BIRD COMMUNITY ECOLOGY AND COMPOSITION IN AFROTEMPERATE FORESTS OF THE DRAKENSBERG MOUNTAINS, SOUTH AFRICA

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Submitted in fulfilment of the academic requirements for the degree of
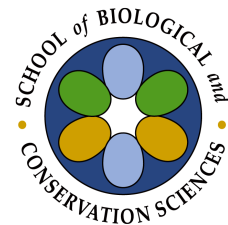
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PREFACE

This dissertation, submitted for the degree of Master of Science in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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Zoë A. Brocklehurst

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I certify that the above statement is correct.

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ABSTRACT

Recent research has emphasized the importance of understanding the consequences of species loss, not just for biodiversity per se, but also for ecosystem resilience and functioning. Firstly, a baseline analysis of the effects of a naturally patchy landscape on avian community composition and resilience in a high altitude Afrotemperate forest landscape in South Africa is presented. Bird data from a point count survey of 706 counts at 31 forest sites was used to test whether taxonomic species diversity, functional species richness and density of birds provide insight into community resilience in this historically patchy ecosystem. Bird species richness of forest patches ranged from 17 to 38, with a total species richness of 50. Density was slightly but negatively related to both area and species richness. That density compensation is occurring in these Afrotemperate forests suggests a level of resilience in this system. Following on from this, cumulative species-area and function-area graphs were derived to quantify the loss of forest area or taxonomic bird species richness that this landscape may potentially sustain before ecosystem functioning is negatively affected.

The concept that species' patterns of distribution, abundance and coexistence are the result of local ecological processes has recently been challenged by evidence that regional-scale processes are equally instrumental in shaping local community composition. The historically and naturally fragmented Afrotemperate forests of the uKhahlamba–Drakensberg Park, South Africa, offer an interesting test case. In this study the relative effects of local and regional-scale processes on species assemblages in a naturally patchy forest system were investigated. By employing species-area and species-isolation relationships, and nested subset analyses, we showed that isolation (regional-scale process) had a greater effect on bird species richness and composition than area (local-scale process), though the species-area relationship was significant. Using generalized linear models and an information-theoretic approach to model selection, patch area, the size of the regional species pool as well as the distance to the nearest Eastern Mistbelt forest were all influential in determining local bird species richness in these montane forests. Thus, localities are regionally enriched within the constraints on species occupancy provided by the available habitat.

Keywords

Afrotemperate forest, avian community ecology, regional enrichment, assemblage structure, species-area relationship

FACULTY OF SCIENCE AND AGRICULTURE

DECLARATION - PLAGIARISM

I, Zoë A. Brocklehurst, declare that:

1.   The research reported in this thesis, except where otherwise indicated, is my original research.

2.   This thesis has not been submitted for any degree or examination at any other university.

3.   This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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   September 2009

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CHAPTER 1

INTRODUCTION

Species diversity and the dynamics of community assemblage are among the most widely studied phenomena in ecology. However, few studies of a broad biogeographical nature have been reported for montane avifauna in Africa. This study examined the ecology and biogeography of montane forest bird communities as part of the biodiversity management plan for the Maloti-Drakensberg Transfrontier Project (MDTP). The geographical location of the study was the Drakensberg mountain range on the South African side of the MDTP planning domain (see Chapter 2). The forests in the Drakensberg are classified as Drakensberg Montane forest and belong to the Northern Afrotemperate Forest Group (Mucina and Rutherford, 2006b). Drakensberg Montane forests are small and have likely experienced several extinction-colonization cycles during climate fluctuations associated with the Quaternary (Eeley et al., 1999; Lawes et al., 2004; Lawes et al., 2007b). These species extinction-filtering events (sensu Balmford, 1996), coupled with the naturally patchy nature of forests and moderate to cool climate in the Drakensberg region, continue to be important determinants of bird community composition and structure. An important aim of this study was to understand how these forest bird communities have been assembled, and to use these insights for the conservation of avian biodiversity in the Drakensberg forests into the future. In particular, I examined the hypothesis that climatic extinction filtering events have resulted in a robust bird community in these montane forests, which, while relatively species poor compared to other lower-lying forest types in the region, are nevertheless more resilient to future climate changes and environmental disturbances.

Montane forest ecology

'Montane' and 'temperate' are descriptive terms used to describe a single forest type, but each term provides information on the locality of the forest i.e. 'montane' generally refers to high altitude forests, while 'temperate' refers to forests of high latitude. In tropical regions climatically suitable sites for forest are associated with high altitude mountains, giving rise to the term 'montane' forest. However, in temperate latitudes, latitude

compensates for altitude. For example, in the tropics montane forests are restricted to mountains above a certain altitude whereas at higher latitudes, where climatically suitable sites exist at lower altitudes, forest may occur almost at sea-level. Thus, in the higher latitudes where forest is not strictly associated with mountains, it is often termed 'temperate' forest. The environmental conditions which affect the distribution of montane forest are an interrelated combination of factors of which rainfall and temperature are primary (Lovett, 1993; Midgley et al., 1997; Amigo and Ramirez, 1998). Montane forest occurs in areas that experience cool temperatures, seasonal variation in temperature and rainfall, and forests are largely confined to higher rainfall areas or where soil moisture is not limiting for extended periods (Cowling, 1983; Mucina and Rutherford, 2006b). In contrast to neighbouring lowland forests, montane forests occupy environments characterized by a much greater climatic range, affecting both species composition and forest size (they are often smaller than lowland forests; Jacobs, 2004). In the southern hemisphere both angiosperm and gymnosperm tree species co-occur, but it is the presence of gymnosperms that differentiate montane forests from their lowland forest counterparts. Furthermore, the presence of the gymnosperm family Podocarpaceae across three southern hemisphere continents (Africa, Australia, South America) establishes an ancestral Gondwana link, providing evidence that montane forests are very old.

Biogeography and history of Afrotemperate forest

Africa's high-lying mountain regions, stretching from Sierra Leone eastwards to Somalia and from the Ethiopian Highlands southwards to the Cape Peninsula, are characterized by a distinct phytochorion classified by White (1978; 1983) as the Afromontane floristic region. These disjunct uplands represent an archipelago-like regional centre of Afromontane flora that displays a reasonable degree of uniformity and continuity despite the large latitudinal and longitudinal range throughout Africa (White, 1981). The disjunct nature of Afromontane forest is the outcome of a complex evolutionary history incorporating geological, climatic and anthropogenic influences to a greater or lesser degree (Hamilton, 1981; Crowe and Crowe, 1982; Kingdon, 1990; Eeley et al., 1999). However, it has been the influence of climate, in particular paleoclimatic events involving repeated and drastic climate shifts during the Quaternary, that were instrumental in determining present day Afromontane forest distribution (Diamond and Hamilton, 1980; Lawes, 1990; Eeley et al., 1999; Prentice and Jolly, 2000). For example, during the Last Glacial Maximum,

approximately 18,000 years BP, conditions were considerably colder and drier than at present, causing a downward elevational shift of forest (Jolly and Haxeltine, 1997; Street-Perrott et al., 1997; Elenga et al., 2000). Forests were likely eliminated at higher altitudes in the Drakensberg, and pushed to lower elevations in suitably protected refugia currently occupied by Eastern Mistbelt forest (Stuckenberg, 1969; Eeley et al., 1999; Mucina and Rutherford, 2006b). As climatic conditions became warmer and moister during the subsequent hyperthermal events, forest remnants are thought to have expanded and re-established in previously suitable sites. The present distribution of forest fauna in southern Africa is thus thought to be largely a consequence of vegetation adjustments following the climatic changes during the Quaternary (van Wyk, 1989; Lawes, 1990; Lawes et al., 2007b).

In contrast to the contemporary changes that are taking place in tropical forests in terms of large-scale anthropogenic fragmentation (Laurance et al., 2006), the Afromontane forests of southern Africa have experienced historical changes in climate since the Quaternary, resulting in a natural expansion and contraction in forest extent (Lawes, 1990). Thus, the forests studied here have experienced natural (rather than anthropogenic) fragmentation over most of their evolutionary history (Eeley et al., 1999), and even the small patches that persist in the landscape today have remained small for at least 60 years, and possibly much longer (Lawes et al., 2004). These differences in historical selection pressure between tropical and Afromontane forest may therefore be a useful tool in explaining current geographical variation in the resilience of forest bird species to modern human-induced impacts. For example, extinction filtering events (sensu Balmford, 1996) that occurred during the climatic perturbations of the Quaternary have likely resulted in Afromontane faunal communities that are robust and relatively resilient to change (Lawes et al., 2000a; Lawes et al., 2007b). This ecological resilience may have predisposed avian communities to cope well with contemporary anthropogenic environmental disturbances as well as to future changes in climate. The natural patchwork mosaic of these forests and their persistence through several climatic and ecological filters poses several questions relating to the biogeography and community ecology of birds in these forests. In accordance with the refugia theory that Eastern Mistbelt forest provided the seed for forest re-establishment of Drakensberg Montane forest during hyperthermal periods, we similarly predict that the Eastern Mistbelt forests provide a regional source of birds as potential colonists for Drakensberg Montane forest. In particular, this thesis addresses whether forest

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size or isolation play a pivotal role in avian community ecology, and whether the Eastern Mistbelt forests act as a species source pool for Drakensberg Montane forests. Furthermore, we determine the redundancy and resilience of Drakensberg Montane forest bird assemblages.

Avian community ecology

In the past few decades, the rapid rate of deforestation has caused localised species extinctions ranging from 1% to 67% of the original forest avifauna (Castelletta et al., 2000; Daily et al., 2001). With over 900 threatened species of forest-utilizing birds (Birdlife International, 2008), it is therefore important to understand the biogeographical processes which determine forest bird communities in order to ensure their persistence. However, much of the research on forest birds has been undertaken in tropical or lowland forests, and because of the different trophic structures and taxonomic compositions between lowland and montane avifaunas (Kattan, 1992; Renjifo et al., 1997; Dowsett-Lemaire and Dowsett, 2001), it is unwise to extrapolate any studied effects from one to the other. Furthermore, it has become increasingly apparent that conservation action must be directed at whole ecosystems rather than individual species (Walker, 1992; Walker, 1995; Balmford, 1996). Recent research has emphasized the importance of understanding the consequences of species loss, not just for biodiversity per se, but also for ecosystem functioning (Dobson et al., 2006; Şekercioğlu, 2006; Cumming, 2007; Cumming and Child, 2009). Biological diversity has repeatedly been found to enhance ecosystem functioning by providing more consistent services over space and time (Rosenfeld, 2002; Tilman et al., 2006; Ives and Carpenter, 2007; Winfree and Kremen, 2008). Increased diversity is thus likely to provide a measure of redundancy to a system (Walker, 1995). Redundancy however does not imply that the loss of any one species may be more ecologically critical than another (Walker, 1992; Walker, 1995), or that some species are superfluous, but refers rather to the ecological equivalence of species.

Functional redundancy is based on the observation that some species perform similar roles in an ecosystem, and may therefore be substitutable with virtually no effect on ecosystem processes (Lawton and Brown, 1993). Studies suggest that when species are lost, increases in the population size of species released from competition can compensate for loss of ecological function (Terborgh et al., 2001; Ives and Cardinale, 2004; Solan et al., 2004). The phenomenon in which the summed population densities of communities in

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species-poor sites may be equivalent to, or greater than, that of species-rich sites is termed 'density compensation' (MacArthur et al., 1972). MacArthur et al. (1972) suggested that species on small islands, because they contained fewer species, were less subject to interspecific competition and predation, which allowed their populations to increase. Mechanisms of density compensation may include expansions in foraging substrates, diet and habitat types (Earle, 1983; Koen, 1988b; Peres and Dolman, 2000; Buckley and Jetz, 2007), all of which may result in greater average population densities for species released from competition. Regardless of its causal mechanisms, density compensation results in lower abundances for residents of diverse communities when compared to depauperate communities (McGrady-Steed and Morin, 2000). The process of density compensation is not an infallible indicator, but if detected, it would lend support to the argument of functional redundancy.

To determine the important ecological functions in a landscape, taxonomic species are frequently placed into functional groups based on the function they perform, or the service that they provide in an ecosystem i.e. sunbirds are pollinators (e.g. Walker, 1992; Naeem, 1998; Fonseca and Ganade, 2001). In terms of practical conservation issues, the concept of functional groups and thus functional redundancy is a double-edged sword. The basic assumption is that a number of species may all perform similar ecological functions (i.e. belong in the same functional group), and redundant species can therefore be lost with minimal impact on ecosystem processes. However, even similar species can only co-exist because they differ to some unknown degree along some functional axis, and may respond differently to different environmental pressures. Thus, although several authors have cautioned the use of discrete functional classifications (Polis and Strong, 1996; Rosenfeld, 2002), identifying redundancy enables biodiversity efforts to initially focus on functional groups or aspects of the ecosystem that require critical attention in order to maintain ecosystem functioning, rather than on individual species.

Regional versus local influences

The contemporary view of community ecology is that both local and regional processes play an important role (Ricklefs, 2004, 2007). The terms 'local' and 'regional' refer to the spatial scales at which ecological and biogeographic processes, respectively, predominate. Thus predation, parasitism, competition, and disturbance occur on a local scale, whereas long-distance dispersal, speciation, widespread extinction, and fluctuation in species'

distribution take place across a broader geographic region. If local diversity is deterministically related to local processes, local assemblages should reach a point of saturation (Ricklefs, 1987). Increasing evidence suggests that, on the contrary, many local assemblages are unsaturated and local diversity is instead dependent upon regional diversity and regional processes (Ricklefs, 1987, 1989; Caley and Schluter, 1997; Lawes and Eeley, 2000). In such an instance, although there may be local interactions among species, these are not sufficient to limit local species richness (Cornell and Lawton, 1992). Indeed, many authors now feel that the regional-scale influence of Quaternary climate change and climatic barriers are much more significant than topographical barriers in determining the zoogeography of Africa (Hamilton, 1988; Grubb, 1990). The more randomly distributed that species are among forest patches, the less likely that bird communities are dominated by local-scale processes. In the case of Drakensberg montane forests, communities are probably assembled by regional and large scale processes (e.g., climatic extinction-filtering) rather than local species interactions (e.g., competition).

Island biogeography

Forest patches are often treated as habitat islands and the interpretation of their ecology is frequently based on the principles of island biogeography theory (MacArthur and Wilson, 1963, 1967). The theory focuses primarily on determinants of species richness, such as island area and distance to mainland, in terms of the balance between colonization and extinction. A fundamental relationship of island biogeography is the species-area relationship (SAR): the tendency for the number of species within a taxon to increase with increasing area (Preston, 1960, 1962; MacArthur and Wilson, 1963, 1967; Connor and McCoy, 1979). The relationship between community composition (measured as species richness) and the availability of suitable habitat is often examined using species-area curves (Wethered and Lawes, 2003). At a simple level, therefore, the species richness of a community appears to be determined by the area of available habitat. This positive response of increasing species richness with increasing area has been consistently documented for avian communities in temperate and tropical forests at several spatial scales (Newmark, 1991; Cornelius et al., 2000; Lindenmayer et al., 2002; Ricklefs and Bermingham, 2004; Castelletta et al., 2005; Watson et al., 2005; Wethered and Lawes, 2005; Hannah et al., 2007; Pavlacky and Anderson, 2007).

SAR's have proved particularly useful for studies of habitat islands. Patch size is important because many species are susceptible to area-dependent extinction effects. Patch spacing is important because it influences the likelihood that a patch will be colonised. The more isolated a patch is the less likely it is to be colonized. The interaction of patch area and isolation means that a large patch area could compensate for a high degree of isolation, or alternatively, that small inter-patch distances could compensate for small patch size. Moreover, given that habitat islands or patches form part of a heterogenous landscape mosaic, and that birds are a highly mobile taxon and are able to disperse through heterogenous environments, patch isolation is often considered a less important variable than patch area. Theoretical models show that increased dispersal leads to lower species turnover and higher homogenization of species compositions (Amarasekare and Nisbet, 2001; Hubbell, 2001; Mouquet and Loreau, 2002; Hovestadt and Poethke, 2005). From the SAR perspective, increasing dispersal ability reduces the slope of SAR by making local assemblages more similar to each other. SAR's in montane bird communities are typically shallow. This is possibly because the species pool is smaller in montane forests (i.e., they are less species rich) and so large forest patches do not contain so many more species than small forest patches. In contrast to the large body of supporting research for the SAR, Prugh et al. (2008) found that patch area and isolation were poor predictors of occupancy, highlighting the fact that other factors, such as the intervening matrix, may also prove useful when studying the effects of habitat fragmentation.

In this study I use species-area theory to describe patterns of diversity and distribution of avian communities in a naturally patchy forest landscape, merely as an aid to describing the putative effects of area-dependence on assemblage structure and diversity.

Nestedness

The spatial arrangement and configuration of patches in a landscape has important implications for avian diversity and community dynamics (Pavlacky and Anderson, 2007). One method of identifying the mechanisms responsible for species richness in a forest patch is by conducting nested subset analyses. Rather than random extinction and colonization of patches by species as suggested by the island biogeography theory, Cutler (1994) and Lomolino (1996) propose that community composition in habitat islands may be the consequence of highly deterministic species extinction or colonization patterns. Differential extinction and differential colonization are not mutually exclusive, and some

nested patterns are thought to be simultaneously affected by both (Lomolino, 1996; Martinez-Morales, 2005). The non-random distribution of species among patches characteristically results in a 'nested subset' pattern across communities (Patterson, 1987; Cutler, 1991, 1994) in which the communities of species-poor sites are a proper subset of those on species-rich sites. Patterson (1987) noted that in a fragmented system perfectly nested by patch size, the larger patch will harbour more species than any number of small patches together, resulting in a wedge-shaped pattern in a presence-absence matrix (Cutler, 1991). In a perfectly nested series it is implicitly assumed that all species are initially dispersed throughout the region, extinctions occur in a consistent sequence on all forest patches and no colonisations occur after isolation of the patch (Cutler, 1994). However, it is highly unusual for natural systems to be perfectly nested, although statistically significant nestedness has been documented for a variety of taxa at several spatial scales across a range of biogeographical regions and habitats (Taylor and Warren, 2001; Berglund and Jonsson, 2003; Feeley, 2003; Wethered and Lawes, 2005; Martínez-Morales, 2005). A departure from perfect nestedness occurs through unexpected absences (holes) of species from large communities, unexpected presences (or outliers) of species in small communities, or both (Cutler, 1991). Analysis of the nestedness of faunas in patchy landscapes is a useful means of identifying both the mechanism of community assembly and the most important patches for biodiversity conservation.

Principles of conservation for forest birds

The development of effective measures to manage and conserve avifaunal biodiversity within forest patches requires knowledge of the patterns and processes involved in determining species assemblages. The SAR, being among the most widely studied phenomena and robust generalizations in ecology, has been used as the focal principle in a conservation debate about the protection of "single large or several small" reserves (Terborgh, 1974; Diamond, 1975; Diamond and May, 1976; Simberloff, 1976; Lomolino, 1994). More recently, the concept of nestedness has been included in the SLOSS debate in determining reserve design (Worthen, 1996; Berglund and Jonsson, 2003; Martínez-Morales, 2005). At one extreme, in systems where species show random occurrences across habitat islands of different areas, a collection of small islands can potentially contain more species than a single large island of equivalent area (Quinn and Harrison, 1988; Peintinger et al., 2003). At the other extreme, in systems with a perfectly nested pattern in species

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composition, a collection of small islands (or reserves) will contain fewer species than a single large fragment (Brown, 1986; Blake, 1991; Atmar and Patterson, 1993). The significance of a species-isolation relationship within a system would imply an increase in the importance of conservation actions designed to mitigate the negative effect of isolation on patch biota. In such a case, small reserves, although perhaps not capable of supporting sustainable populations of target taxa, may be important stepping stones linking larger protected areas (Baum et al., 2004).

The proposed study aimed to describe and investigate the ecological and environmental determinants of avian diversity and community structure in montane forest patches in the Drakensberg, KwaZulu-Natal, South Africa. The influence of extreme climate and small and patchy forests on the diversity, composition and structure of the avifaunal assemblage in forest patches were investigated. Using this approach, we attempted to demonstrate some of the consequences for indigenous fauna in inhabiting an historically patchy, rather than fragmented, forest system.

This thesis is presented as chapters for submission to journals, so some overlap and repetition between chapters has been unavoidable:

Chapter 2. How resilient are Afrotemperate forest bird assemblages?

Chapter 3. Is bird species richness in southern Afrotemperate forests driven by regional-or local-scale processes?

Chapter 4. Summary: Conservation and management.

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CHAPTER 2

HOW RESILIENT ARE AFROTEMPERATE FOREST BIRD ASSEMBLAGES?

Abstract

Montane forests are a threatened habitat-type and the continued loss of montane forests worldwide adversely affects biodiversity in such forests. Recent research has emphasized the importance of understanding the consequences of species loss, not just for biodiversity *per se*, but also for ecosystem resilience and functioning. A baseline analysis is presented here of the effects of a naturally patchy landscape on avian community composition and resilience in a high altitude Afrotemperate forest landscape in South Africa. We use bird data from a point count survey of 706 counts at 31 forest sites to test whether taxonomic species diversity, functional species richness and density of birds, provide insight into community resilience in this historically patchy ecosystem. Forest bird species richness ranged from 17 to 38 in forest patches, with a total species richness of 50. Density was slightly but negatively related to both area and species richness. This density compensation suggests a level of resilience in these Afrotemperate forests. In addition, species-area and function-area analyses were applied to determine the loss of forest area or bird species richness that this landscape may potentially sustain before ecosystem functioning was negatively affected. The bird community in this Afromontane forest system had a taxonomic richness buffer of 12 species. That is, ecosystem functioning would not be impacted if random extinctions were to result in the extinction of a quarter of the bird species across functional guilds. Critical patch size (the smallest patch size capable of full ecosystem functioning) for birds in Drakensberg Montane forests was 3.4 ha. Thus, a large percentage (>95%) of forest patches in this landscape are capable of sustaining a fully functional montane bird community. We argue that, for the very resilient bird community of Drakensberg Montane forests, conservation of even small forest patches provides flexibility in conservation planning and sufficient habitat to maintain the functionality of Afromontane forests.

