Bird Community Structure and Convergence in Afromontane Forest Patches of the Karkloof / Balgowan Range, KwaZulu-Natal

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2001

FOReST
BiODiVERSiTY
PROGRAMME
UNIVERSITY OF NATAL

Bird Community Structure and Convergence in Afromontane Forest Patches of the Karkloof / Balgowan Range, KwaZulu-Natal.

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Submitted in fulfilment of the academic

requirements for the degree of

Master of Science

in the

School of Botany and Zoology

Department of Zoology and Entomology

University of Natal
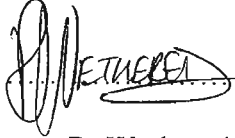
Pietermaritzburg

May 2001

Mom and Dad,

thanks for everything – this is for you!

Preface

This study was carried out in the School of Botany and Zoology, Forest Biodiversity Programme, University of Natal, Pietermaritzburg, from December 1998 to May 2001, under the Supervision of Prof. M. J. Lawes.

The study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work of others, it has been acknowledged in the text.

The chapters of the thesis are written in accordance with the required format for submission to the journal *Biodiversity and Conservation*. The chapters depart from this format in the following areas: 1) tables and figures appear in the text and not on separate sheets at the end of each chapter, 2) one acknowledgements section, and 3) one summary with information on all the chapters, is provided at the beginning of the thesis.

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R. Wethered

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Forest fragmentation is caused by the clearing of patches of indigenous vegetation for agriculture, urban development, and other human land uses. Such action results in patches of remnant natural vegetation being surrounded by altered vegetation. I investigate the effects of forest fragmentation and matrix type on avian diversity and assemblage structure in forest patches of the historically fragmented Karkloof / Balgowan forest range, KwaZulu-Natal, South Africa. This study compares the bird assemblage diversity and composition of indigenous forest patches surrounded by commercial forestry (Gilboa complex) with that surrounded by natural grassland matrix (Balgowan complex).

Insularisation of Afromontane Mistbelt forest in KwaZulu-Natal has led to loss of species where forest fragments support fewer bird species than comparably sized patches of mainland forest. Small fragments within natural grassland have fewer bird species per unit area than larger fragments. Forest patch area-dependent density compensation is evident and bird assemblages appear saturated. Bird assemblages are characterised by a non-random species distribution pattern where area-dependent processes are dominant, and the loss of species from fragments follows a deterministic sequence. In forests in the plantation-dominated matrix no island-effect is detectable and it appears that forest patches are converging on the same bird species richness, regardless of forest size. No density compensation is evident and bird assemblages are not saturated. The sequence of species loss from forest patches is not as predictable, where a random yet prominent colonisation process exists. As commercial plantations provide suitable habitat cover for movement of forest birds, colonisation of both distant and small indigenous forest patches has been possible, reducing the effects of area-dependent extinction in the forest patches but also resulting in lower species richness in larger patches.

Bird species of the Karkloof / Balgowan forest range appear to be fragmentation adapted, and most species are resilient to further landscape change. Certain species are however more prone to local extinction than others. The major predictors of extinction risk are body size, abundance status, and feeding guild. Patch area is the dominant force governing traits in the natural Balgowan complex where larger species with low natural abundance and an insectivorous diet are most prone to local extinction. In the Gilboa complex the nature of the plantation matrix appears to be masking the species natural responses to fragmentation making it difficult to predict which species are most at risk.

In order to preserve maximum bird diversity, including high-risk species, the largest intact forest units ($\geq$302ha) must be conserved. Evidently, the nature of the matrix affects avifaunal diversity and distribution in forest patches, and plantations have the capacity to significantly alter bird assemblage structure and composition in indigenous forest patches. Forest fragments must be considered as integrated parts of a complex landscape mosaic, and this study emphasises the importance of understanding landscape-scale processes. Knowledge of ecological and life history traits proves valuable for predicting community level response to landscape change.

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CHAPTER 1

Introduction

Alteration of habitat by human activity is the greatest threat to the earth's biodiversity. Direct removal of habitat is the most obvious form of habitat alteration and is the major cause of fragmentation of continuous, natural landscapes. Forest fragmentation is caused by the clearing of indigenous vegetation for agriculture, urban development, and other human land uses. Such action results in patches of remnant natural vegetation being surrounded by altered vegetation. This study investigates the effects of forest fragmentation and matrix type on avian diversity and assemblage structure in forest patches of the Karkloof / Balgowan range (Afromontane Mistbelt Mixed *Podocarpus* forest – Cooper, 1985), KwaZulu-Natal province, South Africa. The influence of matrix type, particularly commercial forestry, and the natural grassland matrix, on the diversity, composition, and structure of the avifaunal assemblage in forest patches, are investigated. Using this approach this study seeks to demonstrate some of the consequences of landscape transformation for indigenous fauna in the small and vulnerable forest biome.

Birds are among the most mobile of organisms. It has been suggested that their ability to move among patches may lessen the influence of fragmentation effects on their persistence, more than other taxonomic groups (Rolstad, 1991). On the other hand, some authors have argued that birds may be particularly sensitive to fragmentation of forests because they have relatively large home ranges and are therefore area-demanding (Rolstad, 1991; McIntyre, 1995; Estades and Temple, 1999). Nevertheless, birds have been used as indicators of the ecological effects of forest fragmentation, since several studies have shown that responses of birds to forest fragmentation tend to be individualistic and scale dependent (Jokimäki and Huhta, 1996; Warburton, 1997; Estades and Temple, 1999; Villard *et al.*, 1999). The increasing fragmentation and transformation of forest landscapes necessitates studies of this nature, and are crucial for understanding the ecology, and the wise conservation management, of insular communities.

1.2 Landscape and habitat fragmentation

A fragment is defined as a part broken away from a whole, or an isolated part (Hawkins, 1991). Habitat fragmentation therefore, is the sub-division of a habitat into isolated patches. Fragmentation ultimately results in the (1) loss of original habitat, (2) reduction in habitat patch size, (3) isolation of habitat patches, and (4) increase in area of the surrounding habitat (Forman, 1997; Meffe and Carroll, 1997; Estades and Temple, 1999). All these factors contribute to a decline in biodiversity within the original habitat (Harris, 1984; Wilcove *et al.*, 1986; Saunders *et al.*, 1991; Andrén, 1994; Renjifo, 1999). In general, fragmented landscapes are believed to have a reduced capacity to conserve their natural biota (Blake, 1991; Saunders *et al.*, 1991; Rolstad, 1991; McIntyre, 1995; Warburton, 1997). This is because fragmentation and loss of suitable habitat may reduce a population to a size where stochastic events may cause demographic collapse (Templeton *et al.*, 1990; Rolstad, 1991; Simberloff, 1994; Swart and Lawes, 1996; Meffe and Carroll, 1997).

The biodiversity and landscape-scale consequences of habitat fragmentation are widely discussed in the literature, usually with an emphasis on species-area theory (Bierregaard and Lovejoy, 1989; Newmark, 1991; Stouffer and Bierregaard, 1995; Cornelius *et al.*, 2000), but more recently on metapopulation dynamics (Robbins *et al.*, 1989; Rolstad, 1991; Alvarez-Buylla and Garcia-Barrios, 1993; Hanski, 1994; Forman, 1997; Lawes *et al.*, 2000) and landscape ecology (Andrén, 1994; Jokimäki and Huhta, 1996; Lindenmayer *et al.*, 1999; Robinson and Robinson, 1999; Villard *et al.*, 1999). A landscape is a dynamic mosaic consisting of three basic elements: the matrix, habitat patches, and corridors (Samways, 1994; Hobbs, 1995). Because landscapes are spatially heterogeneous, the structure of, and changes in, landscapes are scale-dependent (Jokimäki and Huhta, 1996). Landscapes, and the biotic populations they include, are not stable through time, with changes occurring as a consequence of small and large-scale disturbances (Fahrig and Merriam, 1994; Wiens, 1994; DeGraaf and Miller, 1996). So while it is important to consider size, shape, and isolation of individual habitat patches, the problem of species distribution and diversity in patches should also be approached from the perspective of changes in the overall landscape.

The spatial scale effects of fragmentation on habitat patches include the increase of boundary length and external habitat, and a decrease in patch size, connectivity, interior-to-edge ratio, and total interior area (Andrén and Angelstam,

1988; Yahner, 1988; Laurance, 1991; Forman, 1997; Kapos *et al.*, 1997; Krüger and Lawes, 1997; Estades and Temple, 1999; Debinski and Holt, 2000). Animal communities respond to these changes in spatial pattern, and in turn ecological patterns and processes are affected. These ecological consequences may range from failure of metapopulation dynamics and disruption of dispersal patterns, to population decline and increased genetic inbreeding (Templeton *et al.*, 1990; Simberloff, 1994; Forman and Collinge, 1996). For example, as a result of reduced forest patch area, forest bird population densities may be reduced. This could lead to the disappearance of some species from small forest fragments (i.e., area-dependent extirpation), and an increased sensitivity of remaining populations to chance events (Fahrig and Merriam, 1994; Wiens, 1994; Estades and Temple, 1999).

Isolation of fragments also has important consequences for their biota, and community structure and composition varies with time since isolation, distance from other fragments, and degree of connectivity between patches (Harris, 1984; Saunders *et al.*, 1991; Forman, 1997). Isolation of fragments may limit recolonisation to a gradual process following local extinctions. As a consequence, species diversity is reduced, and community composition altered, as certain species that are particularly sensitive to these effects, are lost (Bierregaard *et al.*, 1992; Wiens, 1994).

Fragmentation may also affect the physical environment of habitat patches. Fragmentation of the landscape results in changes in the fluxes of physical elements (e.g., wind) across the landscape, the extent of change depending on size, shape, and position in the landscape of the remnant patch (Harris, 1984; Saunders *et al.*, 1991), as well as the nature of the matrix. Alterations in fluxes of radiation, wind, and water can all have important effects on the indigenous remnant vegetation, and may influence the ecology of the fragment (Saunders *et al.*, 1991; Kapos, *et al.*, 1997; Laurance, 1997).

The matrix is the most extensive and most connected landscape element, and therefore plays the dominant role in landscape functioning (Samways, 1994). Human land use practices such as deforestation and monoculture plantation, result in major changes to the natural landscape matrix in many ecosystems (Lawes *et al.*, 1999). One of two patterns may be observed: 1) the natural surrounding matrix may be converted to a different vegetation type, or 2) a naturally continuous matrix, such as extensive indigenous forest or grassland, may become dissected or perforated leaving behind patches or fragments of the original habitat. Most forest ecosystems around the world

are threatened in this way, and recent estimates suggest that over 15 million hectares of tropical forest are being destroyed annually, while another six million are selectively logged (Whitmore, 1997).

1.3 The history of Afromontane forest fragmentation and Extinction filtering

There are two major sources of disturbance that have led to fragmentation of the Afromontane forests of Africa: (1) climatic change during the Quaternary (Hamilton, 1981; Lawes, 1990; Hamilton and Taylor, 1991; Eeley *et al.*, 1999), and (2) anthropogenic disturbance. Eeley *et al.* (1999) suggest that repeated and severe climate changes in the Quaternary have caused Afromontane forests to be fragmented throughout much of their evolutionary history. In addition, the Karkloof / Balgowan forest (Afromontane Mistbelt Mixed *Podocarpus*) range, KwaZulu-Natal, has been selectively logged in the recent past (1870 – 1944; Rycroft, 1944). Furthermore, the spread of cultivation, and lately the encroachment of both commercial plantation forestry and agricultural practises, have been major anthropogenic causes of the fragmentation and transformation of this forest landscape.

Some have argued that the effects of recent fragmentation events on faunal diversity in these Afromontane forests may not be as critical as assumed, because these Afromontane forests are naturally fragmented forests, and presumably contain faunas that have adapted to these effects over time (Balmford, 1996; Danielsen, 1997; Lawes *et al.*, 2000). In fact, there is growing evidence from both palaeontology and conservation biology to suggest that past events may explain the variation seen in species' vulnerability to environmental threats (Blondel, 1990; Balmford, 1996). Historical events may not only determine species diversity of communities (Diamond and Hamilton, 1980; Latham and Ricklefs, 1993), but may also determine the resilience of communities (Balmford, 1996; Danielsen, 1997). For example, a forested region that has a complex topography and high rates of natural disturbance throughout its evolutionary history, may have selected for life history traits that impart resistance to habitat fragmentation effects, particularly recent changes that accompany forest clearance for anthropogenic land use.

Eco-climatically stable regions usually house fragile and complex (specialised) communities, while environments characterised by large and erratic climatic changes, generally house communities that are relatively robust, although simple (Begon *et al.*, 1990; Helle and Niemi, 1996; Danielsen, 1997). Accordingly,

unnatural, anthropogenic disturbances would be expected to have their most detrimental effects on fragile and specialised communities in eco-climatically stable areas with low incidence of habitat disturbance (Begon *et al.*, 1990). On the other hand, they should have the least effect on the simple, robust communities that have evolved in unpredictable environments that have been subject to frequent natural perturbations (Balmford, 1996).

Afromontane Mistbelt forest bird assemblages in KwaZulu-Natal Province may indeed be fragmentation adapted as suggested by Lawes *et al.* (2000). Lawes *et al.* (2000) argue that repeated climate changes in the Quaternary (Diamond and Hamilton, 1980; Hamilton, 1988) have filtered (*sensu* Balmford, 1996) Afromontane forest communities resulting in faunas whose life histories are adjusted to fragmentation. The resulting forest bird assemblages would consequently be highly robust and resistant, and expected to show only slight response, to further anthropogenic change in the landscape. In this study I test these predictions of the general extinction-filtering hypothesis of fragmented faunas.

1.4 Species-area effects

Due to the obvious structural differences between forest fragments and the surrounding matrix, theories of the community ecology of patches of habitat within fragmented forest landscapes have often been compared to that of oceanic islands (Estades and Temple, 1999; Morin, 1999). Consequently, MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography, that is based upon the biogeography of oceanic islands, has often been applied to the investigation of species distribution and richness in habitat islands (Brown, 1971; Terborgh, 1974; Willis, 1974; Diamond, 1975; Whitcomb *et al.*, 1981; Bellamy *et al.*, 1996; Brooks *et al.*, 1999).

Although it is tempting to apply the dynamic equilibrium concept of island biogeography to interpreting patterns of species richness on habitat islands, this should be done cautiously because habitat fragments are unlike oceanic islands in many respects. In particular, habitat islands exist in a complex landscape mosaic, and dynamics within a fragment are affected by external factors that vary as the mosaic structure changes (Andrén, 1994; Wiens, 1994; Jokimäki and Huhta, 1996). Thus, although oceanic islands are surrounded by hostile habitat (i.e., the ocean), habitat fragments are rarely surrounded by an ecologically inhospitable environment, and are

susceptible to influences from the surrounding landscape (Simberloff, 1992; Andrén, 1994; Wiens, 1994; Estades and Temple, 1999).

Moreover, given that habitat islands or patches form part of a heterogeneous landscape mosaic, patch isolation is a less important variable than patch area since most species have evolved mechanisms to move through the heterogeneous environment (Opdam, 1991; Forman, 1997). Furthermore, species sources for a patch may be diffuse and multidirectional rather than unidirectional (Forman, 1997) as island biogeography suggests. Thus, employing studies of oceanic islands and island biogeography theory as a model for predicting faunal extinctions in fragmented landscapes, is not ideal, as such studies probably underestimate the importance of overland vagility and matrix tolerance, and overestimate the significance of traits such as rarity and population stability (Laurance, 1997).

In this study I use species–area theory to describe patterns of diversity and distribution of avian communities in a fragmented forest landscape, merely as an aid to describing the putative effects of area-dependence on assemblage structure and diversity. In using linear least-squares regression in these analyses, my main focus of attention is on the sign and scale of the residual variance in species richness of a forest patch about the average. I do not set out to test the equilibrium theory of species richness on habitat islands. I investigate the latter using analyses of the extent of nested-subsetting of patch species richness. This non-equilibrium approach is discussed in the next section.

1.5 Non-equilibrium theories of community composition: Community convergence and nested subset theory

The Equilibrium Theory of Island Biogeography does not provide information on what species are supported by habitat islands in fragmented terrestrial landscapes (Patterson, 1987; Simberloff, 1992; Gotelli and Graves, 1996; Forman, 1997; Meffe and Carroll, 1997). The theory focuses primarily on determinants of species richness, such as area and distance to mainland, rather than the composition of the biota (Patterson, 1987). In addition, area effects are often confounded by the internal habitat diversity of a patch, as well as the disturbance history (Forman, 1997). Furthermore, the primary assumption of the theory, that species richness in a patch is the consequence of a dynamic equilibrium between the rates of extinction and

colonisation of species in a patch, is seldom thoroughly tested and difficult to test (Brown, 1971).

I tackle the problem of identifying the mechanisms responsible for species richness in a forest patch by assuming that bird species richness in a patch is a consequence of colonisation and extinction of species, but that these processes are not in equilibrium. To explain this approach one must first accept that disturbance effects often dominate the ecology of fragmented landscapes. Disturbance can result in a highly deterministic species succession within a patch and can be a major determinant of species richness and composition (Cutler, 1994; Lomolino, 1996), rather than the random extinction in, and colonisation of, patches by species as suggested by equilibrium theory. Indeed, community composition in habitat islands may be the consequence of highly deterministic species extinction or colonisation patterns (Cutler, 1994; Lomolino, 1996). If this is the case a "nested subset" pattern arises from a non-random distribution of species so that the species that inhabit depauperate islands are a subset of those on richer islands (Patterson and Atmar, 1986).

In a perfectly nested series, species present in a given fauna are also present in all larger faunas, and species absent from a given fauna are also absent from all smaller faunas, resulting in a typical wedge shaped pattern in the presence-absence matrix (Cutler, 1991). This phenomenon arises if sites represent fragments of a once-continuous habitat initially inhabited by a common ancestral biota, and as area continues to decrease, local extinctions of species at the sites produce a nested pattern as extinctions occur in a deterministic sequence (i.e. species will go extinct in order of their specific extinction risks) (Patterson and Atmar, 1986). It is implicitly assumed that all sites share the same potential species pool, and no historical or environmental differences exist between sites (Cutler, 1994). Thus, a perfectly nested pattern results when the following conditions are met (Cutler, 1994): 1) all species were initially dispersed throughout the region (i.e. all fragments begin with precisely the same complement of species); 2) extinctions occur in a consistent sequence on all fragments (i.e. the rules of extinction are the same on all fragments); and 3) no colonisations occur after isolation. However, due to the dynamic and multivariate nature of natural systems a perfectly nested pattern is unlikely to occur. Species distributions deviate from a perfectly nested pattern through unexpected absences of species from large faunas ("holes") and unexpected presences of species in small faunas ("outliers")

(Patterson and Atmar, 1986; Cutler, 1991; Gotelli and Graves, 1996), and failure to satisfy any of the above conditions would produce either one.

Hence, as a forest is fragmented, faunal species composition and abundance patterns change in the fragments relative to those in the original patch. For example, forest birds adapted to forest interior habitats may not be able to maintain viable populations in a small patch where forest edge is abundant (Thiollay, 1992; Bierregaard and Stouffer, 1997; Meffe and Carroll, 1997). If fragmentation is under strong environmental control, such as overwhelming change in the matrix, species loss from fragmented habitat may follow a predictable and deterministic sequence (Patterson, 1987; Cutler, 1991). For instance, forest patches could become dominated by "edge-adapted" or generalist species. Thus, as fragmentation continues the composition of bird communities in similar sized patches will converge as species relaxation takes place (Patterson, 1987). In contrast to this prediction derived from the non-equilibrium scenario, equilibrium theories such as the MacArthur and Wilson model and the random sample hypothesis (Connor and McCoy, 1979; Haila, 1983), predict that the composition of these communities would be random sets of the original community (Atmar and Patterson, 1993; Andrén, 1994; Meffe and Carroll, 1997).

In this study I test the prediction that patterns of species loss from forest fragments (under different levels of environmental control, i.e., natural matrix and afforested matrix) of the Karkloof / Balgowan range are deterministic and not random. I employ nested subset analysis, which tests the non-random nature of communities by comparing the composition of assemblages against a random null model using Monte Carlo simulations (Patterson and Atmar, 1986; Patterson, 1987; Cutler, 1991, 1994; Lomolino, 1996).

An understanding of the primary underlying mechanisms generating nestedness is crucial for understanding the ecology of fragmented ecosystems. Nestedness could result from differential extinction, as a function of area, and/or differential colonisation, as a function of isolation (Lomolino, 1996). Both mechanisms have been proposed to explain nestedness, but because of the generally lesser importance of colonisation processes for habitat islands, recent evidence favours differential local extinction (Patterson and Atmar, 1986; Patterson, 1987, 1990; Cutler, 1991, 1994; Wright and Reeves, 1992; Lomolino, 1996). Furthermore, in terrestrial fragments, the causal factors of nestedness are influenced by variables

such as habitat diversity, disturbance, area of patch interior, matrix heterogeneity, isolation, and edge effects (Forman, 1997). In this study I investigate the relative importance of the putative extinction and colonisation related processes responsible for bird assemblage structure and composition in the forest fragments of the Karkloof / Balgowan range.

1.6 Matrix transformation: species' response to landscape change

I have shown in an earlier discussion that patch species composition and abundance in a fragmented landscape, are dependent on factors at larger scales than the individual's immediate habitat, such as the nature of the surrounding matrix (Pulliam, 1988; Jokimäki and Huhta, 1996; Keitt *et al.*, 1997; Estades and Temple, 1999). Here I revisit this issue and review the response of forest bird species to landscape scale changes and disturbance, and particularly the influence of the matrix.

The nature of the matrix plays an important role in determining movement between habitat fragments. Indeed, the quality of the matrix may be more important for vagile species like forest birds, than the structure of their local habitat (Fahrig and Merriam, 1994; Jokimäki and Huhta, 1996). If the matrix is inhospitable to species dependent on forest (e.g., open grassland) there will be little colonisation of fragments after isolation (Bierregaard *et al.*, 1992; Turner, 1996). However, in many cases the surrounding vegetation is not entirely unsuitable, for example, plantation forestry may support forest birds (Armstrong *et al.*, 1996). In such landscapes, a mosaic of habitat patches of varying quality is created in the process of fragmentation, high quality habitat being provided by forest fragments, and the matrix providing lower quality habitat (Wiens, 1994; McGarigal and McComb, 1995; Armstrong *et al.* 1996; Estades and Temple, 1999). Such a severe change in the matrix as open grassland to closed pine plantation may certainly cause highly deterministic changes in community composition.

As disturbance is a major factor in determining species number (Forman, 1997; Warburton, 1997), one would expect to find that the degree of disturbance affects the rate of convergence. The Karkloof region in the midlands of KwaZulu-Natal is a forest landscape that has become fragmented and dominated by commercial plantation forestry (hereafter referred to as the Gilboa forest complex). Afforestation practises (particularly during and after harvesting) increase and intensify the degree of disturbance otherwise experienced by the indigenous forest patches, especially

disturbance effects along the forest edge (Lovejoy *et al.*, 1986; Armstrong and van Hensbergen, 1996; Estades and Temple, 1999). I predict that these Gilboa forest fragments would converge on the same community composition at a rate faster than would be observed in forest patches in the Balgowan complex that are found in a naturally fragmented landscape, amid a natural grassland matrix.

Responses of species to landscape changes are certainly individualistic and species-specific (Kavanagh *et al.*, 1985; Andrén, 1994; Villard *et al.*, 1995; Fahrig, 1997; Warburton, 1997; Estades and Temple, 1999; Villard *et al.*, 1999). For forest avifauna, this depends largely on mobility (Diamond, 1981; Machtans *et al.*, 1996), home range / territory size (Rolstad, 1991) and migratory patterns (Robbins *et al.*, 1987; Friesen *et al.*, 1999; Morse and Robinson, 1999), as well as life history traits and demography (Karr, 1990; Hansen and Urban, 1992; Stouffer and Bierregaard, 1995). Many traits have been identified and associated with local extinction proneness in populations of forest birds in fragmented landscapes. These include natural rarity (small population size) (Warburton, 1997), large body size (Leck, 1979; Willis, 1979; Karr, 1990), specialised patterns of resource use (Willis, 1974; Thiollay, 1992; Sieving and Karr, 1997), low annual survival rates (Karr, 1990), low fecundity (Sieving and Karr, 1997), terrestrial foraging and nesting (Terborgh, 1974; Willis, 1979; Recher *et al.*, 1987; Stouffer and Bierregaard, 1995), and low tolerance for the surrounding matrix habitat (Bierregaard and Stouffer, 1997; Laurance, 1997; Warburton, 1997).

Matrix tolerance may in fact be a major predictor of vulnerability in insular populations (Diamond *et al.*, 1987; Laurance, 1991; Bierregaard and Stouffer, 1997; Warburton, 1997; Cornelius *et al.*, 2000). When overwhelming change in the landscape matrix occurs, populations of some species will decline or disappear, some remain relatively unaffected, and others increase in fragments (Terborgh, 1992; Laurance, 1997; Warburton, 1997). Most generalist species may be able to use the modified matrix and would be better at dispersing between forest fragments than are those that avoid the matrix. These species would recolonise fragments following local extinctions, strengthening the local populations through the genetic and demographic contributions of the immigrants (Brown and Kodric-Brown, 1977; Lomolino, 1996; Laurance, 1997). Furthermore, species that tolerate or use the modified matrix, are probably adapted to ecological changes in the landscape and habitat patches, such as

edge effects (Laurance, 1997; Dale *et al.*, 2000), and so persist and even thrive in a disturbed environment.

Essentially, the susceptibility of certain life history traits to fragmentation and landscape-level disturbance results in a deterministic pattern of species relaxation and extirpation. This is an extension of arguments already presented in the sections on extinction filtering and nested subset analysis. In this study I aim to identify those life history traits responsible for the deterministic pattern of species relaxation in indigenous forest patches of the Karkloof / Balgowan range.

1.7 Conservation and management

One of the most common patterns in natural communities, the species-area relationship, has been dubbed "one of community ecology's few genuine laws" (Schoener, 1976) and has been observed throughout the 20th century (Arrhenius, 1921; Gleason, 1922; Cain, 1938; Williams, 1943; Hopkins, 1955; Preston, 1960; MacArthur and Wilson, 1963). As a result, the species–area relationship became the focal principle in a conservation debate about the protection of "single large or several small" reserves (SLOSS debate: Terborgh, 1974; Diamond, 1975, 1976; Wilson and Willis, 1975; Simberloff, 1976, 1988; Simberloff and Abele, 1976, 1982, 1984; Simberloff and Gotelli, 1984; Willis, 1984; Doak and Mills, 1994; Lomolino, 1994). However, analyses have revealed weaknesses in the SLOSS theory. The main concern is that management decisions based on habitat area and isolation alone, fail to address a basic feature of community structure: community composition (Worthen, 1996). Soulé and Simberloff (1986) suggested that decisions on reserve area be based on the minimum area needed to sustain the minimum viable populations and habitat diversity. From this it followed that the debate hinged on the similarity among communities in small habitat patches, i.e. community composition patterns, and consequently, composition-area relationships became central to the debate (Worthen, 1996).

The nested subset concept has relevance to the SLOSS debate in management strategies and reserve design in that it is a descriptive tool for revealing an ecologically meaningful non-random pattern, and an exploratory tool for suggesting mechanisms that may structure communities (Blake, 1991; Simberloff and Martin, 1991; Cutler, 1994; Lomolino, 1996; Worthen, 1996). Where community composition of patches is a nested series it is important to conserve the largest intact land units so

that overall species richness is preserved. This conservation requirement arises from understanding that the preservation of any number of small patches, if these have converged to the same community representation, will not support as large species , richness as a large single patch.

In terms of conservation and management, this study aims to estimate the minimum critical forest patch size for maintenance of natural bird diversity in Afromontane forest, and to address the SLOSS debate to examine whether SL or SS is appropriate for the management of Afromontane forest patches to maximise bird biodiversity.

1.8 Summary

In this study I investigate the effects of forest fragmentation and matrix type on avian diversity and assemblage structure in forest patches of the Karkloof / Balgowan forest range, KwaZulu-Natal province, South Africa. Specifically, this study compares the avifaunal community diversity and composition of indigenous forest patches surrounded by commercial forestry (Gilboa complex) with that surrounded by the natural grassland matrix (Balgowan complex), to investigate the possible consequences of such landscape transformation. Throughout this thesis I adopt the working hypothesis that historical fragmentation events have filtered Afromontane forest communities resulting in faunas whose life histories are adjusted to fragmentation, and thus bird communities will show little response to further anthropogenic change in the landscape.

The main objectives of this study are:

1) To investigate the consequences of forest fragmentation, such as the effect of forest patch size, on bird diversity and species distribution among forest fragments.

2) To test the prediction that patterns of species loss from forest fragments under different levels of environmental control in the matrix, i.e., natural matrix and afforested matrix, are deterministic and not random, using nested subset analysis.

3) To determine the dominant process (extinction or colonisation) responsible for bird assemblage structure and composition in forest fragments.

4) To identify those life histories responsible for bird assemblage composition and species relaxation in indigenous forest fragments.

5) To estimate the minimum critical forest patch size for maintenance of natural bird diversity in Afromontane forest, and to address the SLOSS debate for the management of small forest patches to maximise bird biodiversity.

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CHAPTER 2

Insular Effects on Forest Bird Diversity: Species-Area Relationships in a Fragmented Forest Landscape

2.1 Introduction

One of the primary causes of fragmented landscapes is anthropogenic disturbance. Forest fragmentation is caused by the clearing of patches of indigenous vegetation for agriculture, urban development, and other human land uses. This results in patches of remnant indigenous vegetation being surrounded by altered vegetation. In general, fragmented landscapes have a reduced capacity to conserve their natural biota (Blake, 1991; Rolstad, 1991; McIntyre, 1995; Forman, 1997; Warburton, 1997). This is because fragmentation and loss of suitable habitat reduces a population to a size where stochastic events cause demographic collapse (Rolstad, 1991; Swart and Lawes, 1996).

The Afromontane forests of South Africa are thought to have been fragmented throughout much of their evolutionary history due to repeated and severe climate changes in the Quaternary (Eeley *et al.*, 1999). However, there has been further recent fragmentation of the Karkloof / Balgowan forest range, KwaZulu-Natal province, caused by selective logging (1870 –1944; Rycroft, 1944), the spread of cultivation, and lately the encroachment of commercial plantation forestry. Briefly, in this chapter I investigate the effect of this fragmentation and land transformation on forest bird species diversity. I compare the species-area relationships displayed by the avifaunal communities of indigenous forest patches surrounded by a natural grassland matrix (Balgowan complex) with those surrounded by commercial plantation forestry (Gilboa complex).

