - / - | N/A | - / - |
| Cape Longclaw | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Cape Robin-chat | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cape Sparrow | - / - | - / - | - / - | - / - | - / - | N/A | - / - | N/A | N/A |
| Cape Spurfowl | <u>- / #</u> | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A |
| Cape Turtle Dove | - / - | - / - | - / - | - / - | - / - | N/A | - / - | N/A | N/A |
| Cape Weaver | - / - | - / - | - / - | N/A | - / - | N/A | N/A | N/A | N/A |
| Cape White-eye | <u>- / #</u> | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Chestnut-vented Tit-babbler | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Cloud Cisticola | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Common Fiscal | - / - | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A |
| Common Waxbill | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Fiscal Flycatcher | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Grey-backed Cisticola | - / - | - / - | - / - | <u>- / #</u> | N/A | - / - | N/A | - / - | N/A |
| Karoo Prinia | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Karoo Scrub-robin | - / - | - / - | - / - | - / - | N/A | <u># / -</u> | N/A | - / - | N/A |
| Long-billed Crombec | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Malachite Sunbird | - / - | <u># / -</u> | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Neddicky | - / - | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A |
| Southern Double-collared Sunbird | - / - | - / - | - / - | N/A | N/A | - / - | N/A | - / - | N/A |
| Speckled Mousebird | <u>- / #</u> | - / - | <u>** / -</u> | N/A | N/A | - / - | N/A | <u>* / -</u> | N/A |
| Yellow Bishop | - / - | - / - | - / - | N/A | - / - | N/A | - / - | N/A | N/A |
| Yellow Canary | - / - | - / - | - / - | N/A | - / - | - / - | - / - | N/A | N/A |

ECRB/WCRB; Only predictor: #; Predictor null effect: -; Strength: 1st - *, 2nd - **. Size - Fragment area (ha); Isolation - Nearest Neighbour Distance (m); Landscape - Amount of habitat within 5,000 m from sampling points; Grasscover, Shrubcover and Groundcover (%), Grassheight and Shrubheight - Average (cm)

4.4. DISCUSSION

4.4.1 The Influence of Fragmentation Elements and Habitat Quality on Individual Species

The results from this study indicate that bird species differ substantially in their sensitivity to area and isolation effects, landscape configuration and habitat quality. Differences were exhibited at a cross-bioregional scale and comparisons between the same species in the two bioregions showed little similarity. Furthermore, species abundance and occupancy also differed substantially. The Speckled Mousebird was the only species in the ECRB responding to the same predictor regarding abundance and occupancy variation, i.e. average shrub height. It can be argued that this species are therefore more concerned with habitat suitability than fragmentation effects. In the WCRB, however, the bar-throated apalis, the variance of abundances and occupancy of Cape Bulbul and Cape White-eye could be explained by the same predictor, fragment area. Within an inter-bioregional comparison, the similarities were just as rare. The Cape Grassbird was the only species to react to the same predictor in both bioregions. In this case, fragment size was positively correlated with its probability of occupancy. The variation within five species abundances did, however, have similar predictors across the two different bioregions. Both nearest neighbour distance and grass cover predicted cloud cisticola abundances. Fragment area was a consistent predictor for both the Karoo Prinia and Bokmakierie, and average grass height for Yellow Canary abundances. All these abovementioned relationships have a similar direction for both bioregions.

As a whole, the results differ rather substantially between the two bioregions. For fragment area, isolation and habitat within the landscape, the responses that emerged highlighted one major difference between the two bioregions, i.e. a greater importance of area effects on both species abundance and occupancy in the WCRB, contrasting the greater importance of the amount of habitat within the landscape in the ECRB. This is consistent with the pattern that emerged in Chapter 3, regarding assemblage composition, where size was also more important in the WCRB and landscape predictors in the ECRB.

As predicted, species abundance and occupancy correlated positively with fragment area and/or the amount of natural habitat in the landscape and negatively with increased nearest neighbour distances. However, two species, cloud cisticola and African Stonechat, did not conform to these patterns. In the ECRB, cloud cisticola abundance increased with fragment isolation. Similarly, African Stonechat abundance in the ECRB increased as the amount of natural habitat in the landscape decreased, and its probability of occupancy in the

WCRB increased with fragment isolation. These were the only species to exhibit positive relationships with fragmentation. Both these species prefer grassy habitats (Hockey et al., 2005), and grass cover was typically more prevalent in the matrix surrounding the fragments than within the fragments themselves.

All the species used in the analyses were common species, occurring in ten or more of the fragments studied. These species were selected as model species because they had been encountered often enough to show clear trends in abundance and occupancy variation. Common species are important in transformed areas. Species that are highly sensitive to either area or configuration effects may well be confined to large fragments, excluding these species from the greater landscape. Therefore, the onus to perform certain ecological services, e.g. seed dispersal, may well fall on the more common species, or generalists (Mennechez and Clergeau, 2006; Gaston and Fuller, 2008). Therefore, the sensitivity of common species to habitat fragmentation is of great importance.

The greater importance of fragment size in the WCRB and the importance of the amount of habitat in the landscape in the ECRB are consistent with the assemblage level analyses done in Chapter 3. In the ECRB, there are many fragments distributed within the landscape, therefore individual birds have a higher probability of dispersing from one fragment to the next. In the WCRB however, larger fragments are highly isolated and there is no habitat available within the immediate vicinity to accommodate the movements of individual birds. Only fragments farther afield may supply sufficient habitat clustered within the landscape to allow adequate dispersal of individuals, and therefore increase the probability of a species occupying any one fragment. However, size and habitat within the landscape had positive effects on abundance and occupancy in both bioregions, except for the cloud cisticola and African stonechat.

These results indicate that different species respond in unique ways to fragment and landscape scale influences of fragmentation. Moreover, the same species respond differently in different bioregions. This emphasises a critical aspect and central problem within the discipline of conservation biology- the difficulty of making generalisations and to extrapolate results from one region to the next (Okes et al., 2008). Most species analysed occur in both regions, yet only two species within both regions showed shared responses to landscape configuration. Nevertheless, the responses of these species differed substantially.