Keywords

Density compensation, ecological redundancy, ecosystem services, function-area relationship

1. Introduction

Globally, montane forests are considered among the most threatened ecosystems (Aldrich et al., 2001). Throughout Africa montane forests are generally small and patchy in distribution, and it is the larger central African montane forests that are subject to the most severe fragmentation and deforestation (Stuart, 1986; Newmark, 1998). By contrast, the naturally small and intensely patchy Afrotemperate forests in South Africa are largely unaffected by large-scale deforestation. Although in recent times, small-scale selective logging and the encroachment of agriculture has affected Afrotemperate forests (Lawes et al., 2004), most of the Afrotemperate forest of the Drakensberg region has been formally protected since the early 1900's. The small and patchy distribution of Afrotemperate forests, in particular Drakensberg Montane forest, is a result of drastic climate shifts during the Quaternary (Diamond and Hamilton, 1980; Lawes, 1990; Eeley et al., 1999; Prentice and Jolly, 2000). During these paleoclimatic changes, there were perhaps as many as 20 glacial cycles (Shackleton and Opdyke, 1976; Tiedemann et al., 1994), and Afrotemperate forests were likely pushed to lower elevations in suitable refugia (Stuckenberg, 1969; Lawes, 1990; Eeley et al., 1999). As climatic conditions became warmer and moister, forest remnants are thought to have expanded and re-established in previously suitable sites (Lawes, 1990; Eeley et al., 1999). The repeated extinction filtering events (sensu Balmford, 1996) associated with these climatic extremes have likely resulted in Afrotemperate forest communities that are robust and relatively resilient to future climate changes (Lawes et al., 2000a; Lawes et al., 2007c). Measuring the resilience of Afrotemperate forest bird communities in the context of potential climate changes and the patchy nature of forests, will provide valuable insight for conserving the bird diversity of this globally threatened habitat type. This study examines differences in bird species richness and diversity, community composition and bird population densities in forests in a montane landscape.

Recent research has emphasized the importance of understanding the consequences of species loss, not just for biodiversity per se, but also for ecosystem functioning (Dobson et al., 2006; Sekercioglu, 2006; Cumming, 2007; Cumming and Child, 2009). For conservation planning and decision-making, it is critical to know the minimum unit of habitat required to sustain a functional ecosystem, one that is capable of providing a complete suite of ecosystem services. Hypothetically, a single ecosystem service such as seed dispersal may increase with increased land-area conservation. In this case, the target for land conservation should fall at the point where the slope plateaus, suggesting the

minimum area required to ensure that the ecosystem service of seed dispersal is being delivered. Because different ecosystem services require different minimum land areas, it is necessary to bring ecological knowledge about multiple ecosystem services to decision-making (DeFries et al., 2004). Moreover, Armsworth and Roughgarden (2003) recommend increasing the area of land conserved (from an established minimum) to improve stability of the ecosystem.

Ecosystem functions refer variously to the habitat, biological or system processes of ecosystems, whereas ecosystem services represent the benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza et al., 1997). Birds are one of the most diverse groups of ecosystem service providers, whose ecological functions range from pest control to pollination, dispersal and disease control (Sekercioglu, 2006). Given the current and predicted declines in avian diversity (Birdlife International, 2008), it is important to understand that these functions translate to ecosystem services, and to estimate the ecological implications of bird species declines. The use of functional guilds to measure the range of potential ecosystem services and functions provides not only a measure of diversity, but also reflects the biological and functional integrity of an ecosystem (Angermeier and Karr, 1994). The terms 'functional group' and 'guild' are often used interchangeably (for review see Blondel, 2003). However, the two concepts differ in that processes or functions underpin the functional group approach, while competitive relationships within groups of species characterise the guild approach (Blondel, 2003). For example, the sharing by species of a similar resource relates to guilds, while the ecosystem processes these species eventually perform through resource exploitation relate to functional groups. Thus, species within a functional group are by definition ecologically equivalent and provide some degree of redundancy to the system. As a result, quantification of taxonomic species loss alone does not capture the likelihood of ecosystem collapse, because several species may perform similar functions that essentially provide the same ecosystem functions and services. Rather, functional classifications describe species according to what they do, providing an alternative that relates closely to ecosystem functioning (Naeem, 2002; Blondel, 2003; Sekercioglu et al., 2006). A potential downfall of classifying species into coarse functional groups is that the importance of individual species becomes lost. However, estimating the potential loss of species that a system may undergo before collapse provides a tentative measure of the systems resilience.

The function-area relationship (FAR), together with the species-area relationship (SAR), indirectly provides a quantitative assessment of a community's resilience to change by considering the resilience of ecosystem functioning to species loss (Cumming and Child, 2009). Firstly, it is possible to calculate the area of habitat that can be lost before ecological function of the ecosystem declines, and secondly, it provides a measure of the species loss that can be sustained before the community's resilience is affected. This species richness buffer is thus an indirect measure of the redundancy in the community. However, the loss of species important for a particular ecosystem function may not always be compensated by the remaining species (Ernest and Brown, 2001). Different species in a functional group, while all performing the same function, may respond differently to different environmental conditions (Rosenfeld, 2002). Loss of some species may well lead to an increase in abundance of others (i.e. density compensation), but because the diversity of response to environmental conditions has been reduced, net functioning may fluctuate (Rosenfeld, 2002). Therefore, loss of biodiversity may impair ecosystem stability, even if it has a minimal effect on the level of ecosystem functioning (Walker, 1995; Naeem, 1998; Gunderson, 2000).

Population densities are frequently examined taking into account the relative importance of environmental (total resource availability) and ecological (resource partitioning) constraints (Case and Bolger, 1991; Gotelli and McCabe, 2002; Buckley and Jetz, 2007). However, population density *per se* may also provide insights to the functional resilience and integrity of ecosystems by considering density compensation effects (Walker, 1992; Lawton and Brown, 1993). Density compensation is a community-level phenomenon in which the summed population densities of communities in species-poor sites may be equivalent to, or greater than, that of species-rich sites (MacArthur et al., 1972). Evidence for and against density compensation in vertebrates has been varied (MacArthur et al., 1972; Lawes and Eeley, 2000; Stevens and Willig, 2000; Rodda and Dean-Bradley, 2002), and remains largely inconclusive (see review by Connor et al., 2000). The presence of density compensation indicates functional redundancy among species i.e. changes in species diversity may not necessarily lead to measurable changes in ecosystem functioning in situations where density compensation is strong (Walker, 1992; Lawton and Brown, 1993; Jiang, 2007). Functional redundancy means that different species perform the same functional role in ecosystems so that changes in species diversity does not affect ecosystem functioning. However, this redundancy applies to some, but not all ecosystem

properties. The loss of species important for a particular ecosystem function (e.g. keystone species) may not always be compensated for by the remaining species (Ernest and Brown, 2001). Density compensation in response to changes in species diversity or area does not necessarily translate into compensation in response to changes in environmental conditions, which requires differential species responses to environmental change. Therefore, loss of biodiversity may impair ecosystem stability, even if it has a minimal effect on the level of ecosystem functioning. In this chapter I particularly examined the hypothesis that climatic extinction-filtering events have resulted in a resilient bird community by using density compensation and function area relationship to test for redundancy.

2. Methods

2.1 Study area

This study was conducted in the South African portion of the Maloti Drakensberg Transfrontier Project bioregion (MDTP; 28°15' - 31°20'S, 27°10' - 30°E; Fig. 1), a large area which encompasses the uKhahlamba Drakensberg Park, a World Heritage Site. Two Afromontane forest types occur in the area, namely Drakensberg Montane forest (7025 ha) and Eastern Mistbelt forest (8708 ha) (classification follows Mucina and Rutherford, 2006a). The MDTP encompasses the entire distribution of Drakensberg Montane forest in South Africa. Forests are embedded in a grassland matrix and generally occur in moist fire-safe sites on steep south-facing slopes. Drakensberg Montane forest occurs at altitudes of 1500 to 1800 m (850 - 1600 m; Lawes et al., 2007a), and canopy height is generally low in these forests (< 20 m). These mixed evergreen forests are often dominated by the conifer *Podocarpus latifolius.* Most (94%) Drakensberg Montane forests are small (<10 ha; 3.0 ± 7.3 ha, mean ± 1 SD, n = 2352) and only two forest patches (0.1%) were larger than 100 ha, with the largest patch comprising 146.4 ha (Lawes et al., 2007a). These two larger Drakensberg Montane forests are located in the north of the MDTP. The prevailing climate is temperate and seasonal, with summer rainfall and occasional heavy frost and snow in winter, particularly at higher altitudes. The mean annual temperature is 14 °C with a mean annual precipitation of approximately 1240 mm (Schulze, 2006).
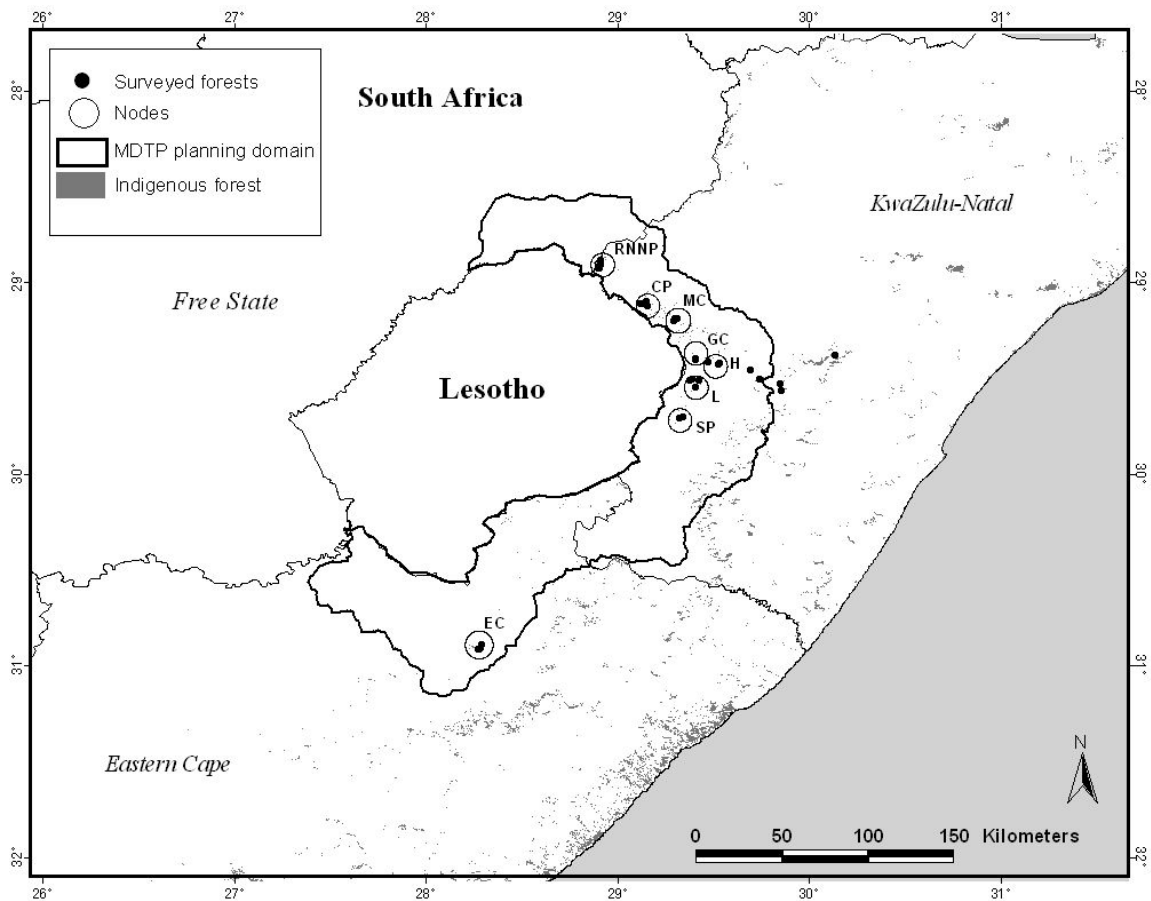
Fig. 1 - Map of study area showing distribution of indigenous forest, and study sites sampled within the MDTP planning domain. The area between SP and EC was not sampled because of logistics. (Abbreviations: RNNP - Royal Natal National Park, CP – Cathedral Peak, MC – Monk's Cowl, GC – Giant's Castle, H – Highmoor, L – Loteni, SP – Sani Pass, EC – Eastern Cape).

2.2 Forest patches sampled

Intensive sampling of forest patches for bird data was undertaken at eight predetermined sampling nodes (Fig. 1). Sampling nodes were selected to take account of the latitudinal gradient within the MDTP, so that each node was within a discrete river catchment and, where possible, to include a range of forest patch sizes. Patches were categorized into three size classes, small (<1 ha), medium (1 - 5 ha), and large (> 5 ha). Thirty-one Drakensberg Montane forests with a size range of 0.6–36.6 ha were sampled, with roughly four forest patches per node.

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2.3 Bird census methods

Bird censuses were conducted in the MDTP (Table 1) during two consecutive breeding seasons (November – March, 2005-2006 and 2006-2007). A modified stationary point count technique (Koen, 1988a) was used. This technique is considered reliable for use in closed-canopy evergreen forests, where vision is limited and bird detection is accomplished by both visual and auditory cues (Koen, 1988a; Sutherland et al., 2004; Buckland, 2006). In the modified stationary point count, birds detected visually or acoustically within a 25 m radius of the observer were recorded, and points were sited >100 m apart (Willson et al., 1994; Ralph et al., 1995; Bibby et al., 2000). A 25 m radius was chosen to ensure more accurate bird detections in the dense habitat (Bibby et al., 2000) and because of the small size of some forest patches. Points were surveyed for 10 min, a time period that maximized detection of all bird species (Lee and Marsden, 2008). Immediately after the 10 min point count a snapshot count of the species present (a record of all individuals present within the 25 m radius survey area at an instant or snapshot in time) was conducted. Bird species density was estimated from both point and snapshot counts. To ensure that sampling effort was similar among the patches, the number of point counts was adjusted for patch size (Table 1). Birds were censused in the 3 h after dawn and in the 3 h before dusk, during the hours of peak bird activity. To avoid biased samples when there was more than one observer, forest patches and survey times were rotated between observers.

Bird species observed were assigned to either forest-dependent (FD) or forest-associated (FA) categories. These were defined as species that live and reproduce only in forest habitats, and species that inhabit forest as well as other habitats and do not breed only in forest, respectively. Species were initially assigned to categories (Lawes et al., 2000a) and assignments were verified from the literature (Harrison et al., 1997; Hockey et al., 2005). The FD and FA categories were adjusted so that species that required wooded habitats, but not necessarily forest, but were restricted to forest in the MDTP, were categorized as forest dependent in this study. Transient bird species, those species observed once in only one patch, were not included in the dataset. Bird nomenclature throughout follows Hockey et al. (2005).

Randomized cumulative sample-species richness curves for birds were plotted for each forest patch to determine sampling saturation (Gotelli and Colwell, 2001). Jackknife2

and Chao2 estimators of species richness were calculated using the program EstimateS (Colwell, 2001).

Table 1 - Summary of surveyed forest patches in each node.

Node	Forest	Area (ha)	No. point counts	Species richness	Forest dependent species
Royal Natal	RNNPA	30	35	30	21
National Park	RNNPB	12	31	33	20
(RNNP)	RNNPC	7.6	17	23	17
	RNNPD	5.7	25	35	22
	RNNPE	1.2	18	25	18
Cathedral Peak	CPA	36.6	46	28	19
(CP)	CPB	16.2	34	24	18
	CPC	6.5	31	33	21
	CPD	2.3	26	32	21
	CPE	0.8	19	25	15
Monk's Cowl	MCA	27.2	32	38	27
(MC)	MCB	19.8	32	29	22
	MCC	16	31	36	24
	MCD	2.5	19	27	20
	MCE	1.7	18	32	22
Giants Castle	GCA	6.8	27	21	17
(GC)	GCB	1.3	13	21	16
	GCC	0.6	7	18	14
Highmoor	HA	4.1	20	27	22
(H)	HB	3.6	27	25	20
	HC	1.2	19	17	16
Loteni	LA	9	20	27	18
(L)	LB	6.1	25	23	16
	LC	4	25	21	16
	LD	1.5	17	18	15
Sani Pass	SPA	4.5	22	17	12
(SP)	SPB	3	22	20	14
Eastern Cape	ECA	14.4	17	26	18
(EC)	ECB	17.7	26	29	21
	ECC	6.2	24	30	21
	ECD	4.8	16	24	17

Species saturation estimates ranged from 85% to 97% for all nodes except Giants Castle, where it ranged from 83% to 88% (Table 2). Thus, the bird species inventories were relatively complete and comparable among nodes.

Table 2. - Comparison of Chao-2 and second-order jackknife (Jack-2) species richness estimates at each node from point count surveys (N). Values are percentage of the estimated total species richness (mean ± 1 SD).

Node	N	Chao-2	Jack-2
Royal Natal National Park	126	95.1 ± 2.8	86.0 ± 5.4
Cathedral Peak	156	95.8 ± 4.9	88.8 ± 7.3
Monk's Cowl	132	92.8 ± 8.5	86.7 ± 11.7
Giants Castle	47	87.9 ± 13.3	82.6 ± 19.5
Highmoor	66	96.6 ± 3.3	90.7 ± 8.7
Loteni	87	97.3 ± 2.1	91.9 ± 8.4
Sani Pass	44	96.8 ± 2.9	88.1 ± 9.3
Eastern Cape	83	90.8 ± 8.2	84.5 ± 10.4

2.4 Analyses

2.4.1 MDTP forests: an African perspective

To determine whether Afromontane forests of the MDTP share similar bioclimatic conditions to Afromontane forests throughout the continent, principal components analysis (PCA) was used. PCA is used to show the role of selected descriptors in the formation of the principal components in reduced space (Legendre and Legendre, 1998). We selected two climate and two environmental descriptors to define 12 Afromontane forests: mean annual temperature, annual rainfall, altitude and latitude. The 12 forest sites were chosen to include the latitudinal (14°N - 34°S) and altitudinal range (450 – 2400 m.a.s.l.) of Afromontane forest in Africa, and included three sites in the MDTP. Ordination was conducted using PC-ORD 4.34 (McCune and Mefford, 1999b).

2.4.2 Bird species diversity

Diversity of birds in forests was summarized using alpha (α), beta (β) and gamma (γ) indices. Alpha diversity was compared among forests using a series of diversity indices that

emphasize either species richness or the relative evenness of an assemblage. Shannon's diversity (H') and evenness indices (J'), Simpson's diversity index ($1/D$) and a suite of indices described by Hill (1973) were calculated for each forest patch. D and H' indices of diversity were used in the derivation of Hill's numbers. Hill's diversity numbers are relatively unaffected by species richness and tend to be independent of sample size (Ludwig and Reynolds, 1988). From Hill's suite of diversity numbers we selected N0, N1 and N2 as measures of species richness and diversity, and E1 and E5 as indices of species evenness (Table 3). The Berger-Parker index was calculated because it provides a simple and easily interpretable measure of dominance (Magurran, 2004).

Two beta diversity indices were calculated to determine bird species turnover between forests within each node and between nodes across the MDTP. The first measure was Harrison et al (1992) β_{H1} modification of Whittaker's (1960) index and the second, a similarity measure ($\beta_{sim)}$ introduced by Lennon et al. (2001). The β_{H1} index provides an effective measure of turnover when comparing samples of different sizes (Magurran, 2004). The β_{sim} index was designed to measure change in assemblage composition and is not affected by local species richness gradients (Magurran, 2004). Gamma diversity (γ) was calculated as the total number of species sampled.

2.4.3 Density

The most problematic summary statistic derived from the point count method is density, since density estimates derived from this method are subject to overestimation (Buckland et al., 2001; Sutherland et al., 2004). To address this problem, a supplementary snapshot count was conducted after each 10 min stationary point count (Buckland et al., 2001; Buckland, 2006). Density was then calculated as the total number of birds recorded within all point counts in each forest, divided by the cumulative area of all the point counts in that same forest (Davies, 2002). To correct for the inflated density estimates derived from this method, the ratio of number of individuals per snapshot to number of individuals recorded in a 10 min count was used to obtain a proportional index.

Density was thus calculated using the following equation:

$$D = [(N/A) \times 10\ 000] \times (s/p) = \text{individuals.ha}^{-1}$$

where D = density estimate of birds per unit area, N = total number of birds in point counts (both seasons), A = total area of all point counts (both seasons), s = number of individuals

in snap-shot count (second season only), p = number of individuals in point count (second season only).

African emerald cuckoo (*Chrysococcyx cupreus*), African harrier-hawk (*Polyboroides typus*), Natal spurfowl (*Pternistis natalensis*) and red-necked spurfowl (*Pternistis afer*) were recorded outside the radius of the point count transects and were therefore not included in population density estimates.