The impacts of forest fragmentation on forest bird communities have been the subject of many ecological studies. Most research is focused on tropical Amazon and other South American forests (Willis, 1979; Bierregaard and Lovejoy, 1989; Kattan *et al.*, 1994; Bierregaard and Stouffer, 1997; Restrepo *et al.*, 1997, Sieving and Karr, 1997; Estades and Temple, 1999), northern hemisphere temperate forests (Lynch and Whigham, 1984; Simberloff and Gotelli, 1984; Wilcove and Robinson, 1990;

Bellamy *et al.*, 1996; Merril *et al.*, 1998; Villard *et al.*, 1999; Robinson and Robinson, 1999), and Australian forests (Kavanagh *et al.*, 1985; Keast, 1985; Loyn, 1985; Saunders, 1989; Warburton, 1997). African forests have received attention only in recent years (Newmark, 1991, 1998; Armstrong and Van Hensbergen, 1996; Castley, 1997; Krüger and Lawes, 1997; Dale *et al.*, 2000; Symes *et al.*, 2000; Van Rensburg *et al.*, 2000). Such studies have shown that forest fragmentation considerably reduces avian diversity through reduction in area of forests, their increased isolation, and the negative effects of increased forest edge on species persistence.

Forest patch size is the best single predictor of species number, probability of occurrence and population densities, especially of forest dependent species (Ambuel and Temple, 1983; Blake and Karr, 1984; Freemark and Merriam, 1986; Van Dorp and Opdam, 1987; Rolstad, 1991). Several studies have shown declines in the diversity of forest birds within fragments over time, and small fragments contain fewer species than larger fragments or similar sized areas within continuous forest (Leck, 1979; Bierregaard and Lovejoy, 1989; Newmark, 1991; Stouffer and Bierregaard, 1995; Bellamy *et al.*, 1996; Jokimäki and Huhta, 1996; Warburton, 1997; Merril *et al.*, 1998; Villard *et al.*, 1999). However, fragment size is correlated with, and is an ecological surrogate for, many other factors that must be taken into account (Forman 1995). These include habitat diversity, disturbance, area of patch interior, fragment shape, edge effects, isolation, connectivity, and matrix heterogeneity (Hobbs, 1995; Forman, 1997; Meffe and Carroll, 1997). Any number of these factors may be invoked to explain observed species-area relationships (Morin, 1999), and in this chapter I investigate how habitat diversity and isolation may influence bird species distribution patterns in the Karkloof / Balgowan forest range.

MacArthur and Wilson's (1967) Equilibrium Theory of Island Biogeography is based upon the biogeography of oceanic islands, but has often been applied to the investigation of species distributions in insular habitats, and species-area equilibrium theory has been used to interpret the observed patterns of community diversity on habitat islands (Terborgh, 1974; Willis, 1974; Diamond, 1975; Whitcomb *et al.*, 1981; Bellamy *et al.*, 1996). Although it is tempting to apply this dynamic equilibrium concept to interpreting patterns on habitat islands, this should be done cautiously because the assumptions of the model are weak evidence for the strong relationship found between species relaxation and habitat patch area (Meffe and Carroll, 1997). With the latter in mind I use species-area theory to describe patterns of diversity and

distribution of avian communities in a fragmented forest landscape, merely as an aid to describing the putative effects of area-dependence on assemblage richness and diversity. I further estimate the minimum critical forest patch size for maintenance of natural bird diversity in Afromontane Mistbelt Mixed *Podocarpus* forest in KwaZulu-Natal.

2.2 Methods

2.2.1 Study area

The Karkloof / Balgowan forest range (29°15' - 29°25'S; 30°00' - 30°30'E) is situated in the midlands of KwaZulu-Natal province, South Africa (Fig. 2.1). These forests are classified as Afromontane Mistbelt Mixed *Podocarpus* forest (Cooper, 1985; Low and Rebelo, 1996). Afromontane forest comprises most of the indigenous forest biome in southern Africa, which is the smallest, most widely distributed and the most fragmented biome of the region (Geldenhuys and MacDevette, 1989). The Karkloof / Balgowan forest range comprises one large, contiguous forest patch (approximately 2900ha in size) and many smaller, peripheral fragments surrounded by mainly one of two matrix types: 1) the natural Moist Upland Grassland (Cooper, 1985; Low and Rebelo, 1996) or 2) commercial plantation forestry species such as pine (*Pinus patula*) and black wattle (*Acacia mearnsii*). This forest complex lies at an altitude of 1500m-1800m and experiences a range in mean annual rainfall of 800mm-1000mm, occurring seasonally – mostly in summer. Temperatures can be extreme (mean minimum temperature: 4.75°C – 15.64°C; mean maximum temperature: 19.81°C – 26.47°C), especially in winter (Low and Rebelo, 1996).

Afromontane Mistbelt Mixed *Podocarpus* forest is the climatic climax forest vegetation of the KwaZulu-Natal mistbelt region (White, 1978). Mistbelt forests are characteristically cool, tall (~15m), inland forests with well-developed and mature soils (Pooley, 1993). Water is a key-limiting factor in this environment, and the forest patches generally occur in fire-safe habitats (Low and Rebelo, 1996), on steep south-facing slopes that are subject to frequent mist, particularly in summer, and with high rainfall, so the region is relatively moist.

KwaZulu-Natal showing the
distribution of Afromontane forest

South Africa

The location of study sites
in the Karkloof / Balgowan range

30°15'E

Leopards Bush

29°20'S

Gilboa complex

Balgowan complex

0   5   10
Kilometers
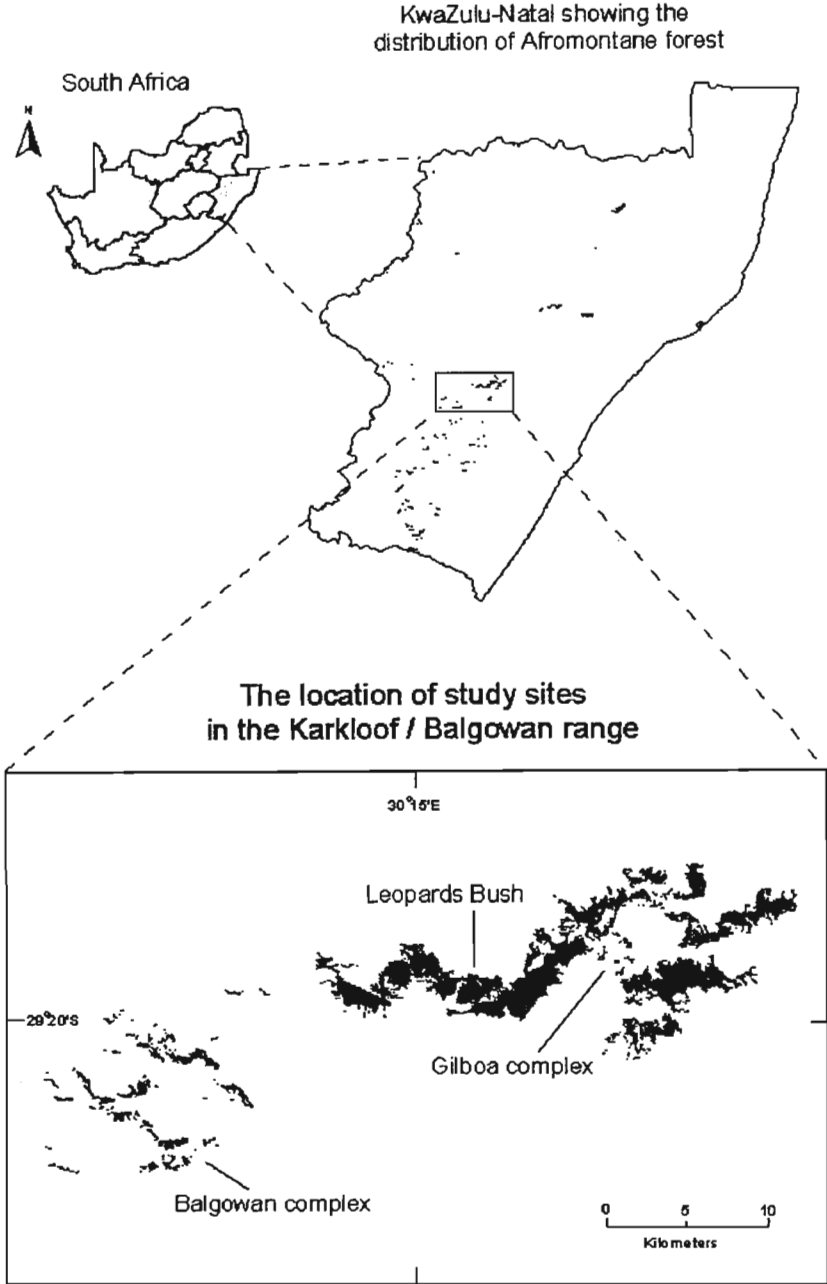
Map produced by the Forest Biodiversity Programme

Figure 2.1. Regional map of KwaZulu-Natal, South Africa, showing the distribution of Afromontane forest and the location of study sites in the Karkloof / Balgowan forest range.

2.2.2 Forest patches sampled

Nineteen forest patches of varying size were selected in the Karkloof / Balgowan range. Nine of these patches were sited in natural grassland in the Balgowan complex, with a size range of 0.5ha to 215ha (Table 2.1). A further nine patches were sited within the Gilboa (Mondi forests) commercial forestry estate in the Karkloof region (hereafter referred to as the Gilboa complex). These patches were surrounded by pine plantation (stand age > 8 years) and had a size range of 0.5ha to 273ha (Table 2.1). Patches of comparable size were selected from each complex and treated as matched pairs in some analyses. A patch of much greater size (Leopards Bush Private Nature Reserve; 705ha), situated in the Karkloof region, served as an ecological control or outgroup, representing the ecological conditions in a large contiguous forest patch, to which the patterns described from the other eighteen smaller forest patches were compared. The forest patches were selected from 1:30 000 aerial photographs from 1996. The total area of each patch in hectares was calculated from digital maps of the area (Macfarlane, 2000) using ArcView version 3.0 (ESRI, 1998). Isolation distances were estimated from the digital maps as the minimum distance to the nearest forest fragment of equal or greater size. In all cases the linear distance between nearest edges was measured (Table 2.1).

2.2.3 Bird census methods

All bird population census techniques have methodological problems (Bull, 1981; Dawson, 1981; Pyke and Recher, 1985). There is no standard census method available for bird community studies in Afromontane forests (Koen, 1988). A reliable technique for working in closed-canopy evergreen forests, where vision is limited and bird detection is accomplished by visual and auditory cues, was sought.

A modified strip transect sampling technique, Kelker's method (Robinette *et al.*, 1974; Burnham *et al.*, 1980), was used to estimate bird species density. For the most part the line transects were straight and thus it was possible to calculate the angle from the path route to the observed bird, and from this the perpendicular transect width. Line transects of varying length adjusted according to patch size were marked out across the dominant environmental gradient (i.e. up the slope and between watercourses) in the forest patches. In this way the maximum gradient of diversity was sampled in each forest patch.

Along each transect the following were recorded: (1) all bird species seen and heard; (2) the number of individuals; (3) estimated straight-line distance from the observer to the bird or centre of a flock; (4) the angle between the straight line transect and the bird (measured using a Suunto KB-77/360RL prismatic compass); and (5) at 10m intervals, a description of the forest structure to ascertain the frequency of occurrence of all forest microhabitats as a measure of forest habitat diversity (see Appendix 2.1).

Cumulative sample-species richness curves were plotted for each transect (or patch) to determine when sampling (number of transects walked) should cease. These curves were asymptotic at approximately 8 transects for the eighteen smaller patches and at 22 transects for the larger control patch (Fig. 2.2). No new species were added at the full sampling effort for each forest patch and all forests were regarded as adequately sampled.
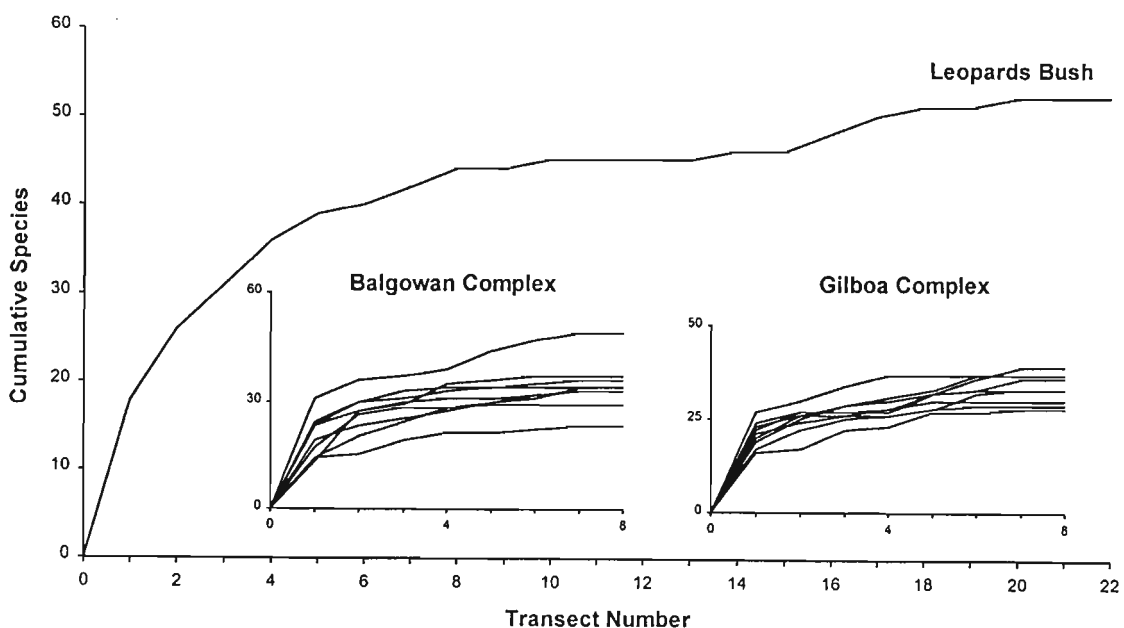
Figure 2.2. Cumulative species curves showing sampling intensity represented by the asymptote. All patches in the Balgowan and Gilboa forest complexes, and the control patch Leopards Bush, are represented.

2.2.4 Data analysis

The most problematic summary statistic required for estimating density from line transects is the measure of transect width. This can be estimated in a number of ways and most methods seek to ensure that this distance includes all individuals observed (i.e. that no birds within this distance from the transect are missed). Because visibility in a forest varies along the line transect, the estimate of reliable transect width can be difficult. Furthermore, birds moving away from the observer may have the effect of increasing width estimates such as means, and thereby decreasing density estimates (Altman *et al.*, 1981; Sutherland, 1996). In order to address these problems, frequency distributions of the calculated perpendicular sighting distances across all species recorded in each patch were plotted (TRANSECT version 2.2; White, 1988). Transect width was then calculated as the maximum reliable perpendicular sighting distance (MRPSD; see Altman *et al.*, 1981), and used to determine the density of bird species in each patch. The MRPSD (Table 2.1) was taken as the lower limit of the first interval (interval widths = 4.2308m) of the frequency distribution at which the number of detection's of individuals dropped significantly (>50%) below that of the immediately previous interval.

Density was calculated using the following equation:

$$D = n / 2LW \times 10\,000 = \text{individuals/ha}$$

    where

        D = Density estimate of animals per unit area

        n = Number of animals seen on transect

        L = Total length of transect (m)

        W = Half the effective transect width (m)

2.2.5 Species diversity

Species diversity was compared among the patches using a series of diversity indices, including those described by Hill (1973). Hill's diversity numbers (see Ludwig and Reynolds, 1988) are the easiest to interpret ecologically, compared to the many other diversity indices (Magurran, 1988). From Hill's family of diversity numbers I selected N0, N1 and N2 for measures of species richness and diversity, and E1 (J') and E5

indices of species evenness (Table 2.1). These evenness indices are recommended above other diversity measures as they are relatively unaffected by species richness, and tend to be independent of sample size (Ludwig and Reynolds, 1988). I also included Hurlbert's (1971) index PIE, which is a simple index of evenness that is easily interpreted as a probability and is unbiased by sample size. Simpson's (λ) and Shannon-Wiener (H') indices of diversity were also calculated and used in the derivation of Hill's numbers.

2.2.6 Rarefaction

The sampling effort (number of individuals recorded in a patch) differed between patches of a size between complexes, therefore I used rarefaction analysis to compare species richness, Shannon-Wiener diversity estimates (H'), and Hurlbert's PIE (evenness index) between forests of equal area (pair-wise analysis) in the two forest complexes. Rarefaction uses probability theory to derive expressions for the expectation and variance of species richness for a sample of a given size (Hurlbert, 1971; Heck et al., 1975; James and Rathbun, 1981; Kotze and Samways, 1999). To detect whether differences in diversity and evenness represented ecological differences between assemblages or simply differences in sampling intensity, samples were rarefied down to a common abundance level and species richness, diversity and evenness then compared using EcoSim version 5.52 (Gotelli and Entsminger, 2000).

2.2.7 Area, isolation, and habitat diversity

A linear multiple regression analysis was performed to determine the dependence of forest bird species richness, on area, isolation, and habitat diversity of the forest patches in each complex. Variables were standardised by subtracting the mean from the value, and dividing the result of this by the standard deviation. After standardisation, all variables had a mean of zero and a standard deviation of one. Results of the standardised data however did not differ from the original data. Forest habitat diversity was calculated using Simpson's diversity index (λ), as it is a widely used index with good discriminatory ability and a low sensitivity to sample size (Magurran, 1998). I used the reciprocal $1/\lambda$ to ensure that the value of the index increased with increasing diversity.

2.2.8 Species-area analysis

i. Species-area curves

Least-squares linear regressions of log-species on log-area for the two complexes were plotted and compared for accuracy of fit to untransformed or semi-log plots. Species-area regressions based on untransformed data fitted best. The island effect or slope for complexes in different habitat matrices was thus compared. Least-squares linear regression analyses were performed using routines in STATGRAPHICS version 7 (Manugistics, 1993).

ii. Minimum critical patch size

Species-area curves can be used to determine the size at which island effects appear to be undetectable. The species-area curve for islands (i.e. forest patches in the two forest complexes) were each compared with the mainland curve (i.e. the control patch Leopards Bush). Bond et al. (1988) suggest that the minimum critical patch size (MCPS) required to avoid loss of species due to insular effects is that minimum area at which island species richness is no different from the mainland (i.e. when an island is no longer an island). MCPS can therefore be inferred as the area that corresponds with the point at which the species-area curve for island patches intersects with the mainland curve.

Contiguous sub-plots (i.e. transect segments) equal in length (i.e. area sampled) to those transect lengths walked in the island forest patches, were used to plot the species-area curve for the mainland forest patch. Nesting sub-transects in this way does violate the regression assumption of random sampling and some authors (e.g. Connor and McCoy, 1979; Bond et al., 1988) suggest the method overestimates species number in small plots. On the other hand Rosenzweig (1995) shows that if sub-transects are not contiguous but random or scattered, the resulting fitted line will show too much curvature and have a steeper slope in a log-species – log-area plot (i.e. underestimates species richness of small plots). Furthermore, using contiguous nested sub-transects is useful in ascertaining whether or not one has sampled an area on a scale that is large enough to include most species coexisting there. This ensures that conservation decisions are made at the same scale as the ecological process in question.

2.3 Results

2.3.1 Bird species richness and diversity

Bird species richness at Leopards Bush (control) was greater ($n = 52$) than in any of the other smaller patches where species richness ranged from 23 to 49 (Table 2.1). Twenty-five of the 61 species recorded in total were classed as forest dependent (Appendix 2.3). Forest-dependent birds were identified from Oatley (1989), and are broadly defined as those species that breed in forest (Krüger and Lawes, 1997; Lawes, Eeley and Piper, 2000). The forest dependent birds were well represented in the forest patches as well as in Leopards Bush. Twenty-four forest dependent species were recorded in Leopards Bush while the number ranged from 8 to 21 in the patches of the two forest complexes (Table 2.1). Total species richness, based on the actual count values and sampling effort, differed between the forest complexes and among patches within a complex (Table 2.1). In general, small forest patches in the Balgowan complex were less species rich than those in the Gilboa complex, and this trend was reversed for patches larger than approximately 50ha (see section: 2.3 Results; *2.3.5 Species-area analysis*; *i. Species-area curves*; Fig. 2.7).

Table 2.1. Diversity of forest patches in each complex, as well as the control, calculated using a variety of diversity indices. Patch area, isolation, transect length and maximum reliable perpendicular sighting distance (MRPSD), is also given for each patch.

Patch	Grassland matrix Balgowan complex									Commercial forestry Gilboa complex									Control
	A	B	C	D	E	F	G	H	I	A	B	C	D	E	F	G	H	I	LB
Area (ha)	215	138.2	123.8	85	45.8	15	3	1.72	0.5	273	149.5	105	81.48	37	13	3.6	1.7	0.5	705
*Isolation (m)	600	250	200	1500	400	450	200	400	750	100	900	400	2500	1400	900	100	100	100	-
Transect length (m)	400	350	300	200	150	150	100	80	80	400	350	300	200	150	150	100	80	80	700
MRPSD (m)	30.2	30.2	30.2	30.2	30.2	30.2	30.2	30	27	30.2	30.2	33	30.2	30.2	26	30	30.6	30	30.2
Species richness (S)																			
Hill's number N0	49	37	34	33	36	34	33	23	29	36	37	39	37	30	29	33	28	33	52
Forest dependent species	21	16	14	14	15	16	12	9	8	17	16	19	18	14	12	15	11	13	24
Diversity																			
Simpsons index (λ')	0.057	0.081	0.069	0.075	0.051	0.087	0.082	0.112	0.060	0.073	0.056	0.082	0.075	0.065	0.077	0.071	0.063	0.052	0.084
Shannon-Wiener index (H')	3.214	2.916	3.001	2.921	3.190	2.862	2.847	2.562	3.075	2.958	3.186	2.959	3.013	3.036	2.910	2.964	2.987	3.174	2.961
Hill's number N1	24.87	18.46	20.12	18.56	24.29	17.49	17.24	12.96	21.66	19.26	24.20	19.28	20.35	20.82	18.35	19.37	19.82	23.90	19.31
Hill's number N2	17.53	12.40	14.59	13.32	19.78	11.54	12.16	8.91	16.72	13.61	18.00	12.24	13.39	15.29	13.00	14.07	15.92	19.24	11.89
Evenness																			
Hurlbert's PIE	0.963	0.945	0.96	0.954	0.977	0.941	0.946	0.928	0.974	0.963	0.971	0.942	0.951	0.967	0.956	0.958	0.972	0.978	0.9339
Hill's index E1 (J)	0.826	0.807	0.851	0.835	0.89	0.812	0.814	0.817	0.913	0.826	0.882	0.808	0.834	0.893	0.864	0.848	0.896	0.908	0.749
Hill's index E5	0.693	0.653	0.711	0.702	0.806	0.639	0.688	0.661	0.761	0.691	0.733	0.615	0.64	0.721	0.692	0.711	0.793	0.796	0.595

* Isolation: minimum distance to nearest forest fragment of equal or greater size

Rarefaction analysis of diversity (H') and evenness (PIE) showed that the two forest complexes were significantly different in both cases. This suggests that the differences detected are ecological (e.g. difference in matrix type) and not simply due to differences in sampling intensity. Small forest patches in the Gilboa complex were more diverse and had higher evenness, while larger patches in the Balgowan complex tended to be more diverse with higher evenness than those of similar size in the Gilboa complex (see Fig. 2.3a-b).
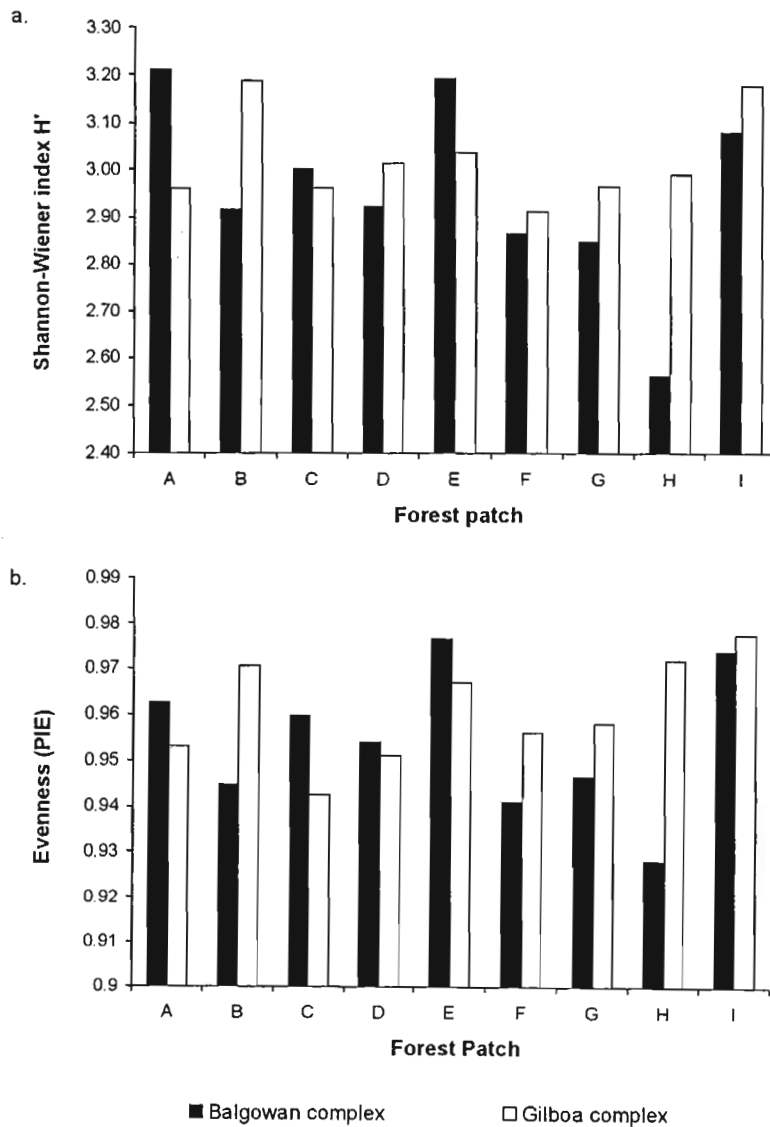
Figure 2.3. Pair-wise comparisons of (a) Shannon-Wiener diversity (H') and (b) Evenness (PIE) between forest patches of similar size in the Balgowan and Gilboa forest complexes.

2.3.2 Population density

Total avian density estimates, calculated from all species seen and heard, ranged from 17.47 individuals/ha to 45.32 ind./ha for forest patches in the Balgowan complex, and from 9.17 ind./ha to 38.96 ind./ha for patches in the Gilboa complex (Appendix 2.2). Total density was significantly lower in forest patches in the Gilboa complex (plantation matrix), than patches in the Balgowan complex (grassland matrix) (paired *t*-test = 3.56, *df* = 60, *P* < 0.0008) (Fig. 2.4).
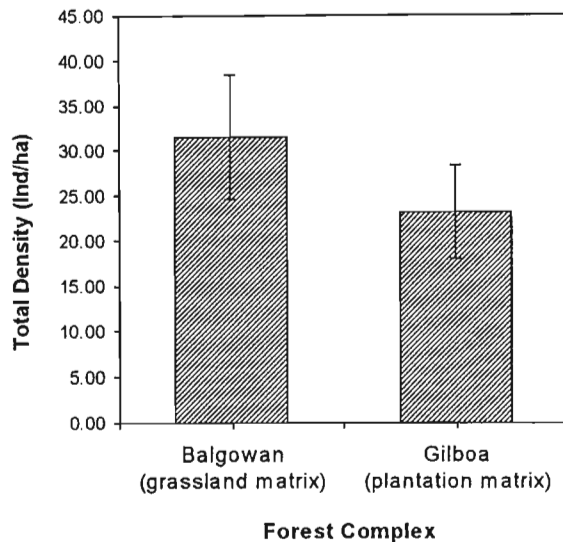
Figure 2.4. Total density (individuals per hectare) of forest birds in each forest complex. Standard error is denoted by I.

The mean species density (Appendix 2.3) was low with 90% (*n* = 53) of the species from the forest patches of the two complexes having densities less than one individual per hectare. Only six species, namely the Sombre Bulbul (*Andropadus importunus*), Yellowthroated Warbler (*Phylloscopus ruficapillus*), Barthroated Apalis (*Apalis thoracica*), Southern Boubou (*Laniarius ferrugineus*), Collared Sunbird (*Anthreptes collaris*), and Cape White Eye (*Zosterops pallidus*), had densities greater than one individual per hectare in the two forest complexes. In the control patch, the mean density of individual species was also low with 96% (*n* = 50) of the species having densities less than one individual per hectare. Only the Sombre Bulbul (*Andropadus importunus*) and Cape White Eye (*Zosterops pallidus*) had densities greater than one individual per hectare.