The problem of making generalizations is daunting even if fragmentation elements are examined alone. However, this study has also highlighted another central dilemma in avian conservation in fragmented habitats – the issue of habitat quality. Many species in the two

bioregions did not respond to any of the fragmentation-related predictors but to habitat quality, or a combination of the two. This is an indication that certain species will only use fragments that are suitable to their needs, and that area or isolation is not as important. It has been suggested that habitat quality may be a more critical factor than area per se, in species-area relationships in fragmented landscapes (Lees and Peres, 2006), especially for habitat-specific species. The issue of habitat quality in fragmented landscapes remains, however, a major obstacle for populations and individuals to overcome. These landscapes fragments may be subject to both different levels and types of disturbance.

However, despite the different patterns that were highlighted in inter-bioregional comparison, these results reveal two major findings at a coarser scale. Firstly, the important role of area effects on many species' abundances and occupancies once the influence of habitat variables have been controlled. Decreasing fragment area with fragmentation can directly influence the abundance of birds in direct ways. As fragments decrease in size, declines in the amount and/or diversity of resources can influence species abundance and occupancy. ii) Alternatively, variation in fragment area also influences the extent of emigration and immigration by individuals (Lomolino, 1990). Indeed, when fragment area decreases to very small sizes, resource deficits or insufficient space may cause fragments to fall below the minimum area requirements of individuals (Stratford and Stouffer, 1999). Smaller areas contain a lower concentration or diversity of resources (Root, 1973), resulting in lower densities of individuals. Lower concentrations of resources can reduce species abundances and occupancy through reduced local recruitment based on declining habitat quality (Matter, 1997). Therefore, declining resource concentrations with decreasing fragment area should have a negative impact on species abundances and occupancy, subsequently increasing extinction probability (Didham et al., 1999), and altering assemblage composition.

The second major finding is the greater importance of area effect over that of landscape effects, once an inter-bioregional comparison falls away. Once all the results are addressed as a unit, area effects are clearly dominant over any other fragmentation element dealt with in this study. Some studies have suggested that abundance is more closely affected by landscape effects at the small scale (Dunning et al., 1995, Renfrew and Ribic, 2008). However, if habitat fragments are not in close enough proximity, area effects becomes an integral part of governing abundances of species, as found in the present study. Some authors have made the statement that quantifying landscape and/or isolation effects on biota is much more difficult than quantifying area effects (Dunning et al., 1995; Lee et al., 2002). In this study, all three

effects (landscape, isolation and area effects) have been incorporated into the analyses. Area effect emerged as the main predictor of both abundance and occupancy models, supporting its well-known role as an important force in determining avian species abundances and occupancy (Biedermann, 2003; Pavlacky and Anderson, 2007).

4.4.2. Implications for Conservation

How do these results contribute to our understanding of the inherent effects of habitat fragmentation and transformation on avian diversity? And how can this guide conservation efforts and practices to better conserve the avifauna of these two regions, and avian diversity in shrublands at the global scale?

That bird species vary in their levels of sensitivity to fragmentation is no novel concept in conservation ecology. The most important result from this research is that some of the same species responded differently in the different bioregions because of the differences in landscape configuration and habitat cover therein (Betts et al., 2007). The spatial arrangements of habitat fragments can have great effects on landscape occupancy and population persistence (Cale, 2003).

Species that are extremely sensitive to fragmentation will be unable to persist in landscapes with little habitat cover, small-sized fragments scattered in the landscape and fragments with low habitat quality (Suorsa et al., 2005). Many studies have predicted that extinction thresholds will increase as habitats become more and more fragmented and as habitat cover and landscape configuration diminish (Burkey, 1995; With and King, 1999; Fahrig, 2002). This increase is well illustrated in this study, with the WCRB having much less habitat scattered in the landscape than the ECRB.

It may be argued that the habitat within the ECRB is more suitably arranged, with habitat fragments being more closely clustered which makes them more accessible, and that species and population persistence in this region has a higher possibility of success than in the WCRB. Both of these regions have experienced habitat loss beyond the 30-20% threshold where fragmentation starts to dominate over pure habitat loss effects (Andrén, 1994; Villard et al., 1999; Fahrig, 1998). Beyond this threshold, the arrangement of the habitat fragments within the landscape becomes crucial. If there is no inter-fragment movement, due to unfavourable arrangement of habitat fragments, the probability of regional extinction then depends on the size of the largest fragment within the landscape (Fahrig, 1998).

However, as mentioned in the previous section, a more holistic point of view reveals that area effects are the overall best predictor of both species abundances and occupancies.

This result supports the findings of most studies, that area effect is indeed critical (Lee and Rotenberry, 2005). In turn, this strengthens the long lasting '*Single Large Or Several Small*' (SLOSS) debate (Burkley, 1995; Cornelius et al., 2000; Ewer and Didham, 2006). If area effects are identified as the most important predictors influencing bird species abundance and occupancy at the greater scale, especially of those common species upon which ecological processes might have come to depend in fragmented landscapes, then conserving large fragments seems to be the better option. However, Renfrew and Ribic (2008) mentioned that, in some cases, area effects could interact with landscape effects such as the amount of habitat within the landscape and landscape configuration. In fact, this is one of the most daunting and significant obstacles with which conservation practitioners are confronted. Is the conservation of large habitat fragments really enough? Much empirical research now implies landscape scale conservation strategies do have many benefits (Mac Nally and Horrocks, 2000). Therefore, rather than focusing on one or the other conservation strategy, an approach that adapts and integrates the two should rather be used. Conserving clusters of fragments that are adequate and favourably configured and incorporating large fragments within these clusters are possibly the best means to conserve avian species in fragmented landscapes. However, as mentioned earlier in this study, habitat suitability should also be considered in selecting fragments to be incorporated in conservation networks (Bakker et al., 2002).

This study has highlighted the importance of a multi-scale approach to examining fragmentation effects on avifauna, and possibly biodiversity. Being able to focus on both fragment-scale and landscape-scale patterns facilitates more thorough and solid predictions and recommendations (Renfrew and Ribic, 2008). Population persistence can be heavily impaired as landscape configuration deteriorates (McGarical and Cushman, 2002). For long, area effects have been advocated as the major threat to birds within fragmented habitat, but the importance of landscape-scale effects is now being more and more appreciated (Miller and Cale, 2002). The science of conservation biology can make important inroads in the predictions and understanding of fragmentation effects on birds when a multi-scale approach rather than a single-scale approach is used. In this particular study, the patch-, landscape- and bioregional scales all contributed to identify species relationships within their environment and how this can affect their persistence within human transformed areas.

