

The biogeography of forest birds in the
Limpopo Province, South Africa

Dale Forbes

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Into the wilderness of the forests I go

in search of intellectual answers,

and passing through it's shade

I return having found much more,

and part of it never to show

Magoebaskloof, August 2002

Preface

This study was carried out in the Forest Biodiversity Programme, School of Botany and Zoology, University of Natal, Pietermaritzburg, between December 2000 and January 2003. The project was supervised by Professor Michael J. Lawes.

This study represents original work by the author and has not been submitted in any form to another university. The use of others' work has been duly acknowledged.

Chapters two and three have been prepared for journal submission and have been written to stand-alone. As a result, there is some repetition between chapters.

Dale Forbes

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Summary

Forest assemblage composition is determined by local ecological (e.g. patch area, species interactions), landscape (e.g. patch connectivity) and regional (e.g. historical change in forest distribution) processes. I investigated the relative effect of these processes on bird and frog assemblage composition in two isolated archipelagos of Afrotropical forest in the Limpopo Province.

The linear relationship between local and regional species diversity suggests that forest bird assemblages in the Limpopo Province are unsaturated. In addition, 66% of bird species and 42% of frog species in southern African forests are generalist species (i.e., forest associated as opposed to forest dependent), suggesting that matrix species have invaded forest assemblages. I thus argue that forest bird and frog assemblage composition is primarily determined by regional (historical) processes and that local ecological processes play a relatively minor role.

Forests in the Limpopo Province were eliminated by major climatic changes during the Quaternary with major forest expansion only in the last 6000 years. Limpopo Province forest assemblages have thus established fairly recently. No forest dependent frogs and one forest dependent bird have established in the Limpopo Province forests from the relatively proximate forests in eastern Zimbabwe. This suggests that the Limpopo River catchment has acted as a significant barrier to the dispersal of forest vertebrate faunas. Cluster analyses showed that the forest bird and frog assemblages are essentially Afrotropical and South African in origin with all forest dependent frogs and 97% of forest dependent birds occurring in the KwaZulu-Natal scarp forests. In addition the most important environmental gradient of change in the southern African forest bird faunas was the geographical distance from northern KwaZulu-Natal. This gradient is congruent with a major northward radiation of faunas from the KwaZulu-Natal scarp into the Limpopo Province. As a result the Limpopo Province forests have low biodiversity values compared to the KwaZulu-Natal scarp because forest frog and bird faunas are largely derived from the latter region. However, the importance of the Limpopo Province forests lies in their protection of threatened vertebrates as well as in providing landscape heterogeneity and ecological services to the surrounding matrix.

Soutpansberg forest bird assemblages appear to be more robust and resilient and comprise a significantly greater proportion of forest associated species than those of the Limpopo Province Drakensberg. This is likely to be a consequence of more severe climatic extinction filtering of these faunas caused primarily by the proximity of the Soutpansberg forests to the arid Limpopo valley during the development of these forests. Consequently, regional and historical processes have played a relatively greater role in determining forest bird assemblages in the Soutpansberg than in the Limpopo Province Drakensberg and species richness in the former region was not significantly affected by local ecological processes (including forest area, isolation and habitat heterogeneity). Forest area and habitat heterogeneity did, however, affect forest bird species richness and abundance in the Limpopo Province Drakensberg where the relatively lower importance of regional processes (compared to the Soutpansberg) has combined with anthropogenic disturbance of smaller forests to increase the influence of local ecological processes. However, the role of local processes in determining local species richness is likely to increase in both archipelagos if the current rates of anthropogenic change and disturbance to forests are sustained.

Forests greater than 138 ha (minimum critical patch size) are needed to avoid an island effect on bird species richness in the Limpopo Province Drakensberg. However, the long-term conservation of vertebrate assemblages in Limpopo province forests depends upon the successful conservation of evolutionary and landscape processes. This can best be achieved by maximising forest connectivity and landscape heterogeneity through the protection of both riparian corridors and forests of all sizes. The maintenance of historical dispersal routes, in particular connectivity along the escarpment with the scarp forests of KwaZulu-Natal, is important. This would require the protection of forests on the KwaZulu-Natal scarp and along the entire northern Drakensberg escarpment.

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Chapter 1

Introduction

This study investigates the relative influences of local and regional (historical) determinants of forest vertebrate assemblage composition in the Limpopo Province, South Africa. Key processes that act on patch, landscape and historical levels are highlighted.

Indigenous forest is the smallest biome in southern Africa, covering only 0.57% of the land surface area (Low and Rebelo 1996). South African forests support the greatest per-area diversity of threatened vertebrates of any habitat type in the region (Castley 1997). Despite the obvious conservation value of forests, approximately 44% of South African indigenous forests have been transformed while only about 18% are conserved (Low and Rebelo 1996).

The indigenous Afrotropical forests of the Limpopo Province are distributed along two mountain ranges, namely; the west-east orientated Soutpansberg and the north-south Drakensberg escarpment. These two forest archipelagos are about 100 km apart and lie on either side of the Tropic of Capricorn. The Limpopo Province is dominated by various forms of bushveld (Low and Rebelo 1996) and supports about 5200 ha and 8100 ha of forest in the Soutpansberg and Limpopo Province Drakensberg, respectively.

Very little is known of the faunal composition and the local ecological processes that maintain forest biodiversity in the Limpopo Province. In addition, an understanding of the history of the forests and the patterns that have resulted is required to better understand the regional processes that have shaped, and continue to shape, forest biodiversity in the region. The Limpopo Province forests represent an interesting biogeographical region delimited to the north by the Limpopo River valley, which in all likelihood has acted as a significant barrier to the southward radiation of species from tropical regions into South Africa (Poynton 1961; Lawes 1990; Clancey 1994). As a result, the forest faunas in the Limpopo Province appear to have been drawn from Afrotropical assemblages within South Africa and it has been argued that these faunas represent a northward radiation of taxa into the Limpopo Province (Clancey 1975; Lawes 1990; Clancey 1994). This study examines the distribution of

forest vertebrates and investigates the putative local and regional (historical) controls on forest vertebrate assemblage composition. This understanding is used to develop conservation and management guidelines.

The Department of Water Affairs and Forestry (DWAF) manages most of the indigenous forests in the Limpopo Province. To improve their policy guidelines for forest conservation, the Conservation Forestry section of DWAF initiated biodiversity assessments within the region. This study investigates vertebrate assemblages in the Limpopo Province forests and is aligned with two other concurrent studies that focus on invertebrate (Swaye in prep.) and plant assemblages (Geldenhuys and Venter 2002). Birds, mammals and amphibians were sampled in this study but this dissertation has focused on birds because of the ease of sampling and their species richness. The local distributions of mammals and amphibians were not investigated because their species richness in the study forests was low. However, the contemporary southern African distribution of amphibians is used as supporting evidence for historical radiation routes of forest vertebrates in southern Africa. In addition, I examine the population status of all forest vertebrates in the Limpopo Province, placing emphasis on threatened species, in order to highlight the conservation importance of the Limpopo Province forests.

The local and regional determination of assemblage composition

The distribution of species in patches can be explained at two spatial scales by looking at the effects of both local and regional processes (Cornell 1993; Lawes *et al.* 2000). The most obvious responses to processes are at a local scale where factors such as habitat features, competition, predation and niche requirements either allow for or exclude a species from a forest (Schluter and Ricklefs 1993a). These factors represent deterministic responses to ecological processes. A larger-scale perspective of species distributions, operating at a regional level, can also be applied and takes into account historical processes (Caley and Schluter 1997). These include the overwhelming effect of climate change on habitat and species distributions (Schluter and Ricklefs 1993b). The regional perspective is that the complement of species found in an area is a consequence of historical changes in habitat and species distributions such that past processes limit contemporary landscape species pools (Cornell 1993; Schluter and Ricklefs 1993a). The number of species in an assemblage is derived from the landscape species pool and is a subset of this

species pool. A local assemblage may be a very small subset of the species pool, and all other things being equal, this has been taken to imply low levels of interaction among species in a local assemblage, i.e. assemblages are unsaturated (Cornell 1993). These assemblages are typically regarded as unsaturated with species. Without assemblage saturation it is not possible to invoke a serious role for deterministic local processes (Cornell and Lawton 1992; Cornell 1993) and unsaturated assemblages are likely to be a consequence of regional (historical) processes (Cornell 1993; Srivastava 1999). Thus, tests of assemblage saturation provide an indication of the relative importance of local versus regional processes in the determination of assemblage composition (Cornell 1993). In this study I investigate the likelihood of assemblage saturation in southern African forest vertebrate assemblages.

One standard test of assemblage saturation examines the nature of the relationship between local and regional species richness (Cornell and Lawton 1992; Srivastava 1999). The premise of local-regional analyses is that in saturated assemblages ecological processes maintain a 'ceiling' in local species richness such that, above a certain level, the local species richness does not increase with an increase in regional species richness (Cornell 1993; Caley and Schluter 1997). On the other hand, in unsaturated assemblages, deterministic processes do not limit local species richness and the number of species in an assemblage is limited only by the size of the species pool (Srivastava 1999). The assemblage composition of non-interactive assemblages is thus largely a consequence of the landscape species pool and the regional scale processes that determine the composition of the species pool (Cornell and Lawton 1992).

In species-saturated assemblages competition for resources is high such that the density of taxa are constrained by competition (MacArthur *et al.* 1972). Competition theory predicts that the removal of species from saturated assemblages would result in the competitive release of the remaining taxa such that a species' density is greatest in species-poor assemblages (density compensation, Wright 1980; Schoener 1988). As a result taxa in species-poor assemblages would be less constrained by competition and would thus be found at greater densities (Ås 1985; Cornell and Lawton 1992; Oberdorff *et al.* 1998). I use density compensation as

another test of assemblage interaction and to evaluate the relative importance of local processes in the determination of assemblage composition.

If assemblages are unsaturated then there should be empty niches (Cornell 1993). The availability of empty niches may allow matrix and generalist species to invade and establish themselves in forest assemblages (Beier *et al.* 2002). Thus, the relative importance of matrix and generalist species in forest assemblages provides an indirect test of assemblage saturation. In addition, obvious competitive exclusion (e.g., where closely related species display a checkerboard distribution among patches) may be indicative of assemblage saturation (Cornell 1993).

Forest assemblage conservation and management

The conservation and management of forests has generally been focussed on local, ecological processes and effects such as patch size, shape and habitat composition (Warburton 1997; Boutin and Herbert 2002). Management and conservation actions at a local (patch) level tend to focus on the maximisation of local species richness but may act at the expense of the species and communities most in need of protection at the regional level (Noss 1983). In addition, management for local diversity may result in the long-term loss of species on a regional level (Noss 1983, 2002).

Recently, however, there has been a shift towards incorporating effects at a landscape-level into conservation assessments (Recher *et al.* 1987; Boutin and Herbert 2002; Lindenmayer *et al.* 2002). This approach emphasises habitat patches within a landscape context so that a mosaic of habitat patches are conserved (Recher *et al.* 1987). Such a mosaic would be founded on the conservation of patches of different sizes, shapes and isolation and, representing a range of habitat features (Noss 1983). At even larger scales, the perpetuation of regional and historical processes involves the maintenance of evolutionary processes and radiation routes (Lindenmayer 2000). The preservation of a heterogeneous landscape would help maintain the regional processes of immigration and colonization with individuals moving between patches both within and between archipelagos (Lindenmayer *et al.* 2002). By ensuring that these regional processes still function, it may be possible to ensure that species in assemblages are free to continue to evolve and respond to environmental change. For unsaturated assemblages, dominated by regional processes, it is important to include the entire region in conservation actions, not just focussing on the deterministic processes that

may affect habitat patches (Noss 1983; Lindenmayer 2000; Lindenmayer *et al.* 2002; Noss 2002). However, the maintenance of regional scale processes without local patch protection is futile, because anthropogenic influences (such as habitat destruction and alteration) can completely overshadow any gains made in regional conservation (Noss 2002).

Forest history and faunal radiation in southern Africa

Species diversity may be affected by at least seven types of processes, four of which operate at a regional level (Schluter and Ricklefs 1993a). Firstly, allopatric speciation increases local endemism and is affected by dispersal barriers, climates and the arrangement of habitats. Secondly, dispersal barriers inhibit the exchange of taxa between regions. Topographical features often act as barriers to dispersal, but unique events (such as climate change e.g., hypothermal periods) may also provide conditions that inhibit the exchange of taxa. Thirdly, these unique events may lead to episodes of extinction where taxa are selectively filtered (*sensu* Balmford 1996) from assemblages. Lastly, the ability of a taxon to diversify ecologically may also affect the species diversity in a habitat if a taxon is able to invade a novel habitat or niche. Chapter 2 investigates the effect of these regional-scale processes on the landscape species pool in the Limpopo Province forests. In particular I focus on the effect of late Quaternary climate changes on forest distribution and their influence on local forest assemblage structure and composition.

Southern African faunal distribution patterns and assemblage composition have been shaped by successive glacial and inter-glacial periods (Hamilton 1981; Deacon and Lancaster 1988; Lawes 1990; Lawes *et al.* 2000). Historical processes, as opposed to simple climatic controls, have been fundamental in shaping and determining African bird assemblages (Crowe and Crowe 1982). Two major forest radiation events in the last 18 000 years have determined the regional species pools in southern African forests (Lawes 1990). The first of these radiations is associated with the post-LGM radiation of Afrotemperate faunas from South African refugia, particularly on the KwaZulu-Natal scarp and the Eastern Cape escarpment (Lawes 1990). In addition, minor refugia in the Western Cape ensured the persistence of a distinct South African Afrotemperate amphibian fauna (Poynton 1961; Poynton and Boycott 1996). An Afrotemperate bird fauna is not as recognizable as in the amphibians (Poynton 1961), but forest bird assemblages in the Limpopo Province

appear to be essentially South African and of Afrotropical origin (Clancey 1975). The second major radiation event was the relatively recent radiation of coastal Afrotropical faunas into South Africa (Lawes 1990). This radiation was associated with the southward expansion of Indian Ocean coastal belt forests out of East African refugia (Diamond and Hamilton 1980; Burgess and Clarke 2000); with initial establishment on the Maputaland coastal plain (Eeley *et al.* 1999). Chapter 2 examines the regional determinants of assemblage composition and those radiation routes that may have determined the regional species pool in the Limpopo Province.

Local determinants of assemblage composition

While regional-scale analyses highlight processes that determine the landscape species pool, analyses at a local scale examine those factors that determine the finer-scale distributions of species (Williams *et al.* 2002). In Chapter 3, I evaluate the efficacy of a variety of ecological and environmental explanatory variables – including patch area, isolation and habitat heterogeneity – in accounting for the distribution and abundance of forest birds in the two Limpopo Province forest archipelagos. From analyses of these deterministic factors, I propose management recommendations that assist in optimising the conservation of vertebrate assemblages in the Limpopo Province forests (Chapter 4).

Forest area is arguably the most important local determinant of assemblage composition and species abundance (Ambuel and Temple 1983; Blake and Karr 1984; Freemark and Merriam 1986; Van Dorp and Opdam 1987; Rolstad 1991; Wethered 2001). Species-area curves describe the increase in species richness with increasing patch size and may be one of the most general patterns in ecology (Lomolino 2000). Preston (1962) found that the general slope of the species-area relationship was approximately 0.26 on a power function (slope = z when Species richness = $c\text{Area}^z$). However, Connor and McCoy (1979) suggest that a slope of 0.26 may arise as a statistical artefact of linear regression. Nevertheless, even under the strict set of constraints employed by Connor and McCoy (1979), observed slopes do depart from expected values (Sugihara 1980). While species-area relationships were first examined using oceanic islands, this approach has subsequently been widely applied to insular 'mainland' habitats where habitat islands are embedded in a matrix of unsuitable habitat (Hanski and Gilpin 1997). Slopes for mainlands are

typically not as steep as those for islands with z values predicted to be between 0.12 and 0.19 for insular habitats (island values = 0.2-0.4, MacArthur and Wilson 1967).

The equilibrium theory of island biogeography (IBT; MacArthur and Wilson 1963, 1967) characterises island species richness according to the area effect and the distance to the nearest mainland (source) population. The underlying premise of IBT is that larger areas and less remote habitat patches will contain greater species diversity (MacArthur and Wilson 1967). The isolation effect is largely because more isolated patches are less likely to be colonized (or supplemented) by faunas from a mainland (Hanski and Simberloff 1997). It has been suggested that the species-area relationship is a direct result of the addition of habitats as area increases (Williams 1943). The antithesis of this argument is the area *per se* hypothesis where larger areas are able to support greater numbers of species with viable and persistent populations (MacArthur and Wilson 1967; Connor and McCoy 1979). Despite habitat heterogeneity having a significant effect on many bird assemblages (MacArthur *et al.* 1962; Gentilli 1992), various insular and island archipelago studies have shown significant relationships between species richness and island size when habitat diversity was not significant (Abbott 1978; Ås 1985; Wethered 2001). In this study I investigate the effect of forest type on bird assemblages based on the floristic and structural classification of Geldenhuys and Venter (2002).

Vegetation structure is the most important habitat characteristic for birds (MacArthur *et al.* 1962; Gentilli 1992) and is investigated using a micro-habitat classification and various other habitat descriptors. A wealth of literature exists on the effects of habitat on bird assemblage composition (MacArthur and MacArthur 1961; MacArthur *et al.* 1962; Cody 1985; Gentilli 1992; Allan *et al.* 1997) and thus, habitat variables are expected to have a significant effect on bird assemblage composition and structure.

Aims and Objectives

This study investigates the major local and regional controls on the biological diversity of vertebrates in the Limpopo Province forests. Specifically, this study examines the contemporary distribution of forest amphibians and birds, in the context of past climatic changes, to suggest the major radiation routes in the establishment of vertebrate assemblages in the Limpopo Province forests. The effects of local ecological processes on assemblage composition are also examined. Furthermore,

the relative importance of local and regional processes in maintaining the species richness of two forest archipelagos in the Limpopo Province are compared and contrasted. This allows a more considered approach to identifying what management guidelines would be appropriate for the two archipelagos.

The main objectives of this study are:

1. To evaluate the relative importance of local and regional processes in the determination of assemblage composition (Chapters 2 and 3).
2. To develop an understanding of the major radiation routes in the establishment of faunal assemblages in the Limpopo Province forests (Chapter 2).
3. To investigate the major local ecological processes responsible for vertebrate assemblage composition in the Limpopo Province (Chapter 3).
4. To develop a set of management guidelines for the conservation of vertebrate assemblages based on an understanding of the major species, population and landscape level controls on biological diversity (Chapters 3 and 4).

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Chapter 2

Regional and historical processes have been fundamental in the determination of forest vertebrate assemblage composition in the Limpopo Province

Introduction

Over the last 50 years, the study of species distributions has been dominated by the local ecology of the species involved (Schluter and Ricklefs 1993). Explanations for animal distributions have derived from theoretical concepts such as the Hutchinsonian niche, competition, competitive exclusion, habitat effects, and patch area and isolation (Schluter and Ricklefs 1993) and recent studies of bird distribution in southern Africa have focussed on ecological and (contemporary) climatic controls on species richness (Fairbanks *et al.* 2001; Van Rensburg *et al.* 2002). Recently, however, a shift in emphasis has seen the re-examination of historical and regional-scale processes as explanations for local species richness (Crowe and Crowe 1982; Ricklefs 1987; Lawes 1990). Such effects include autochthonous speciation and the radiation of faunas from sites of speciation or refuge (Williams and Pearson 1997; Winter 1997). The overriding theme in historical explanations is that the distribution of species is fundamentally shaped by climate and geographic changes acting over hundreds, thousands or millions of years (Hamilton 1981; Schluter and Ricklefs 1993). Species establish in an area from a source population but taxonomic differences in ability to cross dispersal barriers and reach the habitat means that not all species have the same opportunities for colonization (Schluter and Ricklefs 1993). Regional and historical processes are thus fundamental in shaping the landscape species pool (and local assemblage composition) when regional species richness is limited by the 'filtering' of potential colonizers and assemblages are unsaturated.