As a species-specific characteristic, population density might be, at least to some extent, phylogenetically determined (Wethered and Lawes, 2003). Methods used in a previous study of population densities of Afromontane forest birds revealed that the family level of the taxonomic hierarchy accounted for the greatest proportion of variance in population density (Wethered and Lawes, 2003; Lawes et al., 2007a). We therefore adopted a family level approach for comparative analyses of population densities. We regressed the mean density of bird families against the total species richness of a forest patch as well against patch area.

2.4.4 Function-area relationship

'Roberts' Birds of Southern Africa' (Hockey et al., 2005) was used to assign the 50 bird species to functional groups, based primarily on the groupings provided by Şekercioğlu (2006). Şekercioğlu's (2006) classification was modified to generate seven functional groups; raptor, pollinator, grazer, engineer, granivore, frugivore and insectivore. Although most species are clearly capable of performing more than one ecological function, species were limited to a single functional group as this offers a more approachable starting point for linking taxonomic and functional diversity (Cumming and Child, 2009). Cumulatively, the number of functional groups was calculated for forest patches from small to large. In addition, the species-area relationship (SAR) was calculated for taxonomic species. The SAR is commonly defined as $S = cA^z$, where S is the number of taxonomic species; c is a constant; A is the area; and z describes the slope of the curve. Split-line regression was used to determine the asymptote or break-point (and 95% confidence intervals about that point) of the function-area curve that is an estimate of the area that may be lost before ecosystem function declines. The difference between the two curves indicates a 'richness buffer' for the maintenance of ecosystem function (Cumming and Child, 2009; Fig. 2). By substituting the break-point value into the SAR equation it is possible to quantify the resilience of the

system's functional components to species loss i.e. the species richness buffer. Regression analyses were performed using GenStat (GenStat Committee, 2008).
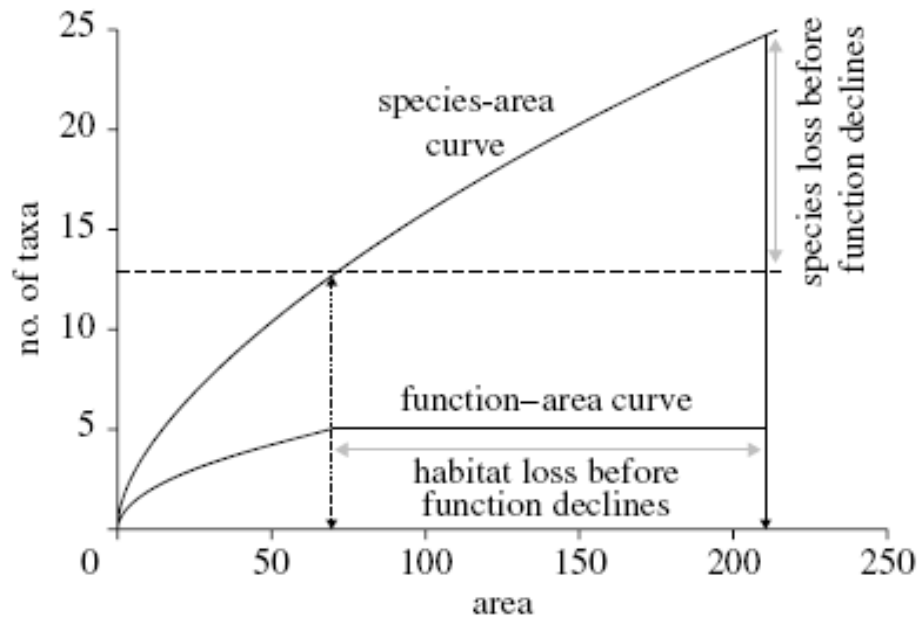
Fig. 2 - Diagram showing species-area and function-area curves. The difference between the two curves indicates the taxonomic species richness buffer, a measure of the redundancy or resilience of the community. The asymptote of the function-area curve indicates the minimum area capable of sustaining a functional ecosystem (from Cumming and Child, 2009).

3. Results

3.1 Drakensberg forests – an African perspective

Variation of climatic and environmental conditions among Afrotemperate forests across Africa was substantially captured by the first two axes of the PCA (77%). Southern African forests (Knysna and three MDTP forests), which are also coastal in location, partially separate from the generally higher altitude equatorial and northern hemisphere Afrotemperate forests along the first principal component (PC1), which in turn describes a latitudinal gradient and an associated gradient in mean annual temperature. The southern African forests are characterized by low PC1 scores, indicating high latitude and low temperature, while the remaining sites experience relatively warmer temperatures at lower latitudes. The second principal component showed the highest correlation with annual rainfall, and the MDTP forests cluster with the equatorial and northern hemisphere forest

sites along this axis. Forests of the MDTP fall within the bioclimatic envelope of the Afrotemperate forest group as a whole, and are not atypical in terms of their climatic and environmental correlates.

3.2 Patterns in the bird community as a whole

We recorded 50 bird species belonging to 25 families during the point count surveys (Appendix A). Most bird species were resident (90%), four species were intra-African migrants, red-chested cuckoo (*Cuculus solitarius*), black cuckoo (*Cuculus clamosus*), emerald cuckoo (*Chrysococcyx cupreus*) and Klaas's cuckoo (*Chrysococcyx klaas*), and one a Palaearctic migrant, black kite (*Milvus migrans*). Two strict South African endemics, greater double-collared sunbird (*Cinnyris afer*) and southern double-collared sunbird (*Cinnyris chalybeus*), and four southern Africa endemic species, bush blackcap (*Lioptilus nigricapillus*), Cape batis (*Batis capensis*), chorister robin-chat (*Cossypha dichroa*), and forest canary (*Crithagra scotops*), were recorded. Total species richness, based on the actual count values and sampling effort, differed between the nodes and among patches within a node (Table 1). Species richness in Drakensberg Montane forest patches ranged from 17 to 36 (26.3 ± 5.7, mean ± 1 SD, n = 31; Table 1). In general, forest patches in the northern nodes were more species rich. The size of Drakensberg Montane forests containing more than 30 bird species varied from 1.7 ha to 30.0 ha, and several larger forests (> 15 ha) contained fewer than 30 species. Thirty of the total 50 recorded bird species (60%) were classed as forest dependent (Appendix A). Furthermore, forest dependent bird species were well represented in all forest patches where they comprised at least 60% of the species assemblage (Table 1).

Table 3 - Summary of diversity measures for birds surveyed in forest patches at each node.

	Alpha diversity indices								Beta diversity indices (within node)	
	Diversity						Evenness			
Forest	Hill's	Simpson's (1/D)	Shannon-Wiener (H')	Berger-Parker	Hill's	Hill's	Hill's	Hill's	βH1	βsim
RNNPA	30	11.03	2.83	0.22	16.91	11.03	0.83	0.63	7.53	0.04
RNNPB	33	14.83	3.03	0.16	20.65	14.85	0.87	0.70		
RNNPC	23	8.83	2.61	0.27	13.61	8.83	0.83	0.62		
RNNPD	35	16.23	3.06	0.13	21.43	16.23	0.86	0.75		
RNNPE	25	10.81	2.70	0.19	14.87	10.81	0.84	0.71		
CPA	28	11.78	2.81	0.20	16.57	11.78	0.84	0.69	10.21	0.09
CPB	24	10.62	2.70	0.22	14.82	10.62	0.85	0.70		
CPC	32	13.64	2.91	0.17	18.32	13.76	0.84	0.72		
CPD	32	16.02	3.08	0.17	21.87	16.02	0.89	0.72		
CPE	25	13.92	2.86	0.16	17.40	13.92	0.89	0.79		
MCA	36	16.02	3.10	0.16	22.23	16.24	0.87	0.70	7.41	0.06
MCB	28	11.44	2.81	0.22	16.62	11.58	0.84	0.66		
MCC	36	14.72	3.04	0.16	20.80	14.72	0.85	0.69		
MCD	27	12.60	2.82	0.20	16.81	12.60	0.86	0.73		
MCE	32	14.37	2.93	0.13	18.75	14.27	0.85	0.75		
GCA	21	9.21	2.56	0.20	12.87	9.21	0.84	0.69	7.50	0.07
GCB	21	9.69	2.52	0.20	12.48	9.69	0.83	0.76		
GCC	18	10.37	2.53	0.24	12.60	10.37	0.88	0.81		
HA	27	10.80	2.77	0.22	15.92	10.80	0.84	0.66	17.39	0.10
HB	25	10.53	2.63	0.19	13.82	10.53	0.82	0.74		
HC	17	6.42	2.26	0.34	9.61	6.42	0.80	0.63		
LA	26	13.20	2.83	0.16	16.87	13.38	0.87	0.76	8.61	0.03
LB	23	12.45	2.72	0.16	15.16	12.45	0.87	0.81		
LC	21	8.76	2.53	0.27	12.58	8.76	0.83	0.67		
LD	18	10.09	2.45	0.16	11.58	10.09	0.85	0.86		
SPA	17	6.66	2.28	0.33	9.75	6.66	0.80	0.65	13.51	0.06
SPB	20	8.04	2.41	0.25	11.16	8.04	0.81	0.69		
ECA	26	10.93	2.73	0.20	15.26	10.93	0.84	0.70	7.03	0.07
ECB	29	10.67	2.75	0.21	15.71	10.67	0.82	0.66		
ECC	30	14.66	2.95	0.14	19.19	14.66	0.87	0.75		
ECD	24	11.09	2.66	0.17	14.34	11.09	0.84	0.76		

Forests varied in terms of their alpha diversity indices (Table 3). Diversity of bird communities in the northern nodes was significantly greater (Simpson's index: $F_{7,23} = 3.26$, $p = 0.01$) and more even than the southern nodes. The southern nodes appeared to be dominated by a few species (Berger Parker index: $F_{7,23} = 1.78$, $p = 0.14$). None of the alpha diversity indices was strongly or significantly correlated with forest patch size. Bird species turnover (beta diversity) between forests, and thus turnover in assemblage composition within nodes, was relatively low by both measures (β_{H1} and β_{sim}; Table 3). Both indices suggest that turnover in assemblage composition was highest between forests at Highmoor, the highest altitude forests in the MDTP. Species turnover between nodes across the MDTP region was low ($\beta_{sim} = 0.095$) and assemblage composition changed little between nodes across the MDTP.

3.3 Density

Total bird density estimates, calculated from all species seen or heard, ranged from 9.79 ind.ha^{-1} (SPA) to 38.49 ind.ha^{-1} (MCA) for Drakensberg Montane forest patches (Appendix B). Mean bird density per node ranged from 12.24 ind.ha^{-1} for Sani Pass to 27.41 ind.ha^{-1} for Giant's Castle (Fig. 3). The mean species density (Appendix C) was fairly low with 48% (n = 22) of bird species from the Drakensberg Montane forest patches having densities less than 1 ind.ha^{-1}. Eleven species (24%) had densities greater than 2 ind/ha, namely the African olive-pigeon (*Columba arquatrix*), bush blackcap (*Lioptilus nigricapillus*), sombre greenbul (*Andropadus importunus*), chorister robin-chat (*Cossypha dichroa*), yellow-throated woodland-warbler (*Phylloscopus ruficapilla*), bar-throated apalis (*Apalis thoracica*), African dusky flycatcher (*Muscicapa adusta*), Cape batis (*Batis capensis*), southern double-collared sunbird (*Cinnyris chalybeus*), Cape white-eye (*Zosterops pallidus*), and forest canary (*Crithagra scotops*). The Cape white-eye (*Z. pallidus*) had the highest mean density of all species (13.57 ind.ha^{-1}).
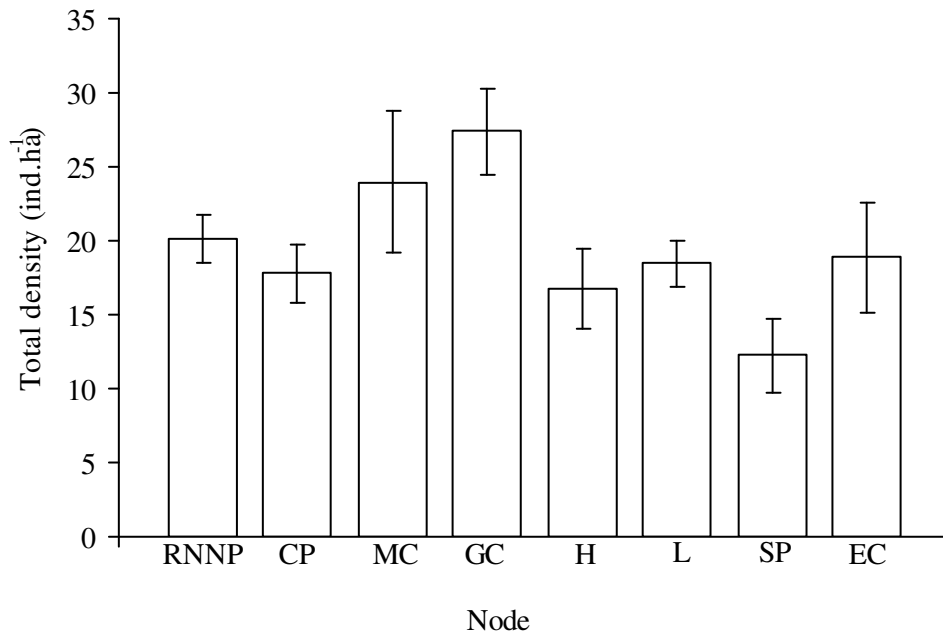
Fig. 3 - Total density (individuals per hectare) of Drakensberg Montane forest birds for the eight nodes. Standard error is denoted by vertical bars. See Fig. 1 for details relating to node acronyms.

3.4 Is density compensation occurring in these forests?

Mean bird family density was negatively correlated with patch area in Drakensberg montane forest patches and was lower in larger forest patches (*Density = -0.591 log Area + 3.16*; $F_{1,29} = 8.53$, $p = 0.007$, $r^2 = 0.23$; Fig. 4). The density of birds at the family level in a patch declined significantly with increasing bird species richness of the patches (*Density = -0.048 Species + 3.99*; $F_{1,29} = 7.71$, $p < 0.01$, $r^2 = 0.21$; Fig. 5), although the shallow slope of the relationship implies slight density compensation. These data suggest that density in forest patches is affected by area and species richness (i.e., competitive interaction), where 23% and 21% respectively, of the variation in bird species density was accounted for. Bird assemblages in Drakensberg Montane forest patches are not saturated with species but are most likely approaching saturation.
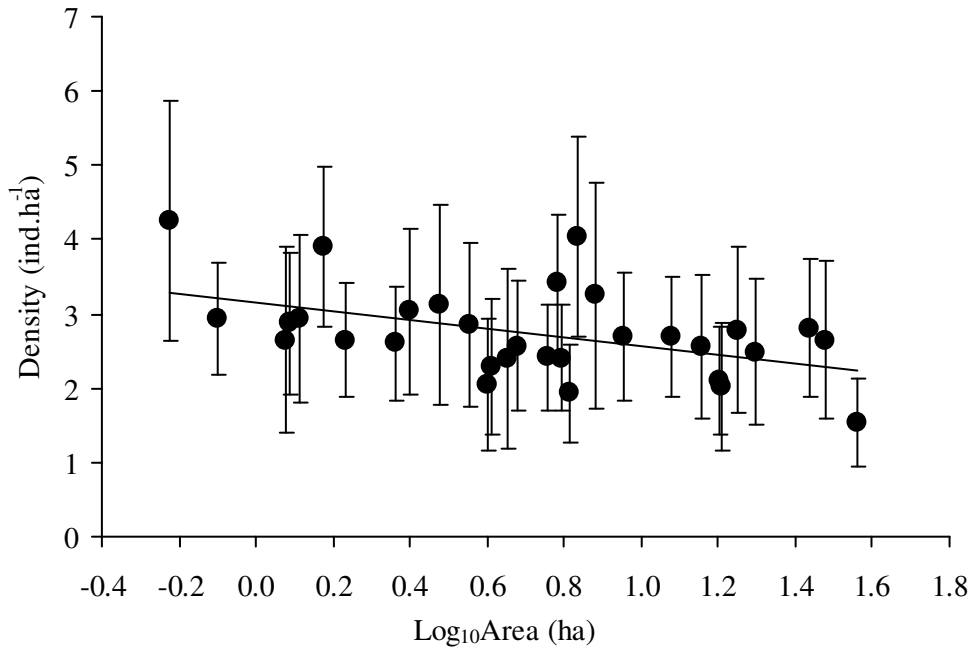
Fig. 4 - Mean density by bird family (ind.ha^{-1}) against log area for all Drakensberg Montane forest patches. Standard error is denoted by vertical bars.
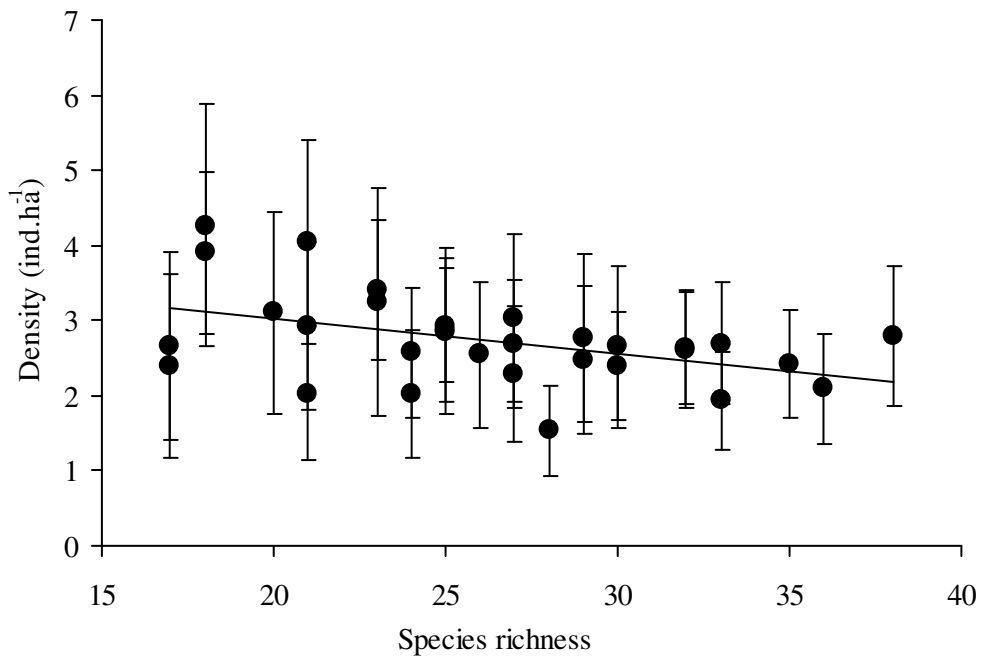
Fig. 5 - Mean density by bird family (ind.ha^{-1}) against total species richness in a patch, illustrating density compensation. Standard error is denoted by vertical bars.

3.5 Community resilience

Drakensberg Montane birds are unevenly distributed between functional groups (Fig. 6).While the avifauna is disproportionately rich in insectivores, there are relatively few birds that function as ecosystem engineers, grazers or pollinators.

The initial slope of the split-line regression for the relationship between forest patch area and functional groups was steep ($z = 0.62$) as functional groups accumulated rapidly with patch area. The breakpoint of the split-line regression for the function-area curve occurs at 3.38 ha (95% confidence intervals: 2.52, 5.95). This corresponds to the area of Drakensberg Montane forest below which functional group loss and the concomitant loss of ecosystem functions would be expected to occur. This threshold area is an approximation because it assumes random species loss from the functional groups, which is unlikely in reality; but it does provide a tentative first estimate of the area of forest that can be lost before the ecosystem functions derived from birds are affected. Interestingly, the breakpoint value 3.38 ha is comparable to the mean size of forest patches in this landscape (3.0 ± 7.3 ha, mean $\pm$ 1 SD, n = 2352). Thus, even though Drakensberg Montane forests are small, most are fully functioning ecosystems, at least from the perspective of the birds occupying them.

Substituting the breakpoint value into the SAR, the species richness buffer for the maintenance of ecosystem functioning is 12 species. That is, approximately a quarter of the bird species (n = 50) of Drakensberg Montane forests are functionally redundant, providing a relatively high level of community resilience to change in this landscape. Again, this is assuming that species loss within the system is random.
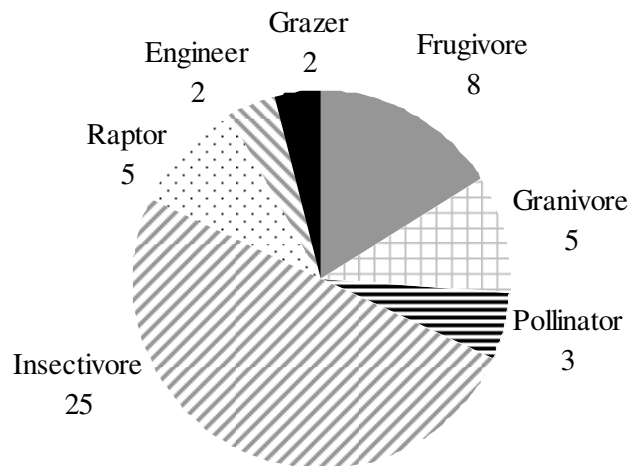
Fig. 6 - Pie chart showing numbers of Drakensberg Montane birds by functional group. The total number of recorded species was 50.