The total avian density estimate at Leopards Bush was comparatively low (8.87 ind./ha; Fig. 2.5), however this forest also had the largest number of rare bird species ($n = 21$, 40%; those with densities ≤ 0.03 ind./ha) approximately half of which were forest dependent ($n = 10$). Twenty-seven percent ($n = 15$) of bird species in the Balgowan complex were rare, as defined by the latter criterion, with 21% ($n = 11$) in the Gilboa complex.
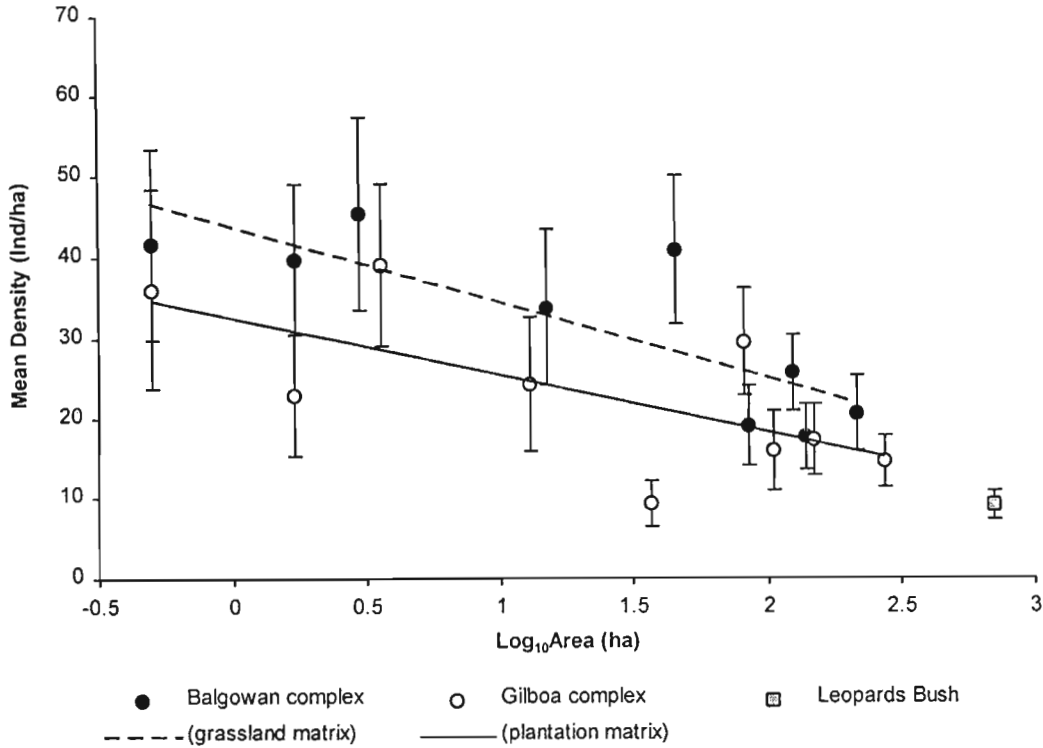
Figure 2.5. Mean bird species density (individuals per hectare) versus log area for forest patches in each complex as well as the control, Leopards Bush. Standard error is denoted by I.

2.3.3 Is density compensation occurring in these forests?

A significant negative relationship existed between the total density of birds in a patch and the area of the patch, and bird density was significantly lower in larger forest patches (*Density* = *-8.34 log Area* + *38.142*; $F_{1, 16} = 15.052$, $P < 0.002$, $r^2 = 0.49$). The negative correlation between density and area was stronger for the Balgowan complex, where there is natural matrix habitat ($P < 0.007$, $r^2 = 0.68$; Fig. 2.5), than for the plantation-dominated Gilboa complex ($P < 0.05$, $r^2 = 0.47$).

In both the Balgowan and Gilboa forest complexes there was no relationship between the total density of birds in a patch and the bird species richness of the patches ($P < 0.2$, $r^2 = 0.297$ and $P < 0.9$, $r^2 = 0.009$ respectively), although a negative trend was evident for the Balgowan complex. However, since density compensation should only occur when communities are saturated with species, and their respective densities are relatively high to account for the adjustments necessary for coexistence, an analysis using only common species (i.e. those species occurring in all of the forest patches and including those with densities > 1 ind./ha; $n = 14$) may be more appropriate. The presence of more rare bird species i.e. those that live naturally at low density and have life histories adapted to this life-style, may underestimate the level of density compensation occurring across the community (Lawes and Eeley, 2000). Although not significant, an obvious negative trend between total common bird species density and species richness was found for the forest patches of the Balgowan complex (*Density = -8.34 sp. + 53.39*; $F_{1,7} = 4.90$, $P = 0.06$, $r^2 = 0.41$; Fig. 2.6), while there was clearly no relationship for the Gilboa complex (*Density = -0.35 sp. + 29.44*; $F_{1,7} = 0.21$, $P = 0.66$, $r^2 = 0.03$).
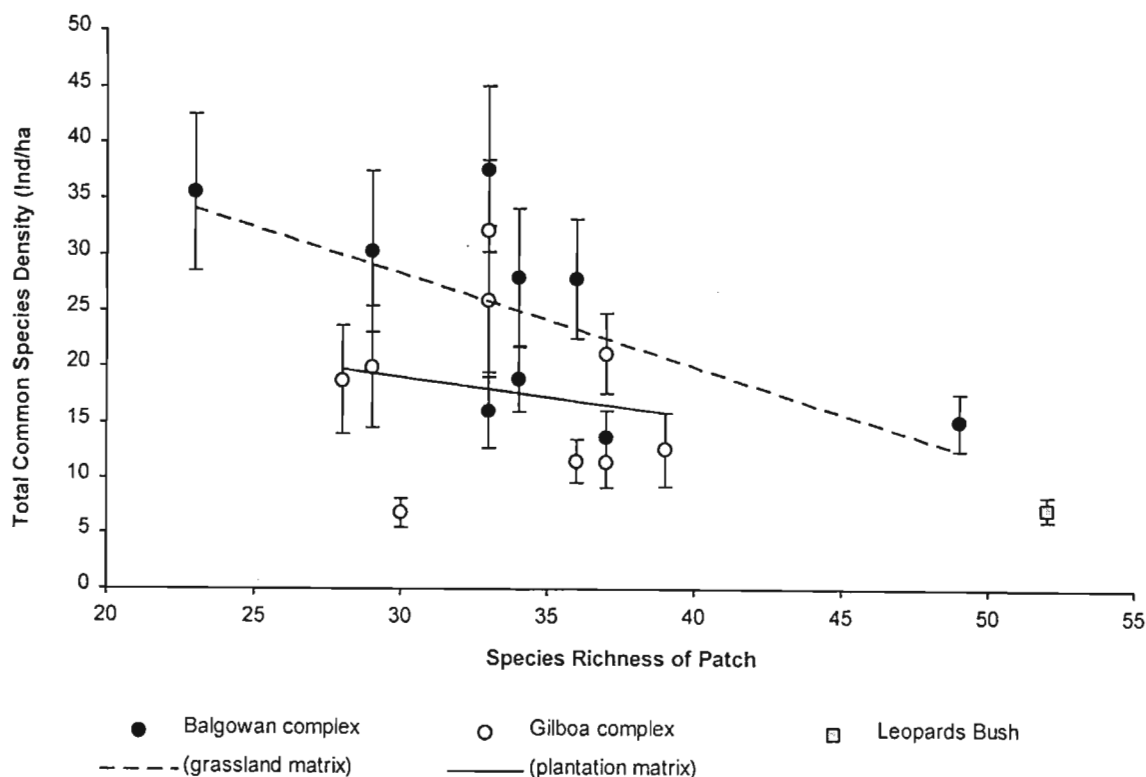
Figure 2.6. Total density (individuals per hectare) of bird species common to all forest patches (including the control) versus species richness. Standard error is denoted by I.

These data suggest that density compensation in the forest patches is generally an area-dependent phenomenon operating at the landscape-level, and only weakly controlled by differences in species richness between forest patches. However, in the Balgowan complex the influence of species packing / richness was more evident, where 41% of the variation in common bird species density was explained by differences in species richness between forest patches, when compared to the Gilboa complex (3%).

It should be noted that, although phylogenetic effects can play an important role in moulding patterns of species occurrence in biogeographical regions, the occurrence of species in habitat patches following short-term disturbance effects such as forest fragmentation due to anthropogenic landscape change, are determined by current ecological effects such as matrix effects and assemblage saturation (Charnov, 1993; Lawes and Eeley, 2000). Phylogenetic effects were therefore not considered in this analysis.

2.3.4 Area, isolation, and habitat diversity

Multiple linear regression models were run for the two complexes separately. In neither case was the fit of the model including the variables area, isolation distance and habitat diversity significant (Gilboa: $F_{3,5} = 1.31$, $P = 0.37$, $R^2 = 0.1$; Balgowan: $F_{3,5} = 3.62$, $P = 0.1$, $R^2 = 0.49$), although the Balgowan complex approached significance ($P = 0.1$) and the area coefficient was significant ($t = 2.95$, $P = 0.03$). These regression models confirm the general lack of an isolation or habitat diversity effect on birds species richness in these forests, but show that patch area is the most important environmental effect, and further that there is no area effect in the plantation-dominated Gilboa complex.

2.3.5 Species-area analysis

i. Species-area curves

The number of species in a forest patch was dependent on patch area (i.e. the island effect) in the Balgowan complex ($S = 28.984 + 0.075A$; $F_{1,7} = 14.74$, $P < 0.007$, $r^2 = 0.68$) and independent of patch area in the Gilboa complex ($S = 31.536 + 0.0273A$; $F_{1,7} = 4.73$, $P < 0.08$, $r^2 = 0.40$; Fig. 2.7). The slopes of the two regressions were thus significantly different ($t = 2.153$, $df = 14$, $P < 0.05$, Zar, 1999). These findings suggest that matrix type has an influence on bird species richness in forest patches – the

species richness of forests surrounded by an unnatural plantation matrix, do not show an island effect, and are generally more species poor than those surrounded by natural grassland.

Comparison of the species-area curves between the two forest complexes suggests that the shallow slope found in the Gilboa is due to species relaxation in the larger patches. In forest patches smaller than 53.4ha there were more bird species in forests in the pine-dominated matrix (Gilboa) than in the natural grassland matrix (Balgowan) (Fig. 2.7). A relatively larger percentage of forest dependent species were also found in the smaller patches (< 4ha) of the Gilboa complex (Gilboa = 74%, n = 17; Balgowan = 59%, n = 13).
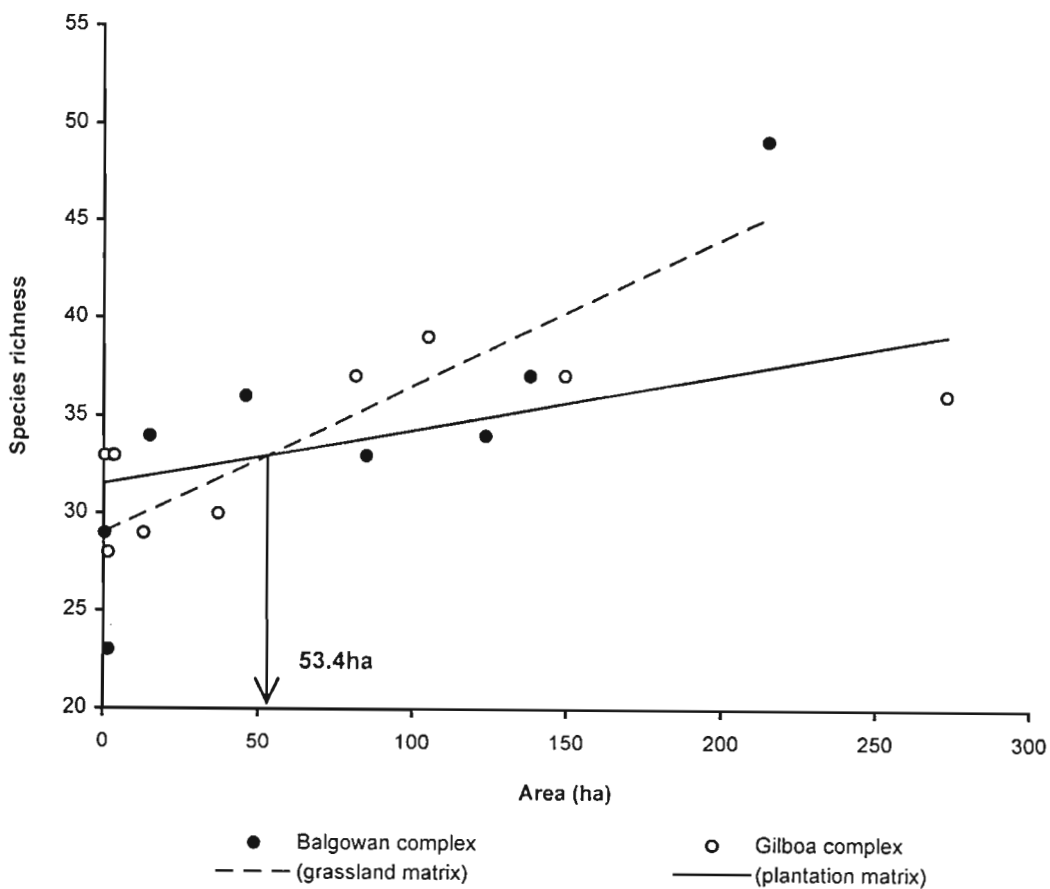
Figure 2.7. A comparison of the species-area regressions as plotted for the Balgowan (natural grassland matrix) and Gilboa (plantation matrix) forest complexes.

ii. Minimum critical patch size

To further determine the influence of matrix type on the island effect, species-area regression curves for the patches ("islands") from the two forest complexes,

Balgowan (natural matrix) and Gilboa (plantation matrix), were compared to the "mainland" curve (control patch) ($S = 36.77 + 0.049A$; $F_{1, 5} = 33.0$, $P < 0.003$, $r^2 = 0.87$) independently (Fig. 2.8a-b). If the mainland or the Leopards Bush data are representative of species richness in extensive tracts of forest in a natural matrix, then the differences between the slopes in terms of species richness, for a particular patch size, indicates species loss attributable to insularisation. The most substantial differences in species richness were for small forest patches in the Balgowan complex (Fig. 2.8a) and for large forest patches in the Gilboa complex (Fig. 2.8b). For example, the smallest patches of the Balgowan complex (< 1.8ha) supported an average of only 72% of the bird species contained in comparable areas of Leopards Bush (Gilboa patches < 1.8ha = 85%). The largest patches of the Gilboa complex (> 138ha) supported an average of only 77% of the bird species contained in similar areas of the mainland (Balgowan patches > 138ha = 91%).

Although the mainland and island curves for the Balgowan complex had similar slopes they nevertheless converged, and the minimum critical patch size (MCPS; i.e., that minimum forest area required to avoid loss of species due to insular effects) was estimated at 302ha for forests within the natural grassland matrix (Fig. 2.8a). Because of the potentially large zone of overlap of intersection of the regression curves, I examined the error associated with this MCPS estimate, i.e. the approximate range in area about the point of intersect over which mainland and island species estimates are essentially the same (following Zar, 1999; p368). However, for conservation purposes, the upper limit of area about the intersection is unimportant, as above the intersect value forest patches are considered to be "mainland" patches where species relaxation due to insular effects is minimal. It is the area value at the point of intersection and the lower limit that are critical because bird species are lost from forest patches smaller than the intersect area. At 130ha, the species estimates for mainland and Balgowan island curves were not significantly different ($t = 2.156$, $df = 12$, $0.1 > P > 0.05$). Thus island effects are negligible above 130 – 302ha for indigenous forest patches situated within the natural grassland matrix (the intersection value being the more critical island size).
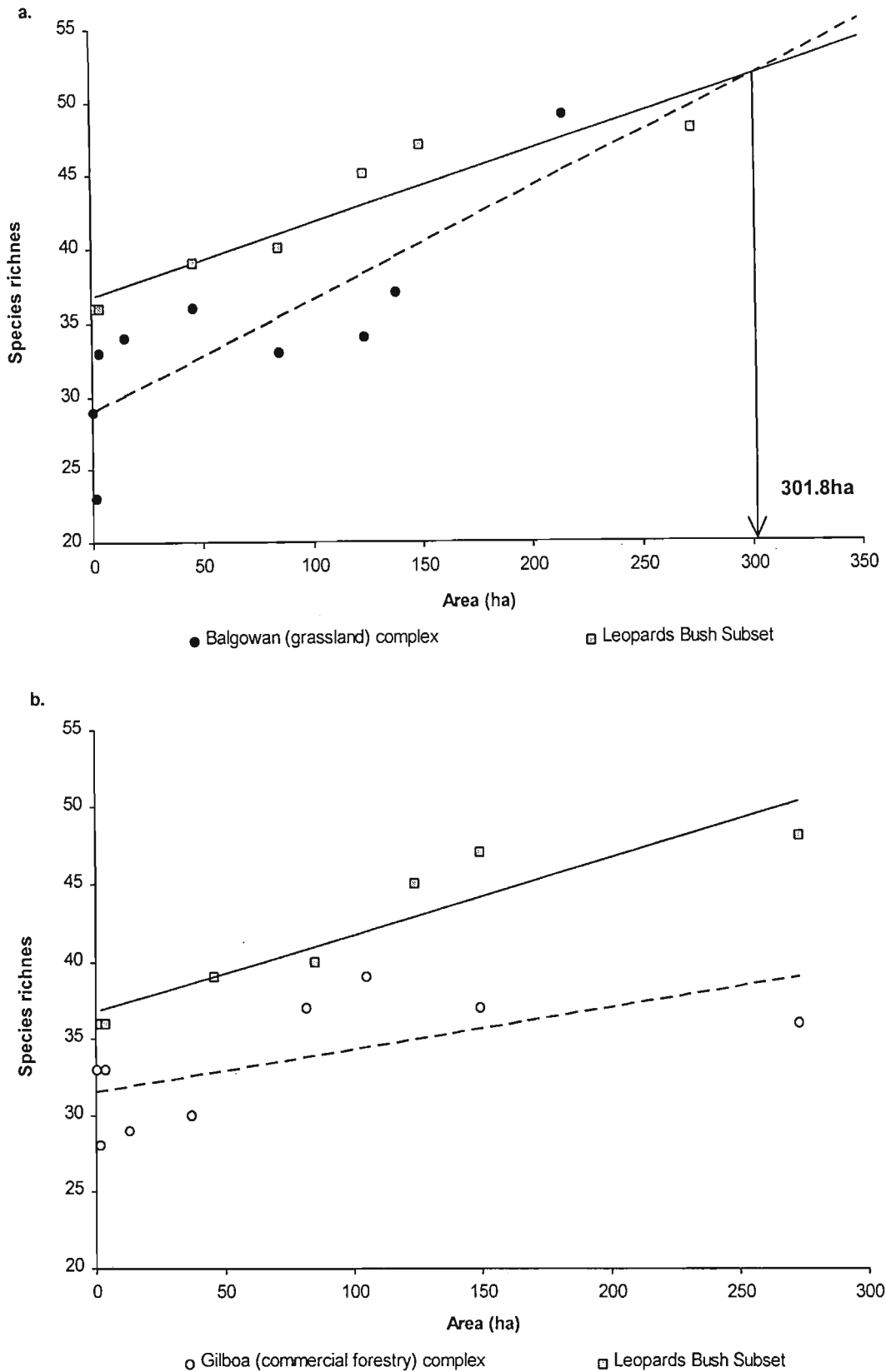
Figure 2.8. Species-area regressions for forest patches of (a) the Balgowan complex and (b) the Gilboa complex, plotted against that for contiguous subplots within the control or mainland patch, Leopards Bush. Minimum critical patch size (MCPS) is represented by the point of intersection in (a) MCPS = 301.8ha.

Mainland and island curves for bird species richness in forests in the plantation matrix (Gilboa complex) did not converge, since the slope of the curve for the Gilboa complex did not differ significantly from zero, and MCPS could not be calculated by the above method (Fig. 2.8b). Theoretically, since the landscape is disturbed (in this case dominated by commercial plantation) and because the slope of the species-area curve is essentially zero), there is no forest fragment in this matrix large enough to reach MCPS. In other words, the plantation matrix influences species richness in these forest patches so that it remains constant about the mean (33.6 species). There is a pervasive negative effect on bird species richness across the forest patch sizes within this matrix type, and forest patches surrounded by commercial plantation will have fewer species than extensive tracts of forest (i.e. forests of area $\geq$ 302ha).

2.4 Discussion

It is generally recognised that insularisation leads to species loss (relaxation) from habitat remnants (Quinn and Hastings, 1987; Rolstad, 1991; Saunders et al., 1991; Simberloff, 1994; Brooks et al., 1999). Species-area equilibrium theory predicts that large areas support larger numbers of species than do small areas (Preston, 1962; MacArthur and Wilson, 1963, 1967). Bird species richness in Afromontane Mistbelt Mixed *Podocarpus* forest patches is characterised by a matrix-dependent island effect where forest patches support fewer bird species than comparably sized contiguous patches of "mainland" forest, and small forest patches surrounded by natural grassland contain fewer species than large forest patches. The island effect is not significant where indigenous forest patches are surrounded by commercial plantation matrix habitat.

Studies of species loss in fragments of tropical rainforest show that small fragments generally contain fewer species of birds (Willis, 1979; Lovejoy et al., 1986; Thiollay and Meyburg, 1988; Newmark, 1991; Bierregaard and Stouffer, 1997; Warburton, 1997; Daily et al., 2001), small mammals and primates (Bierregaard et al., 1992), frogs (Zimmerman and Bierregaard, 1986) and many invertebrate species (Klein, 1989; Fonseca de Souza and Brown, 1994; Weishampel et al., 1997) than larger fragments or areas of similar size in continuous forest. These results are supported by studies from temperate woodlots where forest patch size accounted for

most of the variation in species numbers (Whitcomb *et al.*, 1977; Freemark and Merriam, 1986; Bellamy *et al.*, 1996; Trzcinski *et al.*, 1999). Larger patches can support more diverse assemblages than smaller patches because of greater microhabitat diversity (as shown in this study), including more food sources, nesting sites, and refuge from predators or competitors (Boecklen, 1986; Simberloff, 1992; McIntyre, 1995). Brown *et al.*, (1995) found that among bird assemblages of subtropical dune thicket forest in South Africa, species richness was best explained by increasing habitat complexity with area. In addition, larger forest patches have a larger core area that is unaffected by the environmental and biotic changes associated with edges (Yahner, 1988; Laurance, 1991; Noss and Csuti, 1997). For example, Krüger and Lawes (1997) found a significantly greater turnover of bird species at the forest edge than in core areas of the Ongoye Forest Reserve, South Africa, and attributed this to increased disturbance associated with forest edge.

The exponent "z" of the log species-log area relationship ($S = CA^z$) defines the slope of the regression and so reflects the rate at which species richness declines with island area (MacArthur and Wilson, 1967; Gilbert, 1980; McGuinness, 1984; Gotelli and Graves, 1996). Furthermore, differences between the slope of the island and the mainland species-area regressions provide evidence for the extent of insular effects on species number (Gilbert, 1980; Bond *et al.*, 1988; Warburton, 1997). For the exponent z, Preston (1962) predicted values of 0.20 – 0.40 for real islands (i.e. truly isolated), while MacArthur and Wilson (1967) suggested that for insular habitats within continents, values of z should range from 0.12 – 0.19. In addition, the value of z is usually lower for mainlands (0.10 – 0.20) than for islands (MacArthur and Wilson, 1967; Diamond and May, 1976; Gilbert, 1980). The slope (z) of the log species-log area regression for the Balgowan forest complex (0.07) is lower than the predicted values for habitat islands, while the slope for the Gilboa forest complex does not differ significantly from zero.

In an investigation of fragmentation effects on the avifauna of isolated rainforest remnants in tropical Australia, Warburton (1997) obtained a slope of 0.149 for the log species-log area relationship. Similarly, for bird species in temperate forest patches of east-central Illinois, Blake and Karr (1984) obtained a slope of 0.194, while Stratford and Stouffer (1999) obtained a slope of 0.76 for birds in tropical Amazon forest fragments and 0.3 for control plots within continuous Amazonian forest near Manaus, Brazil. In comparison, the shallow slopes obtained for the Balgowan and

Gilboa forest complexes indicate that species relaxation in these forest fragments is occurring at a rate slower than in other forest habitats mentioned. However, in all the case studies referred to above, the forests are recent remnants of once continuous forest, whereas the Afromontane forests of the Karkloof / Balgowan range are believed to have been fragmented throughout most of their evolutionary history due to repeated and severe climate changes in the Quaternary (Eeley *et al.*, 1999). These climatic changes would have driven the extinction filtering (*sensu* Balmford, 1996) of less resilient species resulting in a community comprised of robust and more resilient species (Lawes, Mealin and Piper, 2000).

The Afromontane avifauna of the Karkloof / Balgowan forest archipelago may thus be more tolerant of fragmentation and less susceptible to local extinctions in response to a decrease in area (hence the shallow "species-relaxation" slopes), than avifaunas in other forest habitats such as those mentioned above. If the "climatic filtering" hypothesis is correct, then it is a matter of considerable concern that, in spite of the putative assemblage resilience to insularisation, large forests surrounded by plantation nevertheless show notable species relaxation. One interpretation of these data is that the effect of commercial plantation forestry on species richness is proportionately greater than the effects of climatic extinction filtering. In fact, the effect of commercial plantation on species loss is probably much greater than suggested by the shallow species-area slope for forests in the Gilboa.

It is certain that the Balgowan forest complex (the natural situation) displays a significant island effect where the smaller patches support fewer species than larger patches, while in comparison, no effect of area on species richness is detectable in the Gilboa forest complex (commercial forestry matrix). I argue that this is indicative of a significant effect of the matrix surrounding the forest patches (since this is the single most important difference between the two forest complexes), on bird species richness. For example, the type of matrix surrounding south-temperate rainforest fragments in Chile had a similar influence on the bird assemblages inhabiting them (Willson *et al.*, 1994). In forest fragments surrounded by non-forest matrix, such as agriculture or pastures for cattle grazing, there was a positive relationship between bird species richness and the size of the forest fragments. However, in central Chile Estades and Temple (1999) found a negative relationship between species richness and fragment size in fragments of the same forest type but surrounded by pine plantations. The nature of the matrix influences patch species richness mainly by

determining the likelihood and success of movement between forest fragments (Turner, 1996). Estades and Temple (1999) found a slightly higher species richness in small coastal deciduous forest fragments surrounded by extensive pine plantation, and suggested that most forest birds were as likely to be found in small fragments as in large fragments, due to their use of the surrounding habitat. Similarly, the relatively low rate of change in species number across the Gilboa forest patches suggests that the pine plantation matrix may equilibrate opportunities for dispersion for some species, by creating a closed environment and providing forest-like cover for arboreal birds to move between indigenous forest patches. Consequently, the plantation matrix is facilitating a higher avian diversity in smaller patches that would ordinarily have experienced a decrease in diversity following fragmentation.

Alternatively, some studies have reported a surprisingly high diversity of wildlife contained in small patches of rainforest in Malaysia, apparently because they receive little human disturbance and are surrounded by extensive tree plantations that act as buffers (Bennet and Caldecot, 1981; Duff *et al.*, 1984). Expanses of planted tree species may form valuable corridors, increasing the connectedness of primary fragments and maintaining higher rates of immigration to them (Turner, 1996). Thus avian forest communities surrounded by plantation might be expected to show less of an island effect than those forest patches within non-forest matrix such as natural grassland as is the case of the Balgowan complex in this study. However, while at first sight this slowing of species relaxation in fragments may appear to be a positive effect of plantations, the transient nature of plantations must be kept in mind. Plantations are harvested and the trees clear-felled. Harvesting occurs every 10-15 years and may provide a metronomic-like disturbance effect on avian assemblage structure. Any species that responds favourably to this regular disturbance would be "selected" for and so plantation forestry has the capacity to significantly alter bird assemblage structure with time.

The forest patches of the Balgowan (natural grassland) complex also exhibit patch area-dependent density compensation (*sensu* MacArthur *et al.*, 1972). Density compensation usually describes an inverse relationship between population density and species richness (McGrady-Steed and Morin, 2000; Stevens and Willig, 2000). However since species richness is a positive function of area, if we assume that the density of a group of species is constant per unit area, then the densities of individual

species must, on average, decrease in larger areas (Schoener, 1986). Density compensation may thus be a natural corollary of density-area effects.

MacArthur *et al.* (1972) found that, on average, island species had higher population densities than mainland species in the Pearl Archipelago off Panama. They 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. However, Schoener (1986) and Connor *et al.* (2000) argue that if total species density is independent of area (as assumed by MacArthur and Wilson, 1967) and if a species-area relationship exists, one need not infer competitive release to account for density compensation. However, for forest patches of the Karkloof / Balgowan range species density is dependent on area, and the trend toward species richness-dependent density compensation in the Balgowan complex suggests that the bird assemblages are approaching saturation if not already saturated with species. The absence of species richness-dependent density compensation in the Gilboa complex therefore implies that bird assemblages are not saturated. This may also be symptomatic of a significant effect of the nature of the matrix surrounding the forest patches, on bird species density. Again, the forest-like plantation matrix of the Gilboa complex may be acting as a "dispersion medium" for the individuals of the bird species in the indigenous forest patches, thereby counteracting both area and species richness effects on density compensation. In other words the pine plantation matrix may facilitate movement between indigenous forest patches.

In both the Balgowan and Gilboa forest complexes the number of forest dependent bird species also decreases with patch size, and the more rare species (i.e. those with densities ≤ 0.03 ind./ha) are lost first from small patches. Studies have revealed that species that live naturally at low density and so are generally scarce, and those with restricted ranges or limited dispersal ability are most likely to disappear first following habitat destruction and fragmentation (Diamond *et al.*, 1987; Newmark, 1991; Simberloff, 1994; Wiens, 1994; Warburton, 1997).

The conclusion that species will be lost with reduction in forest area leads to the notion that there must be a minimum critical size for patches in a fragmented landscape to maintain natural bird diversity (Lovejoy and Oren, 1981). The minimum critical area is essentially an index of how large a patch must be to express its essential structural character, and/or to be representative of a community type

(Forman, 1997). In theory a small fragment will support a smaller population of a given species than a larger one. As a fragment becomes very small, these populations will fall below viable levels and extinction will follow (Turner, 1996). Small populations may be more liable to fluctuations, which will inevitably include local extinctions. Populations will also tend to suffer from genetic drift and inbreeding that reduce genetic variation, increase homozygosity, and in the end, reduce fitness (Caughley, 1994; Mills and Smouse, 1994). However, Thomas (1994) argues that the rapidly changing nature of fragments in the landscape means that demographic collapse is much more likely than genetic collapse mediated by the effects of inbreeding and genetic drift. This likelihood is supported by studies of a forest primate in the mistbelt forests of South Africa (Swart *et al.*, 1993).

Island effects become negligible for bird species in the forest patches of the Karkloof / Balgowan range (that are surrounded by natural grassland matrix habitat), above 302ha (MCPS) and below this size, bird communities decrease in species richness. Consequently, in order to conserve avian diversity in this fragmented forest range; patches of this size and larger are needed to preserve as many bird species as possible. (This does not apply to forest patches surrounded by commercial plantation where no MCPS exists due to the pervasive and negative effects of the surrounding matrix). To compare this MCPS to previous studies, rough estimates of MCPS were calculated using data from Castley (1997) for Afromontane forests of the Eastern Cape, and Koen (unpublished data) for forests of the Oteniqua Mountains of the Eastern Cape, by fitting a quadratic equation to untransformed species-area data and calculating the asymptote. The estimates of minimum critical patch sizes calculated by this crude method for these forested areas were found to be 352ha and 539ha respectively.