Schluter and Ricklefs (1993) suggest that species diversity may be affected by at least seven types of processes, four of which operate at a regional level. Firstly, allopatric speciation increases local endemism and is affected by dispersal barriers, climates and the arrangement of habitats. Secondly, dispersal barriers inhibit the exchange of taxa between regions. Barriers to dispersal are often topographical, but unique events (such as climate change e.g., hypothermal periods) may also provide

conditions that inhibit the exchange of taxa. Thirdly, these unique events may lead to episodes of extinction where taxa are selectively filtered (*sensu* Balmford 1996) from assemblages. Lastly, the ability of a taxon to diversify ecologically may also affect the species diversity in a habitat if a taxon is able to invade a novel habitat/niche.

When a large diversity of species establishes in a habitat, species packing may result in a high level of interaction between competing species (Cornell 1993). In such a saturated assemblage competitive exclusion may result in potential colonizers either being completely excluded or included at the expense of an out-competed species (MacArthur and Wilson 1967). Consequently, species composition in highly interactive assemblages is primarily determined by local ecological processes (Cornell 1993). The effects of local ecology on faunal assemblage composition in the Limpopo Province forests are examined in Chapter 3. In this chapter I investigate the role of regional and historical processes in determining faunal assemblage composition in the forests of the Limpopo Province.

Late Quaternary climate change in southern Africa

Major climatic and vegetation changes over the last 20 000 years (Van Zinderen Bakker Sr. 1978; Deacon 1983; Partridge *et al.* 1990; Scott *et al.* 1997), have dramatically affected the distribution of forests within southern Africa and shaped the evolution of forest vertebrate assemblages (Lawes 1990; Eeley *et al.* 1999).

The Late Pleistocene hypothermal (circa 18 000 BP)

Southern Africa has experienced approximately 20 hypothermals in the last two million years (Eeley *et al.* 1999). The last hypothermal (last glacial maximum; LGM) occurred approximately 18 000 years ago and was characterised by cooler and generally drier climates than present (Van Zinderen Bakker Sr. 1978; Deacon 1983; Partridge *et al.* 1990). Southern African LGM temperatures were about 5 to 7°C cooler than at present (Coetzee 1967; Harper 1969; Scott 1984; Heaton *et al.* 1986; Talma and Vogel 1992; Stute and Talma 1998) and may have dropped by as much as 8 to 10°C (Van Zinderen Bakker Sr. 1978). Estimates from the Wolkberg (Limpopo Province Drakensberg) have suggested that temperature reductions in the Limpopo Province were even greater than elsewhere in South Africa (up to 9.5°C, Talma *et al.* 1974). Thus, hypothermal temperatures in the mountains of the Limpopo Province were at least 5°C cooler than at present.

A reduction in the Indian Ocean sea temperature during the LGM (Vincent 1972; Huston 1980; Prell *et al.* 1980) reduced the atmospheric moisture associated with the contemporary Agulhas Current (Van Zinderen Bakker Sr. 1978; Butzer 1984). Consequently, southern Africa was drier during the LGM, particularly in the east and south of the region (Price-Williams *et al.* 1982; Butzer 1984; Partridge and Dalbey 1986; Tyson 1986). Hypothermal precipitation in southern Africa was almost ubiquitously lower than at present (Partridge *et al.* 1990; Partridge 1997; Tyson and Partridge 2000) with rainfall in northern South Africa 30% lower during the LGM than now (Partridge 1997; Tyson and Partridge 2000).

Much of southern Africa received more winter rainfall than at present (Van Zinderen Bakker Sr. 1978; Prell *et al.* 1980; Van Zinderen Bakker Sr. 1982; Butzer 1984; Lee-Thorp and Beaumont 1990; Botha *et al.* 1992; Stute and Talma 1998). However, there appears to be some evidence to the contrary (Morley and Hays 1979; Lancaster 1981; Deacon 1983). Nevertheless, winter rainfall is unlikely to have reached the Limpopo Province as the anticyclonic influence did not extend more than 10° further north than at present (Van Zinderen Bakker Sr. 1978; Prell *et al.* 1980; Van Zinderen Bakker Sr. 1982).

Climatic changes during the late Quaternary drastically affected the vegetation of southern Africa with the highveld of South Africa being dominated by Afrotemperate grasslands (Van Zinderen Bakker Sr. 1978). A considerably cooler climate depressed vegetation belts by about 1000 m in altitude during the LGM (Van Zinderen Bakker Sr. 1978; Hamilton 1981; Botha *et al.* 1992; Scott 2000) such that the highveld was treeless (Van Zinderen Bakker Sr. 1978). An arid corridor opened up between north-western southern Africa and East Africa, and Karoo vegetation appears to have dominated the Limpopo Province (Van Zinderen Bakker Sr. 1978). Kalahari sands and vegetation currently lie immediately to the north and west of the Soutpansberg Mountains (Hahn 1994), suggesting that the arid corridor lay very close to the Soutpansberg during the LGM. In addition, the deep (~10 m) sands of the Malonga Flats (directly to the north of the Soutpansberg) are aeolian in origin, and were probably sourced from the Limpopo River valley to the west during the LGM (pers. comm., T.C. Partridge and R.R. Maud). The sands are indicative of arid conditions during the LGM with 'virtually no vegetation cover at the time of their formation' (pers. comm., R.R. Maud).

In summary, while rainfall or temperature levels were not stable during the LGM (Scott 2000), average hypothermal temperatures for the Limpopo Province were at least 5°C lower (and probably even lower than those in KwaZulu-Natal, Talma *et al.* 1974) with 30% less rainfall than present (Tyson and Partridge 2000). Rainfall would have fallen predominantly in the summer months (Van Zinderen Bakker Sr. 1978). Thus, cold conditions and the proximity to the arid corridor would have greatly reduced the likelihood of LGM forest refugia in the Limpopo Province, particularly in the Soutpansberg (which flanked the arid corridor).

Climatic changes caused a dramatic reduction in forest area resulting in a very patchy Afrotemperate forest archipelago to the south of the Limpopo Province (LGM forest refugia, Lawes 1990). Forest refugia were separated by large, unforested gaps. Barren aeolian landscapes dominated the arid zone to the north and presented a major barrier to the exchange of forest taxa with Afrotemperate forests to the north, in modern-day Zimbabwe. In terms of the regional processes affecting diversity, major dispersal barriers and unique events would have dramatically affected the species diversity and assemblage composition of the Limpopo Province forest faunas. I suggest that severe climate changes in the late Quaternary were such that most, if not all, contemporary faunal assemblages date from this time, with changes prior to the LGM being relatively unimportant (Lawes 1990).

The Holocene altithermal (circa 4500-7000 BP)

The increase in temperature following the LGM was quite rapid after about 16 000 years ago (Jouzel *et al.* 1987; Partridge *et al.* 1990), with temperatures peaking during the Holocene altithermal (*circa* 4500-7000 BP, Partridge *et al.* 1990; Tyson and Partridge 2000). Altithermal temperatures over most of southern Africa were approximately 1-2°C warmer than at present (Partridge 1997). In contrast, the pattern of precipitation did not change uniformly across southern Africa (Partridge 1997). Coastal KwaZulu-Natal Province received 5-10% more rainfall than at present (Partridge 1997) and along with the increase in temperature, promoted widespread Holocene forest expansion in that region (Eeley *et al.* 1999). In contrast, northern South Africa and southern Zimbabwe are estimated to have been 10-20% drier during the altithermal than at present (Partridge 1997). These warm, dry conditions resulted in the dominance of grassy and fynbos elements in these regions, and potentially resulted in the extension of Lowveld Sour Bushveld into the Soutpansberg

Mountains (Scott 1987). The expansion of *Podocarpus* forests would have been restricted to the cool, damp ravines (Scott 1987). Slightly cooler, wetter conditions following the Holocene altithermal led to the expansion of Afrotropical forests in the Soutpansberg (Scott 1987). This expansion appears to have been reversed around 1500 BP and may be related to the settling of Iron Age people and the consequent effects of man-made fires in the area (Scott 1987).

The range and area expansion of Afrotropical forests during the Holocene would have reduced the effectiveness of dispersal barriers to the south of Limpopo Province, and forested riparian zones developed along the rivers flowing from the highlands in the Limpopo Province (and Mpumalanga) on to the Mozambican coastal plain. In the north of the province, the hot dry Limpopo River valley (Partridge 1997) remained a significant dispersal barrier for fauna throughout the Holocene (Van Zinderen Bakker Sr. 1978; Clancey 1994), temporarily extending the effect of the hypothermal arid corridor.

Thus, the creation of dispersal barriers through Quaternary climate changes are likely to have played a major role in determining the assemblage composition of Limpopo Province forests. In particular, the aridity of the Limpopo River valley throughout much of the Quaternary suggests that the direction of faunal colonization of Limpopo Province forests was from the Afrotropical forests to the south or from the Indian Ocean coastal belt forests to the east. A further prediction is that if Limpopo Province forest faunas were largely re-established since the LGM, primarily from forest regions to the south, then the Limpopo Province forests are likely to be relatively species poor compared to forest regions to the south, east and north.

The origins of Limpopo Province forest assemblages

Historical science (as opposed to hypothetico-deductive science) proceeds through the formulation of multiple alternative hypotheses and the search for evidence that lends support to particular hypotheses over competing hypotheses (Cleland 2001). An understanding of southern African palaeoclimates and the biogeography of KwaZulu-Natal and Eastern Cape forests has been used to formulate a number of alternative biogeographical hypotheses (not necessarily mutually exclusive) to account for the faunal composition of forests in Limpopo Province (Figure 1):

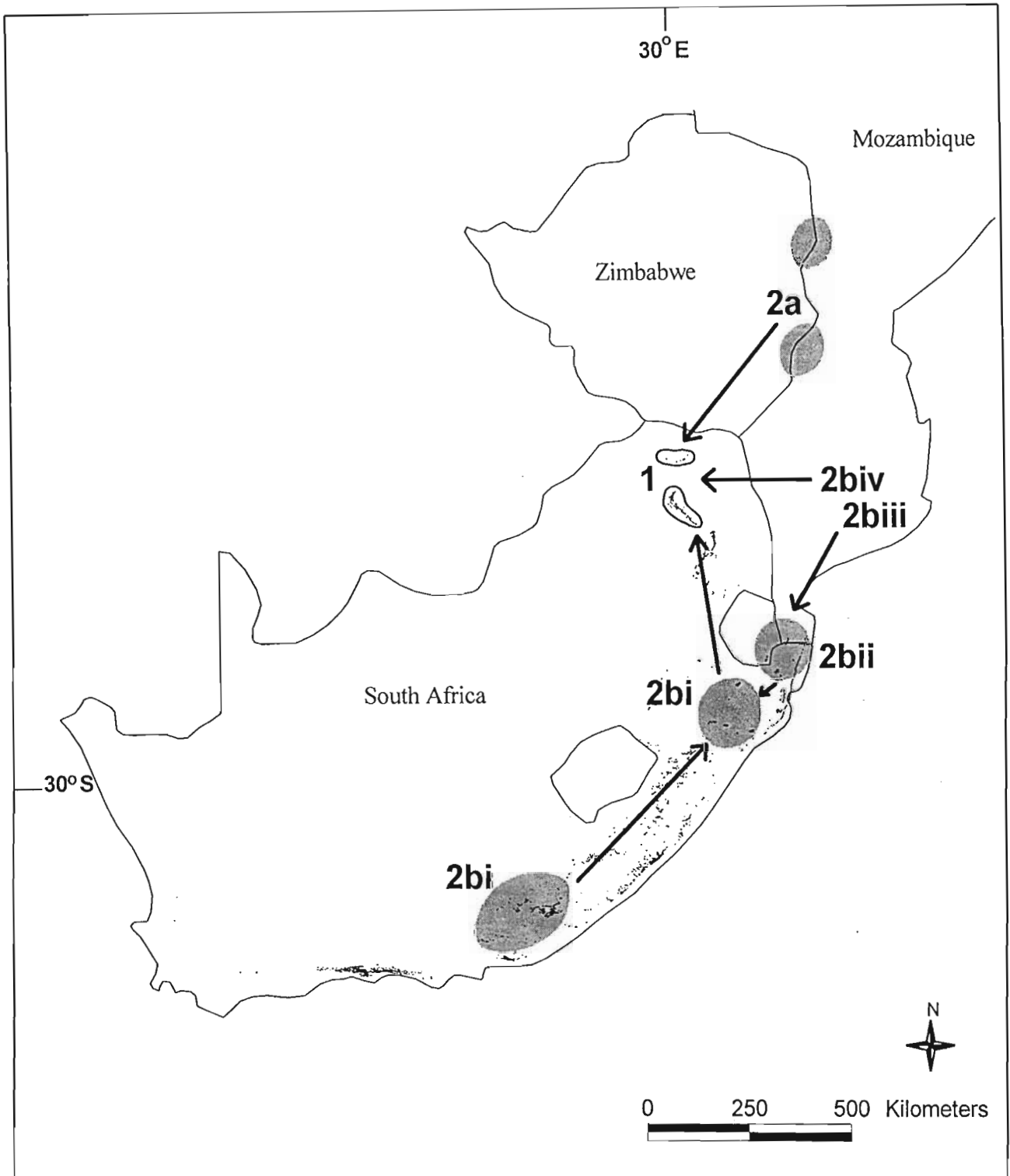


Figure 1. A schematic diagram of the potential radiation routes of faunas into the Limpopo Province. Labels refer to hypothesis numbers given in the text.

1. Forest assemblages persisted through the LGM in the Limpopo Province in forest refugia, despite harsh climatic conditions and the isolation of these forests from those in other areas.
2. If forests did not persist through the LGM in the Limpopo Province then contemporary assemblages have arisen from the re-colonisation by Afrotemperate, Afrotropical (coastal) or matrix faunas (or a combination of these):
 - a. Forest faunas invaded directly from the north after the LGM (from tropical African refugia), and were able to cross the arid Limpopo River valley, a significant barrier to dispersal (Van Zinderen Bakker Sr. 1978; Poynton 1989; Clancey 1994).
 - b. Alternatively, if the Limpopo River valley dispersal barrier was absolute then forest faunas could only have radiated into the region from the south, along the Mpumalanga escarpment, or from the east off the Mozambican coastal plain. While faunas from the east would be of Afrotropical origin (from the Indian Ocean coastal belt forests), if the dominant direction of establishment was from the south, then both Afrotemperate and Afrotropical faunas may be involved. This is because both Afrotemperate and Indian Ocean coastal belt faunas merge in the scarp forests of KwaZulu-Natal and, coastal forests are proximate to the Lebombo Mountains (which link to the Afrotemperate escarpment forests of Mpumalanga Province).
 - i. Afrotemperate faunas may have radiated from LGM refugia in KwaZulu-Natal and the Eastern Cape (Lawes 1990).
 - ii. If Afrotropical refugia survived the LGM on the Mozambican coastal plain (Van Rensburg *et al.* 2000) then these coastal faunas may have dispersed into forests on the Mpumalanga and Limpopo Province escarpments to the northwest, via northern KwaZulu-Natal.
 - iii. Holocene forest expansion resulted in Indian Ocean coastal belt forests expanding from East African coastal refugia, down the Mozambican coast and into KwaZulu-Natal (Lawes 1990; Eeley *et al.* 1999). These faunas may then have radiated from the coastal forests and up the forests of the Lebombo and Drakensberg Mountain ranges, moving from the Mpumalanga escarpment and into the Limpopo Province.

- iv. Afrotropical faunas could also have reached the Limpopo and Mpumalanga Province from coastal East African refugia by dispersing from the Mozambican coast, up wooded riparian zones and into the escarpment forests.
- c. If forest was largely lost during the LGM and barriers to dispersal remained effective during the Holocene then Limpopo Province assemblages should largely comprise matrix species that were able to invade forests. Matrix faunas would have invaded available forest niches regardless of the dominant routes of forest faunal establishment.

Methods

Dispersal, migration and historical processes are major regional controls on assemblage composition (Levine 2002) and different dispersal abilities between taxa highlight subtly different responses to the underlying regional-scale biogeographic processes at work. In order to investigate the response of vertebrates to regional processes two vertebrate classes were selected to represent, at one end of the scale, generally highly mobile taxa (birds) and, at the other end of the scale, taxa with poor dispersal ability (frogs). These two groups were used to examine trends in assemblage composition and saturation across southern Africa and hence, to develop an understanding of the origins of – and major dispersal routes used by – the vertebrate faunas of the Limpopo Province forests.

Birds

Assemblage saturation

If an assemblage is saturated with species then local species richness would not increase regardless of an increase in the regional species pool (i.e. a 'ceiling' in local species richness is reached, Cornell 1993). Theoretically it is possible to use this limitation on species invasions into interactive communities to test for assemblage saturation by examining the relationship between local and regional diversities (Cornell and Lawton 1992; Cornell 1993; Srivastava 1999; Lawes *et al.* 2000). However, if assemblages are unsaturated and largely non-interactive, local diversity would increase linearly with an increase in regional species richness such that there is no ceiling to the numbers of species in an assemblage, i.e. species richness is

determined by the size of the regional species pool (Srivastava 1999). Significant curvilinear relationships that do not reach an asymptote represent assemblages that are approaching saturation but where historical processes have still played an important role (Cornell and Lawton 1992; Srivastava 1999; Lawes *et al.* 2000).

While a linear relationship implies an unsaturated assemblage, a curvilinear relationship does not exclusively characterize saturated assemblages (Cornell and Lawton 1992; Srivastava 1999). The interpretation of local-regional curves in terms of saturation is problematic (Loreau 2000; Koleff and Gaston 2002) as a result, the relative importance of local versus regional processes on assemblage composition should not be assessed only from the relationship between local and regional diversities, but should be supported by other, even circumstantial, evidence (e.g. evidence of density compensation, competition, niche partitioning and, disturbance, major historical changes, Srivastava 1999).

Species richness was estimated for individual forests in twelve southern African Afrotropical forest regions (based on Bailey *et al.* 1999) using both published and unpublished sources (Author's unpublished data, Cody 1983; Koen and Crowe 1987; Castley 1997; Lawes *et al.* 2000). The regions were based on ecological characteristics (Bailey *et al.* 1999) and, although they represent a common Afrotropical origin (Lawes 1990), differences in local and regional ecology are likely to ensure at least some measure of independence in species pools.

In this study, local diversity was defined as the species richness within each individual forest while regional diversity was the total species richness of the forests in the region. Regional estimates of richness were derived from atlas data and were not the sum of the richness of local forests used in the analysis. Thus, estimates of regional richness are independent of local richness. Mean local diversity per region was used over using each individual locality in order to avoid pseudoreplication (Srivastava 1999). The relationship between local and regional diversities was tested using least squares regression for linear and polynomial models. The best model was selected based on superior fit using the F-statistic, r^2 and the residual sum of squares (RSS), provided the coefficients of higher order polynomial terms were significant.

Even though an assemblage may appear unsaturated overall, it may hold a 'core' of species that are interactive. To search for such an interactive core of species, the relationship between local and regional diversities was tested using two

restricted data sets, namely: forest dependent birds and insectivorous forest dependent birds. The latter guild-based restriction was used as there is some evidence suggesting that Limpopo Province and South African insectivorous forest bird assemblages are interactive showing niche partitioning, density compensation and other competition-related responses (Cody 1983; Earlé 1983; Lawes *et al.* 2000). Thus, the insectivorous forest birds are most likely to be interactive and show the effects of competition.

Although Lawes *et al.* (2000) found no significant area effect in KwaZulu-Natal forest bird assemblages, curvilinear relationships may result from area effects (Srivastava 1999). In order to control for species-area effects, species richness estimates were obtained for forest patches greater than 300 ha, an estimate above which area effects appear to be minimal (Wethered and Lawes in prep). In regions where only smaller forests occurred, the largest forests were used. In addition, the effect of forest area on species richness was tested.