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4. Discussion

Notwithstanding the large latitudinal and altitudinal distribution range of Afrotemperate forest in Africa, in terms of bioclimatic conditions, the forests of the MDTP are comparable with Afrotemperate forests throughout the continent. In other words, Afrotemperate forests share similar rainfall and temperature regimes, providing a relatively homogenous climatic environment for forest fauna. This may explain the broad distribution range of a number of bird species found in Afrotemperate forests from southern Africa through to Ethiopia e.g., olive thrush (*Turdus olivaceus*), African dusky flycatcher (*Muscicapa adusta*), African paradise flycatcher (*Tersiphone viridis*), African goshawk (*Accipiter tachiro*), blackheaded oriole (*Oriolus larvatus*), African olive pigeon (*Columba arquatrix*), olive woodpecker (*Dendropicos griseocephalus*), grey cuckooshrike (*Coracina caesia*), red-chested cuckoo (*Cuculus solitarius*), Klaas's cuckoo (*Chrysococcyx klaas*), swee waxbill (*Estrilda melanotis*). However, although climatic conditions may be relatively similar in Afrotemperate forests, bird species richness of forests is not; avifaunal richness declines with increasing latitude (Winterbottom, 1974). Given that climatic conditions are relatively homogenous, and that avian species richness of Afromontane forests differs between the equator and high latitudes, this suggests that factors other than contemporary climate may drive species richness of these forests. Recent research has suggested that historical climatic regimes have been instrumental in determining contemporary forest faunal assemblages (Lawes, 1990; Lawes et al., 2000a; Lawes et al., 2007c). In particular, the extreme climatic perturbations associated with the Quaternary have acted as extinction filtering events, selectively removing species that are not able to adapt or persist through such climatic extremes. Furthermore, as Balmford (1996) points out, because ecologically sensitive taxa tend to be removed by the extinction filtering process, resulting communities, although comparatively species-poor, are ecologically robust and persistent (Coope, 1995; Jackson, 1995; Lawes et al., 2000a). Therefore, in this case, it appears that climatic extinction filtering during the Quaternary has had an influence on the contemporary Afrotemperate forest bird assemblage of the Drakensberg. Notably, the avifauna of the intensely patchy Drakensberg Montane forests display a relatively high degree of redundancy.

Using Cumming and Child's (2009) model, a forest patch of 3.4 ha was found to be ecologically functional in terms of the ecosystem functions that birds provide. It is important to remember that birds are only a part of the ecosystem, and that other taxa are

crucial to the functioning of an ecosystem. In this regard, a patch size of 3.4 ha may not be sufficient for other organisms, but in the context of this thesis, I am dealing strictly with avifauna. Thus, forest patches of 3.4 ha or larger are able to support all the avian functional groups required to maintain ecosystem functionality in the landscape. Furthermore, the model predicts a taxonomic species richness buffer of 12 bird species. In other words, nearly a quarter of the fifty bird species present may be lost before functionality of the system is negatively affected. Together, the small area of forest required to maintain ecosystem functioning, and the relatively high proportion of species that may be lost before functionality is impaired, suggest that the historically fragmented Afrotemperate forests are resilient. A possible reason for the resilience of the avifauna is the climatic extinction filtering that occurred during the Quaternary. Such repeated and extreme changes in paleoclimate have resulted in Drakensberg Montane forests having a species-poor faunal assemblage characterised by robust species (Lawes et al., 2000a; Lawes et al., 2007c). In addition, communities demonstrate far more resilience to modern threats if they have faced similar challenges in the past (Balmford, 1996; Danielsen, 1997). Thus, the avifaunal assemblage of Drakensberg forests may be relatively resilient to potential climate shifts in the future, but only as long as the climatic perturbations are on the spatial and temporal scale of the past. However, contemporary challenges may often be subtly but critically different from historical ones. Thus, even where current threats are broadly similar to those of the recent past, there are no grounds for complacency.

In Drakensberg Montane forest, forest patches of 3.4 ha are ecologically viable units in terms of the ecosystem services provided by the avifauna. Considering that the average patch size of Drakensberg Montane forest is three hectares, the small size of these fully functional forest ecosystems becomes clearer. In particular, the bird communities of these Drakensberg forests have adapted to an intensely patchy landscape, and only those bird communities that are able to survive in small forest patches in such a highly fragmented forest landscape have persisted. Distances between forest patches vary (Chapter 3), but are not sufficient to limit inter-forest movement of this highly vagile taxon. The bird assemblage of the Afrotemperate forests in the Drakensberg are therefore well adapted to life in small, interspersed forest patches, and indeed provide all the ecosystem services necessary to maintain an ecologically functional system. In light of the minimum area required to maintain ecosystem functionality for birds in this landscape, conservation of very small forest patches would ensure a functioning system. However, Armsworth and

Roughgarden (2003) found that the stability of a community increased with increasing reserve size, thus enhancing the value of larger reserves (or in this case larger forest patches). In addition, larger, and therefore more stable ecosystems, can be relied on to provide ecosystem services consistently under fluctuating environmental conditions. Thus, although the model provides us with a current minimum estimate of the area of forest necessary to maintain ecosystem functionality for birds, it is important to recognize that by conserving larger areas we may provide greater resilience to the system (Armsworth and Roughgarden, 2003). This may prove increasingly important under the current changing climate regime.

A key principle of ecosystem function research is the insurance hypothesis, which states that ecosystem functioning is more stable in species-rich communities, where the redundancy of species contributing to the same function provides an "insurance" or buffer against environmental fluctuations (Lawton and Brown, 1993; Naeem, 1998). In other words, ecosystem resilience is enhanced by the presence of functionally redundant species (Walker, 1995). The degree to which communities are likely to have functionally redundant species depends not only on total species richness, but also on the abundance of generalist or specialist species within each functional group (Rosenfeld, 2002). In this study, Afrotemperate forest bird assemblages have relatively low total species richness, but are characterized by many generalist species (Lawes et al., 2007c). Possibly as a result of the preponderance of generalist species, Afrotemperate forest bird assemblages have a relatively high number of redundant species, with nearly one quarter of the bird species present found to be functionally redundant. Thus this system displays a degree of resilience provided by the twelve functionally redundant species. Redundant species, as guarantors of reliable ecosystem functioning, should therefore be perceived as critical features of an ecosystem (Naeem, 1998). Furthermore, declines in bird species that are important for a particular ecosystem function may not necessarily mean a decline in that ecological function if the populations of other equivalent species increase in response (Walker, 1992). In such a case, density compensation may indicate some degree of species redundancy. Our findings support the hypothesis of density compensation. In particular, the significant negative correlation between bird family densities and species richness for Drakensberg Montane forests results in lower abundances for residents of species rich communities when compared to depauperate communities. Wethered & Lawes (2003) and Cody (1983) found similar results to this study, suggesting that density compensation, and therefore

species redundancy, may be ubiquitous for bird assemblages of Afrotemperate forests in South Africa.

Population densities are governed by both total resource availability and the partitioning of resources between species in a community (Damuth, 1981, 1987; Tilman, 1994). The relative importance of environmental (total resource availability) and ecological (resource partitioning) constraints in limiting population density has been widely debated (Case and Bolger, 1991; Gotelli and McCabe, 2002; Buckley and Jetz, 2007). This study provides evidence toward the long-standing question of whether ecological or environmental constraints predominantly determine population densities. While forest patches show significant negative density-area and density-species richness relationships, the two factors account for a similar amount of variation ($r^2 = 0.23$ and $r^2 = 0.21$ respectively). This suggests that ecological (at least as reflected in species richness) and environmental pressures (as reflected in patch area) have a relatively equal influence on avian densities in this heterogenous landscape. Density estimates derived for Drakensberg Montane forests (19.86 ind.ha^{-1}) are comparable to that of the nearby Eastern Mistbelt forests (20.62 ind.ha^{-1}) (Lawes et al., 2007a). Similarly, Cody (1983) found densities in Afrotemperate forests of the Cape region that ranged between 21.44 – 23.68 ind. ha^{-1}. In comparison with density estimates from further afield, Afrotemperate forests in Ethiopia had a very high bird density (98.63 ind.ha^{-1}; Tadesse, 2001), while densities in the temperate *Nothofagus* forests of Chile were more similar to our results (12 - 17 ind.ha^{-1}; Lencinas et al., 2005).

Conservation implications

There is consensus that at least some minimum number of species is essential for ecosystem functioning, and that a larger number of species is probably essential for maintaining the stability of ecosystem processes in changing environments (Loreau et al., 2001). Determining which species have a significant impact on what processes in which ecosystems, however, remains an open empirical question. Although Cumming and Child's (2009) model enables us to quantify the resilience of Drakensberg Montane forests in terms of a minimum viable forest area and the number of redundant species present, it does not predict which species are redundant. To prioritize conservation efforts beyond forest patch size, it may thus be necessary to determine which species are most at risk of extinction. Future research on ecosystem functioning in the Afrotemperate forests of the Drakensberg should therefore focus on determining the relative resilience of individual species (see Isaac et al., 2009).

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Appendix A – Species list for birds recorded in Drakensberg Montane forests including their forest dependency. D = forest dependent.

Common name	Scientific name	Family	FD
African dusky flycatcher	*Muscicapa adusta*	Muscicapidae	D
African emerald cuckoo	*Chrysococcyx cupreus*	Cuculidae	D
African firefinch	*Lagonosticta rubricata*	Estrildidae	-
African goshawk	*Accipiter tachiro*	Accipitridae	D
African harrier-hawk	*Polyboroides typus*	Accipitridae	-
African olive-pigeon	*Columba arquatrix*	Columbidae	D
African paradise-flycatcher	*Terpsiphone viridis*	Monarchidae	D
African wood-owl	*Strix woodfordii*	Strigidae	D
Amethyst sunbird	*Chalcomitra amethystina*	Nectariniidae	-
Barratt's warbler	*Bradypterus barratti*	Sylviidae	D
Bar-throated apalis	*Apalis thoracica*	Cisticolidae	D
Black cuckoo	*Cuculus clamosus*	Cuculidae	-
Black kite	*Milvus migrans*	Accipitridae	-
Black-backed puffback	*Dryoscopus cubla*	Malaconotidae	D
Black-collared barbet	*Lybius torquatus*	Lybiidae	-
Black-headed oriole	*Oriolus larvatus*	Oriolidae	D
Blue-mantled crested-flycatcher	*Trochocercus cyanomelas*	Monarchidae	D
Buff-spotted flufftail	*Sarothrura elegans*	Rallidae	-
Bush blackcap	*Lioptilus nigricapillus*	Sylviidae	D
Cape batis	*Batis capensis*	Malaconotidae	D
Cape robin-chat	*Cossypha caffra*	Muscicapidae	D
Cape turtle-dove	*Streptopelia capicola*	Columbidae	-
Cape white-eye	*Zosterops capensis*	Zosteropidae	D
Chorister robin-chat	*Cossypha dichroa*	Muscicapidae	D
Common waxbill	*Estrilda astrild*	Estrildidae	-
Dark-capped bulbul	*Pycnonotus tricolor*	Pycnonotidae	-
Forest canary	*Crithagra scotops*	Fringillidae	D
Fork-tailed drongo	*Dicrurus adsimilis*	Dicuruidae	-
Greater double-collared sunbird	*Cinnyris afer*	Nectariniidae	-
Grey cuckooshrike	*Coracina caesia*	Campephagidae	D
Hadeda Ibis	*Bostrychia hagedash*	Threskiornithidae	-
Klaas's cuckoo	*Chrysococcyx klaas*	Cuculidae	-
Lemon dove	*Aplopelia larvata*	Columbidae	D
Natal spurfowl	*Pternistis natalensis*	Phasianidae	-
Olive bush-shrike	*Telophorus olivaceus*	Malaconotidae	D
Olive thrush	*Turdus olivaceus*	Muscicapidae	D
Olive woodpecker	*Dendropicos griseocephalus*	Picidae	D
Red-chested cuckoo	*Cuculus solitarius*	Cuculidae	-
Red-eyed dove	*Streptopelia semitorquata*	Columbidae	-
Red-necked spurfowl	*Pternistis afer*	Phasianidae	D
Red-winged starling	*Onychognathus morio*	Sturnidae	-
Rufous-chested sparrowhawk	*Accipiter rufiventris*	Accipitridae	D
Sombre greenbul	*Andropadus importunus*	Pycnonotidae	D
Southern black tit	*Parus niger*	Paridae	D
Southern boubou	*Laniarius ferrugineus*	Malaconotidae	D
Southern double-collared sunbird	*Cinnyris chalybeus*	Nectariniidae	-
Speckled mousebird	*Colius striatus*	Coliidae	-
Swee waxbill	*Coccopygia melanotis*	Estrildidae	D
White-starred robin	*Pogonocichla stellata*	Muscicapidae	D
Yellow-throated woodland-warbler	*Phylloscopus ruficapilla*	Sylviidae	D

Appendix B – Mean densities for bird species recorded in forest patches (Royal Natal National Park to Giants Castle). Total density as well as adjusted densities for each patch.

Common name	RNNPA	RNNPB	RNNPC	RNNPD	RNNPE	CPA	CPB	CPC	CPD	CPE	MCA	MCB	MCC	MCD	MCE	GCA	GCB	GCC
African dusky flycatcher	1.82	1.26	3.74	1.96	2.18	2.55	1.87	1.42	2.82	1.55	3.21	2.45	3.00	0.26	1.09	2.18	3.77	2.10
African firefinch	-	-	-	-	-	-	-	-	-	-	0.15	-	-	-	0.54	-	-	-
African goshawk	0.56	-	-	0.20	-	-	-	-	-	-	0.15	-	-	0.26	-	-	-	-
African olive-pigeon	0.42	-	-	1.76	-	0.21	-	0.63	3.01	-	2.14	-	3.63	1.03	7.34	14.50	10.17	2.80
African paradise-flycatcher	1.26	1.58	-	1.37	0.82	0.85	1.01	0.79	3.39	0.26	2.75	0.61	1.42	-	1.09	2.36	0.75	-
African wood-owl	-	-	-	0.39	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amethyst sunbird	0.70	0.32	-	0.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barratt's warbler	1.68	1.11	3.17	0.78	1.09	-	-	0.32	1.51	1.80	2.75	0.46	-	1.80	-	0.91	2.64	1.40
Bar-throated apalis	7.27	8.21	5.76	10.18	9.52	4.47	3.74	5.84	5.84	2.83	8.72	5.05	5.37	6.18	7.61	2.90	6.02	4.20
Black cuckoo	-	-	-	0.20	-	-	-	-	-	-	0.15	-	-	-	-	-	-	-
Black kite	-	-	-	-	-	-	-	0.32	-	-	-	-	-	-	-	-	-	-
Black-backed puffback	1.12	0.95	1.15	0.78	0.82	0.43	0.86	0.16	0.38	-	0.92	1.84	1.11	1.03	0.82	0.54	0.75	0.70
Black-collared barbet	-	0.32	-	0.59	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-
Black-headed oriole	-	-	-	-	-	-	-	-	-	-	1.22	-	0.32	0.26	0.27	-	-	-
Blue-mantled crested-flycatcher	-	-	-	-	-	-	-	-	-	-	0.92	-	0.47	-	2.45	-	-	-
Buff-spotted flufftail	-	-	-	-	-	-	-	-	0.38	-	0.46	-	-	-	-	-	-	-
Bush blackcap	3.08	3.00	1.44	1.76	0.27	1.28	0.58	3.16	1.88	-	5.05	0.46	0.47	1.03	0.82	2.36	1.13	5.59
Cape batis	3.50	3.16	2.02	3.52	2.72	1.81	1.73	2.37	3.77	1.80	3.98	1.68	2.05	4.38	3.54	1.81	3.77	3.50
Cape robin-chat	0.42	0.47	1.44	1.17	0.27	0.11	0.14	0.79	1.13	5.67	0.15	0.15	-	1.29	0.82	0.54	7.15	4.20
Cape turtle-dove	-	-	-	-	-	-	-	-	-	0.77	-	-	-	-	-	-	-	-
Cape white-eye	16.22	11.69	19.29	10.57	12.24	9.58	11.81	10.74	14.50	12.37	18.20	15.30	14.05	16.49	11.69	18.13	14.69	16.78
Chorister robin-chat	1.82	2.37	1.73	4.50	2.18	1.81	3.31	2.37	2.82	4.64	2.75	2.60	4.26	2.58	3.54	0.54	1.51	0.70
Common waxbill	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dark-capped bulbul	1.82	2.37	1.15	3.13	1.36	1.06	0.43	2.68	1.88	5.15	2.45	2.14	1.89	2.32	2.18	0.91	0.38	-
Forest canary	3.08	2.68	3.17	3.33	3.81	1.38	1.15	2.84	3.95	1.03	5.51	4.13	3.00	3.86	1.90	2.36	0.75	-
Fork-tailed drongo	-	1.89	-	1.37	-	0.43	-	0.32	1.69	2.58	1.38	-	1.26	-	2.99	-	-	-
Greater double-collared sunbird	1.26	0.79	1.44	1.76	0.82	0.74	0.29	2.21	2.45	3.09	0.46	0.76	0.95	1.55	1.09	4.17	1.51	3.50
Grey cuckooshrike	0.56	1.11	-	-	-	0.11	0.29	-	0.94	-	0.92	0.61	0.63	0.26	-	-	-	-
Hadeda ibis	-	-	-	1.17	2.18	0.11	-	0.79	-	1.29	-	-	-	-	-	-	-	-
Klaas's cuckoo	-	0.47	-	-	-	-	-	0.16	0.38	-	-	-	0.16	-	-	-	-	-
Lemon dove	0.42	0.47	-	0.78	0.27	0.11	-	0.16	0.56	-	0.61	0.46	1.11	1.29	1.09	0.54	-	4.20
Olive bush-shrike	0.70	0.79	0.29	0.20	-	-	-	0.32	-	-	0.61	0.31	0.32	-	0.82	-	-	-
Olive thrush	0.28	1.74	1.15	1.57	1.90	0.74	0.29	0.63	1.13	4.12	0.92	1.22	2.37	4.64	1.63	-	0.38	2.80
Olive woodpecker	0.84	1.42	0.58	0.39	0.27	0.11	0.43	0.32	0.94	1.29	1.38	0.61	0.63	1.29	0.27	0.73	0.38	-
Red-chested cuckoo	0.70	1.58	0.58	0.78	0.54	1.06	0.86	0.95	0.56	-	1.38	0.92	0.63	0.52	0.27	-	0.38	0.70

Appendix B – continued (Royal Natal National Park to Giants Castle).

Common name	RNNPA	RNNPB	RNNPC	RNNPD	RNNPE	CPA	CPB	CPC	CPD	CPE	MCA	MCB	MCC	MCD	MCE	GCA	GCB	GCC
Red-eyed dove	0.14	1.26	-	3.13	0.27	0.11	-	-	3.01	8.76	1.53	0.15	0.95	0.52	5.44	1.63	1.51	-
Red-winged starling	0.28	-	0.29	-	-	0.21	0.86	-	1.51	1.29	0.61	0.46	0.32	-	0.82	9.43	0.38	1.40
Rufous-chested sparrowhawk	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sombre greenbul	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Southern black tit	-	-	-	-	0.82	-	-	-	0.75	-	0.61	-	0.95	-	-	1.45	-	-
Southern boubou	0.70	0.16	-	2.35	-	-	-	0.47	0.19	2.58	-	-	0.16	-	0.27	-	-	-
Southern double-collared sunbird	1.54	3.32	2.88	2.35	3.81	1.28	1.73	2.53	1.13	1.55	4.44	2.45	1.89	4.38	2.99	-	-	-
Speckled mousebird	-	-	-	0.59	-	-	-	-	-	0.77	-	-	0.32	-	-	-	-	-
Swee waxbill	-	-	0.58	-	-	-	-	0.16	1.51	-	1.22	0.46	0.32	-	-	-	-	-
White-starred robin	0.70	0.47	1.73	0.20	0.82	0.74	0.58	0.63	1.32	0.52	0.61	0.61	0.47	3.09	-	-	-	-
Yellow-throated woodland-warbler	4.76	5.84	2.30	5.29	7.07	2.13	3.60	4.42	2.07	3.35	3.98	6.27	4.74	3.35	3.54	3.63	1.13	4.20
Total	57.62	60.80	55.86	68.73	56.02	33.42	35.56	48.64	67.40	69.05	82.30	52.16	59.22	63.64	66.90	71.61	59.12	58.74
Proportion*	0.39	0.33	0.34	0.35	0.26	0.37	0.42	0.41	0.35	0.26	0.47	0.29	0.29	0.26	0.48	0.46	0.39	0.44
Adjusted density	22.61	20.27	19.22	24.03	14.61	12.44	15.02	20.03	23.72	17.95	38.49	14.90	17.36	16.56	32.32	33.00	23.35	25.87

*Ratio of average number of individuals in snap-shots to average number of individuals in point counts

Appendix B – continued (Highmoor to Eastern Cape).