2.5 Conclusion

In terms of a management strategy for indigenous forest in the region, clearly our priority remains to conserve the largest, intact forest units, in order to preserve overall species richness. In the Karkloof / Balgowan forest range insularisation has lead to species loss from habitat remnants. Forest fragments support fewer bird species than comparably sized patches of contiguous mainland forest, and small forest fragments within natural grassland matrix habitat have fewer species per unit area than larger forest fragments. In order to conserve as many bird species as possible, forest patches

(surrounded by natural grassland) of 302ha (MCPS) and more are needed, as island effects become negligible for bird species in forest patches above this size, while below this size bird species are lost from forest fragments.

In forests in the plantation-dominated matrix no island-effect is detectable and it appears that forest patches are converging on the same species richness, regardless of forest size. Therefore, a MCPS does not exist for this disturbed forest complex. Nevertheless, in order to conserve as many bird species as possible, it would be wise to preserve the largest intact forest fragments rather than small fragments. I recommend that commercial forestry ventures should avoid growing extensive tree plantations where natural grassland / indigenous forest landscape mosaics exist. At the landscape-level it is clear that the nature of the matrix affects avifaunal diversity and distribution in forest patches, and plantations have the capacity to significantly alter bird assemblage structure and composition in indigenous forest patches. This indicates that forest fragments must be considered as integrated parts of a complex landscape mosaic of different habitat types, and in the following chapter I investigate how the composition of the forest bird assemblages in patches of the Karkloof / Balgowan forest range is affected.

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Appendix 2.1. Habitat diversity of forest patches represented by Simpson's diversity index (λ), calculated using the total number of meters along each transect, occupied by each microhabitat. Descriptions of forest microhabitat categories are given.

		Grassland matrix									Control
		Balgowan complex									
Category	Forest microhabitat	A	B	C	D	E	F	G	H	I	LB
		Total number of meters along each transect occupied by microhabitat									
1	Edge habitat (natural grassland/forest or large clearing within forest)	15	15	5	5	5	10	10	10	10	15
2	Marshy (muddy; little or no undergrowth)	30	10	20	-	-	-	-	-	-	30
3	Old wood (large trees; high, dense canopy; no mid-stratum; sparse undergrowth*)	-	40	-	-	-	-	40	-	30	150
4	Young wood (young, small trees; low, sparse canopy; sparse undergrowth*)	55	30	10	50	20	40	50	-	10	240
5	Mixed wood (young and old trees; high, dense canopy; mid-stratum present; dense undergrowth**	370	160	180	140	115	70	20	50	20	750
6	Closed thicket (low, tangled bushes and vines)	55	60	-	20	10	20	-	-	-	160
7	Open thicket (tangled vegetation; open underneath; no undergrowth)	30	-	45	10	15	10	15	20	20	120
8	Small clearing (small opening in forest canopy (< 10m2) with well developed / hardy ground cover)	30	40	40	-	10	-	-	10	-	40
9	Large clearing (large opening in forest (10 > 50m2) with grass and pioneer and/or exotic tree species)	40	60	-	-	-	20	-	-	-	50
10	Fallen tree	30	10	30	30	20	10	10	20	20	60
11	Stream / water feature	10	-	30	10	-	-	-	-	-	40
12	Rocky area; sparse undergrowth*	20	30	40	10	10	20	5	10	20	55
	Total number of microhabitats	11	10	9	8	8	8	7	6	7	12
	Habitat diversity: Simpson's Index (1/λ)	3.152	5.416	4.005	3.188	2.883	5.000	4.545	4.000	6.259	4.201

*Sparse undergrowth = ferns or thin herb layer; leaf litter well developed
**Dense undergrowth = many species: ferns, grass, shrubs and herbs, creepers

		Commercial forestry								
		Gilboa complex								
Category	Forest microhabitat	A	B	C	D	E	F	G	H	I
		Total number of meters along each transect occupied by microhabitat								
1	Edge habitat (natural grassland/forest or large clearing within forest)	15	-	-	5	-	-	-	-	-
2	Marshy (muddy; little or no undergrowth)	10	30	-	-	-	-	-	-	10
3	Old wood (large trees; high, dense canopy; no mid-stratum; sparse undergrowth*)	30	110	50	30	-	10	-	-	20
4	Young wood (young, small trees; low, sparse canopy; sparse undergrowth*)	20	40	20	2	50	20	-	20	-
5	Mixed wood (young and old trees; high, dense canopy; mid-stratum present; dense undergrowth**	160	180	150	100	70	110	60	30	50
6	Closed thicket (low, tangled bushes and vines)	45	20	20	30	40	10	10	10	10
7	Open thicket (tangled vegetation; open underneath; no undergrowth)	40	10	70	30	-	-	20	20	-
8	Small clearing (small opening in forest canopy (< 10m2) with well developed / hardy ground cover)	60	10	15	10	10	-	10	-	-
9	Large clearing (large opening in forest (10 > 50m2) with grass and pioneer and/or exotic tree species)	50	-	-	-	-	-	-	-	-
10	Fallen tree	30	60	80	40	20	30	20	10	10
11	Stream / water feature	20	-	10	-	-	-	-	-	10
12	Rocky area; sparse undergrowth*	20	20	15	15	10	30	20	5	15
	Total number of microhabitats	12	9	9	9	6	6	6	6	7
	Habitat diversity: Simpson's Index (1/λ)	6.468	4.465	4.911	4.684	4.167	3.041	3.920	4.688	4.433

*Sparse undergrowth = ferns or thin herb layer; leaf litter well developed
**Dense undergrowth = many species: ferns, grass, shrubs and herbs, creepers

Appendix 2.2. Mean densities (individuals per hectare) for individual bird species recorded in all nineteen forest patches, averaged over eight replicate transects in each forest patch of the two complexes, and twenty two replicate transects in the control, Leopards Bush. Total density for each patch is also given.

| Common name | Grassland matrix Balgowan complex | | | | | | | | | Commercial plantation matrix Gilboa complex | | | | | | | | | Control |
	A	B	C	D	E	F	G	H	I	A	B	C	D	E	F	G	H	I	LB
Hadeda Ibis	0.13	-	0.14	0.10	0.55	0.14	-	-	0.43	-	-	-	-	-	-	0.31	-	-	0.04
Crowned Eagle	-	-	0.21	-	-	0.14	-	-	-	-	-	0.06	0.05	0.14	-	-	-	-	0.04
Steppe Buzzard	0.03	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	0.01
Little Sparrowhawk	0.03	-	0.03	-	0.07	-	-	-	-	-	-	0.03	-	-	-	-	-	-	0.02
Black Sparrowhawk	-	0.03	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-
Gymnogene	0.03	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-	0.01
Rednecked Francolin	-	-	-	-	-	-	-	-	-	-	0.06	0.06	-	0.21	-	-	-	-	0.01
Crested Guineafowl	0.03	-	0.17	-	0.07	-	-	-	-	-	0.06	-	-	-	-	-	-	-	0.05
Buffspotted Flufftail	0.03	-	-	-	-	-	-	-	-	-	-	0.03	-	0.07	-	-	-	-	0.01
Rameron Pigeon	0.41	0.89	0.76	0.05	2.35	0.21	0.41	-	-	0.03	0.74	0.13	1.91	0.07	0.24	0.10	-	0.91	0.04
Redeyed Dove	0.26	0.24	0.21	0.26	0.76	0.48	2.38	-	2.46	0.13	0.35	0.19	0.88	0.21	0.48	0.83	0.64	1.30	0.10
Cape Turtle Dove	0.21	0.21	0.41	0.16	0.21	0.21	0.31	-	1.01	-	0.21	0.13	0.21	0.07	-	-	0.38	0.91	0.01
Tambourine Dove	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	0.10	-	-	-
Cinnamon Dove	0.13	0.47	0.76	0.05	1.52	0.14	0.21	0.65	-	0.13	0.27	0.09	0.21	0.14	0.16	0.10	0.26	-	0.03
Knysna Lourie	0.85	0.09	1.24	0.10	2.00	0.48	-	-	-	0.59	0.30	0.28	0.72	0.21	0.32	0.31	-	0.26	0.09
Redchested Cuckoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.09
Black Cuckoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01
Emerald Cuckoo	0.03	0.03	-	-	0.07	-	-	-	-	0.08	0.09	0.09	0.05	0.07	-	-	0.13	-	0.01
Speckled Mousebird	-	-	-	-	0.41	-	-	-	-	-	-	-	-	-	0.40	-	-	-	-
Narina Trogon	0.03	0.03	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-	-	0.04
Redbilled Woodhoopoe	-	-	-	-	-	-	-	-	0.43	-	-	-	-	-	-	-	-	-	-
Redfronted Tinkerbarbet	0.16	0.12	-	-	-	0.07	-	-	-	0.13	-	-	0.31	-	0.08	-	-	-	-
Scalythroated Honeyguide	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02
Goldentailed Woodpecker	0.08	-	-	-	-	-	-	-	-	-	0.06	-	-	-	-	-	0.13	0.52	0.03
Olive Woodpecker	0.49	0.50	0.90	0.72	1.17	1.17	2.28	1.04	1.30	0.28	0.30	0.32	0.83	0.41	0.32	0.94	0.64	0.52	0.23
Grey Cuckooshrike	0.16	-	-	0.41	-	0.41	-	-	-	0.08	0.30	0.22	0.16	-	-	-	-	0.52	0.09
Forktailed Drongo	0.41	0.12	0.03	0.16	0.76	-	0.41	-	0.43	0.13	0.35	0.06	0.21	0.14	0.16	0.42	0.38	0.52	0.11
Squaretailed Drongo	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03
Blackheaded Oriole	0.36	0.03	0.48	0.10	0.83	0.48	0.62	-	0.72	0.31	0.56	0.32	0.62	0.14	0.40	0.73	0.51	1.30	0.08
Southern Black Tit	-	0.12	-	-	0.41	0.14	0.10	0.26	0.29	0.08	0.12	0.09	0.21	-	-	0.52	-	0.39	0.01
Blackeyed Bulbul	0.75	0.12	0.38	1.45	1.03	2.69	2.38	0.39	1.45	0.34	0.41	0.51	0.57	0.62	1.52	1.88	0.77	1.04	0.06
Terrestrial Bulbul	0.47	0.44	0.34	0.88	2.41	1.72	5.17	0.52	2.46	0.34	0.35	0.28	0.57	0.21	1.36	1.88	1.66	1.69	0.15
Sombre Bulbul	2.07	1.69	2.59	2.28	3.79	4.42	4.24	4.69	4.48	2.04	1.36	1.96	2.12	0.55	2.64	3.85	2.43	2.60	1.03
Yellowbellied Bulbul	-	-	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	0.01
Olive Thrush	0.08	0.03	0.14	0.16	0.48	1.31	0.41	0.39	0.87	0.08	0.53	0.06	0.52	-	0.32	-	0.38	0.13	0.04
Orange Thrush	-	-	-	-	-	-	-	-	-	-	-	0.13	0.05	-	-	-	-	-	0.01
Chorister Robin	0.28	0.24	0.38	0.10	0.55	0.07	0.93	0.26	1.30	0.13	0.35	0.13	0.36	-	0.16	0.94	0.13	0.26	0.20
Cape Robin	0.18	0.92	0.24	0.78	0.76	1.24	2.28	1.17	1.59	0.18	0.24	0.03	0.52	0.14	0.48	0.73	1.66	1.04	0.05
Starred Robin	0.10	0.09	0.07	0.36	0.07	0.41	0.10	0.26	-	0.05	0.21	0.35	0.21	0.14	0.16	0.31	0.13	-	0.15
Yellowthroated Warbler	1.47	0.98	1.41	1.29	2.76	1.93	1.55	2.21	2.31	1.09	1.74	0.98	1.40	0.28	1.52	2.71	1.40	3.13	0.67
Barthroated Apalis	1.68	2.54	2.48	1.50	3.93	2.21	4.45	6.90	2.17	1.19	1.66	1.04	3.10	0.55	2.08	4.58	1.91	3.26	0.57
Yellowbreasted Apalis	-	0.41	0.07	-	-	-	-	0.26	-	0.28	0.30	-	0.10	-	-	-	-	0.39	0.01
Bleating Warbler	0.93	0.35	1.35	0.62	1.10	0.55	0.52	3.91	1.16	0.83	0.80	1.14	1.03	0.28	0.96	2.40	0.51	0.52	0.56
Spotted Prinia	0.21	0.06	0.03	0.05	0.14	0.28	0.10	1.04	0.87	-	-	-	-	0.55	-	0.10	-	-	0.01
Spotted Flycatcher	0.03	-	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dusky Flycatcher	0.18	0.21	0.21	0.16	0.28	-	0.10	0.39	0.29	0.10	0.24	0.13	0.31	-	0.32	0.21	0.26	0.26	0.05
Cape Batis	1.01	0.68	1.07	0.93	2.07	0.55	1.45	1.30	1.16	0.65	0.83	0.79	1.50	0.28	0.64	1.04	0.51	1.56	0.33
Chinspot Batis	0.08	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-	0.26	-		0.02
Bluemantled Flycatcher	0.18	0.06	-	0.16	0.07	0.14	0.10	0.10	-	0.05	0.03	0.09	0.05	0.07	-	0.21	0.26	0.39	0.01
Paradise Flycatcher	0.16	0.03	0.62	0.21	0.69	-	0.62	0.65	0.87	0.10	0.15	0.06	0.10	0.07	0.32	0.52	0.38	-	0.04
Southern Boubou	0.80	0.80	2.00	0.52	2.28	1.10	0.72	1.69	2.03	1.11	0.38	0.54	1.81	0.55	1.12	1.98	1.53	1.56	0.61
Puffback	0.72	0.18	0.69	0.26	1.45	0.34	1.14	0.91	1.30	0.44	0.65	0.57	1.19	0.34	0.80	1.25	0.89	1.95	0.31
Olive Bush Shrike	0.05	0.21	0.34	0.05	0.28	0.14	0.10	-	-	0.05	-	-	0.10	-	-	0.21	-	0.26	0.03
Redwinged Starling	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Greater Doublecollared Sunbird	0.57	0.62	0.31	0.78	1.31	1.52	1.35	0.78	1.01	0.08	0.24	0.32	0.16	0.28	0.48	0.83	1.28	1.43	0.28
Black Sunbird	0.13	-	-	-	-	0.21	0.21	-	0.72	-	0.03	-	-	-	-	0.31	-	0.26	-
Collared Sunbird	1.37	0.80	1.10	0.88	1.45	1.59	1.76	1.43	1.88	0.88	0.47	0.98	0.72	0.83	1.60	2.08	0.89	1.95	0.55
Cape White Eye	2.54	3.05	3.97	3.16	2.21	6.83	8.28	8.59	5.93	2.04	1.95	3.13	5.59	1.52	4.41	5.94	2.68	3.52	1.81
Thickbilled Weaver	0.03	-	-	-	-	-	-	-	0.29	-	-	-	-	-	-	-	-	-	-
Forest Weaver	0.18	0.03	0.34	0.10	-	0.21	-	-	0.43	0.28	0.41	0.28	0.36	0.07	0.24	0.52	-	1.04	0.13
Forest Canary	0.13	0.09	-	-	0.34	0.07	0.41	-	-	0.08	-	0.03	0.47	-	0.48	0.10	-	0.26	0.01
Total Density	20.41	17.47	25.49	18.83	40.63	33.60	45.32	39.71	41.67	14.46	17.12	15.75	29.28	9.17	24.20	38.96	22.85	36.07	8.87

- indicates that the species was not recorded in the patch; common species (those species occurring in all of the forest patches and including those with densities > 1 ind./ha) are high-lighted

Appendix 2.3. Mean densities (individuals per hectare) with standard error (SE) for individual bird species, averaged over the nine sites in each complex. Total density for each complex is given. Forest dependent species were identified from Oatley, 1989.

Common name	Scientific name	FD	Balgowan complex Mean density	SE	Gilboa complex Mean density	SE	Control Density
Hadeda Ibis	*Bostrychia hagedash*	A	0.166	0.066	0.035	0.035	0.038
Crowned Eagle	*Stephanoaetus coronatus*	D	0.038	0.026	0.028	0.016	0.038
**Steppe Buzzard	*Buteo buteo vulpinus*	A	0.014	0.011	-	-	0.011
Little Sparrowhawk	*Accipiter minullus*	A	0.014	0.008	0.004	0.004	0.016
Black Sparrowhawk	*Accipiter melanoleucus*	A	0.003	0.003	0.003	0.003	-
Gymnogene	*Polyboroides typus*	A	0.003	0.003	0.004	0.004	0.005
Rednecked Francolin	*Francolinus afer*	A	-	-	0.037	0.023	0.005
Crested Guineafowl	*Guttera pucherani*	D	0.030	0.019	0.007	0.007	0.054
Buffspotted Flufftail	*Sarothrura elegans*	D	0.003	0.003	0.011	0.008	0.005
Rameron Pigeon	*Columba arquatrix*	A	0.564	0.247	0.459	0.212	0.043
Redeyed Dove	*Streptopelia semitorquata*	A	0.782	0.317	0.557	0.131	0.102
Cape Turtle Dove	*S. capicola*	A	0.302	0.096	0.212	0.097	0.011
Tambourine Dove	*Turtur tympanistria*	D	-	-	0.022	0.015	-
Cinnamon Dove	*Aplopelia larvata*	D	0.436	0.162	0.151	0.028	0.032
Knysna Lourie	*Tauraco corythaix*	D	0.530	0.236	0.333	0.071	0.086
*Redchested Cuckoo	*Cuculus solitarius*	A	-	-	-	-	0.086
*Black Cuckoo	*C. clamosus*	A	-	-	-	-	0.011
*Emerald Cuckoo	*Chrysococcyx cupreus*	D	0.014	0.008	0.057	0.016	0.011
Speckled Mousebird	*Colius striatus*	A	0.046	0.046	0.045	0.045	-
Narina Trogon	*Apaloderma narina*	D	0.006	0.004	0.003	0.003	0.038
Redbilled Woodhoopoe	*Pheoniculus purpureus*	A	0.048	0.048	-	-	-
Redfronted Tinkerbarbet	*Pogoniulus pusillus*	A	0.038	0.020	0.058	0.035	-
Scalythroated Honeyguide	*Indicator variegatus*	D	0.017	0.017	-	-	0.016
Goldentailed Woodpecker	*Campethera abingoni*	A	0.009	0.009	0.079	0.057	0.032
Olive Woodpecker	*Mesopicos griseocephalus*	D	1.065	0.180	0.506	0.082	0.226
Grey Cuckooshrike	*Coracina caesia*	D	0.109	0.060	0.141	0.060	0.091
Forktailed Drongo	*Discrurus adsimilis*	A	0.259	0.087	0.264	0.053	0.113
Squaretailed Drongo	*D. ludwigii*	D	0.003	0.003	-	-	0.032
Blackheaded Oriole	*Oriolus larvatus*	A	0.404	0.101	0.543	0.112	0.081
Southern Black Tit	*Parus niger*	A	0.147	0.049	0.157	0.062	0.011
Blackeyed Bulbul	*Pycnonotus barbatus*	A	1.182	0.300	0.850	0.177	0.059
Terrestrial Bulbul	*Phyllastrephus terrestris*	A	1.603	0.528	0.927	0.234	0.145
Sombre Bulbul	*Andropadus importunus*	A	3.360	0.397	2.174	0.304	1.027
Yellowbellied Bulbul	*Chlorocichla flaviventris*	D	-	-	0.006	0.006	0.011
Olive Thrush	*Turdus olivaceus*	A	0.430	0.140	0.225	0.072	0.038
Orange Thrush	*Zoothera gurneyi*	D	-	-	0.020	0.014	0.005
Chorister Robin	*Cossypha dichroa*	D	0.458	0.137	0.273	0.092	0.204
Cape Robin	*C. caffra*	A	1.017	0.218	0.557	0.174	0.048
Starred Robin	*Pogonocichla stellata*	D	0.163	0.048	0.172	0.037	0.151
Yellowthroated Warbler	*Phylloscopus ruficapillus*	D	1.770	0.191	1.582	0.290	0.667
Barthroated Apalis	*Apalis thoracica*	D	3.096	0.576	2.153	0.426	0.570
Yellowbreasted Apalis	*A. flavida*	A	0.083	0.050	0.119	0.053	0.005
Bleating Warbler	*Camaroptera brachyura*	D	1.165	0.360	0.940	0.204	0.559
Spotted Prinia	*Prinia hypoxantha*	A	0.309	0.126	0.073	0.061	0.005
**Spotted Flycatcher	*Muscicapa striata*	A	0.009	0.006	-	-	-
Dusky Flycatcher	*M. adusta*	A	0.201	0.038	0.202	0.035	0.054
Cape Batis	*Batis capensis*	D	1.135	0.149	0.866	0.144	0.328
Chinspot Batis	*B. molitor*	A	0.020	0.013	0.028	0.028	0.022
Bluemantled Flycatcher	*Trochocercus cyanomelas*	D	0.078	0.023	0.128	0.043	0.011
*Paradise Flycatcher	*Terpsiphone viridis*	A	0.427	0.109	0.219	0.054	0.038
Southern Boubou	*Laniarius ferrugineus*	A	1.327	0.224	1.177	0.196	0.613
Puffback	*Dryoscopus cubla*	A	0.777	0.154	0.899	0.167	0.312
Olive Bush Shrike	*Telophorus olivaceus*	D	0.130	0.041	0.069	0.034	0.027
Redwinged Starling	*Onychognathus morio*	A	0.003	0.003	-	-	-
Greater Dblcollared Sunbird	*Nectarinia afra*	A	0.916	0.136	0.565	0.167	0.280
Black Sunbird	*N. amethystina*	A	0.141	0.079	0.067	0.042	-
Collared Sunbird	*Anthreptes collaris*	D	1.362	0.124	1.157	0.191	0.554
Cape White Eye	*Zosterops pallidus*	A	4.949	0.833	3.418	0.531	1.812
Thickbilled Weaver	*Amblyospiza albifrons*	A	0.035	0.032	-	-	-
Forest Weaver	*Ploceus bicolor*	D	0.144	0.054	0.357	0.101	0.129
Forest Canary	*Serinus scotopus*	D	0.116	0.052	0.158	0.066	0.005
Total density			31.46	6.97	23.10	5.12	8.87

- indicates that the species was not recorded in the complex;
FD = Forest Dependence; A = Forest Associated; D = Forest Dependent;
*sp = Short-range breeding migrant; **sp = Long-range non-breeding migrant

CHAPTER 3

Nestedness of Forest Bird Communities in a Fragmented Landscape: Selective Immigration or Extinction?

3.1 Introduction

The biological consequences of fragmentation are the subject of a multitude of ecological studies and the determinants of community structure and composition in fragmented landscapes are hotly debated. Most agree that following fragmentation, local and regional extinctions occur due to changes in the landscape that ensue on many spatial scales (Fahrig and Merriam, 1994; Wiens, 1994; Jokimäki and Huhta, 1996; Villard *et al.*, 1999). Loss of original habitat results in a reduction of habitat area, increased isolation (creating barriers to movement), crowding effects and edge effects (Saunders *et al.*, 1991; Krüger and Lawes, 1997; Meffe and Carroll, 1997). Thus as a consequence of basic assembly rules, species composition in habitat fragments is altered because some species are more vulnerable than others to the changes that accompany the fragmentation process (Andrén, 1994; Simberloff, 1994; Gotelli and Graves, 1996).

Due to the obvious similarity between fragmented terrestrial landscapes and archipelagos of true islands, MacArthur and Wilson's (1967) equilibrium theory of island biogeography, that is based upon the biogeography of oceanic islands, has often been applied to the investigation of species distribution in habitat islands (Brown, 1971; Diamond, 1975; Whitcomb *et al.*, 1981; Bellamy *et al.*, 1996; Brooks *et al.*, 1999). Island biogeography theory assumes that habitat islands are isolated from one another by hostile habitat. However, unlike real islands, an ecologically inhospitable environment rarely surrounds habitat fragments, so fragments are open to influences from the surrounding matrix (Simberloff, 1992; Wiens, 1994; Estades and Temple, 1999). Hence, the equilibrium theory underestimates the importance of overland vagility and matrix tolerance, and overestimates the significance of traits such as rarity and population stability of habitat island fauna (Laurance, 1997). Furthermore, island biogeography theory does not provide information on what species are supported by habitat islands in fragmented landscapes (Patterson, 1987; Simberloff,

1992; Gotelli and Graves, 1996; Forman, 1997). The theory focuses primarily on determinants of species richness, such as area and distance to mainland, rather than the composition of the biota (Patterson, 1987). In this study I examine the composition and structure of forest bird assemblages in a fragmented forest landscape and their relationship to the determinants of species richness.

Fragmentation under strong environmental control, such as overwhelming change in the matrix, may result in highly deterministic changes in community composition (Patterson and Atmar, 1986). As a result of reduced forest patch area, bird population sizes are reduced, leading to the disappearance of some species from small forest fragments (Chapter 2) and an increased sensitivity of remaining populations to chance events (Bierregaard et al., 1992; Fahrig and Merriam, 1994; Wiens, 1994; Estades and Temple, 1999). In addition, isolation of forest fragments may limit recolonisation to a gradual process following local extinctions. Thus, extinction effects can become the dominating influence determining community structure and composition. Forest birds adapted to forest interior habitats may not be able to maintain viable populations in a small patch where forest edge is abundant (Meffe and Carroll, 1997), where as edge-adapted, generalist species may thrive, resulting in a non-random distribution of species among habitat patches. These arguments combine to suggest that assemblage composition in such habitat islands is the consequence of highly deterministic species extinction (or colonisation) patterns. If this is the case a "nested subset" pattern often occurs in which the species that inhabit depauperate islands are a subset of those on richer islands (Patterson and Atmar, 1986). This pattern may also be area-dependent (and thus cannot be tested by species-area regression alone) and species that are present in the smallest patch will tend to be present in all larger, richer ones. Gradually, with increasing fragmentation bird communities in similar sized patches are predicted to converge on the same community composition as species relaxation takes place (Patterson, 1987). In contrast to this prediction derived from a non-equilibrium scenario, equilibrium theories such as the MacArthur and Wilson model and the random sample hypothesis (Connor and McCoy, 1979; Haila, 1983), predict that the composition of these communities would simply be random sets of the original community (Atmar and Patterson, 1993; Andrén, 1994; Meffe and Carroll, 1997). However, in order to apply suitable management plans for the conservation of biodiversity in fragmented landscapes – understanding patterns of community composition and the processes that

may affect them is imperative. In other words, it is important to know whether faunal assemblages are random or non-random sets of the original community. In the past this management requirement was encapsulated in the SLOSS debate (Single Large Or Several Small reserves; Simberloff, 1988). If the faunal assemblages in a fragmented landscape exhibit a non-random species distribution, then the single largest habitat patch should be conserved, while in the case of random assemblage composition a collection of patches would be appropriate.

In KwaZulu-Natal province, South Africa, commercial plantation forestry is a major contributor to the increasing fragmentation of indigenous forest, and the landscape matrix is dominated by plantation forestry in extensive areas of the Karkloof region of the midlands. In this chapter I investigate the effects of fragmentation and matrix conversion (from natural grassland to monoculture pine plantation), on forest bird assemblage composition and structure in indigenous forest patches of the Karkloof / Balgowan range. I test the prediction that patterns of species loss from forest fragments (under different levels of environmental control, i.e., natural matrix and afforested matrix) are deterministic and not random. I employ nested subset analysis, which tests the non-random nature of assemblages by comparing the composition of assemblages against a random null model using Monte Carlo simulations (Patterson and Atmar, 1986; Patterson, 1987; Cutler, 1991, 1994; Lomolino, 1996).

An understanding of the underlying mechanisms generating nestedness is crucial in understanding the ecology of fragmented ecosystems, so that suitable management plans may be applied. Nestedness could result from differential extinction, as a function of area, and/or differential colonisation, as a function of isolation (Lomolino, 1996). However, in terrestrial fragments, the causal factors of nestedness include variables such as habitat diversity, disturbance, matrix heterogeneity, matrix tolerance, and edge effects (Forman, 1997). Here I investigate the contribution of the potentially dominant processes – selective extinction or colonisation, to forest bird assemblage structure and composition in the forest fragments of the Karkloof / Balgowan range. The relevance of nestedness to the SLOSS debate in management strategies and reserve design, for the Karkloof / Balgowan forest range is also considered.

3.2 Methods

3.2.1 Study area

The Karkloof / Balgowan forest range is situated in the midlands of KwaZulu-Natal province, South Africa (Fig. 2.1). These forests are classified as Afromontane Mistbelt Mixed *Podocarpus* forest (Cooper, 1985; Low and Rebelo, 1996), which is the climatic climax forest vegetation of the KwaZulu-Natal mistbelt region (White, 1978). Mistbelt forests are characteristically cool, tall (~15m), inland forests with well-developed and mature soils (Pooley, 1993). Water is a key-limiting factor in this environment, and the forest patches generally occur in moist fire-safe habitats (Low and Rebelo, 1996), on steep south-facing slopes that are subject to frequent mist. The Karkloof / Balgowan forest range lies at an altitude of 1500m-1800m and experiences high rainfall (mean annual rainfall: 800mm-1000mm), particularly in summer.

The forest range comprises one large, contiguous forest patch (approximately 2900ha in size) and many smaller, peripheral fragments surrounded by one of two matrix types: 1) the natural Moist Upland Grassland (Cooper, 1985; Low and Rebelo, 1996) or 2) commercial plantation forestry species such as pine (*Pinus patula*) and black wattle (*Acacia mearnsii*). From 1:30 000 aerial photographs from 1996, nine forest patches were selected in natural grassland in the Balgowan complex, with a size range of 0.5ha to 215ha. A further nine patches were selected within and around the Gilboa (Mondi forests) commercial forestry estate in the Karkloof region (hereafter the Gilboa complex). These patches were surrounded by pine plantation (stand age > 8 years) and had a size range of 0.5ha to 273ha. The patches in the two complexes were matched in pairs by size (Table 2.1). A patch of much greater size (Leopards Bush Private Nature Reserve; 705ha), sited in the Karkloof region, served as an ecological control or outgroup, representing the ecological conditions in a large contiguous forest patch, to which the patterns described from the other eighteen smaller forest patches were compared.