Patterns of species distribution

To better understand the patterns of forest bird distribution and abundance in southern Africa, I analysed data from the Southern African Bird Atlas (Harrison *et al.* 1997). Reporting rate (proportion of cards submitted on which a species was recorded) was used as an index of relative abundance and, although problematic, was suitable for the limited insights we wished to gain from the data (Harrison and Underhill 1997). Data were extracted for $\frac{1}{4}^{\circ}$ by $\frac{1}{4}^{\circ}$ grid cells and only data for forest dependent and forest associated bird species were included. Forest dependent species were defined as species that require forest in which to breed while forest associated species may breed in forest but can survive and breed in other habitats (Lawes *et al.* 2000). Based on the number of forest dependent and associated species, 87 grid cells were selected representing the major forested regions in southern Africa (Figure 2, Appendix 1). Each of the hypotheses for the radiation of forest faunas into the Limpopo Province were evaluated using gradients of species richness and assemblage similarity (Table 1).

While a simple consideration of species richness is of limited ecological value, more meaningful insight can be gained from measures that take into account species abundance (Jenkins 1992). Consequently, I adopted a method similar to Williams (1997), using multivariate statistics for the simultaneous comparison of a large

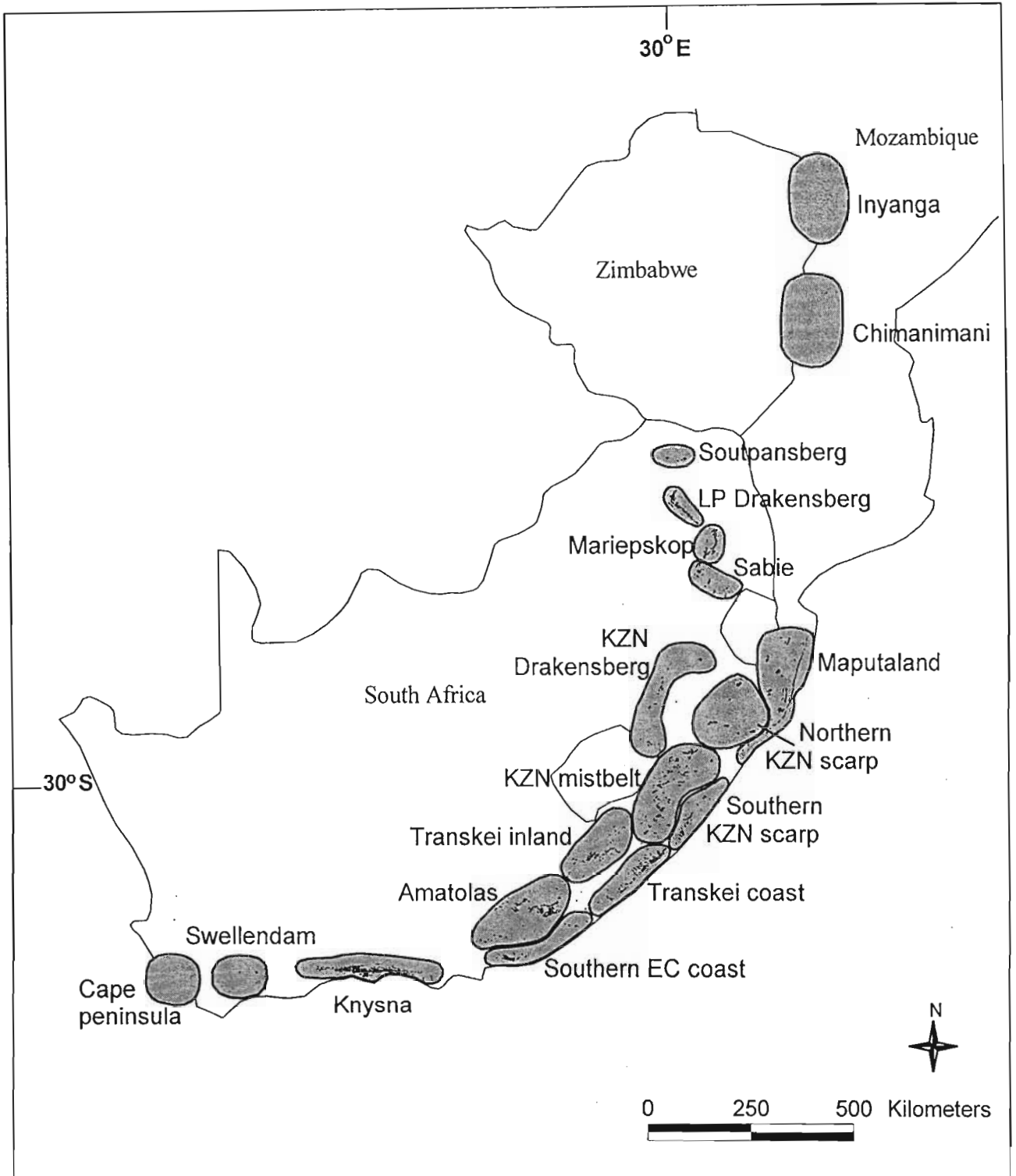


Figure 2. The geographical distribution of forest regions in southern Africa (based on Bailey et al. 1999)

number of sites based on the abundance of all forest bird species found in each grid cell (forest associated species, FAB, and forest dependent species, FDB, only)(Ter Braak 1987). Correspondence analysis was chosen over other ordination techniques because of the nature of the data and the gradient length (FDB: 2.68 SD and FAB: 2.40 SD, Ter Braak 1987). Ordinations were calculated using Canoco IV (Ter Braak and Šmilauer 1998).

The similarity of sites was determined using the Bray-Curtis (Bray and Curtis 1957) similarity measure for both forest dependent and all forest bird species. Simple averaged cluster analysis dendograms were also constructed from the similarity matrix. The Bray-Curtis similarity measure does not require confirmed absence data but relies solely on presence data (Sneath and Sokal 1973; Krebs 1989; De Klerk *et al.* 2002). All correlation and regression statistics were computed using Statistica 5.1 (StatSoft 1998) whilst Simpson's diversity index and Bray-Curtis similarity measure was calculated using Biodiversity Professional (McAleece 1997). The southern African distribution of selected forest taxa was also used in the evaluation of the seven radiation hypotheses.

Frogs

Despite a wide search, I was unable to obtain suitable frog and mammal distribution data from museum specimens or other independent sources. These data may become available in the near future. As a result, the distribution of southern African forest frog species within the 19 southern African forest regions was determined using available texts (Figure 2, Table 3; Passmore and Carruthers 1979, 1995; Carruthers 2001). Frog taxonomy follows Carruthers (2001) and only forest dependent (generally confined to forests) and forest associated species (associated with forests but may also use other habitats) were considered. The binary data available precluded any estimate of forest frog local diversity, as distributional data were only available at the regional level. Consequently, no assessment of assemblage saturation (i.e., relative influence of regional processes) was possible using a local-regional analysis.

Assemblage similarity between sites was assessed using Bray-Curtis simple averaged cluster analyses (using Biodiversity Professional, McAleece 1997).

Results

Birds

Assemblage saturation

Forest bird communities in southern Africa appear to be unsaturated as local species richness increases linearly with an increase in regional richness (Figure 3; $F_{(1,9)}=91.8$, $r^2=0.91$, $P<0.001$, $RSS=362.6$). Neither the polynomial relationship ($F_{(2,8)}=5.2$, $r^2=0.91$, $P>0.05$, $RSS=357.4$) nor the quadratic term were significant ($t_{(8)}=0.3$, $P=0.74$). The same trend was found for forest dependent bird species and forest dependent insectivorous species, where the linear model was the most appropriate as the quadratic term was not significant ($t_{(8)}=0.5$, $P=0.6$ and, $t_{(5)}=0.4$, $P=0.7$, respectively). Therefore, regional, biogeographical processes have been relatively more important in determining bird assemblage composition in southern African forests than local, ecological processes. Forest species richness was independent of area for all species ($F_{(1,31)}=0.004$, $r^2=0.001$, $P=0.8$) and thus area is unlikely to have had a significant effect on the local-regional relationship.

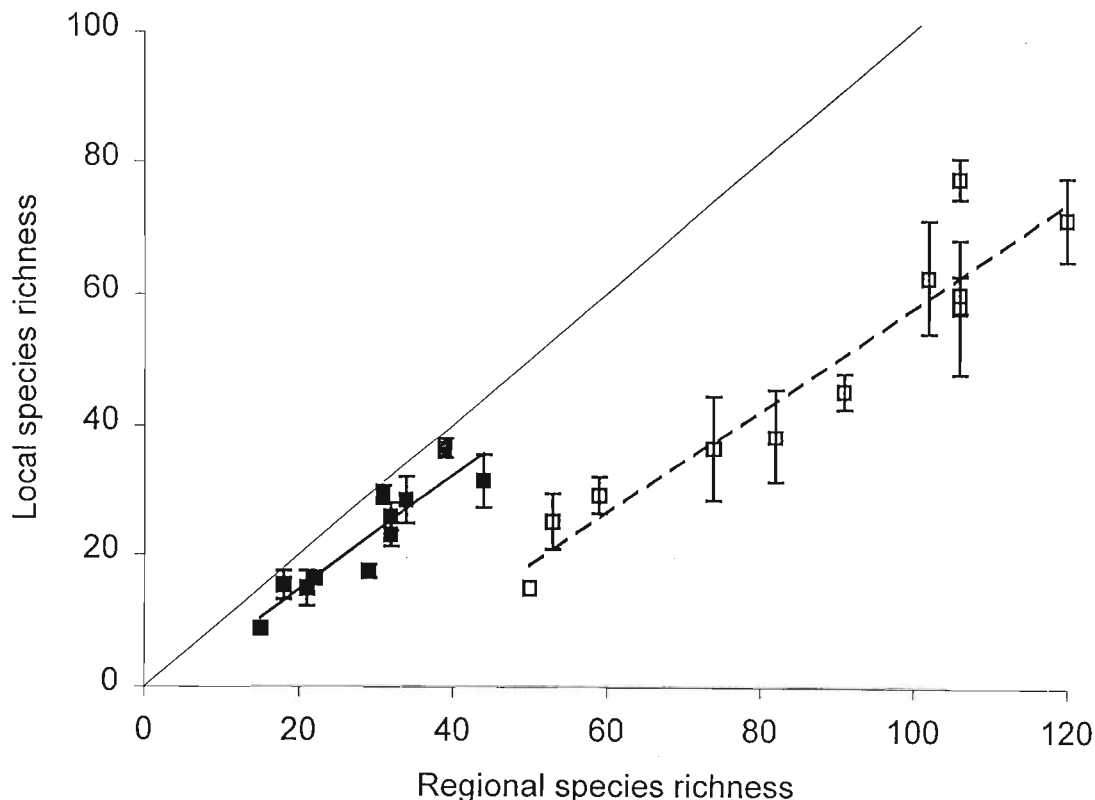


Figure 3: The relationship between local and regional diversity for all forest birds (\square , - - -) and forest dependent birds (\blacksquare , —) in South African Afrotemperate forests. Error bars denote standard error.

Patterns of species richness

Forest dependent bird species richness decreases from northern KwaZulu-Natal, north along the Drakensberg escarpment to the Limpopo Province (Figure 4). The bird species richness of the inland (Afrotropical) forests also decreases southwards to the Transkei Afrotropical forests, is higher in the Amatolas (southern Eastern Cape), and then decreases again to the south. The south-north species richness gradient from KwaZulu-Natal to the Limpopo Province supports hypotheses 2bi, 2bii and 2biii (Table 1).

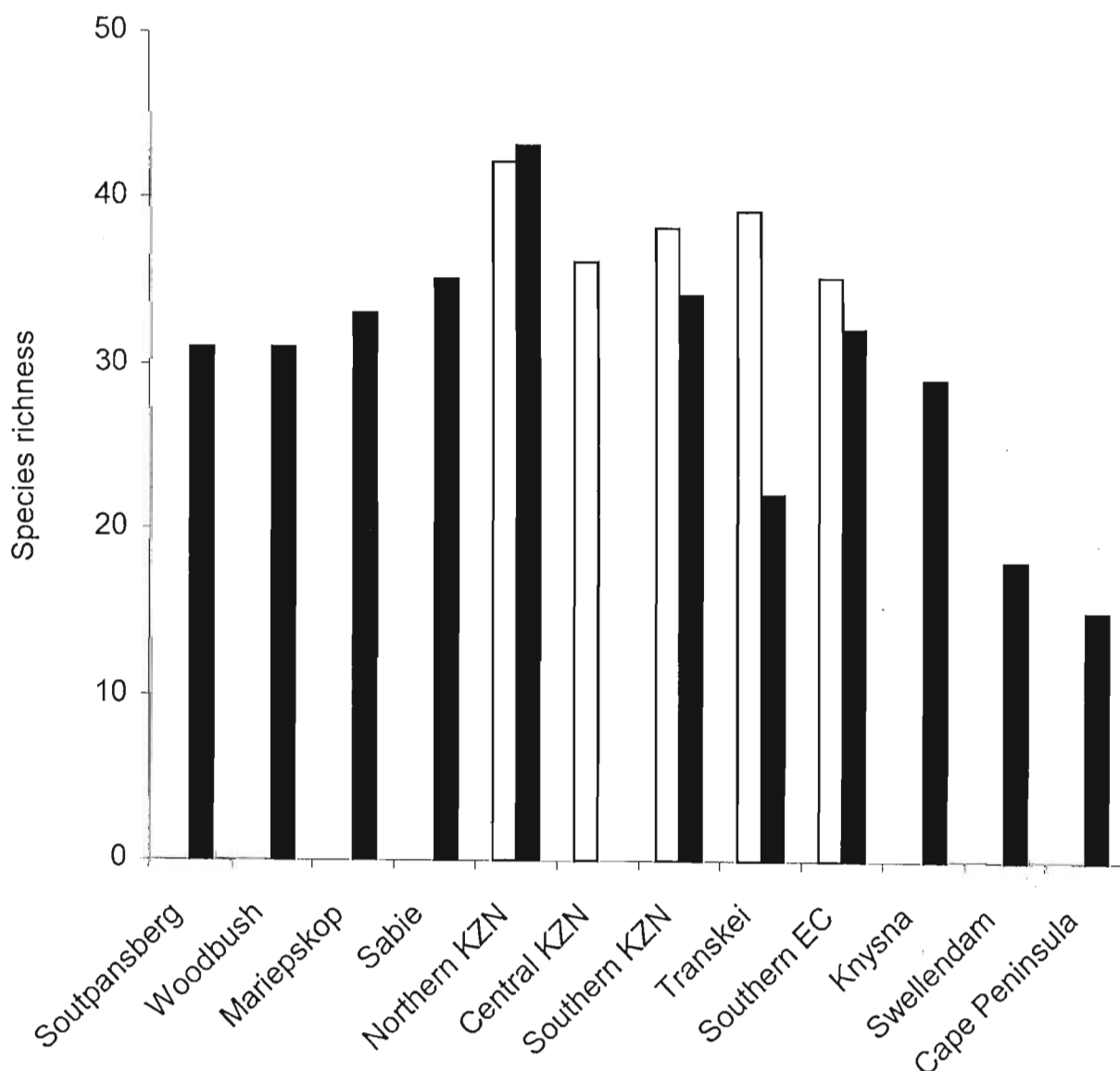


Figure 4: The number of forest dependent bird species in South African forest regions (arranged from north to south). Afrotropical/coastal (□) and Afrotemperate regions (■) are arranged latitudinally from the Soutpansberg in the north, to the Cape Peninsula in the south.

Table 1: Hypotheses explaining the radiation of forest faunas into the Limpopo Province, suggesting how the observation of various patterns would provide evidence for (Y) or against (N) each hypothesis. See text for an explanation of the hypotheses. The last column summarises the results found in this study.

	LP refugia	From Zimbabwe	KZN & EC refugia	Moz. coastal refugia	Down Moz. up Mpum.	Up rivers from Moz.	This study
	1	2a	2bi	2bii	2biii	2biv	
South to North loss of species	-	N	Y	Y	Y	N	Y
North to South loss of species	N	Y	N	N	N	N	N
Strong similarity to Indian Ocean coastal belt assemblages	N	Y	N	N	Y	Y	Y
Endemic species & vicariant distribution	Y	N	N	N	N	N	N
Afrotemperate ¹ versus Afrotropical ² affinities	1	1/2	1	2	2	2	1
Limpopo Province assemblages subsets of those to the south	N	N	Y	Y	Y	N	Y

The main gradient of change in forest bird abundance was that of geographical distance from the Maputaland coastal region with correspondence analysis eigenvector scores decreasing significantly (FDB: $F_{(1,85)} = 80.4$, $r^2=0.48$, $P<0.001$, FAB: $F_{(1,85)} = 57.6$, $r^2=0.40$, $P<0.001$) with increasing distance from Mkuze (grid cell 2732CA, Figure 5). Sites that were more distant from northern KwaZulu-Natal were also less similar (Bray-Curtis similarity) to that region in terms of species assemblage composition (FDB: $F_{(1,85)} = 118.6$, $r^2=0.58$, $P<0.001$, FAB: $F_{(1,85)} = 177.8$, $R^2 = 0.68$, $P<0.001$) such that there was a major gradient of decreasing similarity north to the Limpopo Province (supporting hypotheses 2bi, 2bii and 2biii).

Grid cells in the Soutpansberg had significantly greater axis 1 scores than those in the Limpopo Province Drakensberg ($t_6=29.7$, $P<0.001$). Thus, forest bird assemblages in the Soutpansberg are more similar to those of northern KwaZulu-Natal than would be expected from the general distance gradient. This alludes to some form of assemblage supplementation by Afrotropical faunas either from the Indian Ocean coastal belt forests (hypothesis 2biii), or from the forests of eastern Zimbabwe (hypothesis 2a).

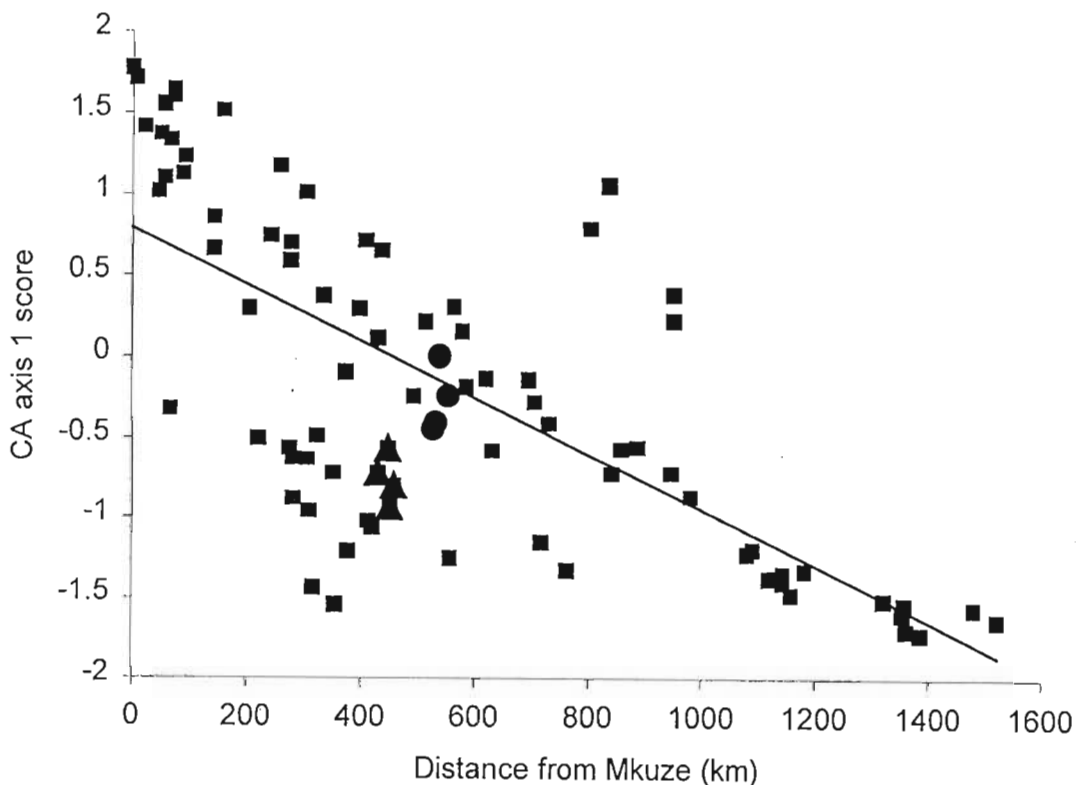


Figure 5: The effect of distance from Maputaland on the correspondence analysis axis 1 scores using the assemblage composition of forest dependent birds in southern African forests. Grid cells in the Limpopo Province Drakensberg (▲) and Soutpansberg (●) are highlighted.