Common name	HA	HB	HC	LA	LB	LC	LD	SPA	SPB	ECA	ECB	ECC	ECD
African dusky flycatcher	2.45	1.63	2.83	2.20	3.33	2.94	2.88	1.56	0.67	1.15	1.69	1.63	0.61
African firefinch	-	-	-	-	-	-	-	-	-	-	-	-	-
African goshawk	0.73	0.18	-	-	-	0.39	-	-	-	-	-	-	-
African olive-pigeon	1.47	0.36	-	0.98	0.39	0.39	-	3.12	4.45	0.29	0.94	1.63	2.45
African paradise-flycatcher	0.73	0.36	0.26	0.73	1.96	1.37	0.29	0.22	1.11	1.15	1.32	1.43	0.92
African wood-owl	-	-	-	0.24	-	-	-	-	-	-	-	-	-
Amethyst sunbird	-	-	-	-	-	-	-	-	-	0.29	-	-	-
Barratt's warbler	0.49	3.99	0.52	2.69	1.76	2.55	0.29	-	0.22	1.44	0.75	0.41	-
Bar-throated apalis	3.92	5.62	2.06	7.59	6.66	2.55	7.49	1.78	3.56	4.61	5.84	5.71	6.42
Black cuckoo	-	-	-	-	-	-	-	-	-	-	-	0.82	-
Black kite	-	-	-	-	-	-	-	-	-	-	-	-	-
Black-backed puffback	1.71	1.81	1.55	-	-	-	-	-	-	-	0.56	-	-
Black-collared barbet	-	-	-	-	-	-	-	-	-	-	-	-	-
Black-headed oriole	-	-	-	-	-	-	-	-	-	-	-	0.20	-
Blue-mantled crested-flycatcher	0.49	-	-	0.98	-	-	-	-	-	-	0.19	1.22	-
Buff-spotted flufftail	-	-	-	-	-	-	-	-	-	-	-	-	-
Bush blackcap	2.20	3.26	0.26	7.83	5.29	1.96	8.35	4.67	8.90	7.77	5.08	7.34	3.06

Appendix B – continued (Highmoor to Eastern Cape).

Common name	HA	HB	HC	LA	LB	LC	LD	SPA	SPB	ECA	ECB	ECC	ECD
Cape batis	4.16	3.44	0.52	3.67	5.48	1.57	0.86	-	2.00	1.15	2.64	3.47	2.45
Cape robin-chat	1.47	0.91	-	5.14	2.35	2.94	5.76	2.00	4.01	0.86	1.88	2.24	1.53
Cape turtle-dove	-	-	-	-	-	-	-	-	-	-	-	-	-
Cape white-eye	13.71	13.78	13.66	11.50	13.12	12.34	10.94	15.35	16.24	12.38	15.25	10.20	10.71
Chorister robin-chat	0.49	2.54	0.26	2.20	2.74	-	0.58	-	-	-	-	-	-
Common waxbill	-	-	-	-	-	-	-	-	1.11	-	-	-	-
Dark-capped bulbul	-	2.72	-	2.94	0.78	0.39	5.47	-	-	0.29	0.19	1.43	1.84
Forest canary	0.98	3.08	3.35	-	-	-	-	0.89	-	0.58	0.75	0.41	-
Fork-tailed drongo	-	-	-	0.24	-	-	-	0.22	1.11	1.73	-	2.04	0.92
Greater double-collared sunbird	0.49	0.36	0.77	0.98	2.55	1.37	4.32	2.45	0.67	0.86	0.94	1.02	0.31
Grey cuckooshrike	0.73	-	-	-	-	-	-	-	-	-	1.32	0.20	0.31
Hadeda ibis	-	-	-	-	-	-	-	-	-	-	-	-	-
Klaas's cuckoo	-	-	-	-	0.20	-	-	-	-	-	-	-	-
Lemon dove	1.47	0.54	-	1.22	0.20	0.20	0.29	0.89	0.45	0.86	1.32	0.61	2.14
Olive bush-shrike	0.49	-	-	-	-	-	-	-	-	-	0.56	-	0.61
Olive thrush	-	1.09	0.52	1.22	-	0.20	0.29	-	-	1.73	0.56	1.43	-
Olive woodpecker	0.73	0.18	1.55	0.49	3.33	0.20	0.86	0.22	1.78	0.58	0.75	-	-
Red-chested cuckoo	-	-	-	-	3.33	0.98	-	-	-	-	0.19	-	-
Red-eyed dove	-	-	-	-	0.20	-	2.02	0.67	0.22	-	0.19	0.41	0.31
Red-winged starling	-	-	-	1.71	2.74	-	-	0.45	-	-	-	-	0.61
Rufous-chested sparrowhawk	-	-	1.03	-	-	-	-	-	-	-	-	-	-
Sombre greenbul	2.20	-	-	-	-	-	-	-	-	4.03	5.84	3.88	3.67
Southern black tit	0.73	-	-	1.47	2.35	0.59	-	-	-	-	-	-	-
Southern boubou	-	2.72	-	0.49	0.20	-	2.30	0.22	0.22	1.15	0.38	1.02	-
Southern double-collared sunbird	0.73	0.36	-	0.49	0.20	0.59	-	-	-	1.44	3.01	2.86	3.06
Speckled mousebird	-	-	-	-	-	-	-	-	-	-	-	-	-
Swee waxbill	-	-	-	-	-	-	-	-	-	-	-	-	-
White-starred robin	0.49	0.36	0.77	-	-	-	-	-	-	0.86	2.64	0.61	-
Yellow-throated woodland-warbler	4.16	3.63	4.38	1.71	5.87	3.92	4.90	2.45	1.34	1.73	2.26	3.06	1.53
Total	47.24	52.94	34.27	58.74	65.01	37.40	57.88	37.16	48.06	46.94	57.05	55.27	43.44
Proportion*	0.26	0.43	0.44	0.33	0.33	0.38	0.32	0.26	0.31	0.39	0.33	0.46	0.30
Adjusted density	12.39	22.84	15.12	19.34	21.67	14.21	18.60	9.79	14.69	18.37	18.56	25.57	12.93

*Ratio of average number of individuals in snap-shots to average number of individuals in point counts.

Appendix C – Mean densities (ind.ha^{-1}) for bird species across all forest patches sampled.

Common name	Scientific name	Mean density	SE
African dusky flycatcher	*Muscicapa adusta*	2.07	0.16
African firefinch	*Lagonosticta rubricata*	0.35	0.20
African goshawk	*Accipiter tachiro*	0.35	0.08
African olive-pigeon	*Columba arquatrix*	2.68	0.71
African paradise-flycatcher	*Terpsiphone viridis*	1.13	0.14
African wood-owl	*Strix woodfordii*	0.32	0.07
Amethyst sunbird	*Chalcomitra amethystina*	0.40	0.11
Barratt's warbler	*Bradypterus barratti*	1.41	0.20
Bar-throated apalis	*Apalis thoracica*	5.60	0.37
Black cuckoo	*Cuculus clamosus*	0.39	0.21
Black kite	*Milvus migrans*	0.32	0.00
Black-backed puffback	*Dryoscopus cubla*	0.92	0.10
Black-collared barbet	*Lybius torquatus*	0.35	0.13
Black-headed oriole	*Oriolus larvatus*	0.45	0.19
Blue-mantled crested-flycatcher	*Trochocercus cyanomelas*	0.87	0.26
Buff-spotted flufftail	*Sarothrura elegans*	0.32	0.10
Bush blackcap	*Lioptilus nigricapillus*	3.22	0.48
Cape batis	*Batis capensis*	2.76	0.21
Cape robin-chat	*Cossypha caffra*	1.96	0.35
Cape turtle-dove	*Streptopelia capicola*	0.77	0.00
Cape white-eye	*Zosterops capensis*	13.57	0.46
Chorister robin-chat	*Cossypha dichroa*	2.22	0.25
Common waxbill	*Estrilda astrild*	1.11	0.00
Dark-capped bulbul	*Pycnonotus tricolor*	1.84	0.26
Forest canary	*Crithagra scotops*	2.43	0.27
Fork-tailed drongo	*Dicrurus adsimilis*	1.30	0.21
Greater double-collared sunbird	*Cinnyris afer*	1.45	0.19
Grey cuckooshrike	*Coracina caesia*	0.61	0.10
Hadeda ibis	*Bostrychia hagedash*	1.11	0.34
Klaas's cuckoo	*Chrysococcyx klaas*	0.27	0.06
Lemon dove	*Aplopelia larvata*	0.84	0.16
Olive bush-shrike	*Telophorus olivaceus*	0.48	0.06
Olive thrush	*Turdus olivaceus*	1.34	0.22
Olive woodpecker	*Dendropicos griseocephalus*	0.81	0.12
Red-chested cuckoo	*Cuculus solitarius*	0.86	0.15
Red-eyed dove	*Streptopelia semitorquata*	1.54	0.46
Red-winged starling	*Onychognathus morio*	1.37	0.53
Rufous-chested sparrowhawk	*Accipiter rufiventris*	1.03	0.00
Sombre greenbul	*Andropadus importunus*	4.28	0.59
Southern black tit	*Parus niger*	1.00	0.19
Southern boubou	*Laniarius ferrugineus*	0.92	0.23
Southern double-collared sunbird	*Cinnyris chalybeus*	2.08	0.25
Speckled mousebird	*Colius striatus*	0.56	0.13
Swee waxbill	*Coccopygia melanotis*	0.71	0.22
White-starred robin	*Pogonocichla stellata*	0.93	0.16
Yellow-throated woodland-warbler	*Phylloscopus ruficapilla*	3.67	0.27
Total mean density		1.56	

CHAPTER 3

IS BIRD SPECIES RICHNESS IN SOUTHERN AFROTEMPERATE FORESTS DRIVEN BY REGIONAL- OR LOCAL-SCALE PROCESSES?

Abstract

The theory that species' patterns of distribution, abundance and coexistence are the result of local ecological processes has been challenged by evidence that regional-scale processes are equally instrumental in shaping local community composition. The historically and naturally fragmented Afrotemperate forests of the uKhahlamba–Drakensberg Park, South Africa, offer an interesting test case. In this study, the relative effects of local and regional-scale processes on species assemblages in a naturally patchy forest system were investigated.

By employing species-area and species-isolation relationships, and nested subset analyses, we show that isolation (regional-scale process) had a greater effect on bird species richness and composition than area (local-scale process). Patch area, the size of the regional species pool as well as the distance to the nearest Eastern Mistbelt forest were all influential in determining local bird species richness in these montane forests. Localities are regionally enriched within the constraints on species occupancy provided by the available habitat.

Overall, both local and regional processes affected species composition in Afrotemperate forests, however, regional processes appear to have played a greater role. This finding emphasizes the need for a broader view of community dynamics in a naturally patchy environment, and furthermore, to conserve a taxon or habitat it is necessary to understand the local and regional processes that affect biodiversity.

1. Introduction

In recent years explanations for geographical patterns of biodiversity have emphasised the importance of historical and geographical factors for local diversity (Cutler, 1991; Lomolino and Perault, 2001; Ricklefs, 2004; Hillebrand, 2005; Lawes et al., 2007b; Ricklefs, 2007; Harrison and Cornell, 2008). The terms 'local' and 'regional' refer to the spatial scales at which ecological and biogeographic processes predominate. Thus predation, competition, and abiotic fluctuations all fall under local processes, whereas long-distance dispersal, speciation, widespread extinction, and fluctuation in species distributions are regional influences. Large-scale processes (speciation, radiation and extinction events) influence regional diversity, which in turn determines the diversity of the species pool from which local communities are assembled (Ricklefs, 1987). The size and structure of local communities that derive from the species pool, may in turn be determined by local ecological processes (dispersal, competition, patch area and isolation) (Cornell and Lawton, 1992; Lawes and Eeley, 2000; Lawes et al., 2000a; Blackburn and Gaston, 2001; Ricklefs, 2004; Harrison and Cornell, 2008). The role of the size of the regional species pool has been contrasted with local processes, such as competition, predation and niche packing, for limiting the number of locally coexisting species (Terborgh and Faaborg, 1980; Ricklefs, 1987; Cornell and Lawton, 1992). In the past, regional processes have been overlooked in favour of local processes by the uncritical application of species-area theory to explain diversity in fragmented landscapes (Connor and McCoy, 1979; Whitcomb et al., 1981; Kitchener et al., 1982; Howe, 1984a). Applied to local landscapes, species-area theory takes account of the influence of regional factors in shaping local communities, though seldom differentiates between fragmented and naturally patchy systems, even though these systems are potentially dominated by ecological processes at different spatial and temporal scales (Kotze and Lawes, 2007; Pavlacky and Anderson, 2007). Thus, for the purposes of this study, local scale processes include the area of a habitat patch and the isolation of that patch from a nearby like patch, while regional processes consider the size of the species pool from which local species assemblages are derived and the isolation of the local patch from the 'mainland' or source species pool.

Patch mosaic landscapes may arise in a number of ways, and fragmentation of once continuous habitat, and the establishment of new habitat patches in an otherwise homogenous matrix, are just two of the causes of patchy landscapes. Broadly, in the former, local and often area-dependent processes are important while in the latter, regional

processes are likely to be more important (Linares-Palomino and Kessler, 2009; Wilson et al., 2009). The Drakensberg Montane forests of the MDTP, South Africa, are small and have been isolated throughout their evolutionary history (Eeley et al., 1999; Lawes et al., 2004). Montane forests share their tree species with and are derived from persistent Afrotemperate forests situated at lower altitudes in the region (Eeley et al., 1999). Their patchy distribution is thus attributed to bioclimatic influences rather than the fragmentation of former continuous forest (Eeley et al., 1999). Their relatively recent origin from Afrotemperate forest at lower altitude implies an important role for regional-scale processes in determining their bird species richness. Regional enrichment of local diversity is an important process in naturally patchy landscapes and species accumulate subject to the constraints that affect specific colonizing ability and the size and proximity of the regional species pool (Butaye et al., 2001; Smith, 2001; Naeslund and Norberg, 2006; Pavlacky and Anderson, 2007). The notion that Drakensberg Montane forest bird assemblages are regionally enriched from former refugia or 'mainland' forests of the Eastern Mistbelt forests of KwaZulu-Natal province is examined in this study.

There are various methods for investigating the relative roles of local versus regional processes in determining diversity (Hillebrand and Blenckner, 2002; Harrison and Cornell, 2008). Most methods infer process from pattern in a site-by-species incidence matrix (Leibold and Mikkelson, 2002). Several kinds of pattern in the distribution of species are recognised, such as nested subsets, checkerboards, gradients, compartmented assemblages (Clementsian gradients) and compound structures of these patterns (Leibold and Mikkelson, 2002; Lewinsohn et al., 2006); all of which have implications for the relative roles of local versus regional processes in determining local diversity. The most popular method of analysis has been to apply regressions of local on regional richness (Ricklefs, 1987; Cornell and Lawton, 1992; but see Hillebrand and Blenckner, 2002; Karlson et al., 2004; Hillebrand, 2005). However, the method used for this study was not strictly a conventional local versus regional analysis because the localities are not embedded in the region from which species are potentially derived. Nevertheless, the analysis does determine whether or not montane bird assemblages derive mainly from the regional temperate forest assemblages. Here several of the measures of local and regional patterns of species distribution are combined to investigate the relative roles of regional and local processes in determining bird community structure and composition in the Afromontane forests of the uKhahlamba Drakensberg Park. An understanding of the roles

of local and regional processes is vital for predicting biodiversity responses to future climate and landscape changes, particularly in terms of conservation initiatives.

2. Methods

2.1 Study area

This study was conducted in the forests of the South African portion of the Maloti Drakensberg Transfrontier Project bioregion (MDTP; 28°15' - 31°20'S, 27°10' - 30°E; Fig. 1). Two forest types occur in the area, namely Drakensberg Montane forest (7025 ha) and Eastern Mistbelt forest (8708 ha; classification follows Mucina and Rutherford, 2006b). The MDTP planning region encompasses the entire distribution of Drakensberg Montane forest in South Africa, and approximately 25% of Eastern Mistbelt forest.
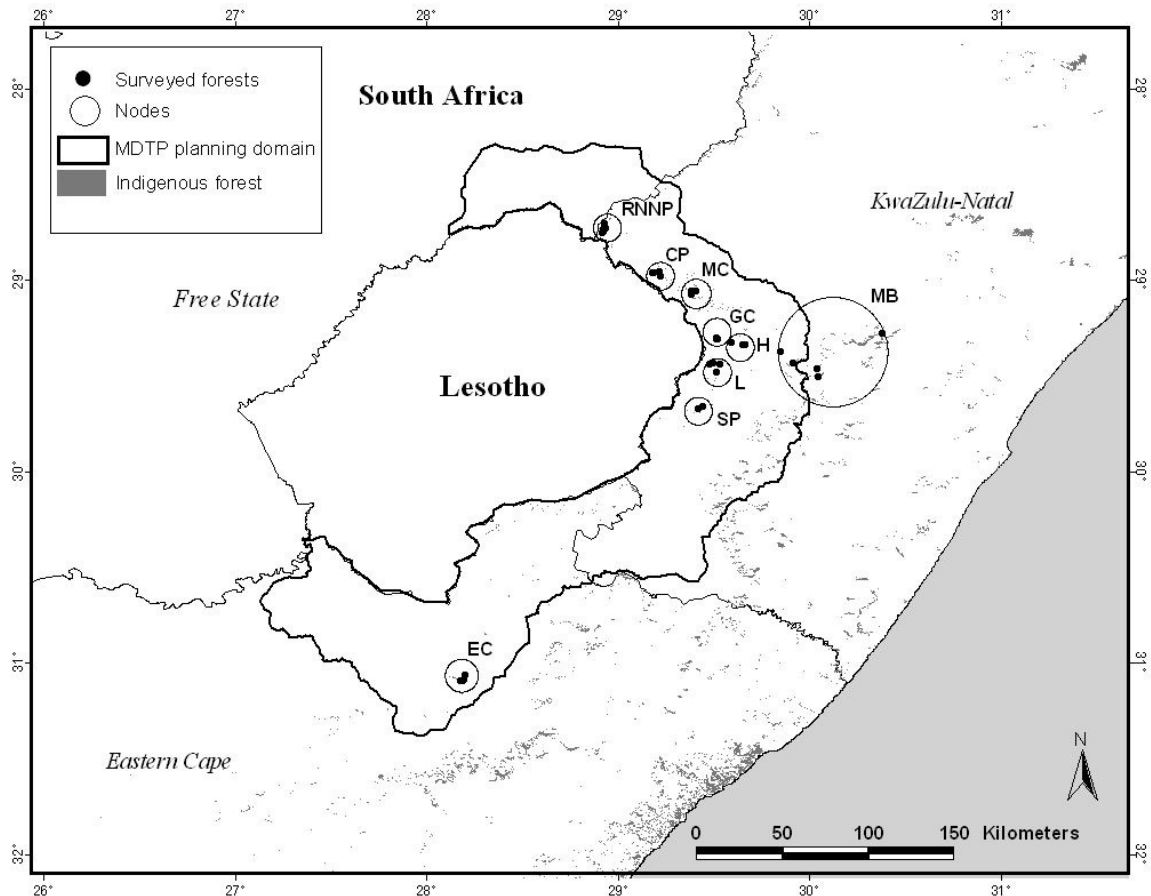

Fig. 1 – Map of study area showing distribution of indigenous forest, and study sites sampled within the MDTP planning domain. Sampled sites outside the planning domain are additional Eastern Mistbelt forests sourced from Wethered & Lawes (2003; 2005). The area between SP and EC was not sampled because of logistics. (Abbreviations: RNNP - Royal Natal National Park, CP – Cathedral Peak, MC – Monk's Cowl, GC – Giant's Castle, H – Highmoor, L – Loteni, SP – Sani Pass, EC – Eastern Cape, MB – Eastern Mistbelt forest).

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Forests are embedded in a grassland matrix and generally occur in moist fire-safe sites, on steep south-facing slopes subjected to high annual rainfall (800-1000 mm; Lawes et al., 2007a). Drakensberg Montane forests occur at altitudes of 1500 to 1800 m and Eastern Mistbelt forest at lower altitudes (850-1600 m; Lawes et al., 2007a). Both these mixed evergreen forests are often dominated by the conifer *Podocarpus latifolius.* Most (94%) Drakensberg Montane forests are small (<10 ha; 3.0 ± 7.3 ha, mean $\pm$ 1 SD, n = 2352) and only two forest patches (0.1%) were larger than 100 ha, with the largest patch comprising 146.4 ha (Lawes et al., 2007a). In the MDTP, the larger Drakensberg Montane forests are in the north. Eastern Mistbelt forests are generally larger than Drakensberg Montane forests (28.0 ± 68.2 ha, mean $\pm$ 1 SD, n = 311), although patch size is similarly skewed with 65.3% of forest patches <10 ha, and only 21 patches (6.7%) exceed 100 ha. The prevailing climate is temperate (mean annual temperature is 14 °C) and seasonal, with summer rainfall and occasional heavy frost and snow in winter, particularly at higher altitudes (Lawes et al., 2007a).

2.2 Forest patches sampled

To describe the landscape pattern of forest across the MDTP, an area characterized by numerous discrete river catchments, a sub-sample of 20 river catchments (quaternary) was examined using Fragstats Landscape Analysis Programme (McGarigal et al., 2002) in ArcView 3.3 GIS (ESRI, 1992-2002). Fifteen catchments contained Drakensberg Montane forest and 5 contained Eastern Mistbelt forest. The following landscape metrics were determined for each of the 20 catchments: patch area (ha), patch density, patch isolation (nearest neighbour within a 1.3 km search radius of the focal patch), mean proximity index (mean ratio between the size and proximity of all patches whose edges were within the search radius), contagion (probability that two randomly chosen adjacent cells belong to different forest types), and cohesion (standardized area-perimeter ratio) (Appendix A). Landscape metric data was sourced from Lawes et al. (2007a).

Detailed sampling of forest patches for bird and/or vegetation data was undertaken in 36 forest patches within nine predetermined sampling nodes (Fig. 1). The sampling nodes were selected to take account of the latitudinal gradient within the MDTP, to fall within a discrete river catchment and, where possible, to include a range of forest patch sizes. Patches were categorized in three size classes, small (< 1 ha), medium (1 - 5 ha), and

large (> 5 ha). Thirty-one Drakensberg Montane forests with a size range of 0.6 –36.6 ha, and five patches of Eastern Mistbelt forest (51.2 – 98.9 ha) were sampled.