4.5. CONCLUSION

The effects of fragment area, landscape configuration and habitat quality on certain bird species' abundances and occupancy are crucial to our understanding of how habitat fragmentation affects species and population persistence in transformed landscapes. I found that species responses to fragmentation were variable and that even the same species can respond differently in different landscapes.

Population persistence in fragmented landscapes is a central component of conservation biology. It is important to know the thresholds at which population persistence starts dwindling because, in fragmented landscapes, maintenance of metapopulation dynamics is essential to ensure the persistence of species at the landscape scale (Hames et al., 2001; Mitchell et al., 2006).

4.6. REFERENCES

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.
- Bakker, K.K., Naugle, D.E., Higgins, K.F., 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16, 1638-1646.
- Betts, M.G., Forbes, G.J., Diamond, A.W., 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* 21, 1046–1058.
- Biedermann, R., 2003. Body size and area-incidence relationships: Is there a general pattern? *Global Ecology and Biogeography* 12, 381-387.
- Burkey, T.V., 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. *Conservation Biology* 9, 527-541.
- Cale, P.G., 2003. The influence of social behaviour, dispersal and landscape fragmentation on population structure in a sedentary bird. *Biological Conservation* 109, 237–248.
- Castellón, T.D., Sieving, K.E., 2006. Landscape history, fragmentation, and patch occupancy: models for a forest bird with limited dispersal. *Ecological Applications* 16, 2223-2234.
- Cornelius, C., Cofré, H., Marquet, P.A., 2002. Effects of habitat fragmentation on bird species in a relict forest in semiarid Chile. *Conservation Biology* 14, 534-543.
- Crawley, M.J., 2002. *Statistical computing: An introduction to data analysis using S-Plus*. John Wiley and Sons Inc. Hoboken, USA
- Cushman, S.A., McGarigal, K., 2003. Landscape-level patterns of avian diversity in the Oregon coast range. *Ecological Monographs* 73, 259–281.
- Dettmers, R., Buehler, D.A., Bartlett, J.G., Klaus, N.A., 1999. Influence of point count length and repeated visits on habitat model performance. *Journal of Wildlife Management* 63, 815-823.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22, 489-496.
- Diefenbach, D.R., Marshall, M.R., Mattice, J.A., Brauning, D.W., 2007. Incorporating availability for detection in estimates of bird abundance. *The Auk* 124, 96-106.
- Donner, D.M., Probst, J.R., Ribic, C.A., 2008. Influence of habitat amount, arrangement, and use on population trends estimates of male Kirkland's warblers. *Landscape Ecology* 23, 467-480.

- Donovan, T.M., Flather, C.H., 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications* 12, 364-374.
- Dunning, Jr, J.B., Borgella, Jr, R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9, 542-550.
- ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, California. Copyright © 1999-2008 ESRI.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117-142.
- Ewers, R.M., Didham, R.K., 2007a. Habitat fragmentation: panchreston or paradigm? *Trends in Ecology and Evolution* 22, 511.
- Ewers, R.M., Didham, R.K., 2007b. The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conservation Biology* 21, 926-936.
- Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. *Conservation Biology* 8, 50-59.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105, 273-292.
- Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12, 346-353.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of the Ecology, Evolution and Systematics* 34, 487-515.
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, Jr., R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315, 238-241.
- FitzGibbon, S.I., Putland, D.A., Goldizen, A.W., 2007. The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. *Landscape Ecology* 22, 1513-1525.
- Foppen, R.P.B., Chardon, J.P., Liefveld, W., 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology* 14, 1881-1892.
- Ford, H.A., Barrett, G.W., Saunders D.A., Recher, H.F., 2001. Why have birds in the woodlands of Southern Australia declined? *Biological Conservation* 97, 71-88
- Gaston K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23, 14-19.

- Gu  nette, J.S., Villard, M.A., 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. *Conservation Biology* 19, 1168-1180.
- Hamer, T.L., Flather, C.H., Noon, B.R., 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landscape Ecology* 21, 569-583.
- Hames, R.S., Rosenberg, K.V., Lowe, J.D., Dhondt, A.A., 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. *Journal of Animal Ecology* 70, 182-190.
- Hockey, P.A.R., Dean, W.R.J., Ryan, P.G., 2005. *Roberts Birds of Southern Africa*. 7th Edn. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hothorn T., Zeileis, A., Millo, G., Mitchell, D., 2008. The lmtest Package. Testing Linear Regression Models.
- Ihaka, R., Gentleman, R., 1996. R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5, 299-314.
- Ims, R.A., Andreassen, H.P., 2005. Density-dependent dispersal and spatial population dynamics. *Proceedings of the Royal Society B* 272, 913-918.
- Jackman, S., Tahk, A., Zeileis, A., Maimone, C., Fearon, J., 2008. The pscl Package. Political Science Computational Laboratory, Stanford University
- Lee, P., Rotenberry, J.T., 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. *Journal of Biogeography* 32, 1139-1150.
- Lee, M., Fahrig, L., Freemark, K., Currie, D.J., 2002. Importance of patch scale vs landscape scale selected forest birds. *Oikos* 96, 110-118.
- Lees, A.C., Peres, C.A., 2006. Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biological Conservation* 133, 198-211.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H., Lindenmayer, B.D., 2002. Effects of forest fragmentation on bird assemblages in a novel landscape context. *Ecological Monographs* 72, 1-18.
- Lomolino, M.V., 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos* 57, 297-300.
- Mac Nally, R., Horrocks, G., 2000. Landscape-scale conservation of an endangered migrant: the Swift Parrot *Lathamus discolor* in its winter range. *Biological Conservation* 92, 335-343.