A Bray-Curtis cluster analysis showed that Afrotemperate forest dependent bird assemblages are largely distinct from their Afrotropical counterparts of the Indian Ocean coastal belt forests (Figures 6 and 7). The assemblages of eastern Zimbabwe were biologically distinct but were most similar to those of the South African Indian Ocean coastal belt forests. The Afrotemperate affinities of the Limpopo Province forests lend support to hypotheses 1 and 2bi. The same trend in assemblage similarities was also found using all forest-associated species.

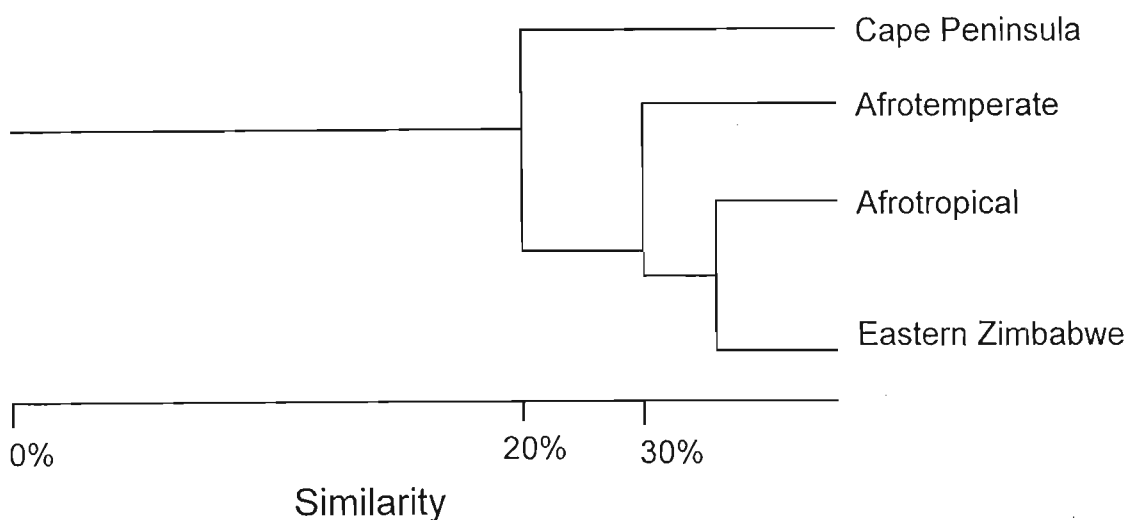


Figure 7: Bray-Curtis cluster analysis dendrogram (simple averaged scaling) for forest dependent bird assemblages in southern African forests.

Limpopo Province assemblages are generally subsets of those to the south with an accumulation of species southwards and 97.1% of Limpopo Province forest dependent bird species occurring in the KwaZulu-Natal scarp forests (Table 2). Thus, the most parsimonious explanation is that the Limpopo Province forest dependent bird assemblages have largely been drawn from assemblages to the south (hypotheses 2bi, 2bii and 2biii). However, this explanation does not account for the distribution of African Broadbill *Smithornis capensis*, Blackfronted Bushshrike *Telophorus nigrifrons* and Crested Guineafowl *Guttera pucherani*, all of which use forested riparian zones (Little 1997; Parker 1997, 1999; Symes and Perrin 2000) and may have used these routes to enter the Limpopo Province. Blackfronted Bushshrike is also the only forest dependent bird species in the Limpopo Province with a distribution to the north but not extensively to the south of the Limpopo Province (i.e. little support for

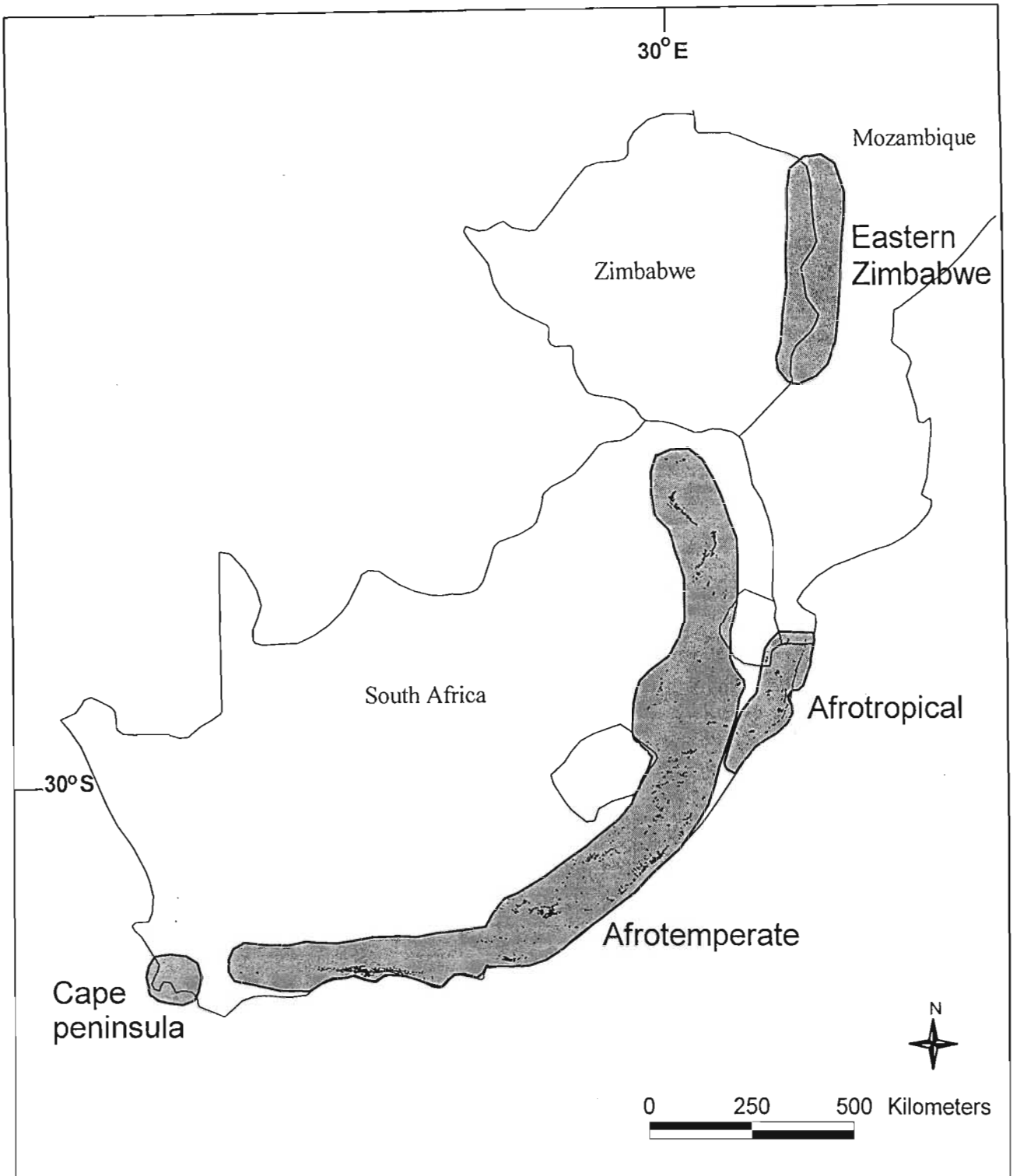


Figure 6. The geographical distribution of the four major cluster analysis groups of forest dependent bird assemblages in southern Africa

Table 2: Forest dependent bird presence in northern South Africa. SOUT Soutpansberg, WB Woodbush, MAR Mariepskop, SAB Sabie, MAP Maputaland, SCA KZN scarp.

Species	SOUT	WB	MAR	SAB	MAP	SCA
African Broadbill	1				1	1
African Goshawk	1	1	1	1	1	1
Barthroated Apalis	1	1	1	1	1	1
Bearded Robin	1		1	1	1	1
Blackbellied Glossy Starling				1	1	1
Blackfronted Bush Shrike	1	1	1			
Bluemantled Flycatcher	1	1	1	1	1	1
Brown Robin	1	1	1	1	1	1
Buffspotted Flufftail	1	1	1	1	1	1
Bush Blackcap			1	1		1
Cape Batis	1	1	1	1	1	1
Cape Parrot		1				1
Chorister Robin	1	1	1	1	1	1
Cinnamon Dove	1	1	1	1	1	1
Collared Sunbird	1	1	1	1	1	1
Crested Guineafowl	1				1	1
Crowned Eagle	1	1	1	1	1	1
Emerald Cuckoo	1	1	1	1	1	1
Forest Buzzard	1	1	1	1		1
Forest Canary	1	1	1	1	1	1
Goldenrumped Tinker Barbet				1	1	1
Green Twinspot	1	1	1	1	1	1
Grey Cuckooshrike	1	1	1	1	1	1
Knysna Lourie	1	1	1	1	1	1
Narina Trogon	1	1	1	1	1	1
Olive Bush Shrike	1	1	1	1	1	1
Olive Sunbird				1	1	1
Olive Woodpecker	1	1	1	1	1	1
Orange Thrush	1	1	1	1		1
Rameron Pigeon	1	1	1	1	1	1
Scalythroated Honeyguide	1	1	1	1	1	1
Squaretailed Drongo		1	1	1	1	1
Starred Robin	1	1	1	1	1	1
Tambourine Dove	1	1	1	1	1	1
Terrestrial Bulbul	1	1	1	1	1	1
Trumpeter Hornbill			1	1	1	1
Wood Owl	1	1	1	1	1	1
Yellowstreaked Bulbul	1	1	1	1	1	1
Yellowthroated Warbler	1	1	1	1	1	1
Total number of species	31	31	33	35	33	36

hypothesis 2a). Alternatively, the unusual (vicariant) distribution of these four species in the Limpopo Province may be indicative of forest refugia in that region (hypothesis 1). However, the lack of endemic taxa in the region and the nested distribution (subsets of forests to the south) provide little support for the persistence of forest refugia (at least for forest birds) in the Limpopo Province.

Fifty-five bird species were dependent on forest in southern Africa, with up to 40 forest dependent species in a grid cell. A high proportion of forest bird species were not dependent on forest (mean \pm SE = 66.4 \pm 3.54%), suggesting that a number of niches within the forest were empty and that forest bird assemblages are not saturated (Begon *et al.* 1996; Beier *et al.* 2002). In addition, there appear to be a number of empty niches in forest frog and bird assemblages in the Limpopo Province, in particular, with a paucity of tree frogs, leaf litter frogs and forest floor birds (unpubl. data, Clancey 1975). The invasion of forest habitat by matrix species has had a noticeable effect on forest bird assemblage richness in southern Africa (hypothesis 2c). Therefore, the most parsimonious explanation of contemporary forest bird assemblage composition in the Limpopo Province comes from hypothesis 2bi where assemblages are largely Afrotropical, being drawn from refugia on the KwaZulu-Natal scarp and Eastern Cape escarpment (Table 1). Some assemblage supplementation has taken place from Afrotropical faunas in the Mozambican and Maputaland Indian Ocean coastal belt forests and from matrix assemblages.

Frogs

Twenty-one southern African frog species were dependent on forests while an additional 15 species were associated with, but not restricted to, forests. All of the South African forest dependent frog species are endemic to South Africa (Table 3, Carruthers 2001). Thus, South African forest dependent frog assemblages show high levels of autochthonous speciation and must have been derived from South African LGM refugia (highlighting only hypotheses 1, 2bi and 2bii).

The forest dependent frog assemblages showed high species turnover across the latitudinal gradient from the Cape to eastern Zimbabwe, with four distinct groups of unique species composition (Table 3). A minimum set including the Cape Peninsula (four species), Knysna (two species), the Eastern Cape mist belt (Amatola

Table 3: The distribution of forest dependent frog species in southern African forest regions, arranged latitudinally. INY Inyanga, CHI Chimanimani, SOU Soutpansberg, LPD LP Drakensberg, MAR Mariepskop, SAB Sabie, MAP Maputaland, SCA KZN scarp, DRA KZN Drakensberg, DBN central KZN coast, MIST KZN mistbelt, SNA Southern KZN scarp, PON Transkei coast, TNK Transkei mistbelt, AMA Amatolas, PE Port Elizabeth, KNY Knysna, SW Swellendam, CT Cape Peninsula.

	INY	CHI	SOU	LPD	MAR	SAB	MAP	SCA	DRA	DBN	MIST	SNA	PON	TNK	AMA	PE	KNY	SW	CT
<i>Breviceps rhodesianus</i>	1																		
<i>Leptopelis argenteus</i>	1	1																	
<i>Arthroleptis xenodactylus</i>	1	1																	
<i>Leptopelis flavomaculatus</i>	1	1																	
<i>Phrynobatrachus parvulus</i>	1	1																	
<i>Arthroleptis troglodytes</i>		1																	
<i>Stephanopaedes anotis</i>		1																	
<i>Breviceps sylvestris</i>			1	1															
<i>Heleophryne natalensis</i>				1	1	1		1	1	1	1								
<i>Breviceps verrucosus</i>					1	1	1	1	1		1	1	1	1	1	1			
<i>Arthroleptis wahlbergii</i>							1	1		1	1	1	1						
<i>Leptopelis natalensis</i>							1	1		1	1	1	1						
<i>Arthroleptella hewitti</i>								1	1		1	1							
<i>Natalobatrachus bonebergi</i>								1		1	1	1	1						
<i>Anhydrophryne rattrayi</i>															1				
<i>Heleophryne regis</i>																	1		
<i>Breviceps fuscus</i>																	1	1	
<i>Arthroleptella lightfooti</i>																			1
<i>Arthroleptella villiersi</i>																			1
<i>Heleophryne rosei</i>																			1
<i>Breviceps acutirostris</i>																			1
Total number of species	5	6	1	2	2	2	3	6	3	4	6	5	4	1	2	1	2	1	4

Mountains, one species) and the KwaZulu-Natal scarp forests (six species), would account for all South African forest dependent frogs (Table 3). Forest dependent frog assemblages in the Limpopo and Mpumalanga Provinces have almost certainly been drawn from the KwaZulu-Natal scarp forests (hypothesis 2bi) as the assemblages of the former are largely sub-sets of the latter and, there is a decrease in species richness, north from KwaZulu-Natal to the Limpopo Province (Table 3). The one exception is *Breviceps sylvestris* which, although considered a forest dependent species in this study, may not be exclusively limited to forests (Passmore and Carruthers 1995) and may have persisted through the LGM regardless of forest persistence. As such, the presence of the locally endemic *B. sylvestris* in the Limpopo Province does not provide convincing evidence for forest persistence through the LGM (hypothesis 1).

A cluster analysis of forest associated frog species separated the Maputaland forest assemblages from those of the rest of KwaZulu-Natal (Figure 8). Three species of frog, not represented elsewhere in KwaZulu-Natal, occur in the Maputaland forests: *Bufo maculatus* and *Arthroleptis stenodactylus* are wide-ranging Afrotropical savanna species, while the Whistling Rain Frog (*Breviceps* sp.) is a species of forest and woodlands occurring in Maputaland, Swaziland and southern Mpumalanga. Although the effect of post-hypothermal radiation from East African refugia has been relatively minor (all forest dependent frogs are endemic), Afrotropical frog species have supplemented South African assemblages with an effect that decreases to the south of KwaZulu-Natal (hypothesis 2a; Table 4).

The scale of the invasion of forest habitat by wide-ranging matrix species (41.7% of species) indicates that matrix species have had an important influence on forest frog assemblage composition in South Africa, particularly in the Limpopo Province (hypothesis 2c). More importantly, this trend implies that matrix species may have been able to establish in forests because forest frog assemblages are unsaturated. South African forest frog assemblages are species poor compared to those of eastern Zimbabwe and East Africa (Table 4 this study, Broadley 1994; Burgess and Clarke 2000). In addition, the attenuation in species richness from KwaZulu-Natal north to the Limpopo Province implies that, at the very least, Limpopo Province assemblages are unsaturated, as not all potential colonisers have reached the Limpopo Province.

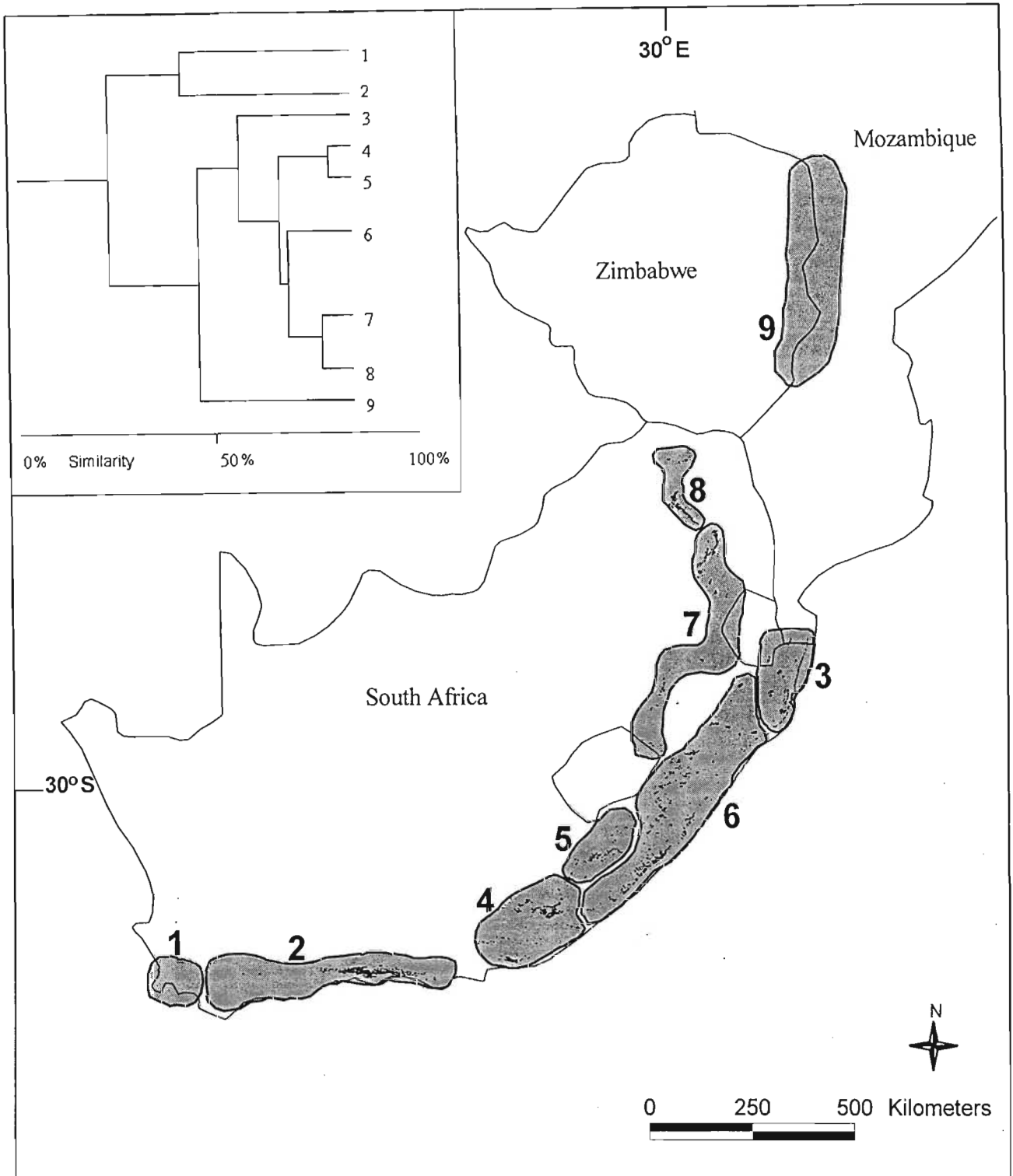


Figure 8. The geographical distribution of the nine major cluster analysis groups of forest associated frog assemblages in southern Africa. Numbers on map refer to cluster analysis groups in the dendrogram (inset)

Table 4: The latitudinal distribution of all forest frog species in southern Africa. See Table B for explanation of locality codes.