2.3 Environmental correlates of forest and bird distribution

Bird species distribution is influenced by vegetation structure and composition (Cody, 1983; Earle, 1983; Owiunji and Plumptre, 1998; Boulinier et al., 2001; Deferrari et al., 2001; Díaz et al., 2005; Reif, 2007). Vegetation in terms of trees was therefore sampled in all 36 forests. In particular, the canopy and sub-canopy woody tree components were sampled to determine measures of tree density (no. individuals per ha) and tree species richness. Using modified Whittaker plots (25 m x 10 m; Obiri et al., 2002), all trees ≥10 cm diameter at breast height (dbh) were identified and measured within randomly placed plots in each of the 36 forest patches. The number of Whittaker plots surveyed varied between forests (2 - 25 plots) and was dependent on forest patch size (0.6 - 237.5 ha). Forest patches were surveyed until species sampling saturation was achieved.

      In addition to the measured vegetation variables, climate and landscape variables were recorded from each forest. Climatic data (current climate) were derived from interpolated climate grids at a resolution of 1' x 1' (approximately 1.6 x 1.8 km at this latitude) (Schulze, 2006) and included: mean annual temperature (MAT), annual temperature range (ATR), mean maximum temperature of the three hottest months December - February (T_{hot}), mean maximum temperature of the three coldest months June - August (T_{cool}), mean annual rainfall (MAR), mean median rainfall for the three driest months June - August (rain.min.), and mean annual potential evaporation (APE). The landscape variables (patch area and altitude) were determined using ArcView 3.3 GIS (ESRI, 1992-2002).

      In addition to the eleven respective vegetation, climate and landscape variables described, three biologically relevant measures of isolation for avifauna were calculated for each of the 31 Drakensberg Montane forests: (1) the distance to the nearest forest patch of any size; (2) distance to the nearest forest patch of larger size; and (3) distance to the nearest Eastern Mistbelt forest larger than 36.6 ha (the largest Drakensberg Montane forest). These distances (km) were estimated as the straight-line distance between forest edges.

2.4 Bird census methods

Birds were censused in 31 Drakensberg Montane forest patches and one Eastern Mistbelt forest patch (MBA) during two consecutive seasons (November – March, 2005-2006 and 2006-2007). The Eastern Mistbelt forest patches, MBB – MBE, were not surveyed for birds. However, bird data for other Eastern Mistbelt forests in the region (Wethered and Lawes, 2003; 2005) were pooled with the MDTP bird data, yielding a sample from 11 Eastern Mistbelt forests with a size range of 0.5 - 705 ha (Table 1). A modified stationary point count technique (Koen, 1988a) was used. This technique is considered reliable for use in closed-canopy evergreen forests where vision is limited and bird detection is accomplished by both visual and auditory cues (Koen, 1988a; Sutherland et al., 2004; Buckland, 2006).

In the modified stationary point count, birds within a 25 m radius of the observer were recorded and points were >100 m apart (Willson et al., 1994; Ralph et al., 1995; Bibby et al., 2000). Points were surveyed for 10 min, immediately after which a snapshot count of the species present was conducted (a record of all individuals present within the survey area at an instant). Bird species density was estimated from both point and snapshot counts. To ensure that sampling effort was similar among the patches, the number of point counts was adjusted for patch size (Table 1). Birds were censused in the 3 h after dawn and in the 3 h before dusk, the hours of peak bird activity. Forest patches and survey times were rotated between observers to avoid bias.

Bird species were assigned to either forest-dependent (FD) or forest-associated (FA) categories. These were defined as species that live and reproduce only in forest habitats, and species that inhabit forest as well as other habitats and do not breed only in forest, respectively. The FD category was adjusted so that species that required wooded habitats (not necessarily forest), but were restricted to forest in the MDTP, were categorized as forest dependent in this study. Species were assigned to categories (Lawes et al., 2000a) and assignments were verified from the literature (Harrison et al., 1997). Transient bird species, those species observed once in only one patch, were not included in any of the statistical analyses. Bird nomenclature follows Hockey et al. (2005).

Randomized cumulative sample-species richness curves for birds were plotted for each forest patch to determine sampling saturation (Gotelli and Colwell, 2001). Jackknife2 and Chao2 estimators of species richness were calculated using the program EstimateS (Colwell, 2001). Species saturation estimates ranged from 85% to 99% for all nodes except Giants Castle, where it ranged from 83% to 88% (Table 2). Thus, the bird species inventories were relatively complete and comparable among nodes.

Table 1 - Summary of forest patches surveyed for birds in each node, including additional Eastern Mistbelt forest patches (Wethered and Lawes, 2003; 2005).

Node	Forest	Area (ha)	No. point counts	Species richness	Forest dependent species	Isolation measures (km) Nearest neighbour (NN)	NN larger forest	NN Eastern Mistbelt
Royal Natal	RNNPA	30.0	35	30	21	0.1	2.9	41.1
National Park	RNNPB	12.0	31	33	19	0.2	0.7	43.7
	RNNPC	7.6	17	23	16	0.1	0.3	45.5
	RNNPD	5.7	25	35	21	0.3	0.4	42.7
	RNNPE	1.2	18	25	17	0.1	0.3	45.0
Cathedral Peak	CPA	36.6	46	28	18	0.1	10.7	55.5
	CPB	16.2	34	24	17	0.1	4.3	57.2
	CPC	6.5	31	33	20	0.8	1.7	54.2
	CPD	2.3	26	32	20	0.2	0.3	55.5
	CPE	0.8	19	25	14	0.2	0.8	55.0
Monk's Cowl	MCA	27.2	32	38	26	0.2	2.3	57.3
	MCB	19.8	32	29	21	0.6	1.5	56.6
	MCC	16.0	31	36	23	0.3	1.1	55.8
	MCD	2.5	19	27	19	0.2	0.3	56.8
	MCE	1.7	18	32	21	0.3	0.3	56.1
Giants Castle	GCA	6.8	27	21	16	0.5	6.3	33.3
	GCB	1.3	13	21	16	0.1	0.7	32.7
	GCC	0.6	7	18	14	0.1	0.2	32.9
Highmoor	HA	4.1	20	27	21	0.1	0.2	18.6
	HB	3.6	27	25	19	0.0	0.6	25.3
	HC	1.2	19	17	16	0.2	0.3	19.2
Loteni	LA	9.0	20	27	17	0.3	9.7	36.7
	LB	6.1	25	23	15	0.4	2.9	32.9
	LC	4.0	25	21	15	0.1	1.5	38.3
	LD	1.5	17	18	14	0.4	0.5	34.1
Sani Pass	SPA	4.5	22	17	11	0.0	2.7	26.8
	SPB	3.0	22	20	13	0.0	2.4	25.5
Eastern Cape	ECA	14.4	17	26	16	0.2	0.4	36.0
	ECB	17.7	26	29	19	0.2	1.4	35.0
	ECC	6.2	24	30	19	0.2	0.4	34.4
	ECD	4.8	16	24	15	0.0	2.8	33.8
Eastern Mistbelt	MBA	96.8	42	41	29			
forest	BA	215.0	-	49	32			
	BB	138.2	-	37	29			
	BC	123.8	-	34	26			
	BD	85.0	-	33	24			
	BE	45.8	-	36	27			
	BF	15.0	-	34	26			
	BG	3.0	-	33	23			
	BH	1.7	-	23	19			
	BI	0.5	-	29	18			
	LpB	705.0	-	52	34			

Table 2 - Comparison of Chao-2 and second-order Jackknife (Jack-2) bird species richness estimates at each node from point count surveys (*N*). Values are percentage of the estimated total species richness (mean ± 1 SD).

Node	*N*	Chao-2	Jack-2
RNNP	126	95.1 ± 2.8	86.0 ± 5.4
CP	156	95.8 ± 4.9	88.8 ± 7.3
MC	132	92.8 ± 8.5	86.7 ± 11.7
GC	47	87.9 ± 13.3	82.6 ± 19.5
H	66	96.6 ± 3.3	90.7 ± 8.7
L	87	97.3 ± 2.1	91.9 ± 8.4
SP	44	96.8 ± 2.9	88.1 ± 9.3
EC	83	90.8 ± 8.2	84.5 ± 10.4
MBA	42	99.4	97.5

2.5 Analyses

2.5.1 Ordination

The spatial, climate and landscape attributes for both bird and tree communities were ordinated using non-metric multidimensional scaling (NMDS). NMDS graphically summarises the association between sites and species (tree and bird), following which the environmental variables are correlated with the axes to evaluate potential relationships between community composition and the selected environmental attributes. The Sorensen dissimilarity measure was used, a random starting configuration, 100 iterations and an instability criterion of 10^{-5} (McCune and Mefford, 1999a). Environmental variables were correlated with the NMDS axes using permutation tests (Oksanen et al., 2006). We reduced the risk of Type I error by adjusting *p*-values using the False Discovery Rate procedure (Verhoeven et al., 2005).

A multi-response permutation procedure (MRPP) using Sorensen's distance and rank transformation (McCune et al., 2002) was used to test for significant differences in community composition and pattern identified from the NMDS, for both tree and bird data. The test statistic (*T*) describes the separation between groups; the more negative *T* is, the stronger the separation between groups. A chance-corrected within-group agreement statistic (*A*) describes within-group homogeneity compared to the random expectation

(McCune et al., 2002). Ordination and MRPP tests were conducted using PC-ORD 4.34 (McCune and Mefford, 1999a).

2.5.2 Species-area and species-distance relationship

The effects of patch area and isolation distance on bird species richness were tested for Drakensberg Montane forest bird communities. Least-squares linear regressions of species richness against area, and species richness against isolation, were compared using goodness of fit for log-transformed or semi-log data. Species-area and -isolation regressions based on log-log data fitted best. Isolation effects were measured at the local (distance to the nearest neighbour) and regional (distance from focal patch to the nearest Eastern Mistbelt forest) level. Regression analyses were performed using routines in GenStat 9.1 (GenStat Committee, 2006).

2.5.3 Analysis of species distribution patterns

To detect patterns of bird distribution, we examined their assemblage structure defined by presence-absence data in species-by-forest matrices using the methods of Leibold and Mikkelson (2002) and Lewinsohn et al. (2006). These methods are contained in the "bipartite" package (Dormann and Gruber, 2008) in R (R Development Core Team, 2008) and provide insights to whether species distribution patterns are nested, arranged along a gradient, or are compartmented (Lewinsohn et al., 2006). Species presence-absence data from the eight Drakensberg Montane sample nodes and 31 forest patches were analysed separately.

Nested species assemblages imply deterministic causes of community assembly. These mechanisms may be competitive exclusion at the local scale, or area-dependent extinction or distance-dependent colonization by species at the regional scale (Cutler, 1991; Lomolino, 1996; Wright et al., 1998). Therefore, it was necessary to determine whether local or regional mechanisms were important (Stone and Roberts, 1992). For insight to the role of local interactions we examined the strength of the checkerboard pattern, implying competitive exclusion, by estimating the C-score (Stone and Roberts, 1990) using the bipartite package in R. The C-score ranges from 0 (aggregation) to 1 (checkerboard).

Nestedness was estimated in two ways. We used the U_t metric of Cutler (1991) based on the RANDOM1 algorithm (Mikkelson et al., 1996), and Lomolino's (1996) Monte Carlo approach to determining the regional causality (selective immigration or

extinction) of nestedness. The assessment of causality of nestedness is strongly influenced by the measure of isolation used in the Lomolino (1996) analysis, and all of the three previously defined measures of isolation were investigated (see section 2.3 for description of isolation measures). A recent review of methods of measuring species nestedness found that Cutler's index of unexpected presences performed best (Ulrich and Gotelli, 2007).

2.5.4 Regional versus local processes: regional enrichment or local interaction?
Regional species richness for FD species was estimated from the South African Bird Atlas Project (SABAP; Harrison et al., 1997) data and was independent of estimates of local FD species richness, which were derived from point counts from the largest forest patch at a sampling node. Here, the question of whether the local richness of Drakensberg Montane forests is dependent on the size of the species pool in adjacent Eastern Mistbelt forests is addressed (Blackburn and Gaston, 2001). There was a scale issue in defining the regional species pool and we used two methods. Firstly, for each sampling node we estimated regional species richness in the catchments including and adjacent to the local forest for one and four adjacent quarter degree squares (QDS). Secondly, we estimated regional richness (or the size of the nearest prospective species pool) from the richness of the nearest Eastern Mistbelt forests within one and four adjacent QDS.

The method applied here was not strictly a conventional local versus regional analysis in design because the localities (Drakensberg Montane forests) do not reside in the region (Eastern Mistbelt forests of the adjacent KwaZulu-Natal midlands) containing the most likely species pool. However, the analysis did determine whether or not montane bird assemblages derive mainly from temperate forest assemblages. The prediction was that if local assemblages are regionally enriched then local richness will increase proportionately with 'regional' Afrotemperate species richness; the regression relationship between local and regional species richness will be a straight-line with a slope > 0 and other correlates such as the distance to the regional species pool may affect the steepness of the regression slope. However, if localities owe their species assembly to local interactions, such as competition for resources, then species richness at localities should be independent of regional richness and likely better explained by other correlates (such as the area of the local forest). Thus, the regional-scale effects that were considered include the species richness of the nearest 'source' Eastern mistbelt forest, and two measures of the distance to the nearest 'source' Eastern mistbelt forest.

Data were analysed by generalised linear models (GLM) with a normal distribution (as is the procedure for conventional local versus regional analysis) and the identity link function. Several independent variables were fitted including regional species richness (separate models for each method of estimating regional richness – see above), the area (ha) of the locality, the straight-line distance to the nearest Drakensberg Montane forest, the straight-line distance from the locality to the nearest Eastern Mistbelt forest in the region, and a corresponding distance following the topography and thus the most likely dispersal route from the nearest large forest in the region. The best fit model was selected using an information theoretic approach based on the second-order bias correction of Akaike's Information Criterion (AIC$_c$), a corrected version of AIC for small sample sizes (Burnham and Anderson, 2002).

3. Results

3.1 Environmental correlates of forest patch distribution

The sampled quaternary catchments ranged from approximately 144 km^2 to 602 km^2 (Appendix A). Percent cover of Drakensberg Montane forest varied from 0.03% in a southern catchment (C1063) to 3.57% in a northern catchment (C887), with generally greater forest cover in the northern areas of the MDTP. Along with a latitudinal decline in total forest area from north to south, there was a decrease in the size and number of individual forest patches. Drakensberg Montane forest patches were more isolated in the south than in the north of the region. Eastern Mistbelt forests were larger and formed bigger clusters than Drakensberg Montane forests (Appendix A), and did not vary in terms of forest area and percent cover in their respective catchments across the latitudinal gradient (Appendix A). The patch cohesion index, a measure of connectivity of the landscape for dispersing organisms, was similarly high for both forest types. Therefore, the potential for species dispersal both within and between forest types was similar throughout the MDTP region.

NMDS results were identical for tree community composition and tree density data, and therefore only tree community composition results are presented here. The first two NMDS axes accounted for 80% of the variance in tree plot data (NMDS axis 1 = 42%; NMDS axis 2 = 38%; Table 3). Forest tree communities were arranged on NMDS axis 1 along an environmental gradient defined by decreasing forest size and increasing annual

temperature variability, with Drakensberg Montane and Eastern Mistbelt forests at opposite ends of the gradient (Fig. 2; Table 3). The smaller Drakensberg Montane forests were located at higher altitudes with lower winter rainfall than Eastern Mistbelt forests. The NMDS revealed a clear separation of the two forest types in terms of their tree species composition. Forests were arranged on the second NMDS axis along a decreasing north-south rainfall gradient. Within Drakensberg Montane forests, the three most northerly nodes (RNNP, CP, MC) clearly separated from the four most southerly nodes (H, L, SP, EC). The Giants Castle node formed a separate and distinct cluster from the other nodes; however it was more similar in composition to the southern nodes (Fig. 2). The tree community composition of the northern (RNNP, CP, MC) and southern nodes (GC, H, L, SP, EC) were significantly different (MRPP: T = -10.23, $P < 0.001$).

Table 3 – Pearson's product-moment correlations between environmental variables and two ordination axes for tree community data of Drakensberg Montane and Eastern Mistbelt forests.

	NMDS 1	NMDS 2
Mean maximum temperature of 3 hottest months	0.02	0.06
Mean maximum temperature of 3 coldest months	-0.41	-0.05
Mean annual temperature	-0.34	0.01
Annual temperature range	0.64 *	0.10
Mean annual rainfall	0.10	0.64 *
Median of mean rainfall of 3 driest months	-0.55 *	0.34
Annual potential evaporation	-0.16	0.17
Patch area	-0.84 *	-0.08
Altitude	0.54 *	-0.35
Mean tree density/ha	0.40	-0.47
Mean tree species richness/ha	0.19	-0.26
Variance explained	42%	38%

* Asterisks denote significant correlations using a threshold False Discovery Rate (α = 0.05) to reduce the likelihood of spurious correlations.

3.2 Bird community composition and distribution

Based on the South African Bird Atlas Project data (Harrison et al., 1997), the 44 QDS within which indigenous forests (Drakensberg Montane and Eastern Mistbelt) occur in the

MDTP planning domain support 101 forest bird species (26 forest dependent and 75 forest associated species). We recorded 74 bird species belonging to 31 families in both Drakensberg Montane and Eastern Mistbelt forest (Appendix B). Bird species richness in the Eastern Mistbelt forests was greater ($n = 65$) than in the Drakensberg Montane forests ($n = 50$), where species richness in forest patches ranged from 17 to 36 (Table 1). Forty-six of the 73 species (63%) recorded in total were classed as forest dependent (Appendix B). Forest dependent species were well represented in the Drakensberg Montane ($n = 28$) and Eastern Mistbelt forests ($n = 42$). Generally, forest dependent species comprised at least 60% of the species assemblage for forest patches of both forest types (Table 1).
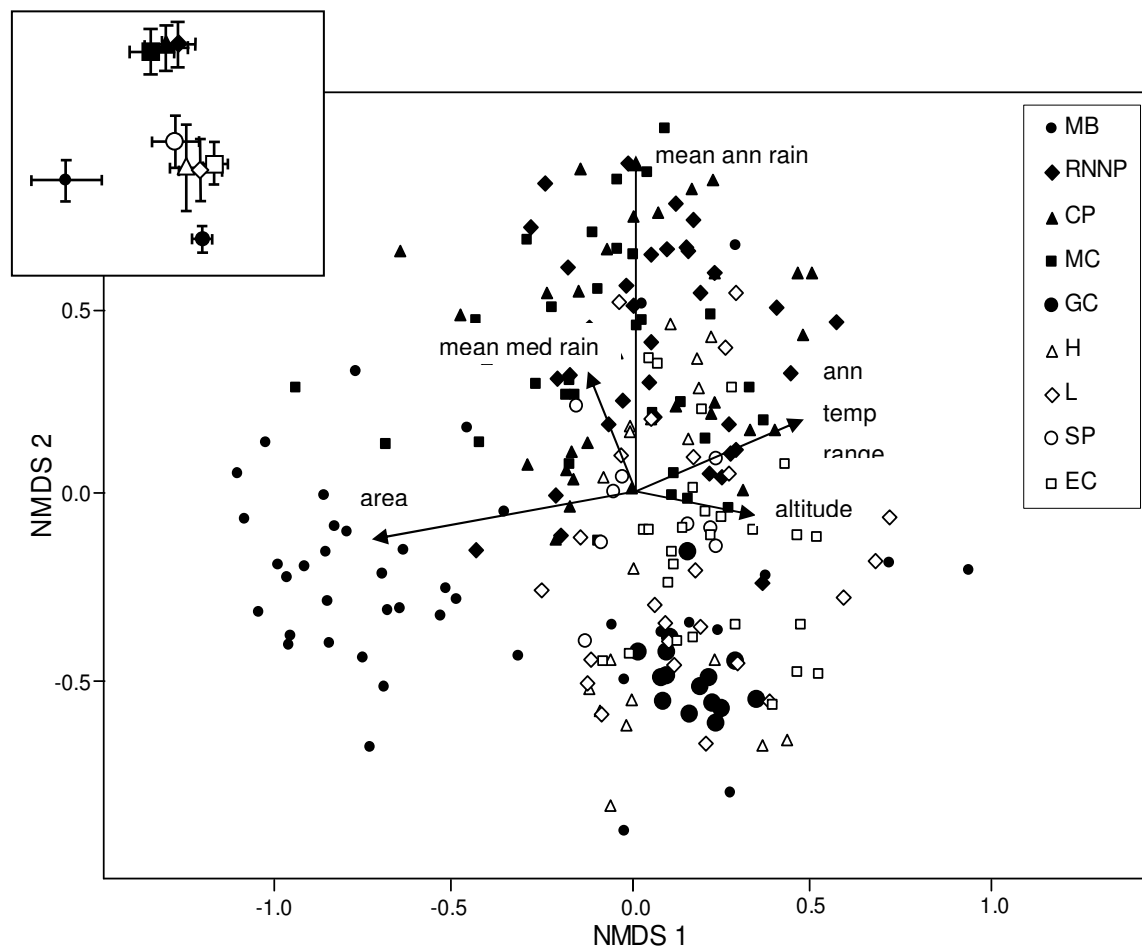

Fig. 2 – Two axes of the three-dimensional NMDS ordination of tree composition data (3D stress = 11.1). The arrows indicate significant correlations of the environmental variables. The length of each arrow indicates the strength of correlations between the variable and the first two ordination axes (see Table 3). See Figure 1 for node abbreviations. Insert: simplified plot showing means ± 2SE of the axes scores of the 9 nodes.