The total area of each patch (ha) was calculated from digital maps of the area (Macfarlane, 2000) using ArcView version 3.0 (ESRI, 1998). Isolation distances were estimated from the digital map as the minimum distance to the nearest forest fragment of equal or greater size. In all cases the linear distance between nearest edges was measured (Table 2.1).

3.2.2 Bird census methods

Line transects of varying length adjusted according to patch size were marked out across the dominant environmental gradient (i.e. up the slope and between watercourses) in the forest patches. In this way the maximum gradient of diversity was sampled in each forest patch. Transects were walked in the early morning, midday and late afternoon to account for variation in bird activity throughout the day. Along each transect, all bird species seen and heard were recorded. Sampling took place through the summer months November to March, over two summer seasons.

Cumulative sample-species richness curves were plotted for each transect (or patch) to determine when sampling (number of transects walked) should cease. These curves were asymptotic at approximately 8 transects for the eighteen smaller patches and at 22 transects for the larger control patch (Fig. 2.2). No new species were added at the full sampling effort for each forest patch and all forest patches were regarded as adequately sampled.

3.2.3 Cluster analysis

When there are a number of sites in an investigation, a good representation of β diversity can be obtained through cluster analysis (Magurran, 1988). From a similarity matrix the two most similar sites are combined to form a cluster. This process continues by successively clustering similar sites until all are combined in a single dendrogram (Magurran, 1988). All forest patches were compared for similarity in species composition, using cluster analysis based on the Jaccard similarity index, which uses presence-absence data (BioDiversity Professional; McAleece et al., 1997).

3.2.4 Correspondence analysis

Using bird species density (individuals per hectare) data, a correspondence analysis for all nineteen forest patches was carried out using the ordination program CANOCO for Windows version 4.02 (ter Braak and Smilauer, 1999). The ordination points for the Balgowan and Gilboa complexes, as well as for the control patch Leopards Bush, were plotted together on the first three hypothetical component axes. By constructing minimum convex polygons around the ordination points for each complex, the variation and differences in community composition in each complex, as well as the

control patch, was compared. Chi-squared distances were used to represent the proportional differences in composition of species at the different sites.

3.2.5 Nested subset analysis

In order to detect convergence of community composition in the forest patches, a nested subset analysis was performed on the presence-absence species data (for the full complement of bird species and forest dependent species separately) for each forest complex (Balgowan and Gilboa).

Many presence-absence matrices form an ordered pattern where faunal assemblages conform to a nested distribution of species (Patterson, 1990; Wright and Reeves, 1992). In a perfectly nested series, species present in a given fauna are also present in all larger faunas, and species absent from a given fauna are also absent from all smaller faunas, resulting in a typical wedge shaped pattern (Cutler, 1991). This phenomenon arises if sites represent fragments of a once-continuous habitat initially inhabited by a common ancestral biota, and as area continues to decrease, local extinctions of species at the sites produce a nested pattern as extinctions occur in a deterministic sequence (i.e. species will go extinct in order of their specific extinction risks) (Patterson and Atmar, 1986). It is implicitly assumed that all sites share the same potential species pool, and no historical or environmental differences exist between sites (Cutler, 1994). Species distributions deviate from a perfectly nested pattern through unexpected absences of species from large faunas ("holes") and unexpected presences of species in small faunas ("outliers") (Patterson and Atmar, 1986; Cutler, 1991; Gotelli and Graves, 1996).

I used Cutler's (1991) U_t metric as an index of nestedness for each forest complex; as it takes into account both holes (representing species extinction) and outliers (representing species colonisation) simultaneously. This is an alternative to Patterson and Atmar's (1986) N index where all deviations from perfect nestedness are treated as unexpected absences (holes), with the complementary N_2 index (Cutler, 1991; Wright and Reeves, 1992) accounting for all unexpected presences (outliers). U_t is the sum of all unexpected absences (U_a) from sites of greater species richness and unexpected presence's (U_p) from sites with less species than a chosen site of intermediate species richness (which is chosen to minimise the sum of the two sub-scores). In effect, the U_t index counts the minimum number of steps required to convert an imperfectly nested pattern into perfectly nested pattern (Cutler, 1991,

1994). The two sub-scores U_a and U_p can then be used to describe whether the matrices are hole (extinction) or outlier (colonisation) dominated.

The significance of the U_t index was tested using the UT and UT01 Monte Carlo simulation programs (UT: Mikkelson and Cutler, 1996; UT01: Mikkelson *et al.*, 1996; which include the programs RANDOM0 and RANDOM1 devised by Patterson and Atmar, 1986). The statistical significance of U_t is assessed using a *t*-test to determine whether the data matrix is significantly more nested than a population of randomised matrices obtained through a large number (1000) of Monte Carlo simulations. The RANDOM1 program runs a more rigorous test as it uses actual values of species richness and actual frequencies of species occurrence in the sites, while the RANDOM0 program is more forgiving as it lacks these constraints (Cutler, 1994).

Percentage deviation from perfect nestedness was calculated for all bird species and for forest dependent species, for each forest complex using the following equation:

$$\% \text{ deviation} = U_t / (\text{number of species x number of sites})$$

3.2.6 Mechanisms of nestedness

The implications of a nested structure for conservation management depend upon the underlying mechanisms generating nestedness (Patterson, 1987; Simberloff and Martin, 1991; Cutler, 1994). Both selective extinction and differential immigration have been invoked to explain nested patterns. To investigate the causality of nestedness in the forest patches, I used a method proposed by Lomolino (1996) that is designed to test the following predictions:

1) If community structure is influenced by selective immigration, then the focal system should exhibit significant nestedness when ordered by increasing isolation;

2) If community structure is influenced by selective extinction, then the focal system should exhibit significant nestedness when ordered by decreasing area.

The following procedures were performed on the presence-absence species data (for the full complement of bird species and forest dependent species separately) for each forest complex, using the randomisation program NESTSEND (Lomolino, 1996). The presence-absence matrix is sorted first by decreasing area and then by increasing isolation. Deviation from perfect nestedness is then calculated by scanning

down each ordered matrix and the number of departures (D), i.e. the number of times the absence of a species is followed by its presence on the next (smaller) island/site, is recorded. The statistical significance of nestedness is determined by comparing the observed D values for each matrix to those obtained for randomly ordered matrices. The statistical significance of nestedness of each ordered matrix is then calculated as the proportion (P) of 1000 random simulations with D values less than or equal to that of the ordered matrices. To enable comparisons between matrices ordered by area or isolation, nestedness is expressed as a percent of perfect nestedness (%PN) using the following equation:

$$\%PN = 100 * [(R - D) / R]$$

where D = the number of departures in the ordered matrix, and R = the mean number of departures for random simulations.

3.2.7 Predictability of extinction

In order to understand the process of extinction, the predictability of extinction sequence can be expressed relative to the extinction rate (Cutler, 1991). I used Cutler's (1991) method for calculating the difference in the pattern of change of species composition between each forest complex, for the full complement of bird species. By comparing the sum of the absolute residuals of the species-area curves for each complex (representing the predictability of extinction rate as implied by richness), to the U_t values obtained from the nested subset analysis (representing the predictability of extinction sequence as implied by composition), the relative importance of extinction processes in each forest complex was ascertained.

3.3 Results

3.3.1 Cluster analysis – how similar are the bird assemblages among patches?

The composition of bird assemblages in the forest patches was classified primarily according to patch size (Fig. 3.1). Larger patches were grouped together as were smaller patches. The size-based classification was stronger for patches in the Balgowan complex than in the plantation-dominated landscape of the Gilboa complex. This difference in classification was expected due to the strong species-area effect found for the Balgowan complex (Chapter 2). Essentially, the classification suggests that assemblage composition of forest patches in the Balgowan complex is controlled by patch size, while forest patches in the Gilboa complex are classified

according to factors other than patch size (species richness was independent of area in the Gilboa – Chapter 2), and assemblage composition and species richness is likely a response to a more dominant landscape effect such as matrix type. The nature of the matrix (plantation) surrounding these forest patches appears to counteract the effect of area-dependent processes, and species richness and assemblage composition is probably determined by factors such as disturbance levels and the dispersal ability of species.

The bird community within the larger Balgowan patch (BA = 215ha) approached the species richness and composition of the mainland patch at Leopards Bush (77% similarity). The smaller patches were fairly similar in assemblage composition and species richness (range: 62.6% - 64.4%; mean = 63.5% similarity).
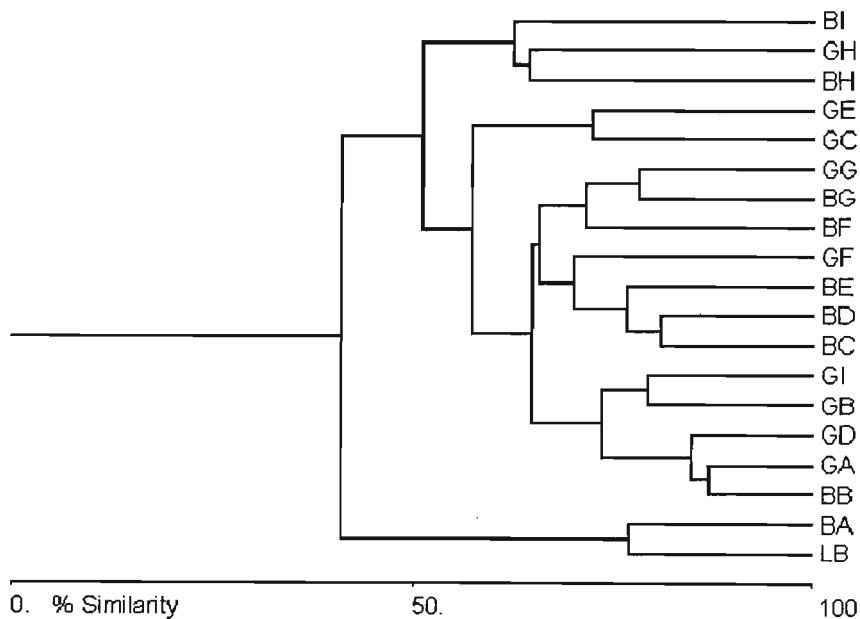
Figure 3.1. Dendrogram based on the Jaccard similarity index from the cluster analysis of all forest patches including the control (LB = Leopards Bush; B = Balgowan; G = Gilboa). Similarity in bird species composition between forest patches is shown.

3.3.2 Correspondence analysis – how variable are the bird assemblages among patches?

Comparison of the ordinations of sites on the 1st and 2nd component axes (Fig. 3.2a) and the 2nd and 3rd component axes (Fig. 3.2b), illustrates that the forest patches of the

two complexes show a relatively equal amount of variation in species assemblage structure and composition. All forest patches including the control appear to be similar in terms of species occupancy (ind./ha) patterns. There appears to be a gradient on the 1st component axis from large patches to small patches. The proportion of variance accounted for by the first three components is 41.84 % (Axis 1 = 18.74 %, Axis 2 = 14.13 %, Axis 3 = 8.97 %).
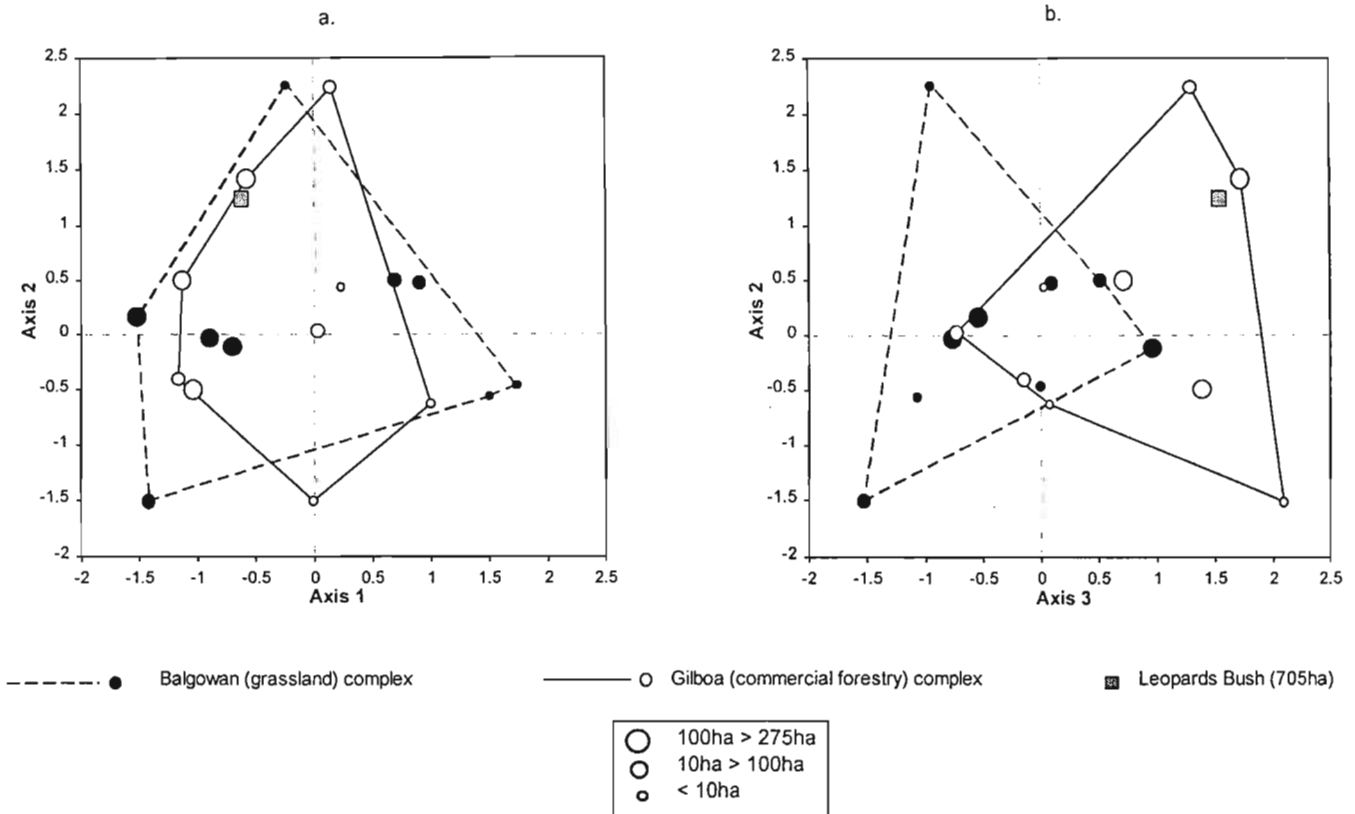
Figure 3.2. Comparison of the ordinations of the forest patches in each complex, as well as the control, on the 1st and 2nd component axes (a.) and the 2nd and 3rd component axes (b.). The proportional differences in composition of species at the different sites are represented here as chi-squared distances.

3.3.3 Nested subset analyses

i. All bird species

The bird assemblages in both forest complexes were significantly nested with assemblages in smaller patches generally nested within larger patches (Balgowan: U_t = 34, P < 0.01; Gilboa: U_t = 39, P < 0.01, Table 3.1). The Balgowan (natural grassland) complex deviated from perfect nestedness by 6.9 % and the Gilboa (plantation forestry) complex by 8.3 % (see Appendix 3.1). Bird assemblage structure

in the Gilboa was outlier dominated (U_p = 23.7; Balgowan U_p = 18.5, Table 3.1) which implies that colonisation is a dominant process in this forest complex so that it is characterised by species that are able to move between forest patches. Furthermore, the occurrence of these outlier species was not nested and did not differ from a random pattern (z = 1.23, P > 0.05). The number of unexplained absences (holes) was low (Balgowan: U_a = 15.5; Gilboa: U_a = 15.33) in both complexes, and significantly different (P < 0.01) from random showing that species relaxation in patches in both complexes follows a deterministic sequence (see Cutler, 1991), but also suggesting a lesser role for selective extinction compared to colonisation in determining assemblage structure.

Table 3.1. Summary of the nestedness analysis of bird assemblages in the Balgowan forest complex and the Gilboa forest complex. Comparative data from three separate studies is also given.

	Sites	Species	Tot. matrix	U_a	U_p	U_t (%)	P
Balgowan complex							
Total species	9	55	495	15.5	18.5	34 (6.9)	P < 0.01
Forest dependent species	9	22	198	3.5	6.5	10 (5.1)	P < 0.01
Gilboa complex							
Total species	9	53	468	15.33	23.67	39 (8.3)	P < 0.01
Forest dependent species	9	23	207	8	10	18 (8.7)	P < 0.01
Southern Cape (Cody, 1993)	5	49	245	11.5	1.5	13 (5.3)	P < 0.01
Alexandria Dunes (Brown, 1990)	14	59	826	27	34	61 (7.4)	P < 0.01
Oteniqua Mountains (Koen, unpub)	9	39	351	14.5	10.5	25 (7.1)	P < 0.01

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.

ii. Forest dependent species

The forest dependent bird assemblages in both forest complexes were also significantly nested with assemblages in smaller patches nested within larger patches (Balgowan: U_t = 10, P < 0.01; Gilboa: U_t = 18, P < 0.01, Table 3.1). The Balgowan (natural grassland) complex deviated from perfect nestedness by only 5.1 % and the Gilboa (plantation forestry) complex by 8.7 % (see Appendix 3.2). The number of unexplained absences (holes) was still low (Balgowan: U_a = 3.5; Gilboa: U_a = 8, Table 3.1) in both complexes, and significantly different from random ($P \leq 0.01$)

showing that forest dependent species relaxation in patches in both complexes follows a deterministic sequence. The higher U_a value for the Gilboa complex implies that selective extinction plays a more important role in determining forest dependent bird assemblage structure in forest patches surrounded by commercial plantation forestry, than for forest patches surrounded by natural grassland.

3.3.4 Mechanisms of nestedness: selective extinction or colonisation?

Nestedness (%PN; Table 3.2) was strongly associated with area for the Balgowan forest complex (for both the full compliment of bird species and for forest dependent bird species). The number of departures from perfect nestedness (D) was significantly less for the area-sorted matrices than for the isolation-sorted matrices (Table 3.2). Selective extinction rather than selective immigration may therefore influence bird species composition in forest patches within natural grassland. For the bird assemblages of the forest patches of the Gilboa complex, nestedness (%PN; Table 3.2) was associated with neither area nor isolation. I suggest that selective extinction and immigration play more or less equal roles in influencing bird species composition in forest patches within the plantation matrix.

Table 3.2. Results of the nested analysis investigating causality, by counting the number of departures from perfect nestedness in a matrix sorted by area and then by isolation.

	Area-sorted matrix			Isolation-sorted matrix			Randomised
	D	P	%PN	D	P	%PN	R
Balgowan complex							
All species	36	0.002	34.5	59	0.779	-7	54.996
FD species	11	0.000	53	26	0.795	-11	23.416
Gilboa complex							
All species	46	0.414	3.14	53	0.932	-11.6	47.492
FD species	20	0.183	13.13	26	0.912	-12.9	23.022

FD = Forest dependent; D = number of departures from perfect nestedness; P = proportion of randomly ordered matrices with
D values ≤ that of the ordered matrix; R = average D value for 1000 randomly ordered matrices; %PN = percent perfect nestedness

3.3.5 Predictability of extinction

The predictability of extinction rate was better than extinction sequence for bird species relaxation in the Balgowan complex (Balgowan: $\sum |\text{residuals}| = 30.27$, $U_t = 34$; Table 3.3). Although a similar result was achieved for the Gilboa complex

(Gilboa: $\sum$ |residuals| = 24.04, U_t = 39), this can be ignored since species richness was independent of area (i.e. there was no area effect; Chapter 2) and no estimate of extinction rate or comparison of extinction rate with extinction sequence is therefore possible. In addition, when comparing U_t values between complexes, the sequence of extinction appears to be more predictable in the Balgowan (natural grassland) complex.

Table 3.3. Predictability of extinction comparison between forest complexes and the control. The sum of the absolute values of the residuals of the species-area curve represents extinction rate and U_t represents extinction sequence.

	Sum |Residuals|	U_t	P
Balgowan complex Total species	30.27	34	$P < 0.007$
Gilboa complex Total species	24.04	39	$P < 0.08$
Control (Leopards Bush) Total species	10.00	-	$P < 0.003$

P refers to the significance of the fit of the species-area regression

3.4 Discussion

The bird assemblages of the two forest complexes of the Karkloof / Balgowan range, exhibit a significant non-random distribution pattern. Bird species assemblages in small, species-poor patches generally constitute a subset of those in larger, more species-rich patches. The degree of bird assemblage nestedness is higher in the Balgowan complex where there is natural grassland matrix habitat, than in the plantation-dominated Gilboa complex. Studies have shown that the distribution of bird species among forests in agricultural landscapes is typically non-random. For example, Blake (1991) found a high degree of nestedness among bird communities in the forest patches of east, central Illinois USA. In central Spain Tellería and Santos (1995) found a similar non-random pattern in forest patches, with all bird species occupying large patches and many species absent from small patches. Warburton (1997) found a nested species distribution among bird communities in isolated rainforest remnants in tropical Australia, while Saunders (1989) documented the loss of many bird species from small habitat remnants since isolation in the wheat-belt of

Western Australia. Nested subset analyses performed on the data from comparative studies in the Afromontane forests of the Southern Cape (Cody, 1983), the Alexandria Dunes (Brown, 1990), and the forests of the Oteniqua Mountains (Koen, unpublished) also revealed highly nested avian assemblages (Table 3.1).

If species distributions within naturally fragmented habitat exhibit patterns of pronounced nestedness, then highly predictable extinction sequences are implied (Blake, 1991; Atmar and Patterson, 1993; Cutler, 1994). However, due to the dynamic and multivariate nature of natural systems a perfectly nested pattern is unlikely to occur, with deviations in the form of holes and outliers. The forest bird assemblages of the Karkloof / Balgowan archipelago deviate slightly (see Table 3.1) from a perfectly nested species distribution pattern through the presence of both holes and outliers, but generally exhibit an outlier-rich pattern. A hole may result from the failure of a species to colonise an area to begin with, or its premature extinction (most likely caused by stochastic events or anthropogenic disturbance) (Cutler, 1991; Wright *et al.*, 1998). An outlier would result from the re-establishment of populations of vagile species by immigrants, or the rescue effect (Brown and Kodric-Brown, 1977), rather than the unlikely survival of the original populations (Blake, 1991; Cutler, 1991; Cook and Quinn, 1995). More vagile taxa are therefore expected to show outlier-rich distribution patterns (high U_p) while less vagile taxa are expected to show hole-rich distribution patters (high U_a) (Cutler, 1991; Cook and Quinn, 1995; Wright *et al.*, 1998). For example, in Brown's (1971; 1978; Brown and Gibson, 1983) study of birds and mammals inhabiting boreal forests in the Great Basin of western North America, both taxa showed highly non-random species distribution patterns, but differed in the mode of departure from perfect nestedness. In the bird matrix, outliers were the dominant type of deviation ($U_a = 4.5$; $U_p = 9.5$), while in the mammalian matrix, holes accounted for most of the departures ($U_a = 13$; $U_p = 8$).

Although differential extinction, rather than differential immigration, is most often considered to be the primary force causing nestedness, both mechanisms have been invoked in previous studies to explain observed patterns of nestedness (Cutler, 1994; Lomolino, 1996). Simberloff and Wilson (1969) attributed nestedness of ant species on defaunated mangrove islands to differential immigration. Nested distributions among bird species in isolated woodlots in Brazil (Terborgh and Winter, 1980), and Illinois (Blake, 1991) were attributed to selective extinction. Many studies on land-bridge islands and other habitats fragmented by post-Pleistocene climatic

changes have also attributed nested patterns to selective extinction. For example, studies on birds, mammals and reptiles on Baja California land-bridge islands (Patterson, 1990), montane mammals in the south-west United States (Patterson, 1984; Patterson and Atmar, 1986), birds and mammals in the Great Basin, North America (Brown, 1971; 1978; Wright and Reeves, 1992), and land birds on islands off New Zealand (Patterson, 1987).

In this study, while both forest complexes show considerable nestedness I suggest that each result from different processes. In the case of the Balgowan complex that is surrounded by a natural grassland matrix, nestedness is attributable to differential extirpation: each bird species tending to occur in the subset of forest patches large enough to prevent extirpation. In the plantation-dominated Gilboa, I ascribe nestedness to selective extinction as well as colonisation processes. As the bird species distribution is substantially outlier-dominated (albeit a random distribution of outlier species), colonisation ability must play a dominant role in determining bird assemblage structure in indigenous forest patches. In other words, species differ in their ability to move through or use the commercial plantation surrounding the indigenous forest patches. However, because commercial plantations provide a suitable habitat and cover for movement of forest birds, colonisation of both distant and small indigenous forest patches has been possible, reducing the effects of area-dependent extinction in these forest patches. This has resulted in more equitable species richness across the forest patches in the Gilboa complex (Chapter 2).

During the extinction process, the rate at which extinctions occur can be compared to the sequence in which species go extinct (Cutler, 1991). While both extinction processes are equally as important, one may be more predictable than the other, yielding a more fundamental understanding of the extinction process (Simberloff and Levin, 1985; Quinn and Hastings, 1987; Brooks et al., 1999). The comparison is informative to conservation biologists who are interested in the fate of individual species and the composition of individual biotas (Zimmerman and Bierregaard, 1986; Cutler, 1991; Simberloff, 1994). In the Balgowan forest complex, extinction rate is more predictable (or shows less variation) than extinction sequence. This is expected considering the comparatively shallow slope (representing species turnover) found for the species-area relationship (Chapter 2). A predictable extinction rate may be indicative of a dominant landscape effect determining species distribution in the forest complexes. In the Balgowan complex where there is a natural grassland

matrix, forest patch size is the major predictor of avian species distribution. In contrast, the nature of the matrix has a dominating influence over bird species distribution patterns in the Gilboa complex. Because there is no effect of area on species richness, the extinction sequence from indigenous forest patches surrounded by commercial plantation forestry is less predictable.

The nested subset concept has important implications for conservation. The deterministic sequence of extinction during species relaxation implied by nestedness indicates that communities in small fragments will in time converge to the same set of extinction-resistant species (Patterson and Atmar, 1986; Patterson, 1987). Therefore, as area-dependent selective extinction is driving the nested distribution of bird assemblages in the Balgowan forest complex (natural grassland matrix), forest patches of similar size have similar community compositions. In the Gilboa complex where colonisation is playing a dominant role, the nature of the matrix is facilitating the dispersal of bird species between indigenous forest patches. This colonisation process is however not a selective one. The plantation matrix creates a closed environment providing suitable forest-like cover, thereby equilibrating opportunities for dispersal for indigenous forest species (including those with limited dispersal ability) as well as widespread generalist species, and thus eliminating area effects. The forest patches are thus converging on the same community representation, regardless of size. In other words a small forest patch has the potential to house the same bird species assemblage as a large forest patch, and vice versa. However, in terms of conservation of bird diversity in forests surrounded by plantation, forest patch selection should depend on the permanency of the plantation matrix (i.e. the matrix effect). Considering that commercial pine plantations are a transient landscape element with a 10-15 year cycle, one would be best advised to manage forests within this matrix type using the same principles that apply to forests within the natural grassland matrix, i.e. the Balgowan complex.

Hence in terms of a management strategy for indigenous forest in the region (SLOSS debate: Simberloff, 1988), clearly our priority remains to conserve the largest, intact forest units, preferably above minimum critical patch size (MCPS: 302ha; Chapter 2), in order to preserve overall species richness and most especially for the forest dependent species. The maintenance of large contiguous forest tracts has repeatedly been recommended for avian conservation (Hurst *et al.*, 1980; Freemark and Merriam, 1986; Blake and Karr, 1987; Dickson, 1988), particularly since a large

contiguous area of forest supports more interior species than does a collection of smaller forest patches equal in total area (McIntyre, 1995).

3.5 Conclusion

Nested subset analysis is a useful descriptive tool for revealing an ecologically meaningful non-random species distribution pattern, and a valuable exploratory tool for suggesting mechanisms that may produce such a non-random assemblage structure. Furthermore, the nested subset concept provides empirical evidence that the non-random nature of extinction may cause assemblage composition of small habitat fragments to converge over time, with the survival of widespread, generalist species and the extinction of local, rare species (Patterson, 1987). Nestedness therefore has important implications for conservation and has direct relevance to the SLOSS debate in management strategies and reserve design. It provides evidence for the preservation of the largest intact land units for the reason that if strong nestedness and a species-area relationship (Chapter 2) exists then small habitats will support depauperate subsets that are unlikely to match the species richness of a single large area (Patterson, 1987; Wright and Reeves, 1992; Cutler, 1994; Worthen, 1996). Bird species assemblages in the Balgowan forest complex are characterised by a non-random species distribution pattern where area-dependent processes are dominant. Thus the preservation of the forest bird assemblages in the region requires the protection of large (≥302ha) forest fragments surrounded by natural grassland habitat.

While the loss of bird species from forest fragments within the natural grassland matrix follows a predictable and deterministic sequence, the sequence of species loss from forest patches surrounded by commercial plantation forestry is not as predictable, where a random yet prominent colonisation process exists. This reflects the lack of an area effect in this complex and further promotes the role of the matrix in influencing the bird assemblage structure in these patches. However, even though no effective forest patch size constraint exists, conserving forest bird diversity in the plantation-dominated Gilboa complex also requires the protection of the largest intact forest fragments. This is considered the most appropriate option given the transient nature of the matrix, and thus the matrix effect. Furthermore, in conserving bird assemblage structure in indigenous forest patches, the management of dispersal processes may be as critical as minimising area-determined extinction processes. This

may be accomplished by maintaining continuity in the natural landscape matrix. If the natural landscape mosaic is preserved, then natural dispersal processes will be maintained. In the following chapter I investigate how individual species respond to the fragmentation and matrix transformation of the Karkloof / Balgowan forest range.

3.6 References

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Appendix 3.1. Species distribution matrix showing patterns of nestedness (shaded areas) for the total compliment of bird species of the Balgowan and Gilboa forest complexes. Percentage deviation from perfect nestedness is given.