	INY	CHI	SOU	LPD	MAR	SAB	MAP	SCA	DRA	DBN	MIST	SNA	PON	TNK	AMA	PE	KNY	SW	CT
<i>Breviceps rhodesianus</i>	1																		
<i>Arthroleptis xenodactylus</i>	1	1																	
<i>Leptopelis argenteus</i>	1	1																	
<i>Leptopelis flavomaculatus</i>	1	1																	
<i>Phrynobatrachus parvulus</i>	1	1																	
<i>Xenopus muelleri</i>	1	1																	
<i>Arthroleptis stenodactylus</i>	1	1					1												
<i>Stephanopaedes anotis</i>		1																	
<i>Arthroleptis troglodytes</i>		1																	
<i>Bufo maculatus</i>	1	1	1	1	1	1	1												
<i>Breviceps adspersus</i>	1	1	1	1	1	1	1	1	1	1	1					1			
<i>Bufo gutturalis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1					
<i>Afrana angolensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
<i>Strongylopus grayii</i>	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1
<i>Xenopus laevis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Breviceps sylvestris</i>			1	1															
<i>Tomopterna natalensis</i>			1	1	1	1	1	1	1	1	1	1	1	1					
<i>Bufo rangeri</i>			1	1				1	1	1	1	1	1	1	1	1	1	1	1
<i>Heleophryne natalensis</i>				1	1	1		1	1	1	1								
<i>Breviceps verrucosus</i>					1	1	1	1	1		1	1	1	1	1	1			
<i>Strongylopus wageri</i>					1	1		1	1										
<i>Breviceps</i> spp (whistling)						1	1												
<i>Arthroleptis wahlbergii</i>							1	1		1	1	1	1						
<i>Leptopelis natalensis</i>							1	1		1	1	1	1						
<i>Natalobatrachus bonebergi</i>								1		1	1	1	1						

<i>Arthroleptella hewitti</i>								1	1			1	1						
<i>Anhydrophryne rattrayi</i>															1				
<i>Heleophryne regis</i>																	1		
<i>Breviceps fuscus</i>																	1	1	
<i>Heleophryne purcelli</i>																	1	1	
<i>Arthroleptella lightfooti</i>																			1
<i>Arthroleptella villiersi</i>																			1
<i>Arthroleptella bicolor</i>																			1
<i>Arthroleptella drewsii</i>																			1
<i>Breviceps acutirostris</i>																			1
<i>Heleophryne rosei</i>																			1
Total associated species	13	14	9	10	10	11	11	14	11	11	13	11	10	7	6	6	6	5	9
Total dependent species	5	6	1	2	2	2	3	6	3	4	6	5	4	1	2	1	2	1	4

Discussion

Southern African forest bird and frog assemblages appear to be unsaturated and assemblage composition is primarily controlled by regional and historical processes. Major climatic changes of the last 18 000 years have fundamentally shaped contemporary assemblages with assemblages in the Limpopo Province being primarily drawn from the post-LGM faunas that survived in Afrotemperate forest refugia on the KwaZulu-Natal scarp.

Local versus regional determination of assemblage composition

This study seeks to establish the relative importance of local versus regional processes in determining forest vertebrate assemblage composition. The data suggest that southern African forest bird assemblages are not saturated (Figure 3) and, by inference, assemblage composition has been primarily determined by regional processes as opposed to local ecology. In other words, the size of the regional species pool determines the size of the local assemblage, and the regional pool is, in turn, determined by the history of establishment of faunas in a region. Cornell and Lawton (1992, p. 1) state that 'unsaturated (type 1) assemblages are likely to be ubiquitous in nature' and most studies suggest that unsaturated, regionally-controlled assemblages are the norm rather than the exception (Caley and Schluter 1997; Gaston 2000; Koleff and Gaston 2002).

A linear relationship between local and regional diversity may be found when the local richness of weakly-interactive, non-specialist species increases with regional diversity despite strong interactions limiting the local richness of specialist species (Cornell and Lawton 1992). However, local-regional analyses of two, more specialist, groups of species (the forest dependent and forest dependent insectivorous species), did not suggest assemblage saturation. Thus, southern African Afrotemperate forest bird assemblages appear to be principally controlled by regional processes. This is not to say that local ecological processes are unimportant but merely that regional processes have had a relatively greater effect on the determination of assemblage composition. Further support for this can be found in the high proportion of non-specialist bird and frog species (forest associated and matrix species) within southern African forests (66.4% and 41.7%, respectively). Climatic changes over the last 18 000 years have had an undeniable influence on the

distribution of species and the composition of contemporary assemblages (Lawes 1990).

Although this study suggests that Afrotropical forest bird assemblages are unsaturated, it is possible that southern African forest bird assemblages may approach saturation at greater levels of regional richness than in the forests examined (i.e. the local-regional curve may reach an asymptote). Lawes *et al.* (2000) also found that a linear local-regional relationship characterised Afrotropical birds but that assemblages in the Afrotropical forests of Maputaland, where regional richness is relatively high, approached saturation.

The regional determinants of assemblage composition

This study has shown that for both birds and frogs there is a general species richness and assemblage similarity gradient north from the KwaZulu-Natal scarp forests to the Limpopo Province, with assemblages in the latter region being Afrotropical in origin and subsets of those to the south. The most parsimonious explanation of these patterns is that Limpopo Province forest vertebrate assemblages have been largely derived from forest refugia on the KwaZulu-Natal scarp and Eastern Cape escarpment (hypothesis 2bi, Table 1). The only bird-related observation not adequately explained by hypothesis 2bi is that of increased Afrotropical affinities in the Soutpansberg, compared to the Limpopo Province Drakensberg forests. I suggest that this is from minor assemblage supplementation by faunas (e.g. Terrestrial Bulbul and Crested Guineafowl) radiating from the Indian Ocean coastal belt forests on the Mozambican coastal plain, up moist, forested riverine systems, and into the Soutpansberg (hypothesis 2biv)(Clancey 1975; Lawes 1990). In addition to refugia on the KwaZulu-Natal scarp and Eastern Cape escarpment, frog taxa also persisted through the LGM in refugia in the Knysna area and the Cape Peninsula.

Historical climate changes, as opposed to simple climatic controls, have been fundamental in shaping and determining African bird assemblages (Crowe and Crowe 1982). This study has shown that the contemporary distribution of forest birds and frogs in southern Africa is consistent with the radiation of southern African forest mammals and the two major radiation events of the last 18 000 years (Lawes 1990). These two radiation events consist of the post-LGM radiation of Afrotropical faunas out of refugia in KwaZulu-Natal and the Eastern Cape and the relatively

recent radiation of Afrotropical faunas associated with the southward expansion of Indian Ocean coastal belt forests (Lawes 1990). Based on forest mammal distributions, Lawes (1990) suggested that forests persisted through the LGM on the scarp of KwaZulu-Natal and on the Eastern Cape escarpment (hypothesis 2bi). The data presented here suggest that this hypothesis is the most likely explanation for the distribution of contemporary forest bird species.

Afrotropical bird species dominate the South African avifauna (Poynton 1961; Clancey 1994). But, nine forest dependent endemic bird species indicate a unique South African Afrotropical forest avifauna with some degree of autochthonous speciation within the region (Clancey 1986). The Limpopo Province bird assemblages are essentially South African in origin (Clancey 1994) with forest bird assemblages being taxonomically more akin to KwaZulu-Natal Afrotropical assemblages than to either eastern Zimbabwe forest bird assemblages or, Afrotropical assemblages on the Mozambican coastal plain (Clancey 1975). In addition, South African Afrotropical bird assemblages must have been primarily derived from refugia within the region, as they are not subsets of, and are relatively dissimilar to (Figure 7), the assemblages of eastern Zimbabwe and the Indian Ocean coastal belt forests. The presence of South African endemic forest bird species and subspecies in the Limpopo Province, but not to the north (Clancey 1975; Harrison *et al.* 1997), provides further evidence for the importance of South African refugia in the determination of Limpopo Province bird assemblages.

South Africa supports a clearly-defined Afrotropical amphibian fauna; distinct from the Afrotropical fauna and its subtraction margin (Poynton 1961; Poynton and Boycott 1996). Fourteen South African endemic frog species are forest dependent (Table 3) with an increase in the number of endemic frog species from Mozambique to the Western Cape (Crowe 1990). These endemic taxa represent the divergence of relict amphibian faunas (Poynton 1961) with forest frog taxa indicating a substantial temporal separation of South and East African forest faunas (Poynton 1989). Thus, South African forest dependent frog assemblages have been completely drawn from South African sites of autochthonous speciation, with four main areas being of particular interest (Table 3), namely; the Cape Peninsula (four species), Knysna (two species), the Eastern Cape escarpment (one species) and the KwaZulu-Natal scarp forests (six species).

While the South African Afrotropical bird and mammal faunas are not as distinct as the frogs (Poynton 1961), the persistence of forests on the KwaZulu-Natal scarp and Eastern Cape escarpment (Lawes 1990) accounts for much of the forest bird diversity. The one obvious exception is the Knysna Warbler *Bradypterus sylvaticus*, but the persistence of two endemic frog species in the Knysna area suggests that patches of thicket-type vegetation may have acted as very minor refugia, unsuitable for most bird species but suitable for the two frog species and the Knysna Warbler.

During the Holocene, Indian Ocean coastal belt forests – and their associated Afrotropical faunas – radiated out of East African refugia and south, into and through Mozambique (Diamond and Hamilton 1980; Crowe and Crowe 1982). This radiation event affected both the eastern Zimbabwe highlands and the Maputaland region (Lawes 1990). This explains the assemblage similarities between eastern Zimbabwe and Maputaland forests (Figure 7) with the contemporary distribution of Woodward's Batis *Batis fratrum* and Livingstone's Lourie *Tauraco livingstonii* mapping this radiation route.

The Maputaland region (and the 18°C mean July isotherm) is the southernmost extension of the climatically tropical region in Africa (Poynton 1961) and is characterised by Afrotropical faunas (Poynton 1961; Crowe 1990; Poynton and Boycott 1996). The Maputaland region has acted as a centre of radiation (if only minor) in both a north and southwestern direction (Figures 5 and 6) and represents the radiation of Afrotropical faunas with the southward expansion of the Indian Ocean coastal belt forests (Eeley *et al.* 1999). It is unlikely that forests were established on the Maputaland coastal plain during the LGM (Eeley *et al.* 1999) and the strongest, yet unpersuasive, avian evidence for a Maputaland refuge centre (hypothesis 2bii) is the restricted distribution of the very distinct Tonga race of the Brown Robin *Erythropygia signata tongensis* (Oatley 1989).

A 'tropical subtraction margin' (*sensu* Poynton 1961) extends south of the Maputaland region such that Afrotropical faunas are lost from assemblages progressively further south (this study, Poynton 1961; Crowe 1990; Clancey 1994; Poynton and Boycott 1996). This subtraction margin represents the decreasing influence of radiating Afrotropical forest faunas south of the Maputaland region. Parallel to this subtraction is the increasing restriction of Afrotropical faunas to the

lowlands with increasing latitude (Poynton 1961; Clancey 1994; Poynton and Boycott 1996). The tropical subtraction terminates in the Western Cape where no Afrotropical faunas enter the Cape sclerophyll area (Poynton 1961). The termination of the subtraction margin coincides with a dramatic shift in rainfall seasonality (Schulze 1997) and the 'Bedford Gap', an intrusion of semi-arid, Karoo vegetation extending from the interior to the coast and acting as an important barrier to species dispersal (Lawes 1990). The 'Bedford Gap' marks the start of a precipitous drop in species richness in the Afrotropical forests to the west (Figure 4, Cody 1983) and is a result of decreasing forest size (Cody 1983), changes in climate (Schulze 1997) and the increasing distance from 'source' populations (i.e. Eastern Cape forest refugia).

Besides the southward expansion of Afrotropical faunas in South Africa, there has also been a radiation of Afrotropical faunas into the Afrotropical forests of Mpumalanga and Limpopo Provinces (Lawes 1990). The recent (4000 BP) development of coastal lowland forests, woodlands and moist, forested riparian zones from the Mozambican coastal plain up to the escarpments of the Limpopo and Mpumalanga Provinces (Scott 1982) has resulted in the direct radiation of some Afrotropical faunas (from the Indian Ocean coastal belt forests) into the Afrotropical forest regions (Lawes 1990). Faunal assemblages in the Soutpansberg appear to have been particularly affected (significantly higher axis 1 scores) and the subspecies of Terrestrial Bulbul found in the Soutpansberg forests (*Phyllastreus terrestris intermedius*) is shared with the Mozambican coastal forests and is distinct from the Afrotropical subspecies found in the Limpopo Province Drakensberg, Mpumalanga and KwaZulu-Natal forests (Clancey 1975).

Thus, faunal assemblages in the Limpopo Province have been primarily drawn from the Afrotropical assemblages that persisted through the LGM in forest refugia on the KwaZulu-Natal scarp and, to a lesser extent, the escarpment of the Eastern Cape (Figure 9). Some assemblage supplementation by Afrotropical and matrix faunas has also taken place.

Would we expect differences in assemblage composition between the Limpopo Province Drakensberg and the Soutpansberg?

Because the scale of this study focused on trends and processes affecting assemblage composition throughout southern African forests, very little insight was gained into the potential differences in assemblage composition between the

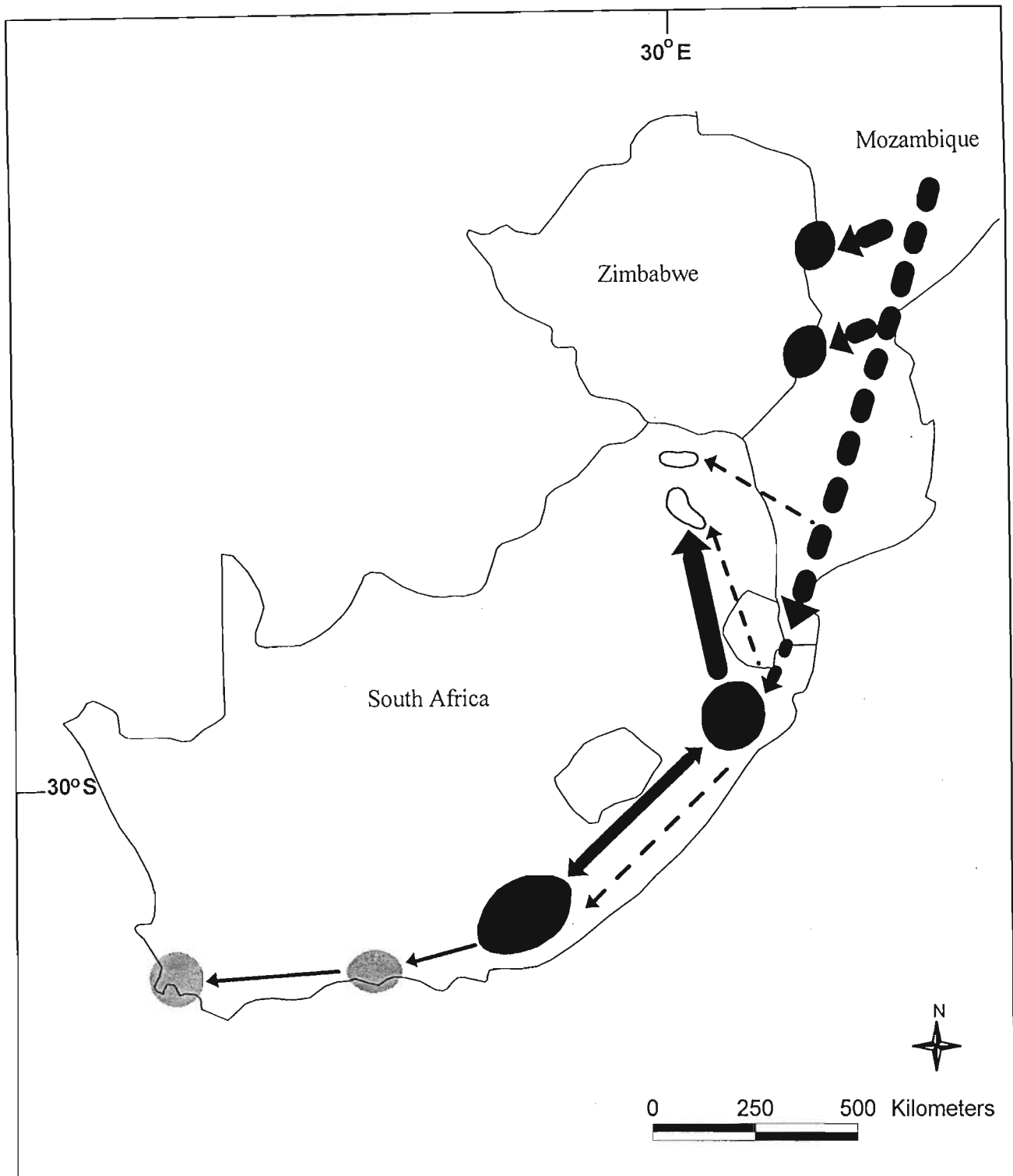


Figure 9. A summary of the post-LGM faunal radiation in southern Africa with particular emphasis on the Limpopo Province. Arrows indicate the major radiations of Afrotemperate (solid) and Afrotropical (dashed) faunas. Arrow weights represent the relative importance of radiation routes from major (black areas; birds, mammals and frogs) and minor (grey areas; frogs) refugia. The position of the Limpopo Province forest archipelagos are outlined.

Limpopo Province Drakensberg and the Soutpansberg forests. As a result, I propose the following speculative explanation for the potential differences between these two forest regions.

All forest dependent birds and frogs in the Soutpansberg are also found in the Limpopo Province Drakensberg (except for the African Broadbill *Smithornis capensis*, Table 2) as the Limpopo Province forest faunas have been principally derived from forest refugia on the KwaZulu-Natal scarp. In addition to being more distant from the KwaZulu-Natal refugia, the Soutpansberg is also separated from the Drakensberg by about 90 km of dry (~ 400-600 mm p.a., Schulze 1997) Mixed Lowveld Bushveld (Low and Rebelo 1996). The relative aridity of this zone would constitute a significant barrier to the dispersal of forest taxa.

Following the cool, dry conditions of the LGM, temperatures peaked during the Holocene altithermal (Partridge *et al.* 1990; Tyson and Partridge 2000). Conditions in northern southern Africa were still dry during the altithermal (10-20% dryer than at present) and rainfall was predominantly associated with tropical easterlies (Tyson and Lindesay 1992; Partridge 1997). As a result, the latitudinally orientated Drakensberg would have received relatively more orographic rainfall than the longitudinally orientated Soutpansberg Mountains. Consequently, at the very least, forest would have been more extensive in the Limpopo Province Drakensberg than the Soutpansberg during the Holocene altithermal.

If temperatures during the Holocene altithermal were 2°C warmer than at present (Partridge *et al.* 1990) then, considering the free air temperature lapse rate of 0.5°C per 100 m rise in altitude (Harper 1969, and references therein), vegetation belts would have been approximately 400 m higher. The Afromontane Forests of the Limpopo Province Drakensberg are concentrated above 1000 m above sea level (asl). At least 2000 ha of forest exists in the Limpopo Province Drakensberg above 1500 m asl (a very conservative estimation from 1:50 000 maps). Thus, all else being equal, at least 2500ha of forest could have persisted through the Holocene Altithermal despite a 2°C rise in temperatures. Thus, by benefiting from orographic rainfall, the Limpopo Province Drakensberg would have been relatively unaffected by climatic changes and general aridity (Partridge 1997).