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NMDS of bird community data revealed a similar separation and grouping of nodes along a north-south latitudinal gradient to that obtained from the tree community data (Fig. 3). The first NMDS axis was significantly correlated only with distance to neighbouring Eastern Mistbelt patches (r = 0.62, P < 0.001) and tree density (r = -0.49, P = 0.05), and highlighted the separation of the three most northerly Drakensberg Montane nodes (RNNP, CP, MC) from all other Drakensberg Montane nodes (Fig. 3). However, although the five southerly nodes were clearly distinct from the northern nodes cluster, the grouping of these southern nodes was less distinct than in the tree community data. There were no significant correlations for the second NMDS axis. Mirroring the tree data, bird community structure was markedly different between Drakensberg Montane and Eastern Mistbelt forests (MRPP: T = -21.96, P < 0.001). Within Drakensberg Montane forests, the bird community composition of the northern (RNNP, CP, MC) and southern nodes (GC, H, L, SP, EC) were significantly different (MRPP: T = -10.02, P < 0.001).
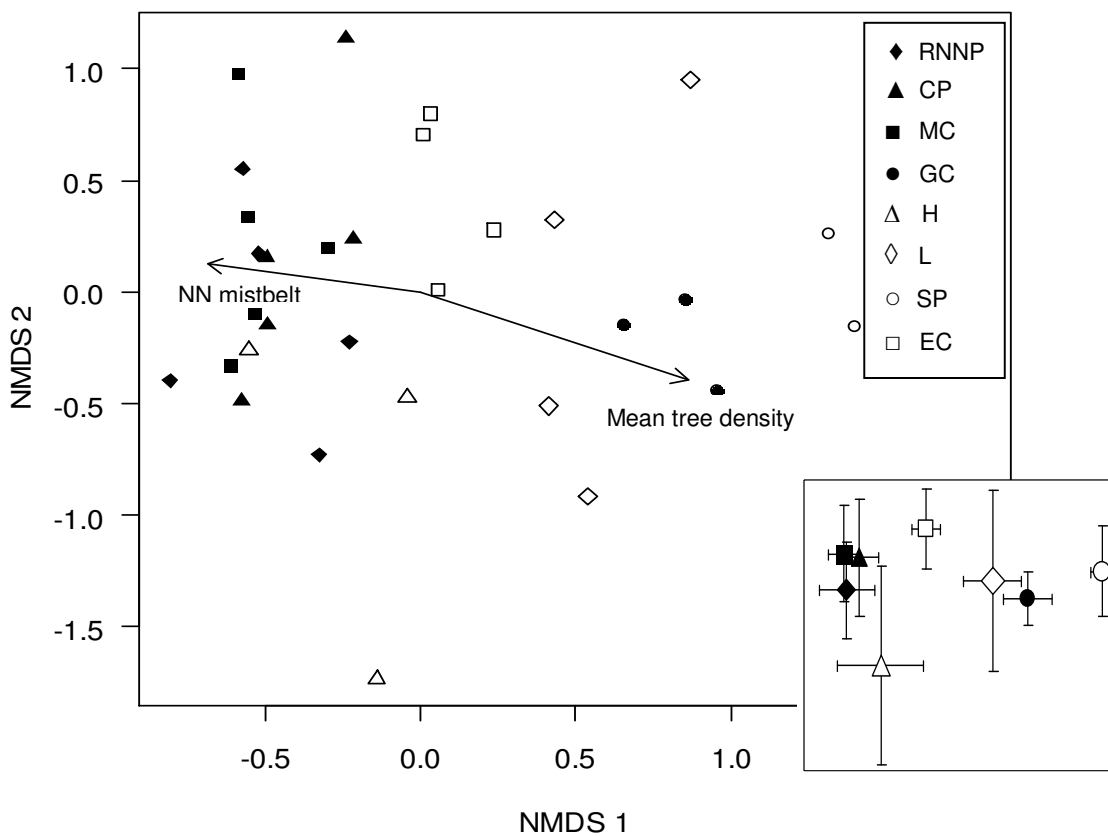

Fig. 3 – First two axes of the NMDS ordination of bird species data (3D stress = 12.7). The arrows indicate significant correlations of two environmental variables, mean tree density and distance to the nearest Eastern Mistbelt forest. The length of each arrow indicates the strength of correlations between the variable and the first two ordination axes. See Figure 1 for node abbreviations. Insert: simplified plot showing means ± 2SE of the axes scores of the 9 nodes.

3.3 Species-area and species-distance relationship

The number of bird species in a forest patch (S) was positively dependent on patch area (A) across Drakensberg Montane forests ($S = 1.33 + 0.10A$; $F_{1,29} = 10.83$, $P = 0.003$, $r^2 = 0.25$; Fig. 4). This suggested some local control on species assembly. However, the overall species-area relationship appeared to be mainly influenced by the species-area relationship in the southern nodes ($S = 1.26 + 0.15A$; $F_{1,14} = 15.21$, $P = 0.002$, $r^2 = 0.49$) and not in the northern nodes where species richness was independent of patch area ($S = 1.44 + 0.036A$; $F_{1,13} = 0.95$, $P = 0.347$, $r^2 = 0.084$). GCC, HC, LD and SPA were all among the smallest forests surveyed (ranging from 0.6 ha to 4.5 ha), other small forests such as RNNPD (5.7 ha), CPD (2.3 ha), MCE (1.7 ha) and HB (3.6 ha) had relatively high species richness (35, 32, 32 species, respectively), suggesting that area is not the main determinant of bird species richness in these forests. (See Fig. 1 for abbreviations.)

Species richness in a patch was positively dependent on isolation (I) for two of the three isolation measures; the nearest neighbour ($S = 1.49 + 0.10I$; $F_{1,29} = 5.24$, $P = 0.03$, $r^2 = 0.12$) and the nearest Eastern Mistbelt neighbour ($S = 0.76 + 0.41I$; $F_{1,29} = 16.39$, $P = 0.001$, $r^2 = 0.34$). Interestingly, the more isolated nodes were characterised by higher bird species richness than less-isolated nodes. The effect of isolation on species richness for northern and southern nodes separately, was insignificant for all three isolation measures. Again, this indicated that bird dispersal in the MDTP was likely occurring and provides support for the colonization-dependent enrichment of local forests.

3.4 Nestedness

Bird assemblages in Drakensberg Montane forests were significantly nested i.e. depauperate assemblages were generally subsets of more species rich assemblages. Drakensberg Montane forests deviated from perfect nestedness by 9.3% ($U_t = 130$, $P < 0.01$; Table 4). Bird assemblage structure was not dominated by either unexplained absences or presences ($U_a = 61.2$, $U_p = 68.8$, Table 4), suggesting a more or less equal role of selective extinctions and colonisations in determining assemblage structure in these forests. The C-score was low (0.057) and did not show a significantly higher observed index value compared to the simulated values.
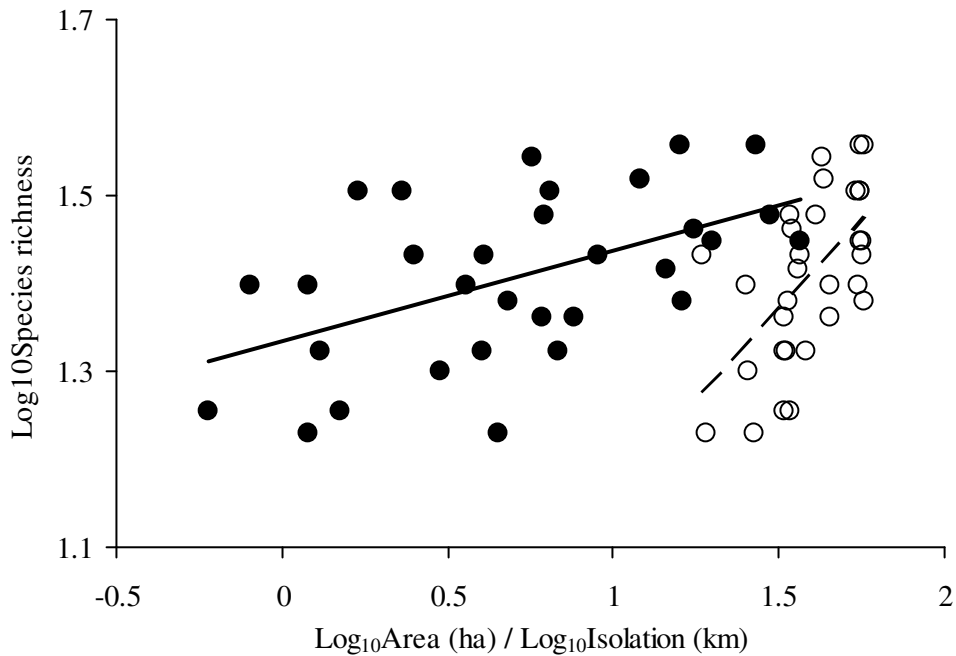
Fig. 4 - Comparison of log species–log area (●,——) and log species–log isolation (nearest Eastern Mistbelt neighbour; ○, ----) regressions of Drakensberg Montane forests.

It appears that bird communities were not structured by strong local competitive interactions, supporting findings that communities in Afrotemperate forests are unsaturated (see Lawes et al., 2000a) and that biological interactions are insufficient to limit local diversity or that diversity is dependent on the size and history of establishment of the species pool.

The forest dependent bird assemblages were also significantly nested. The FD bird assemblage deviated from perfect nestedness by 14.5% ($U_t = 126$, $P < 0.01$; Table 4). In a similar pattern to that of the full suite of species occurring in forest patches, the FD suite of species was also not hole-rich nor outlier dominated ($U_a = 66.0$, $U_p = 60.0$, Table 4).

The potential mechanism of nestedness (%PN; Table 5) was strongly associated with isolation for Drakensberg Montane forests (for both the full complement of bird species and for forest dependent bird species). The number of departures from perfect nestedness (D) was generally fewer for the isolation-ordered matrices than for area-ordered matrices (Table 5). Selective immigration rather than selective extinction influenced bird species composition in Afromontane forest patches. However, comparison of P for the three different isolation metrics revealed that only the "nearest Eastern Mistbelt" metric had a significant effect. Colonisation of Drakensberg Montane forest patches was therefore

mainly from the nearest Eastern Mistbelt forest rather than the nearest forest or the nearest larger forest (Table 5).

The degree of nestedness was not significant for the area-sorted matrix, for either the full bird compliment or the FD species. In general, selective immigration rather than selective extinction appears to play a stronger role in influencing bird species composition in Afromontane forest.

Table 4 – Summary of the analysis of nestedness of bird assemblages, total and forest dependent, in Drakensberg Montane forests. U_a = unexpected absences, U_p = unexpected presences, U_t = total, P refers to the probability that the observed U_t values could be derived from the population of archipelagos simulated by the Monte Carlo program.

	Sites	Species	U_a	U_p	U_t (%)	P
Total species	31	45	61.2	68.8	130 (9.3)	<0.01
Forest dependent species	31	28	66.0	60.0	126 (14.5)	<0.01

Table 5 - Results of the nestedness analysis investigating potential causality by counting the number of departures from perfect nestedness (D) in a matrix sorted by area and then by isolation. P is the proportion of randomly ordered matrices with D values ≤ that of the ordered matrix; %PN is percent deviation from perfect nestedness; R, average D value for 1000 randomly ordered matrices.

	Area-sorted matrix			Isolation-sorted matrix			Randomised
	D	P	%PN	D	P	%PN	R
All species							
- nearest neighbour	160	0.357	1.9	151	0.080	7.4	163.113
- nearest larger neighbour	160	0.381	1.9	173	0.905	-6.1	163.117
- nearest Eastern Mistbelt	160	0.369	1.9	134	0.001	17.8	163.051
Forest dependent species							
- nearest neighbour	99	0.534	-0.1	93	0.166	6.0	98.919
- nearest larger neighbour	99	0.530	-0.2	107	0.938	-8.3	98.817
- nearest Eastern Mistbelt	99	0.527	0.0	81	0.001	18.1	98.959

3.5 Regional versus local analysis

For the GLMs of local species richness as a function of local and/or regional affects, the best fit model included regional richness of FD species derived from Afrotemperate (Eastern Mistbelt) forests in four adjacent QDS, local forest area, the line of sight distance between the locality and the region, and the distance between the locality and the region along the topography (although the latter variable dropped out when one applied the corrected AIC) (Table 6). The only variable excluded by the best fit model was the nearest-neighbour forest distance.

Table 6 – Information-theoretic model selection for the environmental correlates of local species richness. Only the best-fitting model (lowest AIC_c value) is presented for each of four measures of regional species richness (C1, C4, EM1, EM4). w_i is the Akaike weight of evidence in favour of the given model being the best-fit model among the candidate set of models (note: there were a set of candidate models for each estimate of regional species richness), and is provided for the best fit model only. (Abbreviations: Area – size (ha) of the locality, DistLOS - line of sight distance from locality to regional forest, NNdist – distance between locality and nearest forest patch, TopoDist – topographical distance from locality to regional forest, RegSR – regional species richness.)

Regional species richness estimate*	Model	AICc	Deviance	df	w_i
C1	Area + DistLos + TopoDist	94.34	80.34	4	
C4	Area + NNDist + TopoDist + RegSR	81.40	58.07	5	
EM1	Area + DistLos + NNDist + TopoDist + RegSR	57.04	15.04	6	
EM4	Area + DistLos + RegSR	23.68	9.68	5	0.74

* Area used to determine regional species richness: C1 = local catchment of 1 quarter degree square (QDS); C4 = local catchment of 4QDS; EM1 = nearest Eastern Mistbelt forest in 1QDS; EM4 = nearest Eastern Mistbelt forest in 4QDS.

The importance of each variable was estimated as the sum of the model probabilities from all-subsets regression for those models including the variable. Variable weights were 1 for Area, DistLOS and RegSR, confirming the notable effect that these three variables have on local species richness. TopoDist had an effect on local species richness, albeit small (0.255), and NNDist (0.007) had virtually no effect on local species richness. Thus, as expected the area of the locality had an important effect on local species richness, but so did the regional variables, richness of the regional species pool and line of sight distance ($F_{2,7} = 30.11$, $p < 0.001$). Local species richness increased with increasing regional species richness and the area of the local forest, and decreased with increasing distance from the source (regional species pool) (Table 7).

The latter implies that localities were regionally enriched and derived their species from the surrounding region within the constraints of available habitat at a locality. The proximity of a locality to the nearest local forest was not important (0.007) and the distance of the locality from the regional species pool following the topographic contours was relatively unimportant (0.25). The avifauna of Drakensberg Montane forests was clearly enriched from the adjacent regional species pool, and richness at a locality was only constrained by the area of the local forest.

Table 7 – Results of regression analysis (for the best-fit model only) comparing the effects of local and regional variables on local species richness for birds in Drakensberg Montane forests.

Parameter	Coefficient	SE	t	P
Constant	-31.94	5.74	-5.56	<.001
Area	1.592	0.168	9.48	<.001
DistLOS	-0.830	0.118	-7.01	<.001
NNdist	-0.002	0.004	-0.40	0.688
TopoDist	0.030	0.011	2.70	0.007
RegSR	1.295	0.148	8.77	<.001

4. Discussion

The influence of local-scale factors are widely held to be important in determining species richness of communities, though it has been recognized that regional-scale influences also affect community dynamics (Ricklefs, 2007; Harrison and Cornell, 2008). To develop an effective strategy for biodiversity conservation, knowledge of the relative importance of both local and regional scale processes is vital. In the Drakensberg Montane forests of this study, local species richness was affected by both local and regional landscape attributes, as well as by contributions from the regional species pool. In particular, the data show that local bird assemblages accumulate subject to the local constraint of forest patch area, and to the regional constraints of proximity and size of the regional species pool. Thus, the dual effects of local and regional processes are revealed in these findings. This interpretation is similar to many studies where local richness of communities was not strictly dependent on local conditions but was also affected by regional richness (Cornell and Lawton, 1992; Cornell, 1993; Ricklefs and Schluter, 1993; Mouquet et al., 2003; Karlson et al., 2004). The attempts to determine the patterns in and determinants of regional richness variation have led to the emergence of the field of macroecology (Brown and Maurer, 1987; Brown, 1995). Although not the focus of this study, it is important to recognize the potential sources of variation for regional effects. That regional effects are important has been widely studied, and Cornell and Lawton (1992), in their review of local and regional effects on communities, identify habitat heterogeneity, high productivity and habitat stability as three of the main mechanisms. Furthermore, Gotelli and Ellison (2002) found that latitudinal trends, elevation, light availability and vegetation composition were important sources of a regional effect.

This study showed that bird assemblages exhibit significant non-random distribution patterns among forest patches. In particular, species richness of birds was positively, but weakly, dependent on forest patch area. Small forest patches supported fewer bird species than large forest patches. The positive response of bird species richness to increasing area has been extensively and consistently documented both in temperate and tropical forests at several spatial scales (Ambuel and Temple, 1983; Howe, 1984b; Blake and Karr, 1987; Newmark, 1991; Willson et al., 1994; Bellamy et al., 1996; Stratford and Stouffer, 1999; Cornelius et al., 2000). Notably, studies undertaken in Afrotemperate forests reveal similar positive species-area relationships (SAR) to our own (Dowsett-Lemaire and Dowsett, 1980; Newmark, 1991; Wethered and Lawes, 2003), possibly

demonstrating a pervasive role for local (area-based) influences on species richness in Afrotemperate forests.

Similar to our study, Wethered & Lawes (2003) and Castley (1997) obtained a shallow slope for bird species-area relationships in Afrotemperate forest patches. Good dispersal ability reduces the slope of species-area relationships by reducing species turnover between habitat patches, thereby homogenizing local communities (Preston, 1962; Mouquet and Loreau, 2002; Leibold et al., 2004). The slope of the curve in Drakensberg Montane forests ($z = 0.10$) was slightly lower than that predicted by MacArthur & Wilson (1967) for insular habitats within continents (0.12 – 0.19). In comparison, Preston (1962) predicted values of 0.20 – 0.40 for real islands (i.e. truly isolated), while for mainlands or habitat patches within continuous habitats, z values are generally lower (0.10 – 0.20) (MacArthur and Wilson, 1967; Diamond and May, 1976; Gilbert, 1980; Watling and Donnelly, 2006). The shallow "species-relaxation" slope suggests that avian assemblages in these Afromontane forest patches primarily comprise species that either have good dispersal abilities or are highly tolerant of the heterogenous landscape.

In many cases, the fauna of naturally fragmented systems appear to have evolved strategies for coping with a naturally heterogenous environment (McGarigal and McComb, 1995). The apparent resilience of forest-dwelling birds in naturally patchy forests has led some to conclude that these species are adapted to patch discontinuity through long association with historic disturbance regimes (Hejl, 1992; McGarigal and McComb, 1995; Schmiegelow and Monkkonen, 2002; Lawes et al., 2007b). Such is the case for this study, where the long-term adaptation of fauna to an intensely patchy and climatically extreme environment has resulted in a highly mobile and robust faunal community (Lawes et al., 2000b; Lawes et al., 2007b), and this may explain why bird communities of these montane forests are not strongly determined by local area-dependence. That species richness varied significantly but relatively little as a function of area suggests that other factors, mainly regional influences, had a greater influence on local species richness than the local influence of forest area.

Local species richness, while it may reflect the interplay of intrinsic local processes and current environmental conditions that enable species to persist, is also determined by regional richness and the past conditions that have enabled species to accumulate (Brown, 1995). Our results provide further support for this theory, and show that localities were enriched from their respective regions, and that enrichment appeared to be dependent on the

relative size of the locality as well as the size of the respective regional species pools. Similarly, Lawes et al. (2000a) found that local richness of forest birds was strongly influenced by enrichment from the regional pool, but only in regions with low species richness (< approx. 70 species). Furthermore, recent evidence suggests that large scale processes, such as radiation, speciation and climatic extinction filtering can determine the diversity of the regional species pool and therefore set upper limits to the number of species within local assemblages (Ricklefs, 1987; Cornell and Lawton, 1992; Hugueny and Cornell, 2000; Karlson et al., 2004; Ricklefs, 2004).

In the context of local versus regional processes, there are several relevant results from this study. Firstly, local species richness is related, albeit weakly, to the size of the local forest patch and to the distance of the nearest montane forest patch. Thus, local factors do play some role in determining local diversity patterns. Secondly, the diversity of local bird assemblages is strongly related to regional differences in species richness. Thus, local diversity patterns are influenced by more than local environmental factors and a broader regional perspective of drivers of community composition is required to understand them. Birds are a highly vagile taxon and possess good colonising potential, hence their community assemblages, in general, tend to show regional enrichment (Lawes et al., 2000a). Thirdly, regional species richness varies between the eight regions and regional enrichment of localities appears to be dependent on the relative size of the respective regional species pools. Clearly, the dynamics of bird assemblages must be studied at multiple scales. In this case, ecological processes operating at the scale of individual forest patches and larger metacommunities represent potentially important sources of variation in local diversity in Drakensberg Montane forests.

Conservation implications

Understanding the local, historical and biogeographical influences that Drakensberg Montane forests have been subjected to is essential for the effective management of these avian communities. Thus, to conserve Drakensberg Montane forest bird assemblages it is critical to protect Eastern Mistbelt forests, the regional source of species for the Drakensberg. In addition, naturally patchy ecosystems need to be assessed and managed with both local and regional influences in mind, and within the context of landscape mosaics.

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Appendix A - Landscape pattern metrics for forest of 20 catchments within the MDTP, 15 catchments with Drakensberg Montane forest and 5 catchments with Eastern Mistbelt forest.