Balgowan (Grassland) Complex

Common Name	A	B	E	C	F	D	G	I	H
Barthroated Apalis	1	1	1	1	1	1	1	1	1
Blackeyed Bulbul	1	1	1	1	1	1	1	1	1
Bleating Warbler	1	1	1	1	1	1	1	1	1
Cape Batis	1	1	1	1	1	1	1	1	1
Cape Robin	1	1	1	1	1	1	1	1	1
Cape White Eye	1	1	1	1	1	1	1	1	1
Chorister Robin	1	1	1	1	1	1	1	1	1
Collared Sunbird	1	1	1	1	1	1	1	1	1
Greater Doublecollared Sunbird	1	1	1	1	1	1	1	1	1
Olive Thrush	1	1	1	1	1	1	1	1	1
Olive Woodpecker	1	1	1	1	1	1	1	1	1
Puffback	1	1	1	1	1	1	1	1	1
Sombre Bulbul	1	1	1	1	1	1	1	1	1
Southern Boubou	1	1	1	1	1	1	1	1	1
Spotted Prinia	1	1	1	1	1	1	1	1	1
Terrestrial Bulbul	1	1	1	1	1	1	1	1	1
Yellowthroated Warbler	1	1	1	1	1	1	1	1	1
Redeyed Dove	1	1	1	1	1	1	1	1	0
Blackheaded Oriole	1	1	1	1	1	1	1	1	0
Cape Turtle Dove	1	1	1	1	1	1	1	1	0
Cinnamon Dove	1	1	1	1	1	1	1	0	1
Starred Robin	1	1	1	1	1	1	1	0	1
Dusky Flycatcher	1	1	1	1	0	1	1	1	1
Paradise Flycatcher	1	1	1	1	0	1	1	1	1
Olive Bush Shrike	1	1	1	1	1	1	1	0	0
Rameron Pigeon	1	1	1	1	1	1	1	0	0
Forktailed Drongo	1	1	1	1	0	1	1	1	0
Knysna Lourie	1	1	1	1	1	1	0	0	0
Bluemantled Flycatcher	1	1	1	0	1	1	1	0	0
Forest Weaver	1	1	0	1	1	1	0	1	0
Hadeda Ibis	1	0	1	1	1	1	0	1	0
Southern Black Tit	0	1	1	0	1	0	1	1	1
Forest Canary	1	1	1	0	1	0	1	0	0
Black Sunbird	1	0	0	0	1	0	1	1	0
Emerald Cuckoo	1	1	1	0	0	0	0	0	0
Redfronted Tinkerbarbet	1	1	0	0	1	0	0	0	0
Crested Guineafowl	1	0	1	1	0	0	0	0	0
Little Sparrowhawk	1	0	1	1	0	0	0	0	0
Grey Cuckooshrike	1	0	0	0	1	1	0	0	0
Yellowbreasted Apalis	0	1	0	1	0	0	0	0	1
Narina Trogon	1	1	0	0	0	0	0	0	0
Thickbilled Weaver	1	0	0	0	0	0	0	1	0
Chinspot Batis	1	0	0	0	0	0	1	0	0
Steppe Buzzard	1	0	0	0	0	0	1	0	0
Spotted Flycatcher	1	0	0	0	0	1	0	0	0
Crowned Eagle	0	0	0	1	1	0	0	0	0
Redbilled Woodhoopoe	0	0	0	0	0	0	0	1	0
Speckled Mousebird	0	0	1	0	0	0	0	0	0
Black Sparrowhawk	0	1	0	0	0	0	0	0	0
Buffspotted Flufftail	1	0	0	0	0	0	0	0	0
Goldentailed Woodpecker	1	0	0	0	0	0	0	0	0
Gymnogene	1	0	0	0	0	0	0	0	0
Redwinged Starling	1	0	0	0	0	0	0	0	
Scalythroated Honeyguide	1	0	0	0	0	0	0	0	
Squaretailed Drongo	1	0	0	0	0	0	0	0	

Deviation from perfect nestedness = **6.9%**

Gilboa (Pine) Complex

Common Name	C	B	D	A	G	I	E	F	H
Barthroated Apalis	1	1	1	1	1	1	1	1	1
Blackeyed Bulbul	1	1	1	1	1	1	1	1	1
Blackheaded Oriole	1	1	1	1	1	1	1	1	1
Bleating Warbler	1	1	1	1	1	1	1	1	1
Cape Batis	1	1	1	1	1	1	1	1	1
Cape Robin	1	1	1	1	1	1	1	1	1
Cape White Eye	1	1	1	1	1	1	1	1	1
Collared Sunbird	1	1	1	1	1	1	1	1	1
Forktailed Drongo	1	1	1	1	1	1	1	1	1
Greater Doublecollared Sunbird	1	1	1	1	1	1	1	1	1
Olive Woodpecker	1	1	1	1	1	1	1	1	1
Paradise Flycatcher	1	1	1	1	1	1	1	1	1
Puffback	1	1	1	1	1	1	1	1	1
Redeyed Dove	1	1	1	1	1	1	1	1	1
Sombre Bulbul	1	1	1	1	1	1	1	1	1
Southern Boubou	1	1	1	1	1	1	1	1	1
Terrestrial Bulbul	1	1	1	1	1	1	1	1	1
Yellowthroated Warbler	1	1	1	1	1	1	1	1	1
Forest Weaver	1	1	1	1	1	1	1	1	0
Knysna Lourie	1	1	1	1	1	1	1	1	0
Rameron Pigeon	1	1	1	1	1	1	1	1	0
Bluemantled Flycatcher	1	1	1	1	1	1	1	0	1
Chorister Robin	1	1	1	1	1	1	0	1	1
Dusky Flycatcher	1	1	1	1	1	1	0	1	1
Cinnamon Dove	1	1	1	1	1	0	1	1	1
Starred Robin	1	1	1	1	1	0	1	1	1
Olive Thrush	1	1	1	1	0	1	0	1	1
Southern Black Tit	1	1	1	1	1	1	0	0	0
Emerald Cuckoo	1	1	1	1	0	0	1	0	1
Cape Turtle Dove	1	1	1	0	0	1	1	0	1
Forest Canary	1	0	1	1	1	1	0	1	0
Grey Cuckooshrike	1	1	1	1	0	1	0	0	0
Yellowbreasted Apalis	0	1	1	1	0	1	0	0	0
Olive Bush Shrike	0	0	1	1	1	1	0	0	0
Redfronted Tinkerbarbet	0	0	1	1	0	0	0	1	0
Goldentailed Woodpecker	0	1	0	0	0	1	0	0	1
Black Sunbird	0	1	0	0	1	1	0	0	0
Rednecked Francolin	1	1	0	0	0	0	1	0	0
Crowned Eagle	1	0	1	0	0	0	1	0	0
Spotted Prinia	0	0	0	0	1	0	1	0	0
Buffspotted Flufftail	1	0	0	0	0	0	1	0	0
Tambourine Dove	1	0	0	0	1	0	0	0	0
Orange Thrush	1	0	1	0	0	0	0	0	0
Chinspot Batis	0	0	0	0	0	0	0	0	1
Speckled Mousebird	0	0	0	0	0	0	0	1	0
Hadeda Ibis	0	0	0	0	1	0	0	0	0
Black Sparrowhawk	0	0	0	1	0	0	0	0	0
Yellowbellied Bulbul	0	0	0	1	0	0	0	0	0
Crested Guineafowl	0	1	0	0	0	0	0	0	0
Narina Trogon	0	1	0	0	0	0	0	0	0
Gymnogene	1	0	0	0	0	0	0	0	0
Little Sparrowhawk	1	0	0	0	0	0	0	0	0

Deviation from perfect nestedness = **8.3%**

Appendix 3.2. Forest dependent bird species distribution matrix showing patterns of nestedness (shaded areas) for the two forest complexes. Percentage deviation from perfect nestedness is given.

Balgowan Complex									
Common Name	A	B	F	E	C	D	G	H	I
Olive Woodpecker	1	1	1	1	1	1	1	1	1
Chorister Robin	1	1	1	1	1	1	1	1	1
Yellowthroated Warbler	1	1	1	1	1	1	1	1	1
Barthroated Apalis	1	1	1	1	1	1	1	1	1
Bleating Warbler	1	1	1	1	1	1	1	1	1
Cape Batis	1	1	1	1	1	1	1	1	1
Collared Sunbird	1	1	1	1	1	1	1	1	1
Cinnamon Dove	1	1	1	1	1	1	1	1	0
Starred Robin	1	1	1	1	1	1	1	1	0
Olive Bush Shrike	1	1	1	1	1	1	1	0	0
Knysna Lourie	1	1	1	1	1	1	0	0	0
Bluemantled Flycatcher	1	1	1	1	0	1	1	0	0
Forest Weaver	1	1	1	0	1	1	0	0	1
Forest Canary	1	1	1	1	0	0	1	0	0
Grey Cuckooshrike	1	0	1	0	0	1	0	0	0
Crested Guineafowl	1	0	0	1	1	0	0	0	0
Emerald Cuckoo	1	1	0	1	0	0	0	0	0
Crowned Eagle	0	0	1	0	1	0	0	0	0
Narina Trogon	1	1	0	0	0	0	0	0	0
Buffspotted Flufftail	1	0	0	0	0	0	0	0	0
Scalythroated Honeyguide	1	0	0	0	0	0	0	0	0
Squaretailed Drongo	1	0	0	0	0	0	0	0	0

Deviation from perfect nestedness = **5.1%**

Gilboa Complex									
Common Name	C	D	A	B	G	E	I	F	H
Olive Woodpecker	1	1	1	1	1	1	1	1	1
Yellowthroated Warbler	1	1	1	1	1	1	1	1	1
Barthroated Apalis	1	1	1	1	1	1	1	1	1
Bleating Warbler	1	1	1	1	1	1	1	1	1
Cape Batis	1	1	1	1	1	1	1	1	1
Collared Sunbird	1	1	1	1	1	1	1	1	1
Forest Weaver	1	1	1	1	1	1	1	1	0
Knysna Lourie	1	1	1	1	1	1	1	1	0
Bluemantled Flycatcher	1	1	1	1	1	1	1	0	1
Cinnamon Dove	1	1	1	1	1	1	0	1	1
Starred Robin	1	1	1	1	1	1	0	1	1
Chorister Robin	1	1	1	1	1	0	1	1	1
Emerald Cuckoo	1	1	1	1	0	1	0	0	1
Forest Canary	1	1	1	0	1	0	1	1	0
Grey Cuckooshrike	1	1	1	1	0	0	1	0	0
Olive Bush Shrike	0	1	1	0	1	0	1	0	0
Crowned Eagle	1	1	0	0	0	1	0	0	0
Buffspotted Flufftail	1	0	0	0	0	1	0	0	0
Tambourine Dove	1	0	0	0	1	0	0	0	0
Orange Thrush	1	1	0	0	0	0	0	0	0
Crested Guineafowl	0	0	0	1	0	0	0	0	0
Narina Trogon	0	0	0	1	0	0	0	0	0
Yellowbellied Bulbul	0	0	1	0	0	0	0	0	0

Deviation from perfect nestedness = **8.7%**

CHAPTER 4

Species Viability in a Disturbed and Fragmented Forest Landscape – Ecological and Life History Traits

4.1 Introduction

A landscape is a dynamic mosaic of habitat patches, corridors and the surrounding matrix, and because landscapes are spatially heterogeneous, the structure of, and changes that occur in, landscapes are scale-dependent (Jokimäki and Huhta, 1996). I have shown in earlier chapters that bird assemblage composition and abundance patterns in forest patches of a fragmented landscape, are deterministic and dependent on factors at larger scales, such as the nature of the surrounding matrix, than the individual's immediate habitat (e.g. Pulliam, 1988; Jokimäki and Huhta, 1996; Keitt *et al.*, 1997; Estades and Temple, 1999). In this chapter I revisit this issue and investigate the response of forest bird species to landscape scale changes and the influence of the surrounding matrix.

Responses of species to landscape changes are individualistic and species-specific (Kavanagh *et al.*, 1985; Andrén, 1994; Villard *et al.*, 1995; Fahrig, 1997; Warburton, 1997; Estades and Temple, 1999; Villard *et al.*, 1999). For forest avifauna this depends largely on mobility (Diamond, 1981; Machtans *et al.*, 1996), home range / territory size (Rolstad, 1991) and migratory patterns (Robbins *et al.*, 1987; Friesen *et al.*, 1999; Morse and Robinson, 1999), as well as life history traits and demography (Karr, 1990; Hansen and Urban, 1992; Stouffer and Bierregaard, 1995). Many traits have been identified and associated with local extinction proneness in populations of forest birds in fragmented landscapes. These include natural rarity (small population size) (Warburton, 1997), large body size (Leck, 1979; Willis, 1979; Karr, 1990), specialised patterns of resource use (Willis, 1974; Thiollay, 1992; Sieving and Karr, 1997), low annual survival rates (Karr, 1990), low fecundity (Sieving and Karr, 1997), terrestrial foraging and nesting (Terborgh, 1974; Willis, 1979; Recher *et al.*, 1987; Stouffer and Bierregaard, 1995), and low tolerance for the surrounding matrix habitat (Bierregaard and Stouffer, 1997; Laurance, 1997; Warburton, 1997).

Matrix tolerance may be a major predictor of vulnerability in insular populations (Diamond *et al.*, 1987; Laurance, 1991; Bierregaard and Stouffer, 1997; Warburton, 1997; Cornelius *et al.*, 2000). Furthermore, the quality of the matrix may be more important for vagile species like forest birds, than the structure of their local habitat (Fahrig and Merriam, 1994; Jokimäki and Huhta, 1996). If the matrix is inhospitable to species dependent on forest, e.g. open grassland, there will be little colonisation of fragments after isolation (Bierregaard *et al.*, 1992; Turner, 1996). However, in many cases the surrounding vegetation is not entirely unsuitable, for example, plantation forestry may support some forest birds (Armstrong *et al.*, 1996). In such landscapes, a mosaic of habitat patches of varying quality is created in the process of fragmentation, high quality habitat being provided by forest fragments, and the matrix providing lower quality habitat (Wiens, 1994; McGarigal and McComb, 1995; Armstrong *et al.* 1996; Estades and Temple, 1999). Hence, when overwhelming change in the landscape matrix occurs, populations of some species will decline or disappear, some will remain relatively unaffected, and others will increase in fragments (Terborgh, 1992; Laurance, 1997; Warburton, 1997).

Most generalist species may be able to use the modified matrix and would be better at dispersing between forest fragments than are those that avoid the matrix. These species would re-colonise fragments following local extinctions, strengthening the local populations through the genetic and demographic contributions of the immigrants (Brown and Kodric-Brown, 1977; Lomolino, 1986; Laurance, 1997). Furthermore, species that tolerate or use the modified matrix, are probably adapted to ecological changes in the landscape and habitat patches, such as edge effects (Laurance, 1997; Dale *et al.*, 2000), and so persist and even thrive in a disturbed environment.

There are two major sources of disturbance that have led to fragmentation of the Afromontane forests of Southern Africa: (1) climatic change during the Quaternary (Hamilton, 1981; Lawes, 1990; Hamilton and Taylor, 1991; Eeley *et al.*, 1999), and (2) anthropogenic disturbance. Eeley *et al.* (1999) suggest that repeated and severe climate changes in the Quaternary have caused Afromontane forests to be fragmented throughout much of their evolutionary history. In addition, the Karkloof / Balgowan forest range, KwaZulu-Natal, South Africa, has been selectively logged in the recent past (1870 – 1944; Rycroft, 1944), and extensive areas of the Karkloof region have become fragmented and dominated by commercial plantation forestry.

Afforestation practises (particularly during and after harvesting) increase and intensify the degree of disturbance otherwise experienced by the indigenous forest patches, especially disturbance effects along the forest edge (Lovejoy *et al.*, 1986; Armstrong and van Hensbergen, 1996; Estades and Temple, 1999). Since disturbance can be a major determinant of species richness and composition, (Cutler, 1994; Forman, 1997; Lomolino, 1996; Canaday, 1997; Warburton, 1997) a highly non-random species succession within a forest patch may result.

The increased disturbance experienced by indigenous forest patches surrounded by plantation forestry practises may cause disturbance-sensitive species to disappear and allow new, more robust, generalist species to enter the system. In this case, these forest fragments would converge quickly to the same community representation. Essentially, the susceptibility of certain life histories to fragmentation and landscape-level disturbance can result in a deterministic pattern of species relaxation and extirpation producing highly predictable changes in assemblage composition. This is an extension of arguments already presented in Chapter 3 on nested subset analysis. In this chapter I identify those life histories responsible for the deterministic pattern of species relaxation in indigenous forest patches of the Karkloof / Balgowan range. I also compare the species composition of bird assemblages in a disturbed landscape, where forest patches are surrounded by commercial plantation forestry (the Gilboa forest complex), with that of a naturally fragmented forest landscape with natural grassland matrix habitat (the Balgowan forest complex).

There is growing evidence from both palaeontology and conservation biology to suggest that past events may explain the variation seen in species' vulnerability to environmental threats (Blondel, 1990; Hansen and Urban, 1992; Balmford, 1996). Historical events may not only determine species diversity of communities (Diamond and Hamilton, 1980; Latham and Ricklefs, 1993), but may also determine the resilience of communities (Balmford, 1996; Danielsen, 1997). For example, a forested region that has a complex topography and high rates of natural disturbance throughout its evolutionary history, may have selected for life history traits that impart resistance to habitat fragmentation effects, particularly recent changes that accompany forest clearance for anthropogenic land use (Lawes *et al.*, 2000). The Afromontane Mistbelt forest bird assemblages in KwaZulu-Natal may be fragmentation adapted (Lawes *et al.*, 2000). Lawes *et al.* (2000) argue that repeated climate changes in the Quaternary (Diamond and Hamilton, 1980; Hamilton, 1988) have filtered (*sensu* Balmford, 1996)

Afromontane forest communities resulting in faunas whose life histories are adjusted to fragmentation. The resulting Afromontane forest bird community would consequently be robust and resilient, and expected to show only slight response, to further anthropogenic change in the landscape. In this chapter I test these predictions of the general extinction-filtering hypothesis of fragmented faunas.

4.2 Methods

4.2.1 Study area

Afromontane forest comprises most of the indigenous forest biome in southern Africa, which is the smallest, most widely distributed and the most fragmented biome of the region (Geldenhuys and MacDevette, 1989). The naturally fragmented Karkloof / Balgowan forest range is situated in the midlands of South Africa's KwaZulu-Natal province (Fig. 2.1), and forms part of a landscape mosaic comprised of Afromontane Mistbelt Mixed *Podocarpus* Forest and Moist Upland Grassland (Cooper, 1985; Low and Rebelo, 1996). The forest range lies at an altitude of 1500m-1800m and experiences high rainfall (mean annual rainfall: 800mm-1000mm), particularly in summer. Mistbelt forests are characteristically cool, tall (~15m), inland forests with well-developed and mature soils (Pooley, 1993). Water is a key-limiting factor in this environment, and the forest patches generally occur in moist fire-safe habitats (Low and Rebelo, 1996), on steep south-facing slopes that are subject to frequent mist.

The Karkloof / Balgowan forest range comprises one large, contiguous forest patch (approximately 2900ha in size) and many smaller, peripheral fragments surrounded by mainly one of two matrix types: 1) the natural Moist Upland Grassland or 2) commercial plantation forestry species such as pine (*Pinus patula*) and black wattle (*Acacia mearnsii*). From 1:30 000 aerial photographs from 1996, nine forest patches were selected in natural grassland in the Balgowan complex, with a size range of 0.5ha to 215ha. A further nine patches were selected within and around the Gilboa (Mondi forests) commercial forestry estate in the Karkloof region (the Gilboa complex). These forest patches were surrounded by pine plantation (stand age > 8 years) and had a size range of 0.5ha to 273ha. The patches in the two forest complexes were matched in pairs by size (Table 2.1). A forest of much greater size (Leopards Bush Private Nature Reserve; 705ha), sited in the Karkloof region, representing the ecological conditions in a large contiguous forest patch, served as an ecological control or outgroup. The total area in hectares of each patch was calculated

from digital maps of the area (Macfarlane, 2000) using ArcView version 3.0 (ESRI, 1998).

4.2.2 Bird census methods

Line transects of varying length adjusted according to patch size were marked out across the dominant environmental gradient (i.e. up the slope and between watercourses) in the forest patches. In this way the maximum gradient of diversity was sampled in each forest patch. Transects were walked in the early morning, midday and late afternoon to account for variation in bird activity throughout the day. Along each transect, all bird species seen and heard were recorded, including the number of individuals and the estimated categorical height of the bird or flock above the ground (A: ground level; B: above ground; C: lower stratum; D: mid-stratum; E: upper stratum; F: canopy; and G: above canopy). Sampling took place through the summer months November to March, over two summer seasons.

Cumulative sample-species richness curves were plotted for each transect (or patch) to determine when sampling (number of transects walked) should cease. These curves were asymptotic at approximately 8 transects for the eighteen smaller patches and at 22 transects for the larger control patch (Fig. 2.2). No new species were added at the full sampling effort for each forest patch and all forest patches were regarded as adequately sampled.

4.2.3 Species response to fragmentation

Incidence functions (Diamond, 1975) are useful tools for examining and displaying the distributional ecology of individual species as opposed to whole communities. Diamond (1975) described incidence functions as a method of quantifying the survival prospects of a species by illustrating the probability that a species will occur on an island of a particular size or with particular species richness. This method is useful as it enables conservation biologists to predict whether a species is likely to persist in a fragmented landscape when area is used as the independent variable (Taylor, 1991; Hanski, 1994).

To assess how Afromontane forest bird species respond to fragmentation (i.e. a reduction in forest area), incidence functions were plotted (following Diamond, 1975) for all bird species in the Karkloof / Balgowan range. Bird species from all forest patches sampled (including the control) were used in the investigation

(Appendix 4.1). The incidence functions were categorised by grouping together species with similar shaped curves, thereby assessing each species' apparent response to fragmentation. The following categories of species were identified: 1) species that respond positively to fragmentation i.e. those that occur more often in smaller patches than medium or larger patches; 2) species that show little or no response to fragmentation, i.e. those that either occur in all sites or show no consistent response to forest patch area; 3) species that occur in most sites, but occur less frequently in very small patches than in large or medium sized patches; 4) species that occur in all or almost all large sites, are missing from most small patches, and occur in some medium sized patches; and 5) species that occur in large and some medium sites only.

To detect if the matrix had an influence on the way species respond to fragmentation (i.e. are species responding to a landscape effect at a scale larger than forest patch size), incidence functions were plotted for bird species occurring in the Balgowan forest complex (natural grassland matrix; Appendix 4.2) and compared to those found in the Gilboa complex (plantation matrix; Appendix 4.3). A chi-squared test was used to test for differences in species distribution among the five categories between the two forest complexes. Tests were performed using STATGRAPHICS version 7 (Manugistics, 1993).

4.2.4 Ecological and life history traits of bird species

Data on ecological and life history traits were collected from field observations and the literature, for bird species in the two forest complexes (Appendix 4.4). Traits were selected from those considered to be the most important in influencing extinction risk among bird species in fragmented landscapes (Willis, 1974; Leck, 1979; Terborgh and Winter, 1980; Newmark, 1991; Sieving and Karr, 1997; Warburton, 1997; Renjifo, 1999; Stratford and Stouffer, 1999). Two species, namely the Steppe Buzzard (*Buteo buteo vulpinus*) and Spotted Flycatcher (*Muscicapa striata*), were excluded from this investigation as both are non-breeding Palaearctic migrants to the region, and thus breeding is extralimital (Maclean, 1996).

One morphological and five reproductive traits of the forest birds were identified (Maclean, 1996; Tarboton, 2001):

body size (average mass, g);

nest height (average height above ground, m);

nest shape (ranked by decreasing complexity): 1 = hollow / cavity, 2 = ball / closed goblet, 3 = domed, 4 = cup / bowl, 5 = saucer, 6 = platform, 7 = scrape;

clutch size (average number of eggs per brood);

breeding cycles (number of breeding attempts per breeding season);

annual fecundity (the product of clutch size and broods per year).

Nest characteristics of brood parasites, namely the Redchested Cuckoo (*Cuculus solitarus*), Black Cuckoo (*Cuculus clamosus*), Emerald Cuckoo (*Chrysococcyx cupreus*), and Scalythroated Honeyguide (*Indicator variegates*), were recorded as those of their host species, namely the Chorister Robin (*Cossypha dichora*), Southern Boubou (*Laniarius ferrugineus*), Bleating Warbler (*Camaroptera brachyura*), and Olive Woodpecker (*Mesopicos griseocephalus*), respectively.

Four traits associated with diet, social behaviour, and habitat specialisation were identified from the literature (Maclean, 1996; Harrison *et al.*, 1997) and field observations:

feeding guild / trophic level: 1 = frugivore / granivore, 2 = frugivore / insectivore, 3 = nectarivore / insectivore, 4 = granivore / insectivore, 5 = omnivore, 6 = insectivore, 7 = carnivore;

foraging level (ranked by apparent increasing vulnerability to predation): 1 = all levels, 2 = perch / aerial to ground attacker, 3 = upper stratum to canopy, 4 = ground to mid-stratum, 5 = on ground;

groups or pairs (life style / social strategy): 1 = species that live singly or in pairs, 2 = species that live in groups;

habitat preference / forest dependence (ranked by increasing habitat specialisation): 1 = mixed habitat species (non-dependent on forest), 2 = dependent on forest (forest is required for breeding; Oatley, 1989).

Four characteristics of the distribution of the bird species were identified from field observations and the literature (Maclean, 1996; Harrison *et al.*, 1997):

movement patterns (ranked by apparent increasing vulnerability to habitat destruction): 1 = long range intra-African migrant, 2 = nomadic, 3 = short range seasonal migrant, 4 = resident / sedentary;

species status / natural abundance throughout its range (ranked by apparent increasing vulnerability to extinction): 1 = very common, 2 = common, 3 = common localised, 4 = fairly common, 5 = uncommon;

range size (number of grid cells occupied; data from the Southern African Bird Atlas Project (SABAP), Harrison *et al.*, 1997; average grid cell area for the Southern African region = 690km^2);

habitat matrix (habitat surrounding forest in which the species was recorded): 1 = plantation, 2 = plantation and grassland, 3 = grassland.

Principal component analysis (PCA) is an ordination technique that can be used to investigate the overall similarity of variables and to detect major groupings (Magurran, 1988). Using data for all bird species, a PCA was performed using the ordination program CANOCO for Windows version 4.02 (ter Braak and Smilauer, 1999), to detect any co-linearity among the ecological and life history variables. A reduced set of variables was chosen and used in the analyses that follow. These variables included body size, annual fecundity, nest height, and range size (Fig. 4.1).
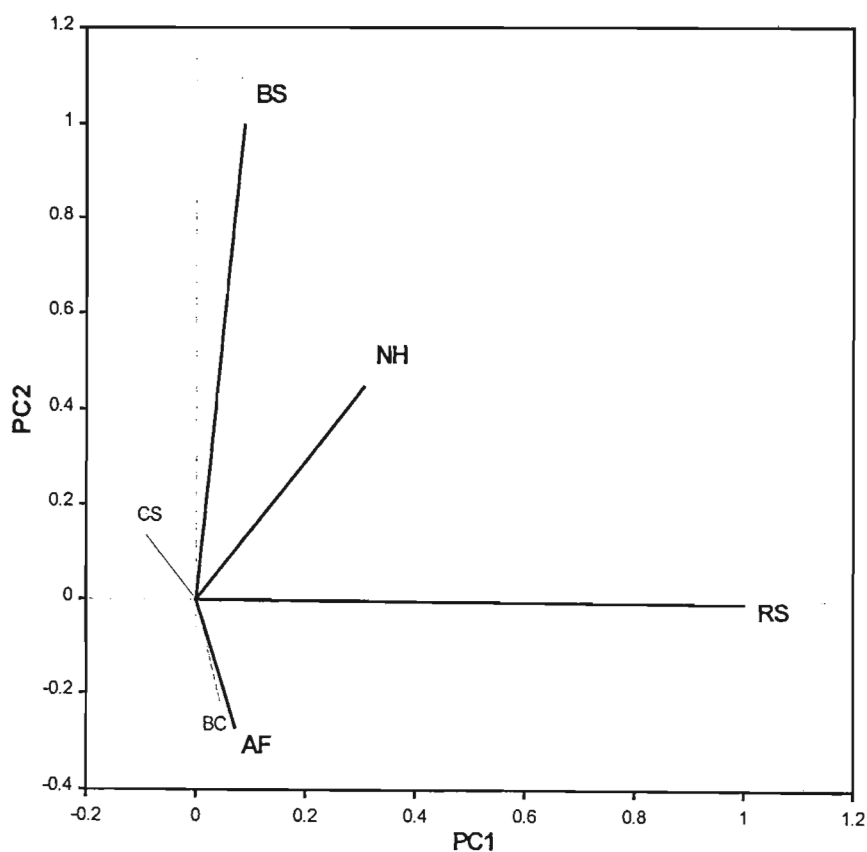
Figure 4.1. Principal component analysis of ecological and life history traits for all bird species in the Karkloof / Balgowan forest range. Important traits are highlighted. The first axis of the ordination accounts for 91% of the variation while the second axis accounts for 9%.

4.2.5 Predictors of local extinction proneness

To investigate the relationship between the bird species' ecological and life history traits, and species proneness to local extinction, a generalised linear model (GLM) was constructed using bird species occupancy (number of forest patches inhabited, n = 19) as the response variable. Because the likelihood of occupancy of a patch was either 1 or 0 by any species, bird species occupancy was modelled using a binomial distribution and a logit link function (McCullagh and Nelder, 1989). The variables discussed below were entered into the model in linear combinations. The GLMs were fitted using Genstat 5 (Genstat 5 committee, 1998). The goodness of fit of a model was assessed using the X^2 statistic in which the actual occupancy was compared with predicted occupancy: X^2 has the useful property that it is asymptotically distributed as χ^2 (Dobson, 1991).

For model selection and parameter estimation a small set of candidate models was formulated *a priori* and the combination of variables and factors for each model were fitted. For each model the Akaike information criterion (AIC) was computed from the sum of the deviance and twice the number of model parameters (Burnham and Anderson, 1998). The difference in AIC between the ith model and the model with the lowest AIC was computed from $\Delta_i = AIC_i - min_i(AIC)$. The significant model with the lowest AIC value (and a difference of at least two AIC values from the other models) is accepted as the model best fitting the data (Anderson and Burnham, 2001) (Table 4.3). The Akaike weights were computed from $w_i = Exp(-1/2\Delta_i)/\Sigma_i Exp(-1/2\Delta_i)$. The weighted estimate of a parameter, θ was computed from $\Sigma_i w_i \theta_i$, where θ_i was the estimate from the ith model (Anderson and Burnham, 2001).