On the other hand, in the Soutpansberg, Afrotropical forest is confined to above approximately 1150 m asl. Below this altitude, Afrotropical forest is

replaced by bushveld (in the relatively arid regions) and broadleaved woodland (in the humid regions in the east). Less than 100 ha of Afrotropical forest occurs above 1500 m in the Soutpansberg with almost no forest above 1550 m (the 400 m increase in contour height). It is unlikely that much Afrotropical forest persisted in the Soutpansberg through the Holocene Altithermal and bushveld expanded with the warm, dry conditions (Scott 1987). Broadleaved woodlands would have persisted in the wetter areas, particularly in the east (Entabeni and Tathe Vondo)(Scott 1987), which would have received relatively more orographic rain from tropical easterlies (Partridge 1997). Consequently, forest taxa that established after the last hypothermal must have been selectively filtered (*sensu*, Balmford 1996) during the Holocene Altithermal, favouring the persistence of species able to survive in small, isolated patches of bush and able to utilise other habitat types (habitat compensation, *sensu* Norton *et al.* 2000). Major forest expansion has only taken place in the last 6500 years (Scott 1987).

Thus, the assemblages of the Soutpansberg forests are more distant from LGM refugia, lie across a potentially significant dispersal barrier, were selectively filtered during the Holocene Altithermal and have only benefited from major forest expansion in the last 6500 years. Consequently, processes acting on a regional scale have had a greater effect on limiting faunal assemblage composition in the forests of the Soutpansberg than in the Limpopo Province Drakensberg. Thus, because of extensive filtering, faunal assemblages in the Soutpansberg are likely to be characterised by more robust and resilient taxa.

Afrotropical forest expanded in the Soutpansberg about 6000 years ago (Scott 1987) while forest probably established in the Limpopo Province Drakensberg soon after the LGM. Thus, forest faunas have had a greater period of time in which to establish in the Limpopo Province Drakensberg compared to the Soutpansberg. As a result, I suggest that not all potential colonizers have reached the Soutpansberg yet and the radiation of forest faunas into the Soutpansberg is probably still in progress.

Conclusion

Overall, southern African forest bird and frog assemblages appear to be largely unsaturated and non-interactive. Regional and historical processes, particularly forest radiation, have been fundamental in determining forest vertebrate assemblage composition.

Limpopo Province forest bird assemblage composition has been fundamentally determined by the climatic filtering of species from forests during the LGM and, the subsequent radiation of Afrotemperate faunas out of LGM forest refugia (on the KwaZulu-Natal scarp and Eastern Cape escarpment). Additional forest bird assemblage enrichment has taken place with the radiation of Afrotropical species out of the Indian Ocean coastal belt forests on the Maputaland and Mozambican coastal plains.

South African forest frog assemblage composition has been primarily determined by radiation from four areas of forest refugia (Cape Peninsula, Knysna, Eastern Cape escarpment and KwaZulu-Natal scarp) with Limpopo Province assemblages being drawn largely from KwaZulu-Natal scarp forest refugia. In addition, assemblage enrichment by matrix species has been important in the determination of assemblage composition for both forest birds and frogs.

Historical climate changes appear to have had a more recent assemblage limiting and filtering effect on faunas in the Soutpansberg than in the Limpopo Province Drakensberg. As a result, assemblages in the Soutpansberg are likely to consist of more robust and resilient taxa.

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Appendix 1: Regional distribution of the 87 grid cells used in the study of southern African bird species distribution patterns.

Region	Grid	Grid ref
Soutpansberg	Thohoyandou	2230CD
Soutpansberg	Schoemansdal	2329BA
Soutpansberg	Louis Trichardt	2329BB
Soutpansberg	Ratombo	2330AA
Limpopo Province Drakensberg	Haenertzburg	2329DD
Limpopo Province Drakensberg	Duiwelskloof	2330CA
Limpopo Province Drakensberg	Tzaneen	2330CC
Limpopo Province Drakensberg	Wolkberg/The Downs	2430AA
Mariepskop	Blyde River Canyon	2430DB
Sabie	Long Tom	2530BA
Sabie	Sabie	2530BB
Sabie	Barbeton area	2531CB
Sabie	Barbeton	2531CC
Sabie	Piggs Peak	2531CD
Maputaland	Ndumu & Border Cave	2632CC
Maputaland	Ndumu & Thembe	2632CD
Maputaland	Kosi	2632DD
Maputaland	NW KZN	2732AA
Maputaland	NW KZN	2732AB
Maputaland	Mkuze	2732CA
Maputaland	Mkuze	2732CB
Maputaland	Phinda	2732CD
Maputaland	Mtunzini & Port Durnford	2831DD
Maputaland	Fanies Island	2832AB
Maputaland	St Lucia	2832AD
Maputaland	Cape Vidal	2832BA
Northern KwaZulu-Natal scarp	Ngome	2731CD
Northern KwaZulu-Natal scarp	Eshowe	2831CD
Northern KwaZulu-Natal scarp	Ongoye	2831DC
Northern KwaZulu-Natal scarp	Hluhluwe	2832AA
Central KwaZulu-Natal coast	Pinetown	2930DD
Central KwaZulu-Natal coast	Ballito	2931CA
Central KwaZulu-Natal coast	Durban	2931CC
Central KwaZulu-Natal coast	Amanzimtoti	3030BB
Central KwaZulu-Natal coast	Pennington	3030BC
KwaZulu-Natal mistbelt / East Griqualand	Nxumeni	2929DD
KwaZulu-Natal mistbelt / East Griqualand	Karkloof	2930AC
KwaZulu-Natal mistbelt / East Griqualand	Karkloof	2930AD
KwaZulu-Natal mistbelt / East Griqualand	Pietermaritzburg	2930CB
KwaZulu-Natal mistbelt / East Griqualand	Richmond	2930CC
KwaZulu-Natal mistbelt / East Griqualand	Eston	2930CD
KwaZulu-Natal mistbelt / East Griqualand	Umzimkulu	3029BD
KwaZulu-Natal mistbelt / East Griqualand	Weza	3029DA
KwaZulu-Natal mistbelt / East Griqualand	Harding	3029DB
Southern KwaZulu-Natal scarp	Friedenow	3030AD
Southern KwaZulu-Natal scarp	Oribi	3030CB
Southern KwaZulu-Natal scarp	Umtamvuna	3030CC

Southern KwaZulu-Natal scarp	Margate	3030CD
Northern Eastern Cape (Transkei) coast	Lusikisiki	3129BC
Northern Eastern Cape (Transkei) coast	Boulder Bay	3129CB
Northern Eastern Cape (Transkei) coast	Hluleka	3129CC
Northern Eastern Cape (Transkei) coast	Coffee Bay	3129CD
Northern Eastern Cape (Transkei) coast	Port St Johns	3129DA
Northern Eastern Cape (Transkei) coast	Port Edward	3130AA
Northern Eastern Cape (Transkei) coast	Mazeppa Bay	3228BC
Northern Eastern Cape (Transkei) coast	Dwesa	3228BD
Northern Eastern Cape (Transkei) coast	Morgan's Bay	3228CB
Northern Eastern Cape (Transkei) inland	Mhlahlane & Kambi	3128BC
Southern Eastern Cape inland	Amatolas	3226DB
Southern Eastern Cape inland	Amatolas	3227CB
Southern Eastern Cape coast	East London	3227DD
Southern Eastern Cape coast	Cintsa	3228CC
Southern Eastern Cape coast	Alexandria	3326CB
Southern Eastern Cape coast	Kenton-on-sea	3326DA
Southern Eastern Cape coast	Port Alfred	3326DB
Knysna	Rondevlei	3322DC
Knysna	Farleigh & Jubilee Creek	3322DD
Knysna	Diepwalle & Gouna	3323CC
Knysna	Whiskey Creek NR	3323CD
Knysna	Tsitsikama west	3323DC
Knysna	Tsitsikama east	3323DD
Knysna	Longmore	3325CC
Knysna	Uitenhage	3325CD
Knysna	Knysna	3423AA
Knysna	Plettenberg Bay	3423AB
Swellendam	East of Montagu	3320CD
Swellendam	Barrydale	3320DC
Swellendam	Lemoenshoek	3320DD
Swellendam	Suurbraak	3420BA
Cape Peninsula	Cape Town	3418AB
Cape Peninsula	Stellenbosch	3418BB
Cape Peninsula	McGreggor	3419BB
Chimanimani	Mt Selinda	2032BB
Chimanimani	Mt Selinda	2032BC
Chimanimani	Mt Selinda	2033AA
Inyanga	Inyanga	1932BA
Inyanga	Inyanga	1932BB

Chapter 3

The importance of local processes on forest bird assemblage composition in the Limpopo Province

Introduction

Forest fragmentation has a considerable influence on bird assemblage composition and structure with fragments being less effective in the conservation of the natural biota (Blake 1991; Newmark 1991; Rolstad 1991; Bierregaard *et al.* 1992; Bierregaard and Stouffer 1997; Sieving and Karr 1997; Warburton 1997). The small populations associated with fragments have a greater chance of extinction as they are more adversely affected by genetic, demographic, and environmental fluctuations (Shaffer 1981; Soulé 1987; Templeton *et al.* 1990; Rolstad 1991). Assemblage composition in forest fragments has most frequently been explained on the basis of deterministic, local effects such as habitat area, isolation, habitat heterogeneity, patch shape and matrix effects (Newmark 1991; Laurance 1997; Warburton 1997; Lindenmayer 2000; Lindenmayer *et al.* 2002). The literature suggests that fragment area is the most important local determinant of species richness, assemblage composition and species abundance (Ambuel and Temple 1983; Blake and Karr 1984; Freemark and Merriam 1986; Van Dorp and Opdam 1987; Rolstad 1991; Wethered 2001). The diversity and density of taxa is also increased at the edge of fragments (Kroodsma 1984; Yahner 1988; Longman and Jenik 1992) while habitat heterogeneity is well-known to have an important influence on bird assemblages (MacArthur and MacArthur 1961; MacArthur *et al.* 1962; Cody 1985; Gentilli 1992). This chapter investigates the importance of local ecological factors in the determination of bird assemblage composition and structure in the Limpopo Province forests. The specific effects of forest area, isolation, and a suite of habitat variables on assemblage composition is investigated. In addition, I test for assemblage saturation as a means to understanding the effects that species interaction has on assemblage composition.

Methods

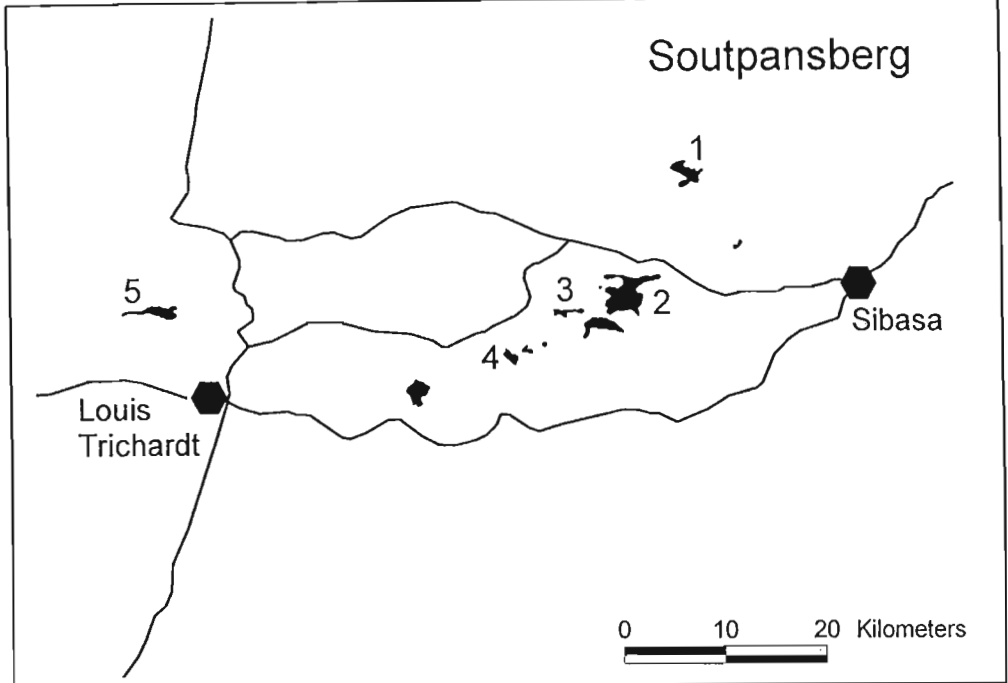
Study Area

The forests of the Limpopo Province are naturally fragmented as a result of climatic factors (Box 1981; Woodward 1987; Midgley *et al.* 1997) and the natural pattern of grassland burning in the region (Granger 1984; Geldenhuys 1994; Bond 1997). Up until about 1950, the forests of the Limpopo Province were selectively logged, mainly for *Ptaeroxylon obliquum* and *Podocarpus falcatus* (Hahn 1994). However, very little actual clearing of forests took place in the area, as plantation forestry was almost exclusively restricted to grassland areas. White (1978) and Scott (1987, referring to the Limpopo Province) independently suggest that forests may have been widely affected by man-made fires and that much forest has been converted to grassland in the last millennium. However, selective harvesting and forest clearing has probably only had a minor influence on the distribution of forests in the Limpopo Province (Hahn 1994).

The forests of the Limpopo Province are located in two isolated archipelagos along the Soutpansberg and Drakensberg escarpments (Figure 1). The Soutpansberg range lies at a latitude of 23°S and extends over a distance of approximately 160 km. Afrotropical forests in the Soutpansberg are concentrated to the east of Louis Trichardt (23°03'S 29°53'E) on the south-facing slopes of the southern-most fold of mountains between 1000 and 1600 m above sea level (asl). Long, relatively shallow, mountain slopes support an extensive ecotone between Afrotropical forest (*sensu* Tinley 1967) and Sour Lowveld Bushveld (Low and Rebelo 1996). Annual average rainfall is approximately 2000 mm in the Afrotropical Forests but is only 618 mm at the base of the escarpment in Louis Trichardt (Geldenhuys and Murray 1993; Hahn 1994). Approximately 95.6% (~ 5000 ha) of the forest in the Soutpansberg lies on State land (pers. comm. Sarah Venter: Department of Water Affairs and Forestry, DWAF) with only about 229 ha on private land (Cooper 1985). The Soutpansberg is separated from forests to the north by approximately 300 km of miombo and mopane woodland (Underwood *et al.* 1998) and, the arid Limpopo River valley (Schulze 1997). The Soutpansberg is separated from the Drakensberg to the south by a 90 km corridor of Mixed Lowveld Bushveld (Acocks 1988; Low and Rebelo 1996) at an altitude of between 500 and 700 m asl.

South Africa

Limpopo Province



Legend



1. Tathe Vondo
2. Matiwe
3. Wonderland
4. Big Ratombo
5. Hanglip
6. Woodbush
7. Samangobos
8. Essenhoutbos
9. Swartbos
10. Baccarat
11. Forest Glens

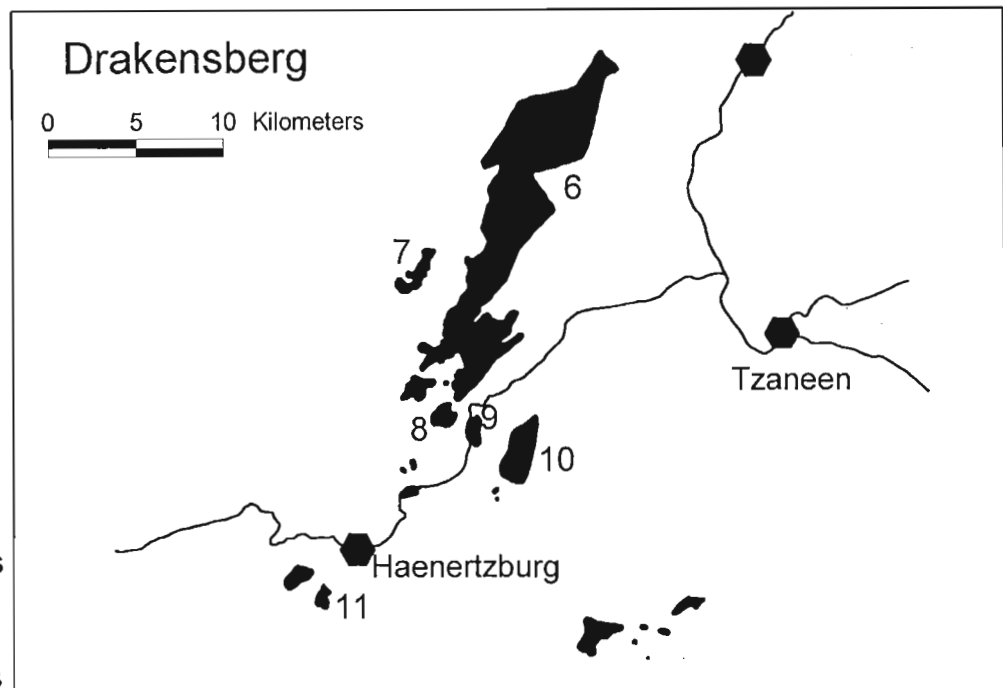


Figure 1. The distribution of forests in South Africa and the location of the larger study sites in the Soutpansberg and the Limpopo Province Drakensberg.

The northern Drakensberg escarpment lies approximately north/south with the study area being between 23°40'S and 24°20'S (approx. 30°E). The Drakensberg mountain range extends south of the study site, through Mpumalanga and KwaZulu-Natal Provinces and terminates in the Eastern Cape. Afrotemperate forests are patchily distributed along the entire mountain range (Cooper 1985). The forests are concentrated between 1200 and 1600 m asl. Almost no natural ecotone exists between Afrotemperate forests and the bushveld because steep slopes characterise the Drakensberg Escarpment and there are extensive tea and tree plantations on the lower slopes of the Limpopo Province Drakensberg.

The Department of Water Affairs and Forestry manages 10 forests in the Limpopo Province Drakensberg totalling 7387 ha – the largest being Woodbush Forest (4952 ha; pers. comm. Sarah Venter: DWAF files). About 700 ha of indigenous forest persists on private land within the Limpopo Province Drakensberg, particularly to the south of the study area (Cooper 1985).

Forests in both archipelagos have been variously classified together (Acocks 1988; Low and Rebelo 1996) and separated (Cooper 1985; Underwood *et al.* 1998; Bailey *et al.* 1999). However, the forests of the Limpopo Province Drakensberg and Soutpansberg are floristically and structurally inseparable, often with more variation within and between forests than between the two archipelagos (Geldenhuis and Venter 2002).

Patches sampled

Nine forests were sampled in the Soutpansberg ranging in size from 3ha to 1853ha. These forests were in a matrix of pine plantations (of various ages) with some forests having a portion of their boundary flanking bushveld. Fourteen forests were sampled in the northern Drakensberg (range=2 – 4952 ha). Pine plantations dominated the matrix surrounding these forests although there was also some Afrotemperate grassland in the matrix.

Patch sizes were calculated using Arcview (pers. comm. Sarah Venter: DWAF). Isolation distances of forests were taken as the shortest distance between a patch and the nearest patch of equal or greater size. Isolation distances were derived from maps (1:50 000 and 1:10 000) and by using a Garmin global positioning system.

Census techniques

Birds

Ringing studies, point counts and strip transects can all be used to estimate bird abundance in forests (Bibby *et al.* 2000). Ringing studies are generally limited to specific strata in the forest and the sampling of canopy and sub-canopy strata requires considerable effort (Bub 1991). Errors in distance estimation are less critical in line transect methods than in point counts as distance estimates are squared in point counts (Bibby *et al.* 2000). Transects are most suited to large homogenous habitats, particularly where bird populations are at low density (Gibbons *et al.* 1996). Transects are further favoured over point counts where individuals are likely to be disturbed by the observer (Gibbons *et al.* 1996) as is the case in the dense vegetation of forests (Koen 1988a).