- Matter, S.F., 1997. Population density and area: the role of between- and within-patch processes. *Oecologia* 110, 533-538.
- McGarigal, K., Cushman, S.A., 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, 12, 335-345.
- Mennechez, G., Clergeau, P., 2006. Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica* 30, 182-191.
- Miller, J.R., Cale, P., 2000. Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. *Ecological Applications* 10, 1732-1748.
- Mitchell, M.S., Rutzmoser, S.H., Wigley, T.B., Loehle, C., Gerwin, J.A., Keyser, P.D., Lancia, R.A., Perry, R.W., Reynolds, C.J., Thill, R.E., Weih, R., White, D., Wood, P.B., 2006. Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. *Forest Ecology and Management* 221, 155-169.
- Mucina, L., Rutherford, C. (Eds), 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.
- Okes, N.C., Hockey, P.A.R., Cumming, G.S., 2008. Habitat use and life history as predictors of bird responses to habitat change. *Conservation Biology* 22, 151-162.
- Pavlacky, D.C., Anderson, S.H., 2007. Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? *Animal Conservation* 10, 57-68.
- Quinn, G.P., Keough, M.J., 2002. Experimental design and data analyses for biologists. Cambridge University Press. Cambridge, United Kingdom.
- Radford, J.Q., Bennett, A.F., 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117, 375-391.
- Renfrew, R.B., Ribic, C.A., 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. *Landscape Ecology* 23, 181-193.
- Root, R.B., 1973. Organization of a plant arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95-124.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777-790.
- SPSS 16.0 for WINDOWS, Release 16.0.1 (Nov. 15, 2007)
- Stockwell, C.A., Hendry, A.P., Kinnison, M.T., 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 8, 94-101.
- Stratford, J.A., Stouffer, P.C., 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* 13, 1416-1423.

- Suorsa, P., Huhta, E., Jäntti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V., Hakkarainen, H., 2005. Thresholds in selection of breeding habitat by the Eurasian treecreeper (*Certhia familiaris*). *Biological Conservation* 121, 443-452.
- Tischendorf, L., Bender, D.J., Fahrig, L., 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18, 41-50.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9, 586-593.
- Tscharntke, T., Şekercioğlu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tlianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89, 944-951.
- Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82, 1205-1218.
- Vance, M.D., Fahrig, L., Flather, C.H., 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84, 2643-2653.
- Villard, M.A., Trzcinski, T.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13, 774-783.
- von Hase, A., Rouget, M., Maze, K., Helme, N., 2003. A fine-scale conservation plan for the Cape Lowlands Renosterveld: Technical Report. Cape Conservation Unit, Botanical Society, Cape Town.
- Welsh, A.H., Cunningham, R.B., Donnelly, C.F., Lindenmayer, D.B., 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* 88, 297-308.
- Wiegand, T., Revilla, E., Moloney, K.A., 2005. Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology* 19, 108-121.
- With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13, 314-326.

Appendix 4.A - List of species used in GLZ and ZIP analyses

| Common Name | Scientific Name |
|-----------------------------------|---------------------------------|
| Cape Spurfowl* | <i>Pternistes capensis</i> |
| Cape Turtle Dove* | <i>Streptopelia capicola</i> |
| Speckled Mousebird | <i>Colius striatus</i> |
| Agulhas Clapper Lark [#] | <i>Mirafra marjorriae</i> |
| Cape Longclaw [#] | <i>Marconyx capensis</i> |
| Cape Bulbul | <i>Pycnonotus capensis</i> |
| Cape Robin-chat | <i>Cossypha caffra</i> |
| Karoo Scrub-robin | <i>Cercotrichas coryphaeus</i> |
| African Stonechat | <i>Saxicola torquatus</i> |
| Cape Grassbird | <i>Sphenoeacus afer</i> |
| Chestnut-vented Tit-babbler* | <i>Parisoma subcaeruleum</i> |
| Neddicky* | <i>Cisticola fulvicapilla</i> |
| Grey-backed Cisticola | <i>Cisticola subruficapilla</i> |
| Cloud Cisticola | <i>Cisticola textrix</i> |
| Bar-throated Apalis | <i>Apalis thoracica</i> |
| Karoo Prinia | <i>Prinia maculosa</i> |
| Long-billed Crombec* | <i>Sylvietta rufescens</i> |
| Fiscal Flycatcher* | <i>Sigelus silens</i> |
| Common Fiscal | <i>Lanius collaris</i> |
| Bokmakierie | <i>Telophorus zeylonus</i> |
| Malachite Sunbird | <i>Nectarinia famosa</i> |
| Southern Double-collard Sunbird | <i>Cinnyris chalybeus</i> |
| Cape White Eye* | <i>Zosterops capensis</i> |
| Cape Sparrow [#] | <i>Passer meuslanur</i> |
| Cape Weaver* | <i>Ploceus capensis</i> |
| Yellow Bishop | <i>Euplectes capensis</i> |
| Common Waxbill | <i>Estrilda astrild</i> |
| Yellow Canary* | <i>Serinus flaviventris</i> |
| Cape Bunting [#] | <i>Emberiza capensis</i> |

Unmarked species have been used for both ECRB and WCRB analyses, [#] - species used in the ECRB analyses, * - species used in the WCRB analyses.

5. FINAL DISCUSSION AND CONCLUSIONS

5.1. INTEGRATIVE DISCUSSION

5.1.1. Similarities, differences and lessons from the West and East Coast Renosterveld Bioregions

The two preceding chapters have encompassed several critical issues concerned with the conservation of avifaunal richness, diversity and integrity. What is more, these were focused on the avifauna of a biodiversity hotspot, the Cape Floristic Region (CFR), a region renowned for its exceptional levels of floristic richness and endemism (Myers et al., 2000; Rouget et al., 2003a). However, despite the value of this region from the biodiversity and conservation perspective, it has undergone major transformation and fragmentation, especially through agricultural expansion, urban sprawl and invasive alien plant introductions (Rouget et al., 2003b). The two bioregions represented in this thesis as they are now formally known (West Coast- and East Coast Renosterveld Bioregions; WCRB and ECRB, respectively) are two of the most threatened bioregions within the CFR with little, and highly fragmented, habitat left for indigenous biota (Kemper et al., 1999; Pressey et al., 2003; Winter et al., 2005).