4.3 Results

4.3.1 Species response to fragmentation

i. Area effects

In the Karkloof / Balgowan forest range as whole (i.e. all forest patches in the study) the largest proportion of bird species (n = 27; 44.3%) showed little or no response to fragmentation (i.e. displayed a response curve typical of category 2). Few species (n = 3; 4.9%) displayed a positive response to fragmentation by occurring in smaller forest patches (<10ha) more often than medium or large forests (category 1), while a large proportion of species (n = 23; 37.7%) responded negatively to fragmentation by

occurring only in large and some medium-sized forest patches (>80ha) (categories 4 and 5). More than half ($n = 13$; 52%) of the forest dependent bird species responded negatively to fragmentation and occurred more often in larger fragments and were absent from small forest patches (i.e. displayed response curves typical of categories 4 and 5) (Table 4.2).

Of the long-range migrant bird species (Palaearctic non-breeding and intra-African breeding migrants), all except one species responded negatively to forest fragmentation, by occurring only in larger forest patches (categories 4 and 5; Table 4.1). This indicates the importance of large forest patches to returning migrant species, especially those that return to breed. The one exception, the Paradise Flycatcher (*Terpsiphone viridus*), showed little response to forest fragmentation (category 2). This species, however, is not a long-range migrant throughout its range. Southeastern African populations, reaching as far as the KwaZulu-Natal south coast, remain relatively sedentary throughout the year. The probability of fragmented Afromontane populations surviving through rescue effects from these sedentary populations is therefore high.

ii. Effect of the matrix: Balgowan / Gilboa comparison

A comparison of the species richness by incidence function category for forest dependent birds and non-dependent bird species separately and between complexes, showed no significant differences (forest dependent birds: $\chi^2 = 4.16$, df = 3, $P = 0.24$; non-dependent birds: $\chi^2 = 4.83$, $df = 4$, $P = 0.31$). At first sight there appears to be no significant effect of the matrix on species response (incidence category) to fragmentation. However, this crude analysis does overlook individual species response. In both forest complexes, the largest proportion of species (Balgowan: $n = 28$, 50.9%; Gilboa: $n = 35$, 67.3%) showed no or little response to fragmentation (category 2), the Gilboa complex comprising a distinctly higher percentage of species in this category (Table 4.2). The most obvious difference between complexes, however, occurred in categories 4 and 5 (i.e. species sensitive to fragmentation). Twenty-nine percent ($n = 16$) of all bird species in the Balgowan complex were in categories 4 and 5, and responded negatively to fragmentation, and only occurred in larger forest patches, while markedly fewer species in these categories ($n = 5$; 9.6%) occurred in the Gilboa complex.

Table 4.1. Afromontane forest bird species and their responses to the fragmentation of the entire forest range, the Balgowan complex, and the Gilboa complex, respectively. Forest dependent species are indicated by *. Long-range migrants are underlined.

| Common Name | Response to fragmentation (incidence function category) | | |
	All forests	Balgowan	Gilboa
Hadeda Ibis	2	2	1
*Crowned Eagle	4	2	2
Steppe Buzzard	5	4	-
Little Sparrowhawk	4	4	2
Black Sparrowhawk	5	2	5
Gymnogene	5	5	2
Rednecked Francolin	5	-	2
*Crested Guineafowl	4	4	2
*Buffspotted Flufftail	4	5	2
Rameron Pigeon	3	3	3
Redeyed Dove	3	3	2
Cape Turtle Dove	2	3	2
*Tambourine Dove	2	-	2
*Cinnamon Dove	3	3	3
*Knysna Lourie	3	3	3
Redchested Cuckoo	5	-	-
Black Cuckoo	5	-	-
*Emerald Cuckoo	4	4	3
Speckled Mousebird	2	2	2
*Narina Trogon	5	5	2
Redbilled Woodhoopoe	1	1	-
Redfronted Tinkerbarbet	2	4	4
*Scalythroated Honeyguide	5	5	-
Goldentailed Woodpecker	2	5	1
*Olive Woodpecker	2	2	2
*Grey Cuckooshrike	4	4	4
Forktailed Drongo	3	2	2
*Squaretailed Drongo	5	5	-
Blackheaded Oriole	3	3	2
Southern Black Tit	1	1	2
Blackeyed Bulbul	2	2	2
Terrestrial Bulbul	2	2	2
Sombre Bulbul	2	2	2
*Yellowbellied Bulbul	5	-	5
Olive Thrush	3	2	3
*Orange Thrush	5	-	2
*Chorister Robin	2	2	2
Cape Robin	2	2	2
*Starred Robin	3	3	3
*Yellowthroated Warbler	2	2	2
*Barthroated Apalis	2	2	2
Yellowbreasted Apalis	4	2	4
*Bleating Warbler	2	2	2
Spotted Prinia	2	2	1
Spotted Flycatcher	5	5	-
Dusky Flycatcher	2	2	2
*Cape Batis	2	2	2
Chinspot Batis	2	4	1
*Bluemantled Flycatcher	4	2	2
Paradise Flycatcher	2	2	2
Southern Boubou	2	2	2
Puffback	2	2	2
*Olive Bush Shrike	4	3	2
Redwinged Starling	5	5	-
Greater Doublecollared Sunbird	2	2	2
Black Sunbird	1	2	1
*Collared Sunbird	2	2	2
Cape White Eye	2	2	2
Thickbilled Weaver	2	4	-
*Forest Weaver	4	3	3
*Forest Canary	2	2	2

- indicates that the bird was not detected in the forest complex.

A similar trend was observed for forest dependent bird species in each forest complex. Most species in the Gilboa complex ($n = 16$; 69.6%) displayed little or no response to fragmentation (category 2), while a small percentage ($n = 2$; 8.7%) responded negatively (categories 4 and 5; Table 4.2). In fact only two species overall, namely the Yellowbellied Bulbul (*Chlorocichla flaviventris*) and the Black Sparrowhawk (*Accipiter melanoieucus*) were adversely affected by fragmentation in this forest complex (Appendix 4.3). A large proportion ($n = 10$; 45.5%) of the forest dependent species occurring in the Balgowan complex showed little or no response to fragmentation (category 2), while a relatively large percentage of species ($n = 7$; 31.8%) responded negatively to the fragmentation of this forest complex (categories 4 and 5). Furthermore, only two of the six long-range migrant species occurring in the Karkloof / Balgowan forest range, occur in the plantation dominated Gilboa complex (Table 4.1). This suggests that the plantation matrix may act as a selective filter for migratory species.

Table 4.2. Total number of bird species in each response-to-fragmentation category for forest dependent (FD) species and non-dependent (ND) species separately (percentage of the total is also given). Data is provided for the Balgowan and Gilboa forest complexes as well as for all forest patches combined.

	Response to fragmentation category				
	1	2	3	4	5
All Forest Patches (including control)					
FD species (n = 25)	0	9 (36)	3 (12)	8 (32)	5 (20)
ND species (n = 36)	3 (8.3)	18 (50)	5 (13.9)	2 (5.6)	8 (22.2)
Balgowan complex (grassland matrix)					
FD species (n = 22)	0	10 (45.5)	5 (22.7)	3 (13.6)	4 (18.2)
ND species (n = 33)	2 (6.1)	18 (54.5)	4 (12.1)	5 (15.2)	4 (12.1)
Gilboa complex (plantation matrix)					
FD species (n = 23)	0	16 (69.6)	5 (21.7)	1 (4.4)	1 (4.4)
ND species (n = 29)	5 (17.2)	19 (65.5)	2 (6.9)	2 (6.9)	1 (3.5)

Categories: 1 = species that occur in smaller sites more often than medium or larger sites; 2 = species that show little or no response to fragmentation; 3 = species that occur in most sites but occur less frequently in small fragments; 4 = species that occur in all or almost all large sites and some medium sized sites, but are missing from most small sites; 5 = species that occur in large and some medium sites only.

4.3.2 Predictors of local extinction proneness

The generalised linear model (GLM) that best fit the data included the variables - body size, annual fecundity, nest height and range size, and the factors – abundance status, forest dependence, feeding guild, foraging level, movement patterns and nest

shape (Table 4.3) (AIC = 202.2 and a weight of 40.8 % compared to the other two competing models; χ^2 = 31.1, df = 43, P = 0.91).

Table 4.3. Coefficient values for the parameters included in the final GLM. Standard error (S.E.) is included.

	Coefficient	S.E.	t value
Constant	6.33	1.52	4.17
Variables			
Annual fecundity	-0.3398	0.0639	-5.32
Body size	-0.001350	0.000379	-3.56
Nest height	-0.0409	0.0474	-0.86
Range size	-0.0003509	0.00008	-4.39
Factors			
Forest dependence			
Dependent	2.529	0.454	5.57
Habitat matrix			
Plantation and grassland	4.366	0.592	7.37
Grassland	0.251	0.700	0.36
Groups / Pairs			
Groups	-1.143	0.333	-3.43
Abundance status			
Abundant	-2.721	0.713	-3.82
Abundant localised	-2.339	0.917	-2.55
Fairly abundant	-4.380	0.737	-5.94
Rare	-7.32	1.10	-6.66
Movement patterns			
Nomadic	-4.418	0.920	-4.80
Seasonal movements (within range)	-0.472	0.896	-0.53
Resident / sedentary	-1.055	0.598	-1.76
Feeding guild			
Frugivore / Insectivore (F / I)	-4.329	0.698	-6.20
Nectarivore / Insectivore (N / I)	-0.766	0.800	-0.96
Granivore / Insectivore (G / I)	-4.401	0.968	-4.55
Omnivore (O)	-1.261	0.624	-2.02
Insectivore (I)	-3.167	0.612	-5.17
Carnivore (C)	0.56	1.15	0.48
Foraging level			
Perch / aerial to ground attacker	-2.873	0.538	-5.34
Upper stratum to canopy	0.047	0.425	0.11
Ground to mid-stratum	0.576	0.548	1.05
Ground	-1.639	0.592	-2.77
Nest shape			
Ball / closed goblet	-0.359	0.422	-0.85
Dome	-0.58	1.02	-0.57
Cup / Bowl	-0.251	0.377	-0.67
Saucer	-0.417	0.650	-0.64
Platform	0.665	0.586	1.14
Scrape	2.458	0.892	2.75

Forest dependent bird species had a higher likelihood of occurring in all forest patches than non-dependent species (Fig. 4.2a). This is a natural corollary of the fact that forest dependent birds require forest for breeding. Bird species that are able to

tolerate both grassland and plantation matrix habitat (i.e. those species found in forest patches in both the Balgowan and Gilboa forest complexes) had a higher likelihood of occurring in all forest patches than species found only in forests in the plantation matrix or the grassland matrix. There was no difference between matrix types *per se* in the probability of occupancy (Fig. 4.2b).
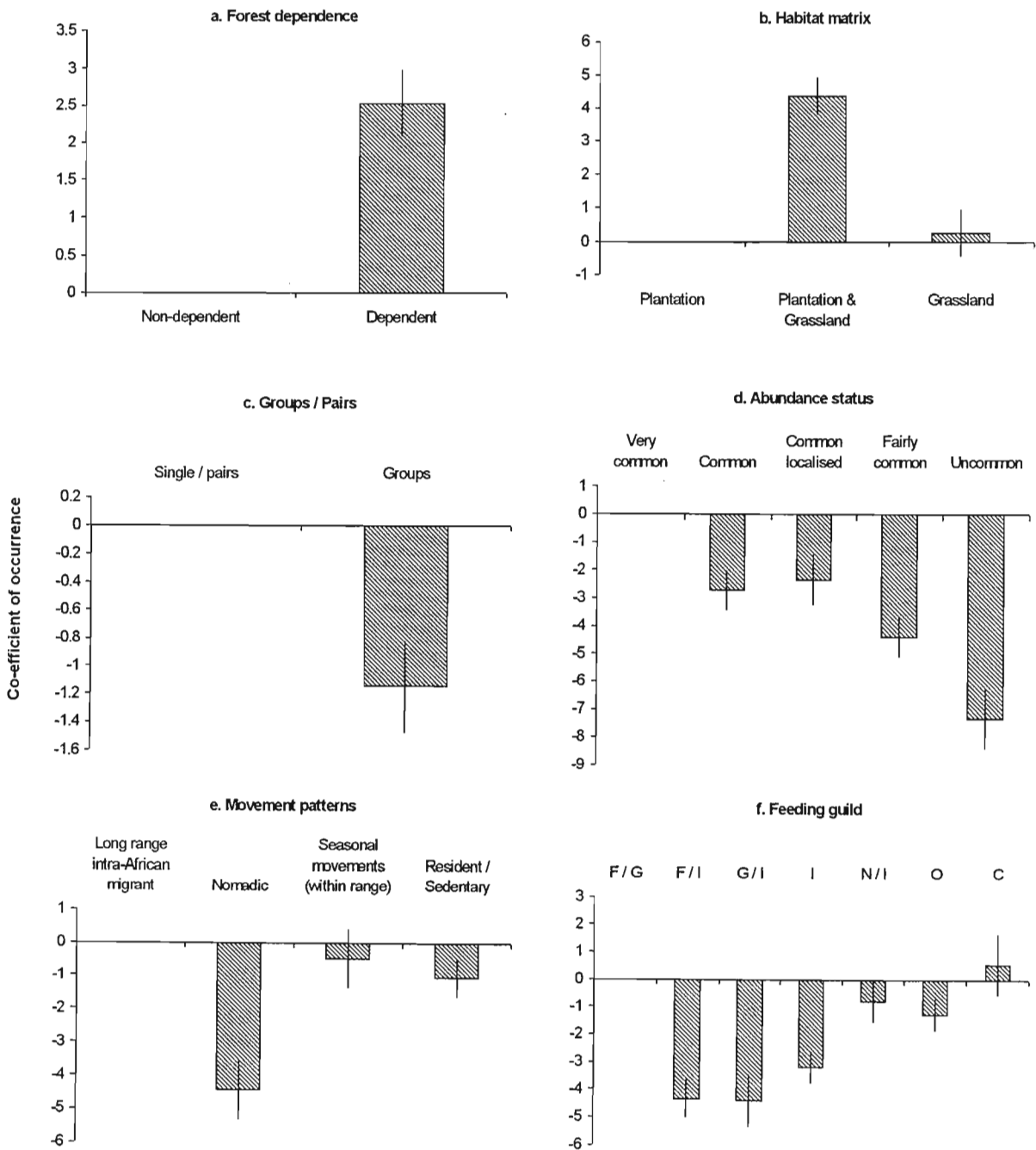
Figure 4.2. Coefficient of occurrence in all forest patches for all forest bird species. The effect of each factor is plotted relative to the constant; so that negative values indicate lower likelihood of occurrence relative to the constant (blank category on graph).

Bird species living singly or in pairs were more likely to occur in a patch than those that live in groups (Fig. 4.2c), while uncommon (naturally rare) bird species were least likely to occur in forest patches compared to common or locally abundant species (Fig. 4.2d). Nomadic species had a lower probability of occurrence than migrant species, within-range seasonal migrants, and sedentary species (Fig. 4.2e), while insectivorous species were less likely to occur in forest patches than non-insectivorous species (Fig. 4.2f). The two remaining factors, namely foraging level and nest shape, proved to be uninformative.

Most life history traits have some association with other life history traits. Certain traits may be strongly influenced by and dependent on other, more dominant traits. For example, many traits scale with body size, for instance fecundity is often dependent on body size. Thus, although the variables body size, annual fecundity, range size, and nest height were included in the final GLM, the relationship between each variable and the various factors, showed similar trends. These trends were most easily explained using body size as the interactive variable (Fig. 4.3).

Overall, the probability of a species occurring in all forest patches decreased with increasing body size. Large, non-dependent bird species had a lower probability of occurring in forest patches than large forest dependent species (Fig. 4.3a). Occupancy was independent of the interaction of body size and matrix tolerance. There was a weak trend for lower occupancy by very large bodied birds (Fig. 4.3b). Large social bird species had a lower probability of occurrence than large solitary bird species (Fig. 4.3c). Regardless of body size, annual fecundity, and range size, the probability of occurrence of uncommon or naturally rare (very low density) bird species was extremely low and declined with increasing value of each variable (Fig. 4.3d). Nomadic species had the lowest probability of occupancy and this declined steeply with increasing body size, compared to migratory and sedentary species (Fig. 4.3e). The probability of occurrence of insectivorous bird species and those that incorporate insects into their diets was lower than non-insectivorous species, and decreased markedly with increasing body size (Fig. 4.3f). No informative relationships were found for nest height.
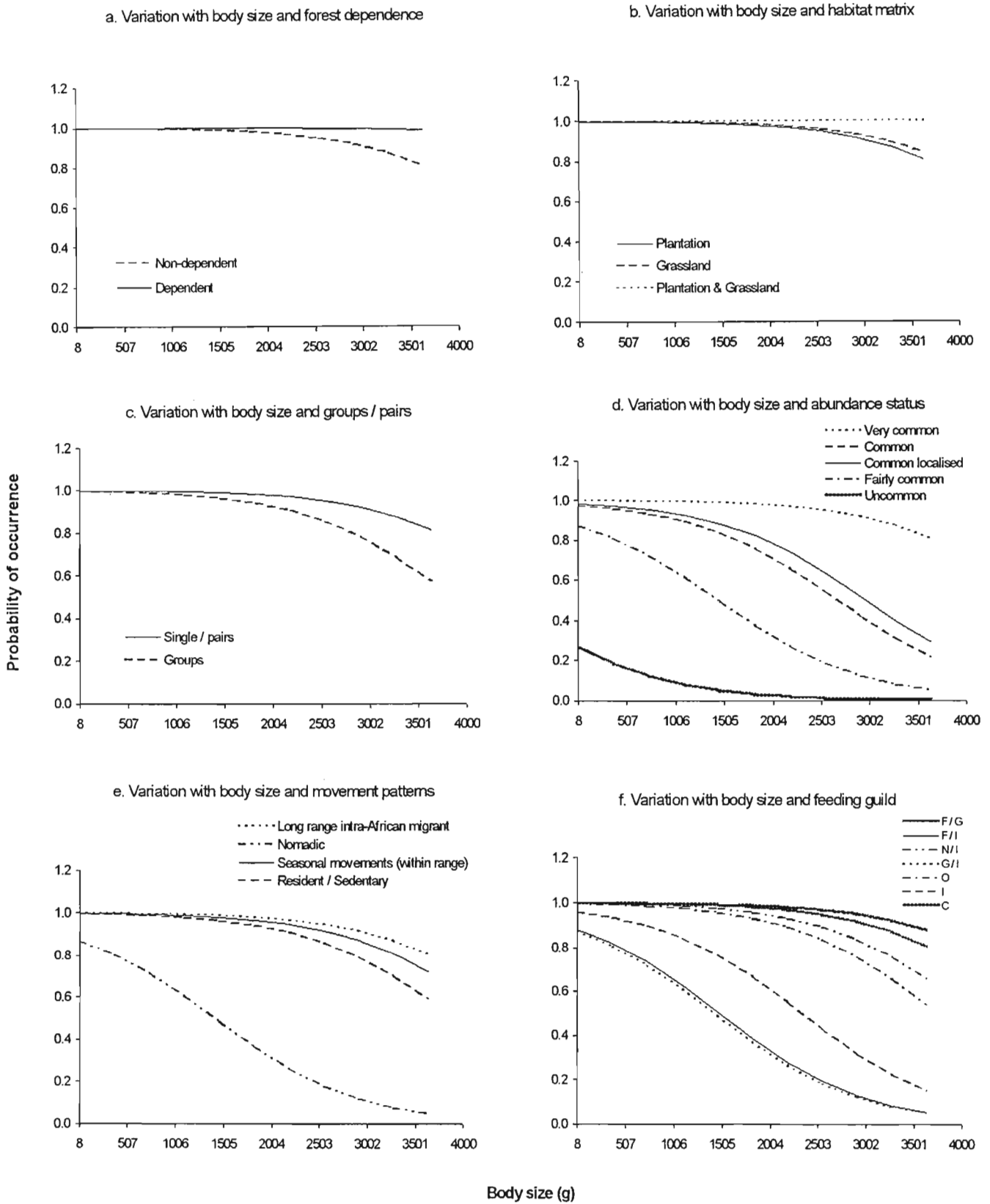
Figure 4.3. Probability of occurrence of bird species in all forest patches versus body size for each ecological factor category. Probabilities were calculated as logits from the coefficients of the best fit generalised linear model (GLM) (probability = $e^{(coeff.)}/(1+e^{(coeff.)})$).

In summary, those birds most prone to local extinctions following fragmentation are those that are naturally rare, forest dependent, group living, matrix intolerant, nomadic, insectivorous species and large in size. Large, insectivorous birds living at naturally low densities (i.e. rare or uncommon species) appear to be most vulnerable (Table 4.3). Key predictors of vulnerability to forest fragmentation for forest bird species include body size, natural abundance status, and feeding guild.

Therefore, in the Karkloof / Balgowan forest range, bird species most vulnerable to fragmentation include the Crested Guineafowl (*Guttera pucherani*), the Buffspotted Flufftail (*Sarothura elegans*), the Emerald Cuckoo (*Chrysococcyx cupreus*), the Narina Trogon (*Apaloderma narina*), the Scalythroated Honeyguide (*Indicator variegatus*), the Grey Cuckooshrike (*Coracina caesia*), the Squaretailed Drongo (*Dicrurus ludwigii*), the Orange Thrush (*Zoothera gurneyi*), and the Bluemantled flycatcher (*Trochocercus cyanomelas*).

4.4 Discussion

In order to conserve the biodiversity of a fragmented or disturbed landscape effectively, not only is it necessary to understand the way species assemblages respond to ecological processes, but an understanding of the innate character of individual species is essential. Predicting the way species respond to forest fragmentation and anthropogenic landscape alteration, by categorising species by their relative risk of extinction, is imperative for providing a basis for proactive management of forest ecosystems. Recent studies have focused upon identifying traits of species that predict vulnerability to forest fragmentation and anthropogenic landscape alteration (Estrada *et al.*, 1997; Desrochers *et* al., 1999; Kemp, 1999; Renjifo, 1999; With and Wing, 1999; Davies *et al.*, 2000; Miller and Cale, 2000; Daily *et al.*, 2001).

This study identified three major predictors of local extinction proneness and vulnerability to fragmentation (reduction in forest area) for forest bird species. These ecological and life history traits include body size, abundance status, and feeding guild. To a lesser extent, forest dependence, annual fecundity, and range size are also important. While a large proportion (44.3%) of bird species found in the Karkloof / Balgowan forest range show a high degree of resilience to fragmentation, those that respond negatively to fragmentation and display high extinction proneness are those with large body sizes, low natural abundance, and that depend on insects as part or all

of their diet. Furthermore, results from a density analysis (Chapter 2) indicate that the more rare bird species are lost first from smaller forest patches after insularisation.

The findings of this study receive wide support from other studies of forest birds. For instance, Soulé *et al.* (1988) found that species density and body size were good predictors of extinction proneness for forest bird species in Western North America. Renjifo (1999) found that sub-Andean forest bird species with small geographic ranges, as well as those that were scarce or rare throughout their range, and large bodied species such as certain raptors, terrestrial insectivores, and large frugivores, were highly prone to extinction.

It has been predicted in theory and shown empirically that populations of rare bird species tend to disappear first during the process of forest fragmentation (Leck, 1979; Pimm *et al.*, 1988; Newmark, 1991; Willson *et al.*, 1994; Stouffer and Bierregaard, 1995; Warburton, 1997; Brooks *et al.*, 1999; Renjifo, 1999). Species with small population sizes or that occur naturally at low abundance are likely to be more prone to extinction than species with large populations or high abundance, as small populations are most vulnerable to stochastic events that may cause demographic collapse and ultimately local extinction (Diamond *et al.*, 1987; Quinn and Hastings, 1987; Newmark, 1991; Rolstad, 1991; Meffe and Carroll, 1997; With and Wing, 1999; Davies *et al.*, 2000). Small populations may suffer from genetic drift and inbreeding that reduce genetic variation, increase homozygosity, and in the end, reduce fitness (Caughley, 1994; Mills and Smouse, 1994). However, the rapidly changing nature of fragments in a human-dominated landscape means that demographic collapse is much more likely than genetic collapse mediated by the effects of inbreeding and genetic drift (Thomas, 1994; Swart and Lawes, 1996).

Similarly, restricted range size has been associated with increased extinction risk in forest birds, as such species are vulnerable to localised destructive processes such as deforestation and afforestation (Rolstad, 1991; Simberloff, 1994; Brooks *et al.*, 1999; Renjifo, 1999). Such processes cause localised extinctions, which lead to a break down of metapopulation dynamics, which in turn leads to the extinction of the species from its range. However, a species range size is often closely correlated with its abundance status (Terborgh and Winter, 1980; Rabinowitz *et al.*, 1986; Meffe and Carroll, 1997; Brooks *et al.*, 1999), thus a species may be rare due to its restricted range, and visa versa.

Large body size has been consistently identified as a trait of extinction prone forest bird species (Leck, 1979, Willis, 1979; Terborgh and Winter, 1980; Karr, 1990; Kattan *et al.*, 1994; Restrepo *et al.*, 1997; Estades and Temple, 1999; Renjifo, 1999). Large species tend to have large territories making them more area-sensitive than species with smaller territories (Leck, 1979; Shaffer, 1981; Rolstad, 1991; Turner, 1996). Possessing large territories renders their population sizes smaller in habitat remnants following fragmentation, and increases their extinction risk in fragmented landscapes compared to smaller bodied species with smaller territory sizes (Sieving and Karr, 1997). Many large non-predatory bird species, such as the Crested Guineafowl (*Guttera pucherani*), also possess traits such as terrestrial foraging and nesting, low dispersal ability, and low annual fecundity, which make them vulnerable to fragmentation effects (Diamond, 1981; Karr, 1990; Stouffer and Bierregaard, 1995). Such species are more susceptible to predators, especially when a reduction in forest fragment area reduces the number of available nest sites, which may lead to nest crowding (Hagan *et al.*, 1996; Keyser *et al.*, 1998). Populations of these species may also suffer reduced rescue effects due to restricted dispersal ability (Wright, 1985) and reduced annual survival rates due to a combination of low annual fecundity and loss of individuals as a consequence of reduction in forest area (Sieving and Karr, 1997; Burke and Nol, 2000).

Understorey and terrestrial insectivorous birds, especially large bodied species, have emerged as extinction-prone in many studies (Bierregaard and Lovejoy, 1989; Thiollay, 1992; Kattan *et al.*, 1994; Bierregaard and Stouffer, 1997; Canaday, 1997; Christiansen and Pitter, 1997; Renjifo, 1999; Stratford and Stouffer, 1999; Miller and Cale, 2000). Fragmentation and landscape alteration may have direct consequences for insectivorous birds through changes in microclimate, which alter the insect prey base (Saunders *et al.*, 1991; Canaday, 1997; Stratford and Stouffer, 1999). Furthermore, insectivorous species may be more sensitive to habitat change due to a high degree of ecological specialisation (Kattan *et al.*, 1994; Bierregaard and Stouffer, 1997; Canaday, 1997; Renjifo, 1999). Species with specialised resource requirements, especially when the resource is unpredictable through time and space are usually vulnerable to extinction (Meffe and Carroll, 1997). Species that depend on resources that fluctuate seasonally or annually are prone to population variability, which predisposes them to a higher risk of extinction (Pimm *et al.*, 1988). It is known that tropical insects undergo seasonal variation in abundance and are more abundant and

readily available throughout the year than at higher latitudes (Wolda, 1978; Rautenbach *et al.*, 1988). Furthermore, there is less seasonal variation closer to the tropics than at higher latitudes (Lack, 1986; Rautenbach *et al.*, 1988). In the forests of southern Africa there is a decline in numbers of invertebrate species from autumn to winter (Koen and Crowe, 1987), and in KwaZulu-Natal, there is a predicted general lack of insects from forests during the dry winter months (Lawes, 1991). This seasonal fluctuation in the insect food base may explain the fact that insectivorous birds are more prone to extinction in forest patches of the Karkloof / Balgowan range than non-insectivorous species.

As a predictor of extinction proneness in birds of the Karkloof / Balgowan forest range, matrix tolerance is an important trait. The fact that most species (82%) are found in both the Balgowan and Gilboa complexes suggests that most Afromontane forest birds are in fact tolerant of modified matrix habitats, such as commercial pine plantations, surrounding the forest patches. Results from previous chapters imply that bird species in the Gilboa complex are able to disperse between indigenous forest fragments by moving through the forest-like plantation matrix. Similarly, Estades and Temple (1999) suggested that most forest bird species in the coastal Maule region of central Chile were using the surrounding pine plantation to disperse between indigenous forest patches.

The matrix surrounding indigenous forest patches does however have an influence over the way bird species have responded to forest fragmentation. In the Balgowan forest complex where the habitat matrix is natural grassland, while many bird species (50.9%) display a degree of resilience to fragmentation, a large proportion (29%) respond negatively and occur only in larger or medium-sized patches (i.e. patches > 80ha). Thus forest patch area is the dominant force influencing bird species response in the Balgowan complex, and patch size may be a predictor of extinction rate following fragmentation. This may be expected as this forest complex is naturally and historically fragmented, and the bird species' life histories have consequently been moulded and adjusted to the area of the forest fragments throughout time.

In the plantation dominated Gilboa complex, area effects seem less prominent as most bird species (67.3%) appear to be relatively unaffected by forest fragmentation, with only a small percentage (9.6%) responding negatively to a reduction in forest area. The plantation matrix is arguably facilitating the common

distribution of bird species across the forest size classes. This is supported by the absence of a species-area effect for this forest complex (Chapter 2). Furthermore species richness is lower in the larger forest patches of equivalent size in the Gilboa compared to the Balgowan (Chapter 2). Species response in the Gilboa complex may thus be a consequence of a more dominant landscape effect than patch area. Because species richness is essentially independent of area, bird species are not responding the way they would if area-determined processes were in place, as is the case for the Balgowan complex. In other words, the plantation matrix is effectively masking the bird's natural responses governed by their ecological and life history traits. The landscape matrix has become the dominant influence (instead of the species innate characteristics) over the way species are responding to changes in the landscape. For conservation purposes this makes predicting traits characteristic of species prone to extinction following fragmentation, difficult in forest patches surrounded by commercial plantation forestry.