Kelker's method of strip sampling was used (Robinette *et al.* 1974) where, at each encounter with an individual or group, the species was recorded as well as the perpendicular distance from the transect path to the individual (or centre of the group) and the number of individuals in the group. Each transect was divided into 100m sections. Species accumulation curves were plotted to determine whether sufficient transects had been completed to achieve sampling saturation. Approximately ten replicate transects were needed for adequate sampling in each forest patch (Figure 2).

Forests were sampled in Winter (July-August 2001), Spring (October-December 2001) and Summer (January-February 2002). Time and logistical constraints precluded the sampling of all forests in each season. Nevertheless, the largest forests in each region (Woodbush and Matiwe) were sampled in each season. A large enough sample of forests repeated across seasons was obtained to show that season did not significantly affect forest bird assemblage composition or abundance (Monte Carlo permutation test, Drakensberg: $F=1.274$, $P=0.275$; Soutpansberg: $F=2.271$, $P=0.105$). Thus, all samples and seasons were included in analyses.

Vegetation

Because vegetation structure is usually the most important habitat characteristic affecting birds (MacArthur and MacArthur 1961; MacArthur *et al.* 1962; Gentilli 1992;

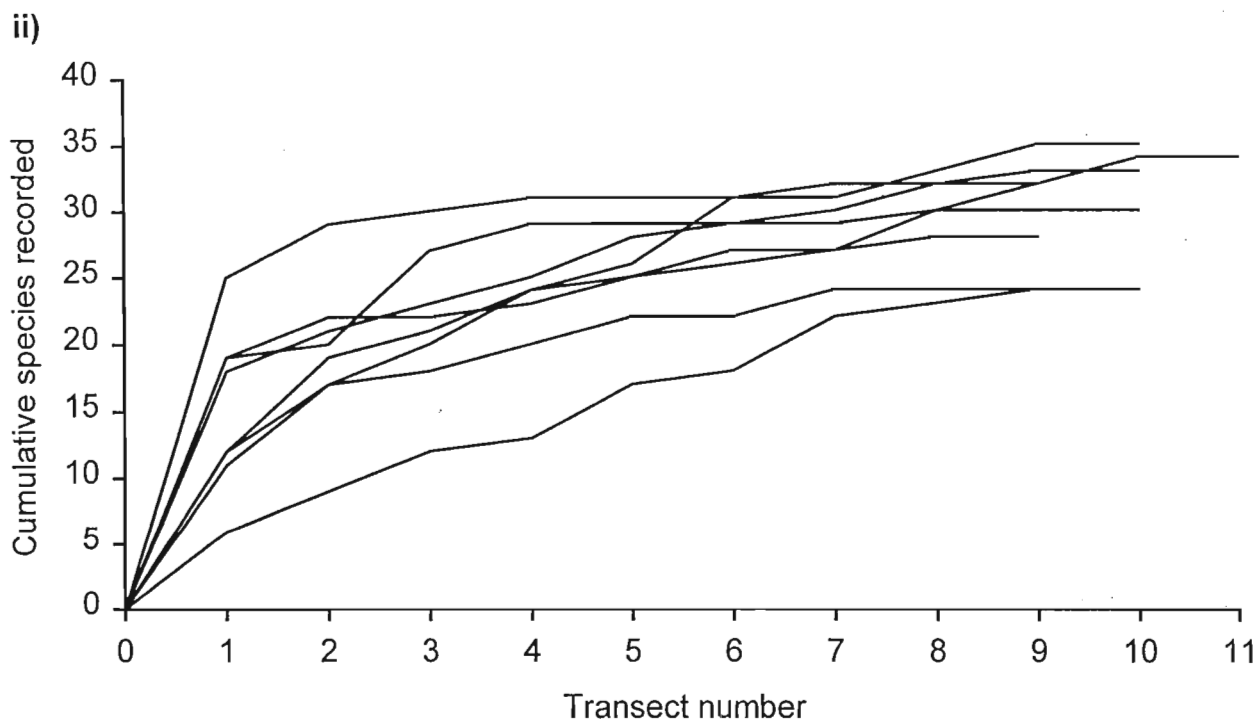
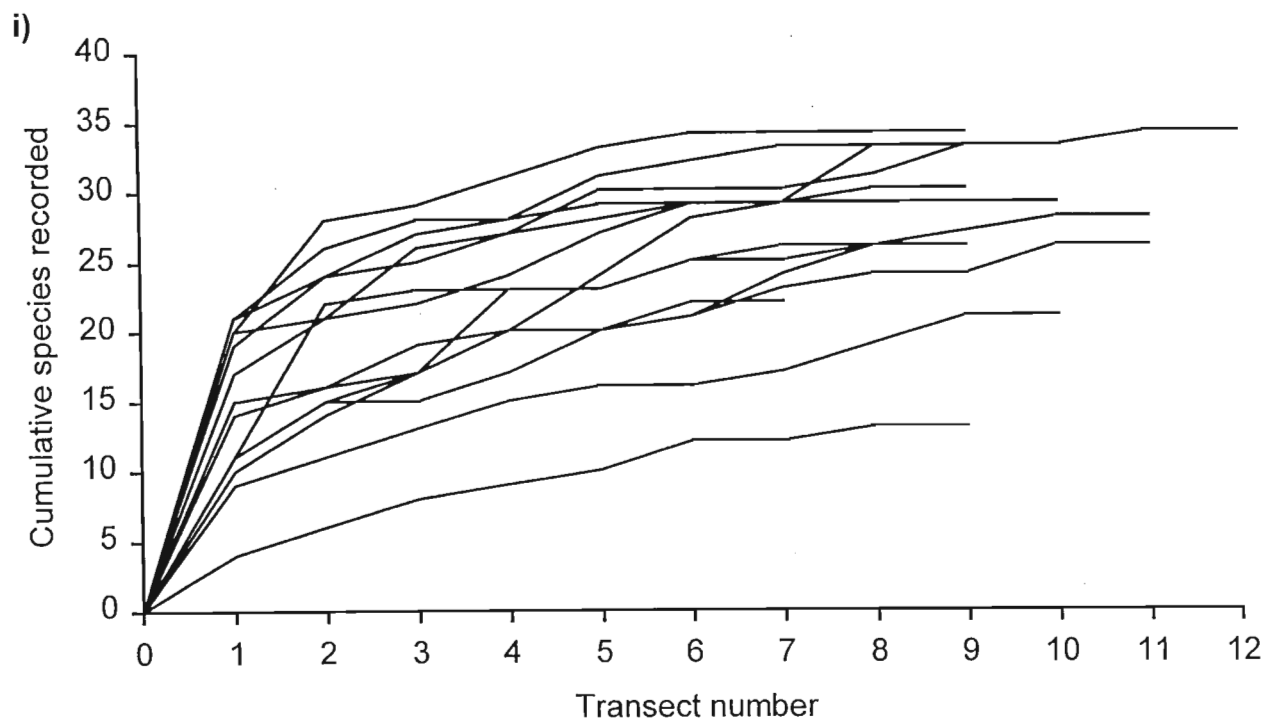


Figure 2: Cumulative species richness curves for all forests sampled in i) the Limpopo Province Drakensberg and, ii) the Soutpansberg. Curve asymptote represents the number of transects required for sampling saturation.

Allan *et al.* 1997), the structural heterogeneity of each forest was described using a habitat classification that emphasized differences in forest structure (Table 1). Habitat heterogeneity was estimated using the number and extent of habitats along each of the strip transects and Simpson's diversity index (calculated using Biodiversity Professional, McAleece 1997).

In each forest the canopy height was estimated at more than 30 arbitrarily located points along the strip transect (a minimum of 10 estimates were taken for small patches). Each patch was classified into forest type and sub-type (Geldenhuys and Venter 2002).

Table 1: Habitat classification scheme adapted from Wethered (2001).

Forest habitat categories

1	Edge habitat (the effects of the forest margin are clearly visible)
2	Old forest (large trees, high canopy, sparse undergrowth)
3	Mixed forest (both large and small trees, high canopy, well developed undergrowth)
4	Young forest (mainly small trees with low, sparse canopy)
5	Closed thicket (low, tangled bushes and vines)
6	Open thicket (tangled vegetation but with open undergrowth)
7	Small clearing (small opening in forest canopy, $\approx 10\text{m}^2$, well developed groundcover)
8	Large clearing (large opening in forest, $\geq 50\text{m}^2$ with grass and pioneer species)
9	Fallen tree
10	Stream

Data analysis

Species diversity

Shannon's and Simpson's diversity indices were used to characterize the faunal diversity of forests (Ludwig and Reynolds 1988). In addition, the evenness of the assemblage diversity was calculated using Pielou's (1977) J evenness index.

Multivariate analysis

The effects of explanatory variables on forest bird abundance and distribution has been examined using multivariate statistics (Lindenmayer *et al.* 2002; Mac Nally and Horrocks 2002; Williams *et al.* 2002). Thus, I used direct gradient analyses and Monte Carlo permutation tests to initially identify those environmental variables that have the greatest effect on bird species abundance in the Limpopo Province forests. These variables included patch area, isolation, latitude, longitude, habitat diversity, mean (and variance of) canopy height, forest class, mean altitude and season of sampling. The mean number of individuals encountered per kilometre of transect was used as a measure of bird species abundance. As both the Soutpansberg and Drakensberg forest bird assemblages showed short gradients of change (1.386 and 1.739 SD), linear analysis techniques were used to analyse the multivariate variation in the data (Ter Braak and Šmilauer 1998). All multivariate statistics and Monte Carlo permutation tests were computed using CANOCO version 4 (Ter Braak and Šmilauer 1998).

Explanatory variables determining species richness

I tested for the explanatory variables determining forest species richness using generalised linear models (GLM), based on the understanding gained from the multivariate analysis. A logarithm link function was used with the GLMs and models were tested using Genstat 5.1 (Genstat 1987). I selected the most important explanatory variables as being those that represented the greatest independent variation in a principal components analysis (eigenvalues: axis 1= 0.44, axis 2 = 0.23, CANOCO version 4, Ter Braak and Šmilauer 1998). Explanatory variables that were collinear or co-variable with those already selected were not included in further analyses. In this way, the variables log-Area, number of habitats, isolation distance and altitude, were selected for inclusion in the models. To avoid data dredging (i.e.,

repeatedly building new models using all possible combinations of variables or factors) and Type I errors, only a limited number of models were tested. Models were selected based on the results of the multivariate analysis. Patterns of bird species richness were investigated separately for the Limpopo Province Drakensberg and Soutpansberg. The most parsimonious model was selected using Akaike's Information Criterion (AIC), which balances the fit of the model against the number of parameters used in the model (Anderson and Burnham 2001). The model with the lowest AIC value and, with at least two AIC units difference from other models, was selected as the model best fitting the data (Anderson and Burnham 2001; Quinn and Keough 2002).

The species-area relationship

The relationship between species richness and forest area was compared for both archipelagos using linear least squares regression (Statistica, StatSoft 1998). The best fit model for the relationship between species richness and area was selected based on the comparison of residual mean sums of squares for the regressions of log-log (power), semi-log (exponential) and untransformed (linear) data, provided the regression fit was significant in each case.

Minimum critical patch size

The minimum critical patch size (MCPS) is that patch size above which a patch is an ecological equivalent to a mainland, and below which mainland species are lost at an accelerated pace (Bond *et al.* 1988). The MCPS can be estimated as the intercept between an island species-area regression and that for a nested sub-sample of a mainland habitat (on linear axes, Bond *et al.* 1988; on log-log axes, Wethered 2001). The mainland species-area regression was calculated using a nested series of transect segments (i.e. sub-plots) equal in length (i.e. area sampled) to those from the forest patches sampled (Connor and McCoy 1979; Coleman 1981). Nested sampling was used as the accumulation of randomly placed samples tends to overestimate the slope (Goodall 1952; Kobayashi 1974, 1976), even though nested sampling violates the assumption of independence of x-axis values (Connor and McCoy 1979).

Bird density and saturation effects

The estimation of bird density is highly problematic and has been much debated in the literature (Bibby *et al.* 2000). Because sighting probability decreases away from

the observer, I used the Fourier series distance estimator to calculate the maximum reliable perpendicular sighting distance (MRPSD) for all bird species in a forest (using Transect version 2.2, White 1988). The MRPSD was used to estimate transect width in the calculation of density (Equation 1, Altman *et al.* 1981). The MRPSD was calculated from the frequency distributions as the lower limit of the interval in which the frequency dropped by more than 50% compared with the previous interval.

$$\text{Density (individuals.ha}^{-1}\text{)} = n/2LW*10000 \quad \text{Equation 1}$$

where, n = total number of individuals seen on the transect

L = total length of transect (metres)

W = minimum reliable perpendicular sighting distance

In species-saturated assemblages, competition for resources is high such that the density of taxa is constrained by competition. Competition theory predicts that the removal of species from saturated assemblages would result in the competitive release of the remaining taxa such that a species' density is greatest in species-poor assemblages (density compensation, Wright 1980; Schoener 1988). As a result taxa in species-poor assemblages would be less constrained by competition and would thus be found at greater densities (Ås 1985; Cornell and Lawton 1992; Oberdorff *et al.* 1998). I used density compensation to test for competition effects on forest bird assemblages in both the Limpopo Province Drakensberg and the Soutpansberg.

Population density may be affected by the density of related taxa because phylogenetically similar taxa are more likely to share behaviour, morphology and ecology than less related taxa (Wethered and Lawes in prep). Thus, species density data may not be independent. As a result, an analysis of higher nodes (Harvey and Pagel 1998) was used to determine the phylogenetic level at which variation in bird species density was independent of phylogenetic effects. A hierarchical analysis of variance was used to partition the variance associated with each of four phylogenetic levels, namely; order, family, genus and species (using Statistica, StatSoft 1998). Family accounted for most of the variance (Drakensberg, 57.3%; Soutpansberg, 41.7%) and an analysis at the family level was considered to be independent of phylogenetic effects. The variance associated with lower phylogenetic levels was

attributed to additional, but not independent, evolutionary events and was discarded (Wethered and Lawes in prep). Thus, in a test of density compensation the mean density of families was regressed against the total species richness of a forest.

Because season had no significant effect on the abundance of the forest bird species in this study (Drakensberg $F=4.2$, $P=0.105$; Soutpansberg $F=3.3$, $P=0.29$), all samples were treated equally. However, one sample was excluded from the analyses (spring sample in Hanglip Forest, Soutpansberg) where a high density of fruiting *Trema orientalis* on the transect path attracted large numbers of Cape White-eye *Zosterops pallidus* into the area (creating anomalously high overall density estimates).

The insectivorous forest birds form the guild most likely to show competition effects and stratal separation (and hence density compensation) in South African forests (Earlé 1983; Koen and Crowe 1987; Koen 1988b). Cody (1983) found that not all species (and insectivores) of low-diversity assemblages are involved in density compensation but that the density of Cape White-eye decreased significantly as assemblages became more diverse. As a result, I tested for density compensation in the Cape White-eye, a species likely to respond to competitive release.

I looked for differences between the density of birds at the forest edge and core in the largest forest in order to determine whether density compensation effects are purely a result of fragment species richness or if total density is higher in small fragments because of edge effects. To test for edge effects in the largest forest (Woodbush 4952 ha), bird densities for the first 100 m leading into the forest were compared to the average density in the forest core (at least 900 m from the edge).

Results

Species diversity

In the northern Drakensberg, bird species richness was greatest in Woodbush and Baccarat Forests (34 species) with 19 and 20 forest dependent species being found in these forests, respectively (Table 2). Swartbos, Essenhoutbos and Forest Glens had the most diverse (Shannon H') and even (J' evenness) bird assemblages but Forest Glens had relatively few forest dependent bird species. Of the Soutpansberg forests, Wonderland (23°00'S 30°14.5'E), Big Ratombo and Small Ratombo held the

most diverse and even bird assemblages (Shannon's and Simpson's indices, J' evenness). However, the two Ratombo forests had relatively few forest dependent bird species compared to the 19 forest dependent species found in Wonderland. Between 24 and 35 bird species were found in each of the Soutpansberg forests, of which between 11 and 19 species were dependent on forest. Assemblages in the Soutpansberg had a greater proportion of forest associated species (mean \pm SE = 38.1 \pm 2.79%) than in the Limpopo Province Drakensberg (40.8 \pm 2.03%, t_{27} =2.86, P <0.01) suggesting that relatively more generalist matrix species have invaded forests in the Soutpansberg.

General patterns of species distribution and abundance

Forest area, the number of habitats and the proportional area of each habitat significantly affected forest bird abundance and distribution in the Limpopo Province Drakensberg (F =5.34, P =0.02; F =8.7, P =0.01; F =7.3, P =0.005, respectively). Further Monte Carlo permutation tests showed that the effects of season, latitude, longitude, altitude, isolation and canopy height (mean and variance) were not significant. Forest bird distribution and abundance in the Soutpansberg was significantly affected by longitude and isolation (F =4.8, P =0.010 and F =4.6, P =0.015, respectively) but, these had no significant effect on species richness ($F_{1,14}$ =0.004, r^2 =0.0003, P >0.5 and $F_{1,14}$ =0.06, r^2 =0.004, P >0.2, respectively). Soutpansberg forest bird abundance was not significantly affected by altitude, patch area, canopy height (mean and variance), latitude, forest type (broadleaved woodland or Afrotropical forest), Simpson's habitat diversity, proportions of each habitat, the number of habitats or season. Forest bird abundance was poorly explained by the various habitat variables, suggesting that forest bird species in the Soutpansberg may have broader habitat tolerances (habitat compensation, *sensu* Norton *et al.* 2000) than those in the Limpopo Province Drakensberg (where habitat variables had a significant effect).

Table 2: Bird species diversity in forest patches in the Limpopo Province Drakensberg and Soutpansberg. Patch area and transect length are also given. See Appendix 1 for geographical location of forests.

	Area (ha)	Transect length (m)	Species richness	Forest dependent	Shannon H'	Simpsons (1/D)	J'
Drakensberg							
Tea	2	100	13	7	0.66	2.42	0.59
Ducklands	3	200	21	10	0.85	3.81	0.64
Magic	4	100	26	12	1.14	6.80	0.81
Forbidden	4	100	22	10	1.10	7.49	0.82
Crystal Valley	8	100	28	14	1.08	5.84	0.74
Ravine	10	400	26	14	0.85	3.33	0.60
Brown Robin Rd	12	300	26	14	1.09	8.14	0.77
Swartbos	52	1100	29	18	1.15	8.11	0.79
Forest Glens	71	400	30	14	1.18	10.25	0.80
Samangobos	108	1000	33	19	0.97	4.82	0.64
Essenhout	129	600	29	16	1.24	11.96	0.85
Baccarat	309	800	34	20	1.11	6.20	0.72
Woodbush	4952	2100	34	19	1.10	7.38	0.72
Soutpansberg							
Mahogany	3	100	24	11	1.08	7.72	0.80
Spot	4	200	24	11	0.79	2.77	0.57
Small Ratombo	40	300	32	11	1.26	13.34	0.83
Corridor	60	900	34	18	1.19	10.43	0.78
Wonderland	120	900	35	19	1.26	12.61	0.82
Big Ratombo	130	1000	33	13	1.26	12.98	0.84
Hanglip	354	1100	28	11	1.12	9.35	0.77
Tathe Vondo	500	1000	30	17	1.16	8.34	0.78
Matiwe	1853	2100	32	18	1.14	9.37	0.76

Environmental determinants of species richness

Using the general patterns of bird abundance from the multivariate analysis, I selected a series of appropriate models for GLM testing of species richness gradients. The logarithm of area (alone) best explained the variation in species richness in the Limpopo Province Drakensberg forests (GLM: AIC=11.0, Weight=37.1%, chi-squared=15.2, 14df, $P < 0.001$). A more complex model (log-Area + no. habitats) was not significantly different (AIC=11.9).

The variation in species richness in the Soutpansberg was not well explained by the environmental variables (no models had significant chi-squared values). However, the logarithm of area (alone) had the lowest AIC value and approached significance (AIC=9.1, weight=31.9%, chi-squared=3.8, 11df, $P = 0.052$).