These two bioregions showed remarkable variability in how their avifaunal composition and occupancy and abundances of species responded to habitat fragmentation at two spatial scales measured here, i.e. fragment- and landscape-scale. The landscapes, within which these two bioregions fall, are very different in habitat configuration and arrangement of remaining fragments (see fig. 3.1, chapter 3). The WCRB consists of several large fragments with few small fragments in between, and the remaining fragments within the WCRB form clusters scattered within this landscape. In the ECRB, the average fragment size is much smaller than in the WCRB, but the spatial distribution, or arrangement of the fragments, is more uniform within the landscape. Fragments are scattered within the landscape, but in such way that connectivity through stepping-stones allows for easier dispersal through the matrix.

In the case of the ECRB, there was a very strong influence from landscape configuration in affecting bird assemblage composition and species abundance. This may be because of the distribution of these stepping-stone fragments. Stepping-stones have been

advocated as one of the more successful means to increase connectivity in fragmented landscapes (Beier and Noss, 1998; Gjerde et al., 2004; Rouget et al., 2005; Haslem and Bennet, 2008). When individuals utilise these stepping-stones they can acquire more of the resources occurring throughout the landscape as they facilitate dispersal. The arrangement of fragments in the ECRB enables species to colonise and utilize fragments.

Opdam et al. (2003) defined the concepts of network, spatial and landscape cohesion. Network cohesion is composed of three elements of a landscape, i.e. the size, the quality and the configuration of habitat fragment within the landscape. Spatial cohesion is a measure of the value of the networks with the landscape, whereas landscape cohesion is based on the overall ecological quality of the entire landscape, including untransformed and transformed elements. The ECRB may have more small fragments than the WCRB, but despite this, the arrangement of these fragments increases the network, spatial and landscape cohesion of the bioregion. The measure of landscape configuration used in the present study exclusively explained the amount of habitat in different buffers around each fragment. This measure of habitat configuration and isolation has already been used by Bender et al. (2003) and Tischendorf et al. (2003). They showed that this is the best measure of isolation and landscape configuration. Fahrig (2003) suggests that the strong effect of habitat amount on dispersal also suggests that the effects of patch isolation and of landscape-scale habitat amount are equivalent. The latter links to the three levels of cohesion (Opdam et al., 2003). The configuration of the landscape within the ECRB seems to have a higher level of cohesion than that of the WCRB.

The WCRB's avifaunal composition was influenced much more by area effects. This could, however, still be interpreted as an effect of landscape configuration. In short, the arrangement of the remaining fragments is of such a nature that it emphasises the effect that area has on the avifauna of this bioregion. Area effects are known to have serious repercussions for avifaunal diversity and richness in various ecosystems, including forests (Raman, 2006), shrublands (Freudenberger and Brooker, 2004) and grasslands (Johnson and Igl, 2001).

Area effects can influence assemblages and species abundances in two different ways. Firstly, assemblages are maintained through the resources found within habitats (Fletcher et al., 2007). If these resources are compromised (through area reductions), the carrying capacity of that particular fragment may decrease, leading to shift in assemblage composition and species abundance. Secondly, fragment size has a crucial role to play in immigration and

emigration of individuals between fragments. Small fragments are, generally, more difficult to locate within the landscape and will therefore be less likely to attract dispersing individuals.

In the WCRB, both of the above mechanisms can be important. The fragments within the bioregion are much more isolated from one another than the fragments in the ECRB. This makes movement between fragments a risky and costly affair. Therefore, birds may well rely on those fragments that are large enough to sustain higher levels of resources.

Although the way in which assemblages and species respond to area and landscape effects might be important, population persistence within these fragmented landscapes are equally important (Fahrig, 2002; Lindenmayer et al., 2002). Limpila et al. (2005) found strong effects of landscape configuration and isolation on population persistence. Unfavourable landscape configuration can have serious repercussions on metapopulation dynamics (Opdam et al., 2003). Fragment area also plays a key role in population persistence at the fragment, or patch, scale (Fahrig, 2002). In this study, various common species have been shown to be sensitive to either landscape configuration and/or fragment area in their probability of occupancy, an indicator of persistence. What makes this finding extraordinary is that it shows that even common species can have their populations put in jeopardy by habitat fragmentation. Most empirical research focuses on specialist, rare or highly sensitive species, and area and landscape effects are often cited as key drivers in population extinctions in specialist species (Limpila et al., 2005). However, this study shows that in the ECRB and the WCRB, even common species are adversely affected by fragmentation and might well be in other fragmented habitats.

Why has this study elected to focus on generalist and common species? These species are generally expected to be either favoured, or at least not negatively affected by transformation, with sensitive species receiving highest conservation priority (Gil-Tena et al., 2007; Arriaga-Weiss et al., 2008). However, generalist species may be vital in sustaining ecological services in fragmented landscapes. Generalist pollinators and seed dispersers are of great importance in such a landscape, taking over the roles of more specialist species that cannot persist within the landscape or may be confined to larger fragments (Aguilar et al., 2006; Mennechez and Clergeau, 2006; Albercht et al., 2007). It is therefore important to understand how both specialist species and generalist species respond to the various fragmentation effects, and how their persistence in a landscape is affected.

The ECRB and WCRB showed different responses to habitat fragmentation with regard to their avifaunal assemblage and guild composition. This study has shown that the extent of fragmentation, the effects that it has on the size distribution, and arrangement of habitat

fragments can have a variable influence on avian assemblages. Here, the bioregion that was most severely fragmented, with the least amount of habitat within the overall landscape, was the WCRB. However, the ECRB, with its more homogenous distribution of fragments within the landscape, shorter distances between the habitat fragments, and the amount of habitat within the landscape, together were the determinants of the avian assemblages. Furthermore, this study showed that even common, or generalist, species may be sensitive and vulnerable to fragmentation. The occupancies and abundances of the most common species in both of these bioregions confirmed the compositional discrepancies that has discussed above. However, three valuable conclusions also came from looking at these species. These were that fragment area is the most important factor influencing species occupancy and abundance, area effects are generally more important in determining occupancy and abundance than landscape elements and that, finally, habitat suitability is of utmost importance in fragments.