The fact that most bird species appear to be relatively unaffected by forest fragmentation indicates that the bird assemblages in Afromontane Mistbelt forests of KwaZulu-Natal Province are by-and-large fragmentation adapted, as suggested by Lawes *et al.* (2000). The life history traits of a species are a product of natural selection and evolutionary forces, and thus represent a long-term interaction between the species demography and its environment (Hansen and Urban, 1992). Furthermore, species that are able to adjust their life histories to changing environmental conditions are the species that will persist (Begon *et al.*, 1990). Thus, varying conditions such as repeated climatic changes in the Quaternary (Diamond and Hamilton, 1980; Hamilton, 1988) might have filtered (*sensu* Balmford, 1996) Afromontane forest communities resulting in faunas whose life histories are adjusted to fragmentation (Lawes *et al.*, 2000). The resulting Afromontane forest bird community is consequently resilient, showing only slight response to further anthropogenic change in the landscape.

4.5 Conclusion

Bird species of the Karkloof / Balgowan forest range appear to be fragmentation adapted, and most species are resilient to further forest fragmentation and landscape change. Certain species are however more prone to local extinction than others. The major predictors of extinction risk are body size, abundance status, and feeding guild.

Forest patch area is the dominant force governing these traits in the natural Balgowan complex where larger species with low natural abundance and those that incorporate insects in their diet are most prone to local extinction. Thus, in order to conserve maximum bird diversity, including high-risk species, large forest fragments above 302ha (MCPS, Chapter 2) must be preserved. In the Gilboa complex the plantation matrix is masking the species natural responses to fragmentation making it difficult to predict which species are most at risk.

With a better understanding of the interaction between inherent species traits and environmental processes influencing species responses, it is possible to minimise the probability of extinction through habitat management that includes control over anthropogenic effects on the environment. I recommend that in the future, commercial forestry ventures must avoid naturally fragmented forest landscapes in order to preserve the natural processes that operated within the mosaic of natural habitats. The results of this chapter emphasise the importance of understanding landscape-scale processes in conserving forest bird communities, and a knowledge of ecological and life history traits is useful for predicting community level response to landscape change.

4.6 References

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Appendix 4.1. Incidence functions for 61 forest bird species in the Karkloof / Balgowan forest range, illustrating 5 types of responses to fragmentation. All forest patches, including the control, were used in the investigation. Forest dependent birds are indicated by *. Horizontal axes represent forest patch size classes (1: >200ha; 2: 80>200ha; 3: 10>80ha; 4: <10ha). Vertical axes represent the percentage of sites in each size class in which the species occurred.
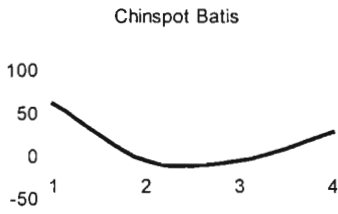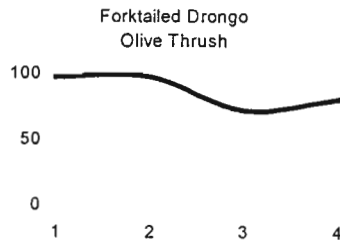
Category 1

Southern Black Tit

Black Sunbird

Redbilled Woodhoopoe

Category 2

*Barthroated Apalis
Blackeyed Bulbul
*Bleating Warbler
*Cape Batis
Cape Robin
Cape White Eye
*Collared Sunbird
Greater Dblcollared Sunbird
*Olive Woodpecker
Puffback
Sombre Bulbul
Southern Boubou
Terrestrial Bulbul
*Yellowthroated Warbler

*Tambourine Dove

Dusky Flycatcher

*Chorister Robin
Paradise Flycatcher

*Forest Canary

Cape Turtle Dove

Spotted Prinia

Hadeda Ibis

Redfronted Tinkerbarbet

Goldentailed Woodpecker

Category 2 cont.

Chinspot Batis

Thickbilled Weaver

Speckled Mousebird

Category 3

Redeyed Dove
Blackheaded Oriole

Rameron Pigeon

*Cinnamon Dove
*Starred Robin

*Knysna Lourie

Forktailed Drongo
Olive Thrush

Category 4

*Bluemantled Flycatcher

*Forest Weaver

*Olive Bush Shrike

*Grey Cuckooshrike

*Emerald Cuckoo

*Buffspotted Flufftail

Category 4 cont.

Little Sparrowhawk
*Crested Guineafowl

Yellowbreasted Apalis

*Crowned Eagle

Category 5

Gymnogene

*Scalythroated Honeyguide
*Squaretailed Drongo
*Yellowbellied Bulbul

*Narina Trogon

Steppe Buzzard

*Orange Thrush

Black Sparrowhawk
Spotted Flycatcher

Redchested Cuckoo
Black Cuckoo
Redwinged Starling

Rednecked Francolin
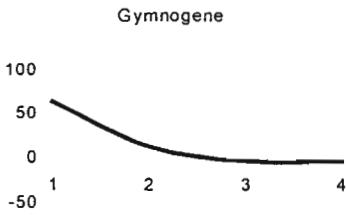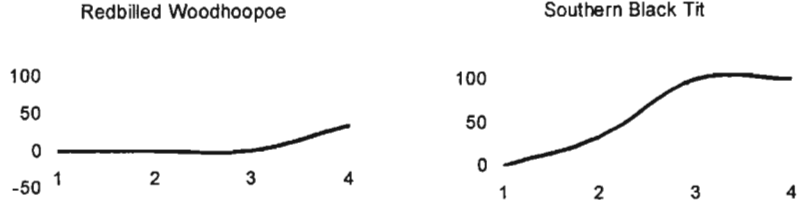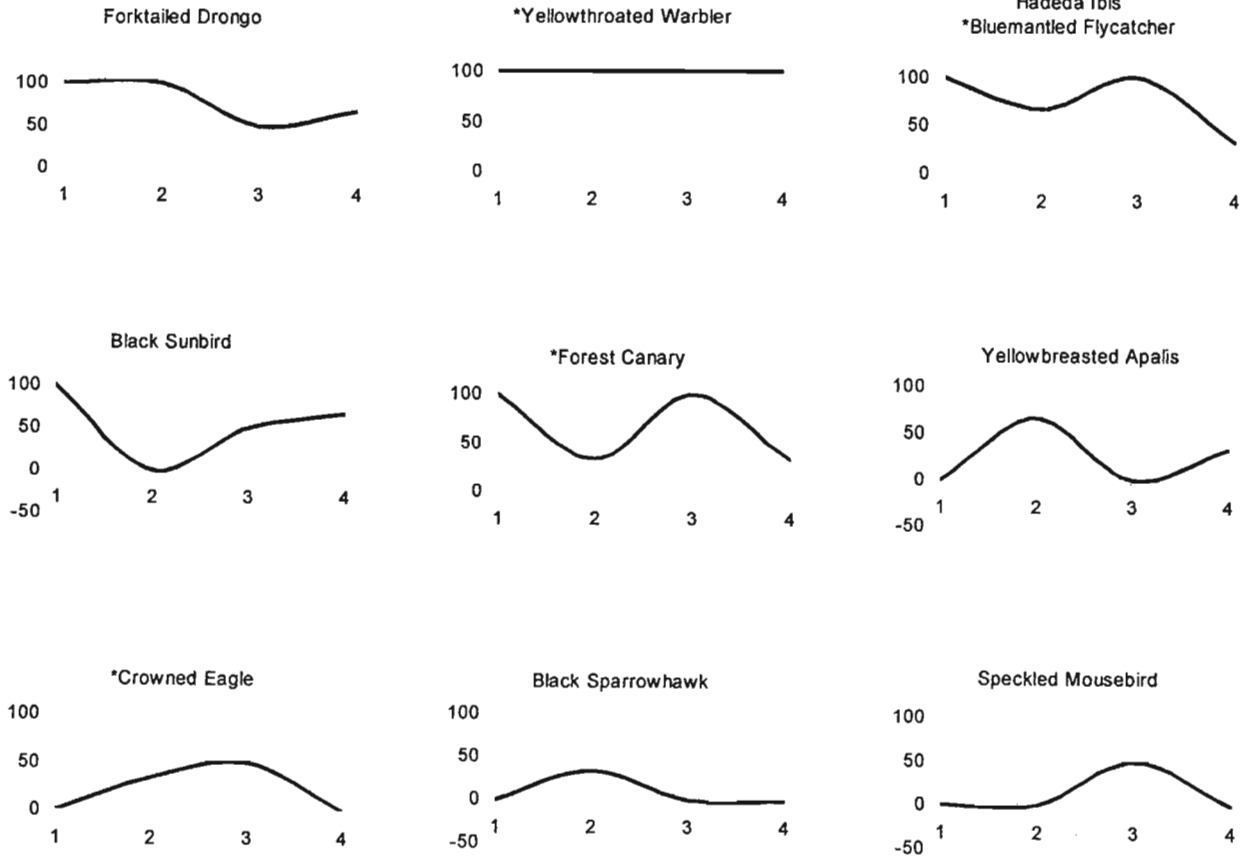
Appendix 4.2. Incidence functions for 55 forest bird species in the Balgowan forest complex (grassland matrix), illustrating 5 types of responses to fragmentation.

Category 1

Redbilled Woodhoopoe

Southern Black Tit

Category 2

*Barthroated Apalis
Blackeyed Bulbul
*Bleating Warbler
*Cape Batis
Cape Robin
Cape White Eye
*Chorister Robin
*Collared Sunbird
Greater Dblcollared Sunbird
Olive Thrush
*Olive Woodpecker
Puffback
Sombre Bulbul
Southern Boubou
Spotted Prinia
Terrestrial Bulbul
*Yellowthroated Warbler

Dusky Flycatcher
Paradise Flycatcher

Forktailed Drongo

Hadeda Ibis
*Bluemantled Flycatcher

Black Sunbird

*Forest Canary

Yellowbreasted Apalis

*Crowned Eagle

Black Sparrowhawk

Speckled Mousebird

Category 3

Redeyed Dove
Blackheaded Oriole
Cape Turtle Dove
*Cinnamon Dove
*Starred Robin

*Olive Bush Shrike
Rameron Pigeon
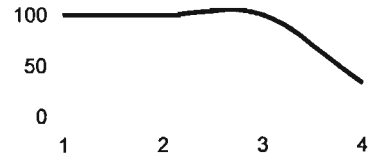
*Knysna Lourie
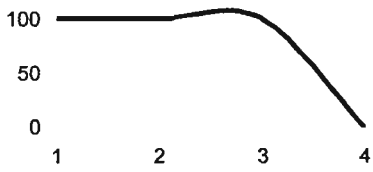
*Forest Weaver
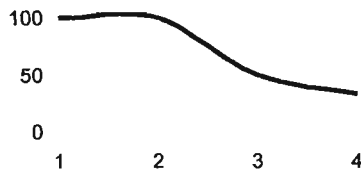
Category 4

Redfronted Tinkerbarbet
*Grey Cuckooshrike
*Crested Guineafowl
Little Sparrowhawk
*Emerald Cuckoo
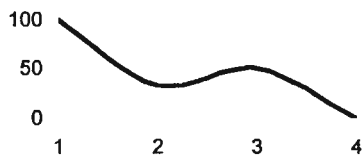
Chinspot Batis
Steppe Buzzard
Thickbilled Weaver

Category 5

*Buffspotted Flufftail
Goldentailed Woodpecker
Gymnogene
Redwinged Starling
*Scalythroated Honeyguide
*Squaretailed Drongo
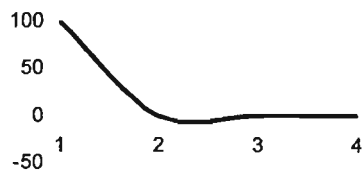
*Narina Trogon
Spotted Flycatcher
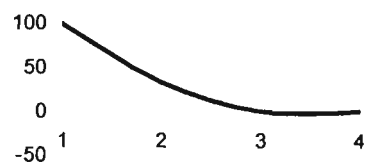
Appendix 4.3. Incidence functions for 52 forest bird species in the Gilboa forest complex (commercial plantation matrix), illustrating 5 types of responses to fragmentation.
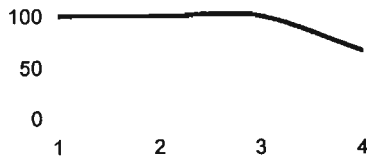
Category 1

Goldentailed Woodpecker
Black Sunbird

Spotted Prinia

Chinspot Batis
Hadeda Ibis

Category 2

*Barthroated Apalis
Blackeyed Bulbul
Blackheaded Oriole
*Bleating Warbler
*Cape Batis
Cape Robin
Cape White Eye
*Collared Sunbird
Forktailed Drongo
Greater Dblcollared Sunbird
*Olive Woodpecker
Paradise Flycatcher
Puffback
Redeyed Dove
Sombre Bulbul
Southern Boubou
Terrestrial Bulbul
*Yellowthroated Warbler

Southern Black Tit

*Bluemantled Flycatcher
*Chorister Robin
Dusky Flycatcher

*Forest Canary

*Olive Bush Shrike

Rednecked Francolin
*Crowned Eagle

*Orange Thrush

Cape Turtle Dove

*Buffspotted Flufftail

Speckled Mousebird

*Tambourine Dove

Category 2 cont.

*Crested Guineafowl
*Narina Trogon
Gymnogene
Little Sparrowhawk

Category 3

*Forest Weaver
*Knysna Lourie
Rameron Pigeon
*Cinnamon Dove
*Starred Robin

Olive Thrush

*Emerald Cuckoo

Category 4

Yellowbreasted Apalis

Redfronted Tinkerbarbet

*Grey Cuckooshrike

Category 5

Black Sparrowhawk
*Yellowbellied Bulbul

Appendix 4.4. Ecological and life history traits of forest bird species recorded in the Karkloof / Balgowan forest range. Information on morphology, reproduction, habitat preference, diet, and distribution is provided (see text for categories). Systematic information is also provided.

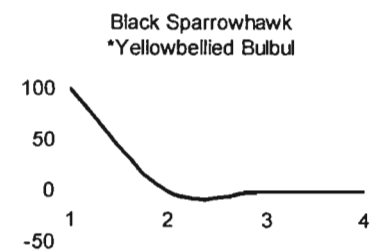| Robert's #	Common Name	Scientific Name	Order	Family	NH	NS	CS	BC	AF	BS	FG	FL	GP	FD	MP	SS	RS	HM
94	Hadeda Ibis	*Bostrychia hagedash*	Ciconiiformes	Plataleidae	5	6	3	1	3	1262	6	5	2	1	4	1	1643	2
141	Crowned Eagle	*Stephanoaetus coronatus*	Falconiformes	Accipitridae	17.5	4	2	1	2	3637	7	2	1	2	4	4	362	2
157	Little Sparrowhawk	*Accipiter minullus*	Falconiformes	Accipitridae	13	6	2	1	2	87.3	7	2	1	1	4	5	812	2
158	Black Sparrowhawk	*Accipiter melanoleucus*	Falconiformes	Accipitridae	13.5	6	3	1	3	699.3	7	2	1	1	4	5	472	2
169	Gymnogene	*Polyboroides typus*	Falconiformes	Accipitridae	15	6	2	1	2	725.2	7	2	1	1	4	2	12287	2
198	Rednecked Francolin	*Francolinus afer*	Galliformes	Phasianidae	4.5	7	5.5	1	5.5	674.7	5	5	2	1	4	3	250	1
204	Crested Guineafowl	*Guttera pucherani*	Galliformes	Numididae	0	7	6.5	1	6.5	1315	5	5	2	2	4	5	124	2
218	Buffspotted Flufftail	*Sarothrura elegans*	Gruiformes	Rallidae	0	2	4	2	8	42.4	4	5	1	2	4	4	169	2
350	Rameron Pigeon	*Columba arquatrix*	Columbiformes	Columbidae	7.5	6	1	4	4	421.7	1	3	2	1	2	3	460	2
352	Redeyed Dove	*Streptopelia semitorquata*	Columbiformes	Columbidae	5	6	2	4	8	246.3	1	5	1	1	4	2	2178	2
354	Cape Turtle Dove	*Streptopelia capicola*	Columbiformes	Columbidae	3.5	6	2	4	8	152.9	2	5	1	1	3	1	4111	2
359	Tambourine Dove	*Turtur tympanistria*	Columbiformes	Columbidae	2.5	6	2	3	6	74.9	5	5	1	2	4	4	408	1
360	Cinnamon Dove	*Aplopelia larvata*	Columbiformes	Columbidae	3	6	2	2	4	157	5	5	1	2	4	4	215	2
370	Knysna Lourie	*Tauraco corythaix*	Musophagiformes	Musophagidae	4.5	6	2	3	6	310	2	1	2	2	4	4	263	2
377	Redchested Cuckoo	*Cuculus solitarus*	Cuculiformes	Cuculidae	5	4	1	2	2	72.4	4	3	1	1	1	2	1238	3
378	Black Cuckoo	*Cuculus clamosus*	Cuculiformes	Cuculidae	2	4	1	3	3	87.2	6	2	1	1	1	4	1183	3
384	Emerald Cuckoo	*Chrysococcyx cupreus*	Cuculiformes	Cuculidae	0.8	2	1	2	2	34.2	2	2	1	2	1	4	277	2
424	Speckled Mousebird	*Colius striatus*	Coliiformes	Collidae	3	4	3	4	12	51.1	5	1	2	1	4	2	1156	2
427	Narina Trogon	*Apaloderma narina*	Trogoniformes	Trogonidae	4	1	3	2	6	65.5	5	2	1	2	4	5	323	2
452	Redbilled Woodhoopoe	*Pheoniculus purpureus*	Coraciiformes	Phoeniculidae	4.5	1	3.5	3	10.5	70.8	3	3	2	1	4	2	1704	3
469	Redfronted Tinkerbarbet	*Pogoniulus pusillus*	Piciformes	Lybiidae	1.5	1	3	1	3	10	2	3	1	1	4	4	241	2
475	Scalythroated Honeyguide	*Indicator variegatus*	Piciformes	Indicatoridae	7	1	1.5	2	3	48.6	5	3	1	2	4	5	200	3
483	Goldentailed Woodpecker	*Campethera abingoni*	Piciformes	Picidae	1.5	1	3	2	6	70.6	6	3	1	1	4	4	1368	2
488	Olive Woodpecker	*Mesopicos griseocephalus*	Piciformes	Picidae	7	1	2.5	1	2.5	46.1	6	1	1	2	4	4	274	2
540	Grey Cuckooshrike	*Coracina caesia*	Passeriformes	Campephagidae	17.5	4	2	1	2	97	6	3	1	2	3	5	188	2
541	Forktailed Drongo	*Dicrurus adsimilis*	Passeriformes	Dicruridae	5	5	3	2	6	40	5	2	1	1	4	1	3192	2
542	Squaretailed Drongo	*Dicrurus ludwigii*	Passeriformes	Dicruridae	5	4	3	1	3	30	3	2	1	2	4	4	99	3
545	Blackheaded Oriole	*Oriolus larvatus*	Passeriformes	Oriolidae	7.5	4	3	2	6	63.6	5	3	1	1	4	2	1387	2
554	Southern Black Tit	*Parus niger*	Passeriformes	Paridae	2.5	1	4.5	2	9	21.2	6	3	1	1	4	2	1408	2
568	Blackeyed Bulbul	*Pycnonotus barbatus*	Passeriformes	Pycnonotidae	3	4	3	4	12	37.2	5	1	1	1	3	1	1490	2
569	Terrestrial Bulbul	*Phyllastrephus terrestris*	Passeriformes	Pycnonotidae	1.25	4	2	1	2	29.9	5	4	2	1	4	4	752	2
572	Sombre Bulbul	*Andropadus importunus*	Passeriformes	Pycnonotidae	2	4	2	3	6	31.8	5	1	1	1	4	2	604	2
574	Yellowbellied Bulbul	*Chlorocichla flaviventris*	Passeriformes	Pycnonotidae	2.5	4	2	3	6	41.3	5	1	2	2	4	4	630	1
577	Olive Thrush	*Turdus olivaceus*	Passeriformes	Turdidae	5	4	2	2	4	74	5	5	1	1	4	2	1196	2
579	Orange Thrush	*Zoothera gurneyi*	Passeriformes	Turdidae	1.5	4	2	1	2	59.4	5	5	1	2	4	5	44	1
598	Chorister Robin	*Cossypha dichroa*	Passeriformes	Turdidae	5	4	3	1	3	40.3	2	4	1	2	3	3	215	2
601	Cape Robin	*Cossypha caffra*	Passeriformes	Turdidae	0.75	4	2.5	2	5	29.1	5	4	1	1	3	2	1373	2
606	Starred Robin	*Pogonocichla stellata*	Passeriformes	Turdidae	0	3	3	1	3	20.4	2	4	1	2	4	3	153	2
644	Yellowthroated Warbler	*Phylloscopus ruficapillus*	Passeriformes	Sylviidae	0	3	3	1	3	7.7	6	3	1	2	4	4	186	2
645	Barthroated Apalis	*Apalis thoracica*	Passeriformes	Sylviidae	1.5	2	3	2	6	10.3	6	1	1	2	4	2	968	2
648	Yellowbreasted Apalis	*Apalis flavida*	Passeriformes	Sylviidae	2	2	3	3	9	7.6	5	1	1	1	4	5	597	2
657	Bleating Warbler	*Camaroptera brachyura*	Passeriformes	Sylviidae	0.8	2	3	3	9	10.1	6	4	1	2	4	2	1463	2
686	Spotted Prinia	*Prinia hypoxantha*	Passeriformes	Sylviidae	0.5	2	4	2	8	11	6	4	1	2	4	2	1005	2
690	Dusky Flycatcher	*Muscicapa adusta*	Passeriformes	Muscicapidae	4	4	2	2	4	10.7	2	4	1	1	3	3	566	2
700	Cape Batis	*Batis capensis*	Passeriformes	Muscicapidae	2.5	4	2	2	4	11.7	6	1	1	2	4	4	508	2
701	Chinspot Batis	*Batis molitor*	Passeriformes	Muscicapidae	3	4	2	3	6	11	6	3	1	1	4	2	1556	2
708	Bluemantled Flycatcher	*Trochocercus cyanomelas*	Passeriformes	Muscicapidae	1.5	4	2	1	2	10.1	6	3	1	2	4	5	230	2
710	Paradise Flycatcher	*Terpsiphone viridus*	Passeriformes	Muscicapidae	3	4	3	2	6	14.4	6	3	1	1	1	2	1610	2
736	Southern Boubou	*Laniarius ferrugineus*	Passeriformes	Malaconotidae	2	4	2.5	3	7.5	59.5	5	4	1	1	4	2	814	2
740	Puffback	*Dryoscopus cubla*	Passeriformes	Malaconotidae	5.5	4	2.5	3	7.5	27.6	6	3	1	1	4	2	1485	2
750	Olive Bush Shrike	*Telophorus olivaceus*	Passeriformes	Malaconotidae	3	5	2	3	6	33.7	2	3	1	2	4	4	332	2
769	Redwinged Starling	*Onychognathus morio*	Passeriformes	Sturnidae	15	4	3	3	9	128.3	5	1	1	1	4	2	1500	3
785	Greater Doublecollared Sunbird	*Nectarinia afra*	Passeriformes	Nectariniidae	2.5	2	2	3	6	10.9	3	1	1	1	4	4	488	2
792	Black Sunbird	*Nectarinia amethystina*	Passeriformes	Nectariniidae	3.5	2	2	3	6	12.8	3	1	1	1	2	2	1161	2
793	Collared Sunbird	*Anthreptes collaris*	Passeriformes	Nectariniidae	1.75	2	2.5	2	5	7.8	3	1	1	2	4	3	424	2
796	Cape White Eye	*Zosterops pallidus*	Passeriformes	Zosteropidae	2	4	2.5	3	7.5	11.8	5	1	2	1	4	1	1591	2
807	Thickbilled Weaver	*Amblyospiza albifrons*	Passeriformes	Ploceidae	1.5	2	3	2	6	45.7	5	3	2	1	3	4	342	3
808	Forest Weaver	*Ploceus bicolor*	Passeriformes	Ploceidae	5	2	3	1	3	35	5	3	2	2	4	5	175	2
873	Forest Canary	*Serinus scotopus*	Passeriformes	Fringillidae	3.45	4	3	3	9	15.5	1	3	1	2	4	5	215	2

NH = nest height; NS = nest structure; CS = clutch size; BC = breeding cycles; AF = annual fecundity; BS = body size; FG = feeding guild; FL = foraging level; GP = groups / pairs; FD = forest dependence;
MP = movement patterns; SS = species status; RS = range size; HM = habitat matrix

CHAPTER 5

Summary: Conservation and Management

5.1 Implications for conservation: important findings

In the Karkloof / Balgowan forest range insularisation has led to species loss (relaxation) from habitat remnants. Forest fragments support fewer bird species than comparably sized patches of contiguous mainland forest.

1. Small forest fragments within the natural grassland matrix (Balgowan complex) have fewer species per unit area than larger forest fragments, while in forests in the plantation matrix (Gilboa complex), no island-effect is detectable and it appears that forest patches are converging on the same species richness, regardless of forest size.

2. The relatively low rate of change in species number across the Gilboa forest patches suggests that the plantation matrix may equilibrate opportunities for dispersion for some species, by creating a closed environment and providing forest-like cover for arboreal birds to move between indigenous forest patches. Consequently, the plantation matrix is facilitating a higher avian diversity in smaller patches that would ordinarily have experienced a decrease in diversity following fragmentation. In addition, larger patches in the Gilboa complex have fewer species when compared to forests of similar area in the Balgowan complex. Hence, the overriding effect of the plantation matrix is to reduce species numbers in the complex as a whole.

3. Forest patch area-dependent density compensation is evident in forest fragments within natural grassland (Balgowan), and bird assemblages are approaching saturation if not already saturated with species. The absence of density compensation in fragments of the plantation dominated Gilboa complex implies that bird assemblages are not saturated. This may be symptomatic of the effect of the surrounding matrix on bird species density, where the forest-like plantation may be acting as a "dispersion medium," facilitating the movement of individuals between forest patches. Species packing in this forest complex is therefore not evident.

4. Bird species assemblages in forest fragments within natural grassland are characterised by a non-random species distribution pattern where patch-area dependent processes are dominant, and the loss of bird species from fragments follows a predictable and deterministic sequence. Nestedness is attributable to differential extirpation: each bird species tending to occur in the subset of forest patches large enough to prevent extirpation.

5. The sequence of species loss from forest patches surrounded by commercial plantation forestry is not as predictable, where a random yet prominent colonisation process exists. Because commercial plantations provide a suitable habitat and cover for movement of forest birds, colonisation of both distant and small indigenous forest patches has been possible, reducing the effects of area-dependent extinction in these forest patches.

6. Extinction rate is more predictable than extinction sequence. This is indicative of a dominant landscape effect determining bird species distribution in the forest complexes. In the Balgowan complex forest patch size is the major predictor of bird species distribution, while the nature of the matrix has the dominant influence over bird species distribution patterns in the Gilboa complex.

7. At the landscape-level it is clear that the nature of the matrix affects avifaunal diversity and distribution in forest patches, and plantations have the capacity to significantly alter bird assemblage structure and composition in indigenous forest patches. Consequently, for the conservation of indigenous forest and the management of commercial plantation, forest fragments must be considered as integrated parts of a complex landscape mosaic of different habitat types.

8. While bird species of the Karkloof / Balgowan forest range appear to be fragmentation adapted and resilient to further fragmentation and landscape change, certain species are more prone to local extinction than others. The major predictors of extinction risk are body size, abundance status, and feeding guild.

9. Forest patch area is the dominant force governing ecological and life history traits in the natural Balgowan complex where larger bird species with low natural abundance and an insectivorous diet are most prone to local extinction. In the Gilboa complex the nature of the plantation matrix appears to be masking the species natural responses to area-dependent processes, making it difficult to predict what characteristics place bird species most at risk.

10. The results of this study emphasise the importance of understanding landscape-scale processes, and knowledge of ecological and life history traits proves valuable for predicting community level responses to landscape change, for forest bird species.

5.2 Management recommendations

The dominant theme throughout this study is the importance of forest area to bird species in Afromontane Mistbelt Mixed *Podocarpus* forests of KwaZulu-Natal. In terms of a management strategy, clearly our priority remains to conserve the largest, intact forest units. The preservation of forest bird assemblage structure and diversity in the region requires the protection of forest fragments within natural grassland of a minimum critical patch size (MCPS = 302ha) and larger. Island effects become negligible for bird species in forests above this size, while below this size bird species are lost from forest fragments. In the plantation dominated Gilboa complex no effective forest patch size constraint exists (and therefore no MCPS exists), and this is a consequence of the effect of the plantation matrix on species richness in patches.

If species distributions within naturally fragmented habitat exhibit patterns of pronounced nestedness, then highly predictable extinction sequences are implied, and thus again it is important to conserve the largest intact land units so that overall species richness is preserved. This conservation requirement arises from understanding that the preservation of any number of small patches, if these have converged to the same community representation, will not support a species richness equivalent to that of a single large patch. In addition, those species more prone to local extinction through a loss of forest area will not be preserved in small patches or a collection of small patches, as these species tend to occur only in forests of more than 80ha in area.

If the "climatic filtering" hypothesis is correct, then it is a matter of considerable concern that, in spite of the putative assemblage resilience to insularisation, large forests surrounded by plantation nevertheless show notable species relaxation. One interpretation is that the effect of commercial plantation forestry on species richness is proportionately greater than the effects of climatic extinction filtering. In fact, the effect of commercial plantation on species loss is probably much greater than suggested by the shallow species-area slope for forests in

the Gilboa. Nevertheless, considering that commercial pine plantations are a transient landscape element, one would be best advised to manage forests within this matrix type using the same principles that apply to forests within the natural grassland matrix.

With a better understanding of the interaction between inherent species traits and environmental processes influencing species responses, it is possible to minimise the probability of extinction through habitat management that includes control over anthropogenic effects on the environment. I recommend that in the future, commercial forestry ventures must avoid naturally fragmented forest landscapes or manage plantations in a way that preserves the natural processes that operated within the mosaic of natural habitats and affect forest bird communities.