Metrics	Catchment ID	North									South
		C774	C813	C807	C818	C853	C836	C887	C884	C900	C941
	Forest Type	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane	Drakensberg Montane
Area	Forest area (ha)	674.41	28.26	49.41	192.77	718.93	751.91	828.21	459.18	159.62	221.93
	Catchment area (ha)	25 244.73	28 338.33	14 404.31	25 263.21	31 348.54	29 378.39	23 170.03	34 155.63	28 026.11	41 814.23
	% of catchment	2.67	0.10	0.34	0.76	2.29	2.56	3.57	1.34	0.57	0.53
	No. of patches	158	16	10	115	283	165	120	112	139	105
	Patch density	0.63	0.06	0.08	0.51	0.99	0.61	0.60	0.35	0.59	0.26
	Mean patch size (ha)	4.22	1.66	4.50	1.44	2.32	4.21	5.91	3.65	0.97	2.02
	Patch size SD	6.55	2.01	9.37	3.61	6.20	11.51	15.7	9.14	1.35	3.24
Isolation	Mean Euclidean nearest neighbour	109.64	485.21	1418.88	158.99	118.25	125.93	107.90	287.38	221.93	229.31
	Euclidean nearest neighbour SD	114.26	941.24	2622.65	252.80	206.27	211.25	132.25	739.86	366.46	254.95
Proximity	Mean proximity index	43.22	3.09	8.29	31.37	26.64	33.20	86.96	24.50	5.79	13.56
	Proximity index SD	115.61	4.33	22.93	103.99	78.47	71.99	220.02	51.81	15.23	51.90
Contagion	Clumpiness index	0.91	0.88	0.94	0.86	0.88	0.91	0.93	0.93	0.85	0.88
Connectivity	Patch cohesion index	96.84	95.58	98.98	95.87	96.5	97.77	97.93	97.31	93.11	96.03
Size classes	<2 ha	89	11	8	94	211	103	60	70	118	76
	2-10 ha	50	5	0	18	58	45	45	30	21	24
	10-20 ha	13	0	1	1	8	10	5	10	0	5
	20-60 ha	6	0	1	2	5	6	8	1	0	0
	60 -100 ha	0	0	0	0	1	0	1	1	0	0
	>100 ha	0	0	0	0	0	1	1	0	0	0
	Largest Patch	42.60	6.53	29.49	29.57	80.57	121.61	146.39	92.02	6.33	19.61

Metrics	Catchment ID	North				South	North				South
		C952	C961	C997	C1063	C1076	C966	C986	C998	C1002	C1024
		Drakensberg	Drakensberg	Drakensberg	Drakensberg	Drakensberg	Eastern	Eastern	Eastern	Eastern	Eastern
	Forest Type	Montane	Montane	Montane	Montane	Montane	Mistbelt	Mistbelt	Mistbelt	Mistbelt	Mistbelt
Area	Forest area (ha)	103.55	100.61	51.38	15.02	20.09	462.26	1 075.37	1 490.07	220.97	1 641.42
	Catchment area (ha)	33 700.72	39 208.14	32 733.18	50 865.51	60 192.68	29 334.71	32 716.30	37 899.33	25 546.23	46 144.53
	% of catchment	0.31	0.26	0.16	0.03	0.03	1.58	3.29	3.93	0.86	3.56
	No. of patches	61	74	22	11	26	26	32	42	19	49
	Patch density	0.19	0.19	0.07	0.02	0.04	0.11	0.10	0.11	0.06	0.11
	Mean patch size (ha)	1.64	1.29	2.33	1.36	0.77	13.89	26.46	28.48	13.92	18.16
	Patch size SD	2.25	1.42	2.81	1.37	0.59	28.45	56.68	52.74	19.03	66.35
Isolation	Mean Euclidean nearest neighbour	220.46	376.85	295.37	1 256.84	669.90	355.17	328.78	190.00	1 005.46	438.88
	Euclidean nearest neighbour SD	342.29	644.73	379.54	1769.78	1004.35	1323.05	494.35	225.58	2091.30	687.47
Proximity	Mean proximity index	8.67	4.13	1.51	0.21	1.20	52.82	144.37	294.25	2.07	38.74
	Proximity index SD	24.12	12.02	1.57	0.25	2.04	110.36	369.09	991.16	3.12	90.29
Contagion	Clumpiness index	0.86	0.85	0.89	0.85	0.81	0.96	0.95	0.96	0.61	0.97
Connectivity	Patch cohesion index	95.13	93.78	96.41	95.41	91.66	98.84	99.16	99.19	84.73	99.20
Size classes	<2 ha	46	59	15	9	24	9	6	13	6	25
	2-10 ha	14	15	7	2	2	8	11	11	8	13
	10-20 ha	1	0	0	0	0	4	4	6	2	1
	20-60 ha	0	0	0	0	0	2	5	5	2	5
	60 -100 ha	0	0	0	0	0	1	4	3	1	1
	>100 ha	0	0	0	0	0	2	2	4	0	4
	Largest Patch	12.42	8.25	8.73	4.75	2.78	122.41	329.84	329.84	69.29	488.73

Appendix B - Species list for birds recorded in Drakensberg Montane and Eastern Mistbelt forests (x indicates a species presence), including the forest dependency (FD) of each.

Common name	Scientific name	Family	FD	Drakensberg Montane	Eastern Mistbelt
African dusky flycatcher	*Muscicapa adusta*	Muscicapidae	D	x	x
African emerald cuckoo	*Chrysococcyx cupreus*	Cuculidae	D	x	x
African firefinch	*Lagonosticta rubricata*	Estrildidae	-	x	
African goshawk	*Accipiter tachiro*	Accipitridae	D	x	
African harrier-hawk	*Polyboroides typus*	Accipitridae	-	x	x
African olive-pigeon	*Columba arquatrix*	Columbidae	D	x	x
African paradise-flycatcher	*Terpsiphone viridis*	Monarchidae	D	x	x
African wood-owl	*Strix woodfordii*	Strigidae	D	x	
Amethyst sunbird	*Chalcomitra amethystina*	Nectariniidae	-	x	x
Barratt's warbler	*Bradypterus barratti*	Sylviidae	D	x	x
Bar-throated apalis	*Apalis thoracica*	Cisticolidae	D	x	x
Black cuckoo	*Cuculus clamosus*	Cuculidae	-	x	x
Black kite	*Milvus migrans*	Accipitridae	-	x	
Black sparrowhawk	*Accipiter melanoleucus*	Accipitridae	-		x
Black-backed puffback	*Dryoscopus cubla*	Malaconotidae	D	x	x
Black-collared barbet	*Lybius torquatus*	Lybiidae	-	x	x
Black-headed oriole	*Oriolus larvatus*	Oriolidae	D	x	x
Blue-mantled crested-flycatcher	*Trochocercus cyanomelas*	Monarchidae	D	x	x
Buff-spotted flufftail	*Sarothrura elegans*	Rallidae	-	x	x
Bush blackcap	*Lioptilus nigricapillus*	Sylviidae	D	x	x
Cape batis	*Batis capensis*	Malaconotidae	D	x	x
Cape robin-chat	*Cossypha caffra*	Muscicapidae	D	x	x
Cape turtle-dove	*Streptopelia capicola*	Columbidae	-	x	x
Cape white-eye	*Zosterops capensis*	Zosteropidae	D	x	x
Chinspot batis	*Batis molitor*	Malaconotidae	-		x
Chorister robin-chat	*Cossypha dichroa*	Muscicapidae	D	x	x
Collared sunbird	*Hedydipna collaris*	Nectariniidae	D		x
Common waxbill	*Estrilda astrild*	Estrildidae	-	x	
Crested guineafowl	*Guttera edouardi*	Numididae	D		x
Crowned eagle	*Stephanoaetus coronatus*	Accipitridae	D		x
Dark-backed weaver	*Ploceus bicolor*	Ploceidae	D		x
Dark-capped bulbul	*Pycnonotus tricolor*	Pycnonotidae	-	x	x
Drakensberg prinia	*Prinia hypoxantha*	Cisticolidae	-		x
Forest canary	*Crithagra scotops*	Fringillidae	D	x	x
Fork-tailed drongo	*Dicrurus adsimilis*	Dicuruidae	-	x	x
Goldentailed woodpecker	*Campethera abingoni*	Picidae	D		x
Greater double-collared sunbird	*Cinnyris afer*	Nectariniidae	-	x	x
Green-backed camaroptera	*Camaroptera brachyura*	Cisticolidae	D		x
Green wood-hoopoe	*Phoeniculus purpureus*	Phoeniculidae	-		x
Grey cuckooshrike	*Coracina caesia*	Campephagidae	D	x	x

Common name	Scientific name	Family	FD	Drakensberg Montane	Eastern Mistbelt
Hadeda ibis	*Bostrychia hagedash*	Threskiornithidae	-	x	x
Klaas's cuckoo	*Chrysococcyx klaas*	Cuculidae	-	x	
Knysna turaco	*Tauraco corythaix*	Musophagidae	D		x
Lemon dove	*Aplopelia larvata*	Columbidae	D	x	x
Little sparrowhawk	*Accipiter minullus*	Accipitridae	D		x
Narina trogon	*Apaloderma narina*	Trogonidae	D		x
Natal spurfowl	*Pternistis natalensis*	Phasianidae	-	x	
Olive bush-shrike	*Telophorus olivaceus*	Malaconotidae	D	x	x
Olive thrush	*Turdus olivaceus*	Muscicapidae	D	x	x
Olive woodpecker	*Dendropicos griseocephalus*	Picidae	D	x	x
Orange ground-thrush	*Zoothera gurneyi*	Muscicapidae	D		x
Red-chested cuckoo	*Cuculus solitarius*	Cuculidae	-	x	x
Red-eyed dove	*Streptopelia semitorquata*	Columbidae	-	x	x
Red-fronted tinkerbird	*Pogoniulus pusillus*	Lybiidae	D		x
Red-necked spurfowl	*Pternistis afer*	Phasianidae	D	x	x
Red-winged starling	*Onychognathus morio*	Sturnidae	-	x	x
Rufous-chested sparrowhawk	*Accipiter rufiventris*	Accipitridae	D	x	
Scaly-throated honeyguide	*Indicator variegatus*	Indicatoridae	D		x
Sombre greenbul	*Andropadus importunus*	Pycnonotidae	D	x	x
Southern black tit	*Parus niger*	Paridae	D	x	x
Southern boubou	*Laniarius ferrugineus*	Malaconotidae	D	x	x
Southern double-collared sunbird	*Cinnyris chalybeus*	Nectariniidae	-	x	x
Speckled mousebird	*Colius striatus*	Coliidae	-	x	x
Spotted flycatcher	*Muscicapa striata*	Muscicapidae	-		x
Square-tailed drongo	*Dicrurus ludwigii*	Dicuruidae	D		x
Steppe buzzard	*Buteo vulpinus*	Accipitridae	-		x
Swee waxbill	*Coccopygia melanotis*	Estrildidae	D	x	
Terrestrial brownbul	*Phyllastrephus terrestris*	Pycnonotidae	D		x
Thick-billed weaver	*Amblyospiza albifrons*	Ploceidae	-		x
White-starred robin	*Pogonocichla stellata*	Muscicapidae	D	x	x
Yellow-bellied greenbul	*Chlorocichla flaviventris*	Pycnonotidae	-		x
Yellow-breasted apalis	*Apalis flavida*	Cisticolidae	D		x
Yellow-throated woodland-warbler	*Phylloscopus ruficapilla*	Sylviidae	D	x	x

CHAPTER 4

CONSERVATION AND MANAGEMENT

The small, isolated forests of the Drakensberg region provide an interesting situation to examine how a naturally and historically patchy landscape affects community assemblage and resilience of forest avifauna.

- Drakensberg Montane and the lower altitude Eastern Mistbelt forests have distinct bird species assemblages. Notably however, the Drakensberg Montane bird assemblages are a subset of the more species rich Eastern Mistbelt assemblages. This suggests that Eastern Mistbelt forests act as a species source pool for Drakensberg Montane forests.
- Small forest patches have fewer species per unit area than larger forest patches, suggesting some local control on species assembly. However, the weak island-effect suggests that factors other than area are also having an effect on species composition.
- Isolation of forest patches, particularly from Eastern Mistbelt forests, had a strong influence on species richness. This suggests that distance from the 'source' forest influences species composition, highlighting the role of regional-scale processes in determining species assemblages.
- Bird species assemblages are characterised by a non-random species distribution pattern where isolation-dependent processes are dominant, and the immigration of bird species from patches follows a predictable and deterministic sequence. Nestedness is attributable to selective immigration rather than area-based extinction.
- Drakensberg forest assemblages are enriched from the adjacent Eastern Mistbelt forests, and the species richness of the Eastern Mistbelt forests (regional source pool) directly influenced the species richness of the locality.
- Local species richness (of Drakensberg forests) is attributable to both local and regional influences. Localities are regionally enriched within the constraints of available forest habitat.
- At the landscape level it is clear that the Eastern Mistbelt forests affect the species composition of Drakensberg Montane forests. Consequently, for the conservation of

Drakensberg Montane avifauna, Eastern Mistbelt forests must be considered an integral part of the landscape mosaic.

- Small forest patches (≥ 3.4 ha) are able to support a fully functional avian community, one that is able to provide all the ecosystem functions necessary for continued ecological functioning and thus persistence of the forest avifauna.

- The forest bird community of Drakensberg Montane forests is very resilient, with 25% of the bird species exhibiting functional redundancy. The high level of redundancy therefore imparts resilience to the bird community as a whole.

- The results of this study emphasise the importance of understanding local- and landscape-scale processes, both past and present, and prove valuable for predicting community level responses to landscape change, for forest bird species.

The forest-grassland mosaic of the high-altitude Drakensberg Mountains, KwaZulu-Natal, South Africa, presents a number of challenges to the local forest fauna. Firstly, the region experiences marked seasonal climatic fluctuations, often with snow and frost. Secondly, the forests are very small, on average 3 ha in area. Lastly, the forests are isolated from one another, as well as from the larger 'mainland' Eastern Mistbelt forests. Thus, fauna of Drakensberg Montane forests must contend with climatic extremes and an intensely patchy network of small forests. To understand how the contemporary avifauna persist in such a landscape, it is useful to understand the biogeographical history of the landscape. The forests of the Drakensberg are not the result of modern anthropogenic fragmentation. Rather, these forests are naturally small and patchy as a result of the repeated and drastic climate changes of the late Quaternary. During the cold, dry conditions of the Last Glacial Maximum (18000 y BP), Drakensberg Montane forests were likely forced to lower elevations and potentially occupied sites currently occupied by Eastern Mistbelt forest (Eeley et al., 1999). As climatic conditions became warmer and moister, forests re-established in previously occupied sites. The process of forest shrinkage and expansion occurred repeatedly, and the extinction filtering events (*sensu* Balmford, 1996) during these climatic extremes have resulted in resilient forest communities that display good colonizing ability, high persistence and tolerance of extreme environments (Lawes et al., 2000b; Lawes et al., 2005; Kotze and Lawes, 2007; Lawes et al., 2007a). The Drakensberg forests are thus relatively resilient, both in terms of the small size of functioning forest patches, and the relatively high number of functionally redundant bird species (Chapter 2). Furthermore, both

local (area) and regional (isolation from Eastern Mistbelt forests) factors emerge as important determinants of faunal composition in these forests (Chapter 3).

It is interesting to note that the avifaunal assemblage of Drakensberg Montane forests have no endemic species, rather, all the bird species that occur in Drakensberg Montane forests also occur in the Eastern Mistbelt forests or in other habitat types. This is the exception rather than the 'norm', as Afrotemperate forests throughout the continent tend to support a number of endemic birds. In particular, endemism for birds peaks in the tropical montane forest ecoregions of the Cameroon Highlands of western Africa, the Albertine Rift of central Africa and the Eastern Arc of eastern Africa (Burgess et al., 2006). The lack of endemism in Drakensberg Afrotemperate forests may be a result of climatic conditions. In the broad analysis of where MDTP forests fall within the bioclimatic envelope of Afrotemperate forests throughout Africa, it was found that MDTP forests experience lower mean annual temperatures than the other forests. Thus, the current climate, and possibly the drastic and repeated climatic fluctuations of the past, may have played a role in the lack of avian endemism in Drakensberg Montane forests.

The best way to minimize species loss is to maintain the integrity of ecosystem function (Walker, 1992). To achieve this it is necessary to quantify the area of habitat required to sustain an ecologically functional unit. In this study, that minimum area to maintain montane forest bird communities is 3.4 ha. Although the model predicts 3.4 ha as a functioning unit, in all likelihood the avifauna of this system require a larger network of forest patches and grassland matrix to persist. The highly vagile nature and the good colonizing potential of birds in this historically patchy system tends to suggest that birds may derive necessary resources not just from a single forest patch, but also from the surrounding forests and matrix. Thus, forest patches in this landscape do not function as true islands. Against this background, defining a minimum forest area required for maintaining a functioning and resilient ecosystem may not be entirely valid. Moreover, by conserving a greater number of forests, and where possible larger forest patches, the stability of the ecosystem is increased (Armsworth and Roughgarden, 2003). Cook and Quinn (1995) suggest that if colonization is important in generating a nested pattern, as in this study (Chapter 3), minimum critical areas for conservation may be difficult to determine, and protection of multiple sites may be required. Therefore, to maintain a functional ecosystem that is resilient to future change, it is necessary to conserve the largest possible area encompassing a mosaic of multiple forest patches and interspersing grassland.

In addition, to further focus conservation efforts, we need to establish how much (or how little) redundancy there is in the species composition of ecosystems (Chapter 2). Redundancy provides resilience to a system against potential environmental changes, both natural and anthropogenic, and is therefore essential for continued ecosystem functioning. A system with a high level of species redundancy would thus be capable of withstanding relatively high levels of environmental disturbance. In contrast, a system with little species redundancy would need to be intensively managed to withstand any form of disturbance, if a fully functioning ecosystem were to be maintained. Thus, given that this Drakensberg forest system has a high level of species redundancy, it is advisable to focus conservation efforts on maintaining the patterns and processes that underlie the system. In this regard, biodiversity conservation issues are ultimately concerned with higher-level processes and are rightly addressed over broad spatial scales (Urban et al., 1987; Gustafson and Parker, 1994). Although species may be maintained by local processes in the short-term, stable ecosystem functioning is possible only when regional-scale processes are addressed. The design of conservation reserves must consider the spatial relationships of habitat reserves in the context of the broader landscape. In terms of avian conservation in the Drakensberg, we need to conserve the regional source pool of species for the Drakensberg Montane forests, as well as the local forests themselves (Chapter 3). Following the initial migration of birds from the Eastern Mistbelt forests to the Drakensberg Montane forests, birds are likely to move amongst and between Drakensberg Montane forests. However, movement between forests may be limited to forests within the same catchment, as a steep watershed may hinder movement between catchments. Nevertheless, species composition is similar throughout the forests, with very little species turnover (Chapter 2). Notably, the continued movement of birds from the Eastern Mistbelt forests to the Drakensberg Montane forests is critical for the long-term persistence of the Drakensberg Montane avifauna.

An important component in contemporary conservation management planning is the potential impact of climate change on ecosystems. Climate change has received much attention as a major factor influencing biodiversity, and as such needs to be addressed. In light of the numerous climatic perturbations that the Afrotemperate forests in the Drakensberg have undergone during the Quaternary, and that communities demonstrate far more resilience to modern threats if they have faced similar challenges in the past (Balmford, 1996; Danielsen, 1997), it may seem that this system is unlikely to experience drastic biodiversity losses due to current climate change. Rather, it has been suggested that

the robust and persistent suite of bird species in Afrotemperate forests (a result of repeated extinction filtering events during the Quaternary) is adapted to climatic fluctuations (Lawes et al., 2000a; Lawes et al., 2007c). However, it is worth noting that the response of Drakensberg Montane forest avifauna to climate change is dependent on the similarity of contemporary climate change to that of the past. This poses a problem as current climate changes are occurring on a much shorter time scale than historically. Thus, although this system has been through numerous extinction filtering events it is likely that current climate changes, occurring at such an unprecedented rate, may very well have some impact on the avifauna, though the loss of biodiversity in Drakensberg Montane forests may not be as drastic as the avifaunal communities of historically climatically stable forests.

Management and conservation recommendations

- The conservation of forest bird assemblage structure and diversity in Drakensberg Montane forests requires the protection of forest patches of a minimum critical patch size (3.4 ha). However, the positive species-area relationship and the presence of nestedness clearly suggest that in terms of a management strategy, the priority remains to conserve the largest forest patches.

- Birds form only a part of the broader ecosystem in the Drakensberg Montane forests, and it must be remembered that the minimum critical patch size of 3.4 ha does not consider the requirements of other taxa.

- In addition to conserving local forest patches, conservation initiatives need to include the regional species source, the Eastern Mistbelt forests. All Drakensberg Montane forests currently fall within the Maloti Drakensberg Transfrontier project bioregion and are therefore afforded varying levels of protection, whereas only 25% of Eastern Mistbelt forests fall within the bioregion. Conservation initiatives should therefore focus on conserving Eastern Mistbelt forests throughout the province.

- If the 'climatic filtering' hypothesis is correct, and the resilience of the contemporary forest avifauna is a result of past climate change, then it is likely that future climate change may not affect this species community as dramatically as landscapes that have had a climatically stable history. Nevertheless, considering that current climate change is occurring at an unprecedented rate, there may still be cause for concern as the bird assemblages of this landscape are not adapted to such intense change.

- With a better understanding of the processes that influence interactions between the forest avifauna and the Drakensberg forest-grassland landscape, it is possible to conserve species through habitat management that aims to preserve the ecological processes that operate to maintain a stable avian community.

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