5.1.2. Lessons from other vegetation types, regions and hotspots

The East and West Coast Renosterveld Bioregions from part of the Cape Floristic Region (CFR), proclaimed as a global biodiversity hotspot (Myers al., 2000; Rouget et al., 2003; Winter et al., 2005). By definition, these are regions that have high richness in rare, endemic and taxonomically unique species. However, despite the high biological and conservation priority of these regions, they are under immense pressure from the human population (Brooks et al., 2002).

This is the first study on the influences of habitat fragmentation on the indigenous avifauna from a multi-scale perspective in the CFR, and possibly elsewhere. Most studies have only addressed the issue from either a fragment scale or landscape scale (Lee et al., 2002), and in some cases a combination of these two scales. But no studies were found that have also included the geographic- or bioregional scales as well.

The majority of studies addressing the effects of fragmentation on birds within global biodiversity hotspots have been done in forest biomes, e.g. Maputaland Centre of Endemism, southern Mozambique (Wilson et al., 2007) and the Sundaland forests, Borneo (Cleary et al., 2007). Only a few studies have been conducted in the shrubland-type habitats within the hotspots, e.g. the Mediterranean Basin (Falcucci et al., 2007; Sirami et al., 2008). Compared to the fragmentation of a shrubland, such as the Renosterveld, forest fragmentation can be much more drastic. If forest cover is reduced and fragmented, the contrast between the edges

of the fragment and the matrix are usually much higher than that of shrubland fragments and the matrix (Watling and Donnelly, 2006).

Wilson et al. (2007) found that fragment area and species richness and species abundance were positively correlated in the Maputaland Centre of Endemism. This strong effect of fragment area is an expected phenomenon and has been repeatedly recorded in the literature. It is, for example, a prominent predictor of species richness, diversity and abundances in forest biomes (Castellón and Sieving, 2006; Scott et al., 2006), and even in habitats that differ greatly from forests from a structural point of view, such as grassland. Area effects are a main driver of species richness in the grasslands of the USA, an indication that area effects are indeed vital in avifaunal composition, regardless of habitat complexity (Johnson and Igl, 2001; Davis, 2004). However, Johnson and Igl (2001) highlighted the fact that the same species showed variable responses to fragment area in different geographical regions. The present study has shown similar results. Species that were sensitive to area effects in the WCRB were found to be more sensitive to landscape configuration in the ECRB. Consistent with the result from the WCRB, Watson et al. (2004) also found that insectivorous species were the most sensitive guild to decreasing fragment area. This is yet another compelling similarity of area effects on avifaunal diversity. Their study was conducted in the littoral forest remnants, south-eastern Madagascar, and focus was on forest-dependent or -specialist species. In the WCRB, it was also the insectivorous species that were highly sensitive to area effects. However, these were all common and/or generalist species. Specialist species, such in case of Watson et al. (2004), are expected to be sensitive fragmentation, with generalists often overlooked, as it is assumed that they will not be as sensitive to fragmentation and area effects as their counterparts. Yet this study in the WCRB clearly showed that even generalist/common species may be sensitive to decreasing fragment area.

There are many possible reasons why species richness, diversity and abundance may decrease as fragments become smaller in size. Larger fragments have greater areas for territories, more resources and better conditions for feeding and breeding (Helzer and Jelinski, 1999; Watson et al., 2004; Parker et al., 2005; Kaiser and Lindell, 2007). The other explanation is that habitat-dependent species are lost as fragments become smaller and as edge to area ratios increase, with concurrent deterioration of habitat condition (Briggs et al., 2007).

The dominance of area effects in the WCRB is mainly due to the lack of habitat within the landscape. This is consistent with Watson et al. (2005), who suggest that area effects are

manifested in landscape pattern or configuration. Landscape configuration has an undisputed role to play in avian diversity in many habitats, including forests, grasslands and shrublands. Coppedge et al. (2001) found that landscape configuration was equally important in landscapes of different degrees of fragmentation. However, in the two bioregions that were sampled in the present study, this was not the case. Landscape configuration seems to be more important when the landscape has enough habitat fragments left within it to sustain healthy populations and assemblages. Many authors have shown the significance of landscape configuration (Bani et al., 2006; Cushman and McGarical, 2003). Villard et al. (1999) showed that landscape configuration and forest cover had a major influence on species occurrence and occupancy within fragmented landscapes. Mitchell et al. (2001) showed that landscape characteristics, when measured at appropriate scales, are an accurate predictor of the distribution of some bird species inhabiting managed forests in coastal South Carolina.

Landscape configuration is a complex concept that encompasses the arrangement of habitat fragments, the amount of habitat within the landscape and the connectivity between those fragments (Fahrig, 2003; Ewers and Didham, 2006). Landscape-scale effects, such as configuration, are often more visible at the community-level than at the species-level (Rodewald and Yahner, 2001; Mitchell et al., 2006). If landscape configuration is favourable, it will allow individuals to more readily disperse between fragments and keep a constant turnover and flow of individuals and species within the landscape (Robinson, 1999). Landscape configuration can therefore have great effects on avifaunal composition.

More importantly, landscape configuration can affect the persistence of species within the landscape, through maintaining viable metapopulations (Fahrig and Merriam, 1994). If habitat fragments within the landscape are arranged in such a manner that does not allow movement of individuals to and from fragments, population persistence in the landscape can be compromised. However, if the fragment arrangement is of such a nature that species can move between fragments, metapopulation dynamics can sustain populations within the landscape (Bani et al., 2006). Landscape configuration has a strong effect on metapopulations. It is the configuration of the landscape that determines rates of immigration and emigration between fragments that can subsequently rescue populations from local extinctions (With and King, 1999; Ewers and Didham, 2006).

It is therefore important to understand the importance of landscape-scale pattern, such as fragment arrangement, amount of habitat and connectivity (Bélisle and Desrochers, 2002; Bowen et al., 2007) and how it influences avifauna, as well as biodiversity as a whole. The strong effect of landscape configuration in the ECRB, and its effect on species persistence

and/or occupancy in both the studied bioregions is a great indicator of landscape pattern importance. The effects of landscape scale pattern are a recognised threat to avian diversity in many habitat types and landscapes (Donovan and Lambertson, 2001; Quevedo et al., 2006). The shift from patch-scale research to landscape-scale research is a major step in the right direction, and will yield many new results with regard to species conservation within fragmented landscapes. It is, however, important to view each landscape as unique and to determine the best conservation strategy for a specific landscape. This means that the conservation strategies for the WCRB are not necessarily the same as those for the ECRB.

5.2. FINAL CONCLUSIONS

The adverse effects of habitat fragmentation on avian diversity are a major concern worldwide. The WCRB and ECRB were shown here to have highly variable responses to the different spatial scales at which they were examined. Area effects have been generally considered as the main driver of avian species losses, but the recent shift to establishing the effects of landscape configuration on birds, and biodiversity as a whole, has shown that fragmentation is a far more complex process than previously thought.

Landscape configuration is becoming more and more recognised as one of the key drivers in avian integrity in fragmented landscapes. The present study confirms this notion. What this study has also revealed is that different components within assemblages react to different elements of fragmentation, depending exclusively on the scale at which it is being examined. I would therefore recommend that more research be done from a multi-scale perspective. Studying birds at the fragment, landscape and bioregional scale was shown to yield interesting and important results.

Between the two bioregions of this study two very different patterns emerged. However, the dominance of area effects in the WCRB can be related to landscape configuration and habitat amount. The arrangement of habitat fragments and the amount of habitat left within the landscape are key drivers to shifts occurring in avian assemblages. Moreover, for population persistence, the interplay between landscape configuration and appropriately-sized fragments is critical in both the two bioregions. However, what this study has also shown is that an avifaunal response to fragmentation is complex.

The conservation of various interactions, vulnerable populations and threatened species is no longer a problem to be tackled at just the scale of the fragment. Conservation is moving towards a more comprehensive and sophisticated landscape scale approach, which forms a sound knowledge base towards a more realistic conservation biology.

5.3. MAJOR CONSERVATION RECOMMENDATIONS

Generalisations are often difficult to make in the discipline of conservation biology (Okes et al., 2008). However, there are some valuable conservation recommendations that can be made from this study.

1. *Conserving large fragments:* Large fragments provide sufficient resources, shelter and habitat for birds. These fragments remain valuable conservation areas, especially in landscapes that are highly fragmented. Large fragments must receive the highest conservation priority and should be included in formal and statutory nature reserves.
2. *Follow a landscape scale approach:* The landscape remains the main factor governing the integrity of avifaunal composition. If there is enough habitat within the landscape (e.g. the ECRB) area effects are far less pressing than in landscapes with less habitat. Therefore, it is crucial that conservation strategies must look at landscape scale conservation, complementing single fragment reserves. This may increase immigration and emigration between source fragments and the landscape, promoting metapopulation persistence. Clusters of fragments that can promote the movement of individuals within that cluster should receive high priority in conservation planning, focusing conservation efforts at the broader scale, rather than simply at the scale of the fragments.
3. *Corridors:* Although corridors are generally thought of as linear strips of habitat that connect fragments, the importance of fragment arrangement is starting to become more and more popular as stepping-stone habitats that function as corridors. It therefore is important to maintain and conserve small and medium-sized fragments scattered within the landscape, as stepping-stone habitats connect large fragments.

4. *Selecting surrogate species and/or guilds:* This study has shown that species and feeding guilds respond differently to the different elements of fragmentation. Conservation science must tease out which species and guilds are most sensitive to fragmentation, and also to which effects, whether area or landscape configuration effects, etc. These species/guilds can be used as surrogates, being valuable monitoring tools and indicators to overall avian integrity.
5. *Multi-scale conservation approaches:* The future of research and conservation practises are now moving towards a new era, that of multi-scale approaches. From a spatial point of view, looking at the fragment, landscape and (bio) regional scales, different patterns and mechanisms emerge. It is extremely important to recognise these differences, and subsequently implement appropriate conservation strategies that contribute to effective conservation of avian diversity at each of these scales. In this study, two vegetation types, that are structurally and functionally very similar, exhibited very different patterns regarding fragmentation effects. These area-specific differences must be recognised in order for conservationists to be successful in biodiversity conservation in fragmented landscapes.

Furthermore, these different components within the avian assemblages can give insights into the patterns that are observed from coarse scales alone. Assemblages change because of fine-scale changes within. It is therefore important to be aware of these fine-scale components and how they respond to fragmentation.

6. *Further research:* For conservation practice to keep up with ever-changing landscape patterns and new emerging pressures on avian diversity, research must be carried out on a constant base, looking into fine- and coarse-scale solutions and problems. Understanding patterns is important, but so too is understanding processes. Through ongoing research and adequate communication between the scientific community and managers, the science of conservation will go forward. Adaptive management in reserves and landscape is key to the success of conservation efforts and all relevant parties, scientists, managers, private landowners, governmental sectors and non-governmental organisations must work together in asking the right questions for finding the right solutions.

5.4. REFERENCES

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9, 968–980.
- Albrecht, M., Duelli, P., Müller, C., Kleijn, D., Schmid, B., 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology* 44, 813–822.
- Arriaga-Weiss, S.L., Calmé, S., 2008. Bird communities in rainforest fragments: guild responses to habitat variable in Tabasco, Mexico. *Biodiversity Conservation* 17, 73–190.
- Bani, L., Massimino, D., Bottoni, L., Massa, R., 2006. A multiscale method for selecting indicator species and priority conservation areas: a case study for broadleaved forests in Lombardy, Italy. *Conservation Biology* 20, 512–526.
- Beier, P., Noss, R.F., 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12, 1241–1252.
- Bélisle, M., Desrochers, A., 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* 17, 219–231.
- Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Evaluation of patch isolation metrics for predicting animal movement in binary landscapes. *Landscape Ecology* 18, 17–39.
- Bowen, M.E., McAlpine, C.A., Housec, A.P.N., Smith, G.C., 2007. Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. *Biological Conservation* 140, 273–296.
- Briggs, S.V., Seddon, J.A., Doyle, S.J., 2007. Structures of bird communities in woodland fragments in central New South Wales, Australia. *Australian Journal of Zoology* 55, 29–40.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, G., 2002. Habitat loss and extinction in hotspots of biodiversity. *Conservation Biology* 16, 909–923.
- Castellón, T.D., Sieving, K.E., 2006. Landscape history, fragmentation, and patch occupancy: models for a forest bird with limited dispersal. *Ecological Applications* 16, 2223–2234.

- Cleary, D.F.R., Boyle, T.J.B., Setyawati, T., Anggraeni, C.D., van Loon, E.E., Menken, S.B.J., 2007. Bird species and traits associated with logged and unlogged forests in Borneo. *Ecological Applications* 17, 1184-1197
- Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2001. Avian responses to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications* 11, 47-59.
- Cushman, S.A., McGarical, K., 2003. Landscape-level pattern of avian diversity in the Oregon coast range. *Ecological Monographs* 73, 259-281.
- Davis, S.K., 2004. Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in Southern Saskatchewan. *The Auk* 121, 1130-1145.
- Donovan, T.M., Lambertson, R.H., 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. *Ecology* 82, 1170-1179.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117-142.
- Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12, 346-353.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of the Ecology, Evolution and Systematics* 34, 487-515.
- Fahrig, L., Merriam, G., 1994. Conservation of fragmented populations. *Conservation Biology* 8, 50-59.
- Falcucci, A., Maiotano, L., Boitani, L., 2007. Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecology* 22, 617-631.
- Fletcher, Jr., R.J., Ries, L., Battin, J., Chalfoun A.D., 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology* 85, 1017-1030.
- Freudenberger, D., Brooker, L., 2004. Development of the focal species approach for biodiversity conservation in the temperate agricultural zones of Australia. *Biodiversity and Conservation* 13, 253-274.
- Gil-Tena, A., Saura, S., Bortons, L., 2007. Effects of forest composition and structure on bird species richness in a Mediterranean context: implications for forest ecosystem management. *Forest ecology and Management* 242, 470-476.
- Gjerde, I., Sætersdal, M., Rolstad, J., Blom, H.H., Storaunet, K.O., 2004. Fine-scale diversity and rarity hotspots in northern forests. *Conservation Biology* 18, 1032-1042.

- Haslem, A., Bennet, A.F., 2008. Birds in agricultural mosaics: the influence of landscape pattern and countryside heterogeneity. *Ecological Applications* 18, 185-196.
- Helzer, C.J., Jelinski, D.E., 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* 9, 1448-1458.
- Johnson, D.H., Igl, L.D., 2001. Area requirements of grassland birds: A regional perspective. *The Auk* 118, 24-34.
- Kaiser, S.A., Lindell, C.A., 2007. Effects of distance to edge and edge type on nestling growth and nest survival in the wood thrush. *Condor* 109, 288-303.
- Kemper, J., Cowling, R.M., Richardson, D.M., 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation* 90, 103-111.
- Lampila, P., Mönkkönen, M., Desrochers, A., 2005. Demographic responses by birds to forests fragmentation. *Conservation Biology* 19, 1537-1546.
- Lee, M., Fahrig, L., Freemark, K., Currie, D. J., 2002. Importance of patch scale vs. landscape scale selected forest birds. *Oikos* 96, 110-118.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H., Lindenmayer, B.D., 2002. Effects of forest fragmentation on bird assemblages in a novel landscape context. *Ecological Monographs* 72, 1-18.
- Mennechez, G., Clergeau, P., 2006. Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica* 30, 182-191.
- Mitchell, M.S., Lancia, R.A., Gerwin, J.A., 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications* 11, 1692-1708.
- Mitchell, M.S., Rutzmoser, S.H., Wigley, T.B., Loehle, C., Gerwin, J.A., Keyser, P.D., Lancia, R.A., Perry, R.W., Reynolds, C.J., Thill, R.E., Weih, R., White, D., Wood, P.B., 2006. Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. *Forest Ecology and Management* 221, 155-169.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.
- Okes, N.C., Hockey, P.A.R., Cumming G.S., 2008. Habitat use and life history as predictors of bird responses to habitat change. *Conservation Biology* 22, 151-162.
- Opdam, P., Verboom, J., Pouwels, R., 2003. Landscape cohesion: an index for the conservation potential of landscape for biodiversity. *Landscape Ecology* 18, 113-126.

- Parker, T.H., Stansberry, B.M. Becker, C.D., Gipson P.S., 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conservation Biology* 19, 1157-1167.
- Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* 112, 99-127.
- Quevedo, M., Bañuelos, M.J., Obeso, J.R., 2006. The decline of *Cantabrian capercaillie*: How much does habitat configuration matter? *Biological Conservation* 127, 190-200.
- Raman, T.R.S., 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantation in the Western Ghats, India. *Biodiversity and Conservation* 15, 1577–1607
- Robinson, W.D., 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conservation Biology* 13, 85–97.
- Rodewald, A.D., Yahner, R.H., 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82, 3493–3504.
- Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T., Kerley, G.I.H., 2005. Designing large-scale conservation corridors for pattern and process. *Conservation Biology* 20, 549-561.
- Rouget, M., Richardson, D.M., Cowling, R.M., 2003a. The current configuration of protected areas in the Cape Floristic Region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biological Conservation* 112, 129-145.
- Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W., Lombard, A.T., 2003b. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112, 63-85.
- Scott, D.M., Brown, D., Mahood, S., Denton, B., Silburn, A., Rakotondraparany, F., 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation* 127, 72-87.
- Simari, C., Brotons, L., Burfield, I., Fonderflick, J., Martina, J., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. *Biological Conservation* 141, 450-459.
- Tischendorf, L., Bender, D.J., Fahrig, L., 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18, 41-50.

- Villard, M.A., Trzcinski, T.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13, 774-783.
- Watling, J.I., Donnelly, M.A., 2006. Fragments as islands: a synthesis of faunal responses to patchiness. *Conservation Biology* 20, 1016-1025.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31, 1791-1807.
- Watson, J.E.M., Whittaker, R.J., Freudenberger, D., 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* 32, 1353-1370.
- Wilson, J.W., van Aarde, R.J., van Rensburg, B.J., 2007. Effects of habitat fragmentation on bird communities of sand forests in southern Mozambique. *Ostrich* 78, 37-42.
- Winter, S.J., Esler, K.J., Kidd, M., 2005. An index to measure the conservation attitudes of landowners towards Overberg Coastal Renosterveld, a critically endangered vegetation type in the Cape Floristic Region, South Africa. *Biological Conservation* 126, 383-394.
- With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13, 314-326.