The species-area relationship

Species richness increased significantly with area in the Limpopo Province Drakensberg under linear, semi-log and log-log models (Species=0.1004Area^{0.12}, $F_{1,10}=16.6$, $r^2=0.62$, $P=0.002$). The log-log model fit the data best and had the lowest residual sums of squares (RSS: linear=204.8, semi-log=95.5, log-log=15.1, Figure 3). In the Soutpansberg, the log-log relationship accounted for 42.9% of the variation of species with area. However, this relationship was not significant ($F_{1,6}=4.5$, $P=0.078$, RSS=9.8).

Although the log-log regressions for the Soutpansberg and the Limpopo Province Drakensberg intersected, they did not differ significantly in either slope ($t=1.0$, 16df, $P > 0.2$, Zar 1984, p. 292) or elevation ($t=0.9$, 16df, $P > 0.2$, Zar 1984, p. 296). Nevertheless, the intersections of the two regressions indicates that below 196.8 ha, forests in the Soutpansberg are slightly more species rich.

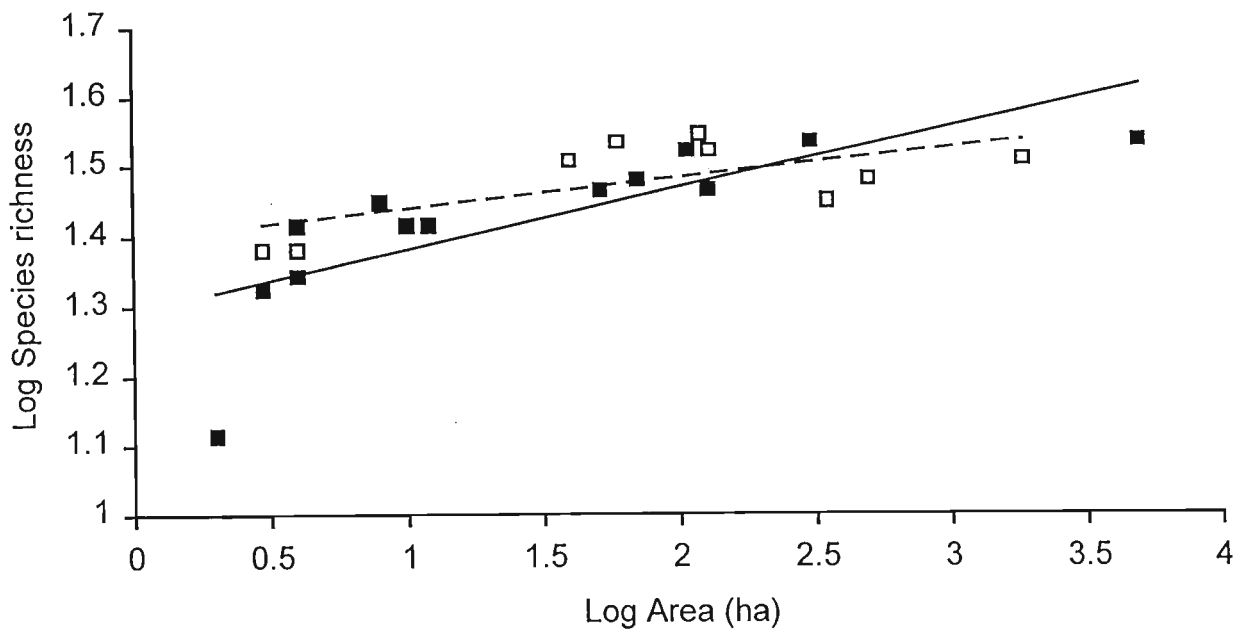


Figure 3: Species area relationships in the Limpopo Province Drakensberg (■, —) and the Soutpansberg (□, - - -) forest archipelagos.

Minimum Critical Patch Size

In the Limpopo Province Drakensberg, island effects are ecologically unimportant above 137.5 ha (MCPS; Figure 4). However, this estimate had a large standard error (SE=73.1 ha, following the delta method of Morgan 1992) mainly because many of the smaller forests had species richness values approaching that of Woodbush Forest. Thus, forests are ecological equivalents to mainlands above 137.5 ha even though they may approach equivalent species richness at lower patch size.

An estimate of minimum critical patch size for the Soutpansberg was not determined because species richness was independent of area (i.e. the slope of the species-area regression approached zero). Nevertheless, the species richness in forests above about 40-60 ha was equivalent to that of the large mainland forests (Figure 3). Species appear to be lost from fragments below about 40-60 ha.

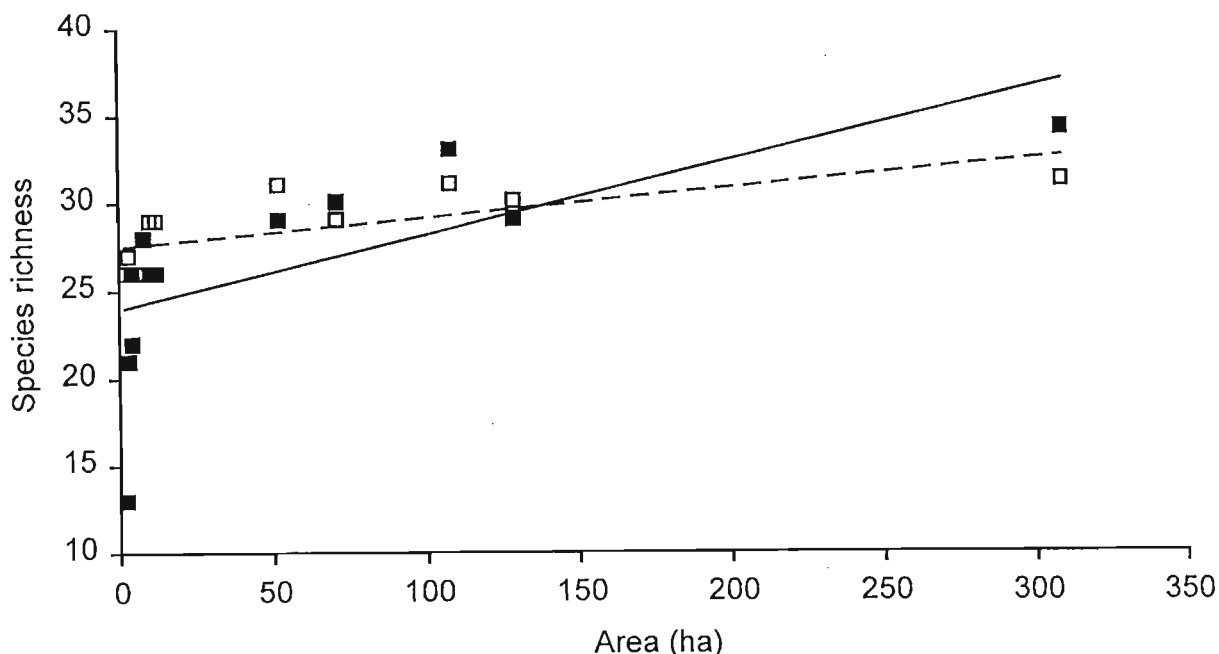


Figure 4: Minimum critical patch size determination for forests in the Limpopo Province Drakensberg. The regressions of sampled forests (■, —) and nested samples within Woodbush Forest (□, - - -) intersect at 137.5 ha.

Bird density and saturation effects

Total bird density estimates ranged from 8.36 to 44.77 ind.ha⁻¹ in the Limpopo Province Drakensberg and, from 8.28 to 31.82 ind.ha⁻¹ for forests in the Soutpansberg (Table 3). The mean (\pm SE) bird density for the largest forest in each region were 10.87 ± 2.76 ind.ha⁻¹ (Woodbush) and 12.93 ± 4.16 ind.ha⁻¹ (Matiwe), respectively.

Weak density compensation was found in the Limpopo Province Drakensberg where total bird density decreased significantly with increasing species richness, forest area and number of habitats ($F_{1,14}=7.5$, $r^2=0.35$, $P=0.016$; $F_{1,14}=5.5$, $r^2=0.28$, $P=0.034$ and; $F_{1,14}=15.1$, $r^2=0.5$, $P=0.0016$, respectively). In the Soutpansberg, total bird density decreased significantly with increasing area and habitat heterogeneity but not with increasing species richness ($F_{1,10}=6.5$, $r^2=0.40$, $P=0.029$; $F_{1,10}=6.7$, $r^2=0.40$, $P=0.027$ and; $F_{1,10}=2.4$, $r^2=0.19$, $P=0.155$, respectively).

In the Limpopo Province Drakensberg, the average density of families was significantly greater in forests that had low species richness (Figure 5), were small

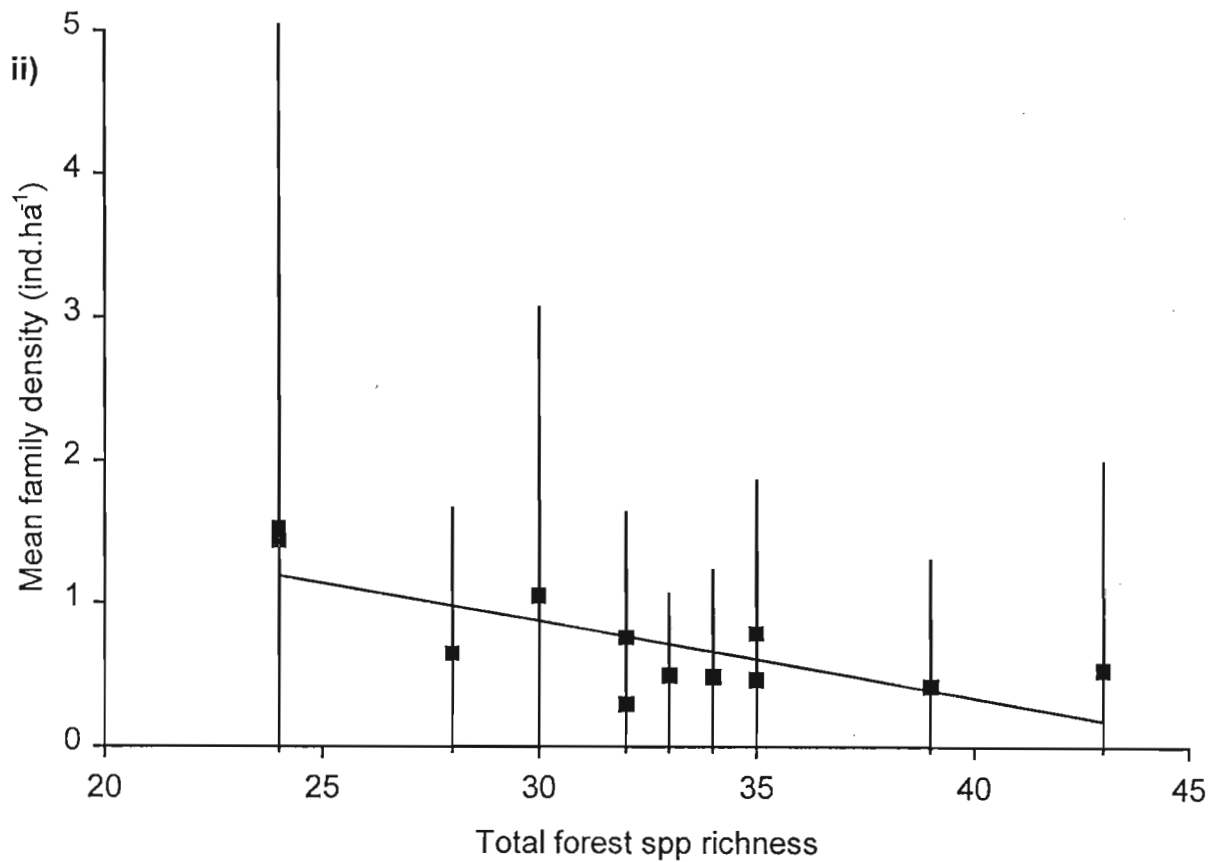
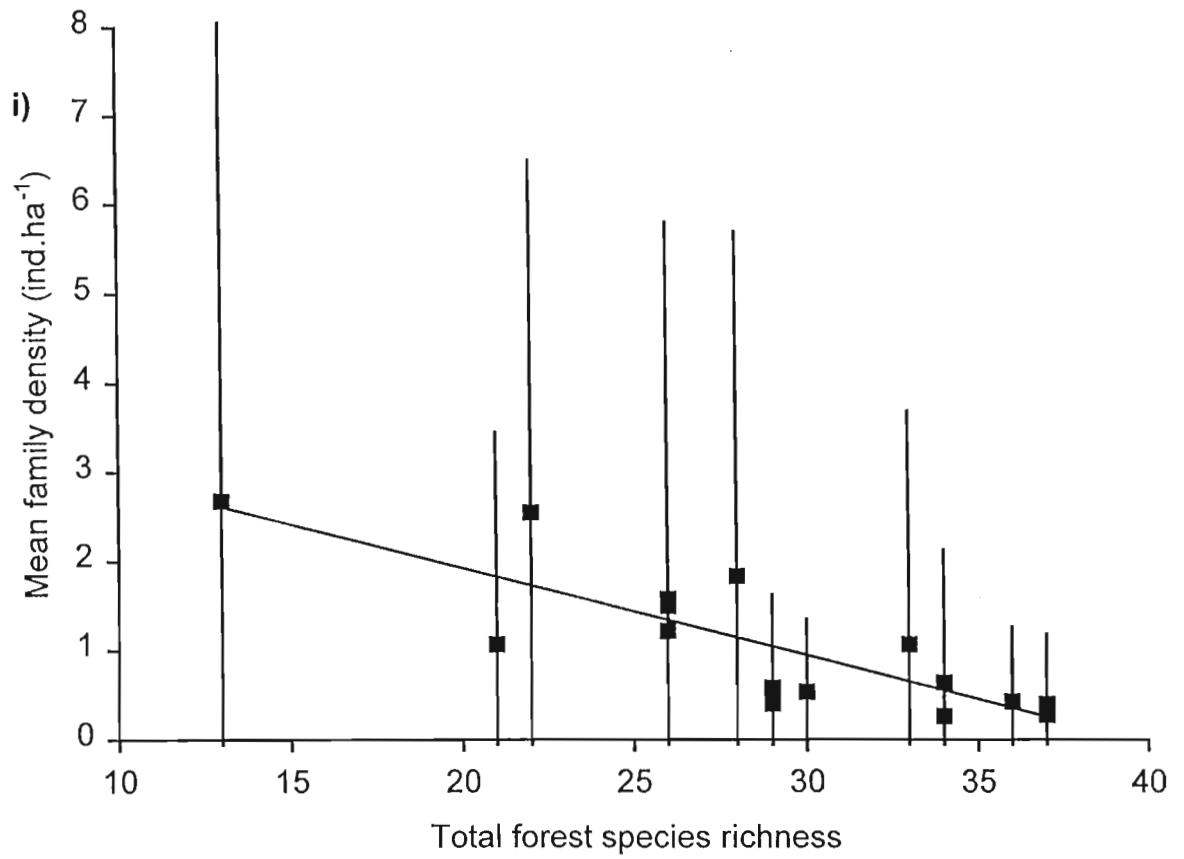


Figure 5: Mean density (\pm SE) of bird families for forest species richness in i) the Limpopo Province Drakensberg and, ii) the Soutpansberg.

Table 3: Total forest bird density estimates (ind.ha⁻¹) for forest fragments in the Limpopo Province Drakensberg and Soutpansberg.

Drakensberg	Total density (ind.ha ⁻¹)	Soutpansberg	Total density (ind.ha ⁻¹)
Tea	28.71	Mahogany	31.82
Ducklands	20.07	Spot	23.40
Magic	28.28	Small Ratombo	24.89
Forbidden	44.77	Corridor	15.31
Crystal Valley	40.73	Wonderland	23.39
Ravine	32.39	Big Ratombo	19.50
Brown Robin Rd	28.35	Hanglip	16.99
Swartbos	14.73	Tathe Vondo	29.15
Forest Glens	15.67	Matiwe	8.28
Samangobos	25.71		
Essenhoutbos	11.86		
Baccarat	17.08		
Woodbush	8.36		
Mean	24.36	Mean	21.41

and had few habitats ($F_{1,14}=30.1$, $r^2=0.68$, $P<0.001$; $F_{1,14}=22.3$, $r^2=0.61$, $P<0.001$ and, $F_{1,14}=18.2$, $r^2=0.57$, $P<0.001$, respectively). The same trend was found, but to a lesser extent, in the Soutpansberg ($F_{1,10}=12.2$, $r^2=0.55$, $P=0.006$; $F_{1,10}=19.0$, $r^2=0.66$, $P=0.001$ and, $F_{1,10}=9.3$, $r^2=0.48$, $P=0.012$, respectively). Thus, significant, but weak, density compensation was found in both archipelagos after the effects of phylogeny had been removed. This suggests that deterministic local processes operate to some degree in both archipelagos and at least some species are competitive.

The Cape White-eye formed the bulk of the total bird density estimates (Drakensberg: mean \pm SE = 33.69 \pm 12.49%, range = 18.91-63.04%, Soutpansberg: mean \pm SE = 27.61 \pm 13.09%, range = 12.84-58.97%). Thus, any Cape White-eye-specific density compensation effects are likely to be evident in an assemblage-wide analysis. The Cape White-eye appears to benefit from competitive release in the Limpopo Province Drakensberg and shows significant density compensation in that

region ($F_{1,14}=15.5$, $r^2=0.53$, $P=0.002$). The density of Cape White-eye was independent of species richness in the Soutpansberg ($F_{1,11}=0.2$, $r^2=0.02$, $P=0.65$). This explains and corroborates the finding of reduced overall density compensation in the Soutpansberg and suggests that bird assemblages in the Soutpansberg are less affected by assemblage saturation and other local determinants of assemblage composition.

Forest bird density was significantly greater at the edge of Woodbush Forest than in the forest core (winter 30.4 vs 9.5 ind.ha⁻¹, $t_{21}=6.3$, $P<0.001$ and spring 31.0 vs 11.4 ind.ha⁻¹, $t_{27}=4.7$, $P<0.001$, respectively).

Discussion

Deterministic local processes significantly affected bird assemblage composition in the Limpopo Province Drakensberg as forest area and habitat heterogeneity significantly affected forest bird abundance, distribution and species richness. The effect of local ecological processes in the Soutpansberg is less clear where none of the environmental variables had a significant effect on forest bird assemblage composition and species richness. Weak density compensation, suggesting some degree of assemblage interaction, was detected in both archipelagos but was relatively more important in the Limpopo Province Drakensberg.

Why are local processes more pronounced in the Limpopo Province Drakensberg than in the Soutpansberg?

One explanation is that regional and historical processes have had a greater effect on limiting faunal assemblage composition in the Soutpansberg forests. Climatic changes during the Quaternary filtered (*sensu* Balmford 1996) South African Afrotropical forest faunas, making contemporary assemblages less species rich but comprising more robust and resilient species (Chapter 2, Lawes *et al.* 2000). Holocene climatic changes appear to have had an additional filtering effect on forest faunas in the Soutpansberg, with major forest expansion only in the last 6500 years (Scott 1987). Thus, assemblages in the Soutpansberg are likely to be more robust and resilient than those in the Limpopo Province Drakensberg. The significantly greater proportion of generalist (forest associated) species found in the forests of the Soutpansberg ($t_{27}=2.86$, $P<0.01$) further suggests that assemblages in the

Soutpansberg have been exposed to greater extinction filtering than those in the Limpopo Province Drakensberg (Balmford 1996).

The alternative explanation is that local processes have played a greater role in the determination of bird assemblage composition in the Limpopo Province Drakensberg, despite the overwhelming role of historical processes (Chapter 2). I discuss the local processes of forest area, habitat heterogeneity and saturation effects below.

The effect of forest area on assemblage composition

A significant power relationship between species richness and patch area produced a slope of 0.12 in the Limpopo Province Drakensberg. This z value is at the lower end of MacArthur and Wilson's (1967) prediction for habitat islands ($z = 0.12-0.19$), and while being comparable to that for forest birds in East Africa ($z = 0.11$, Newmark 1991; $z=0.12$, Mlingwa *et al.* 2000), is shallower than those for other forest regions around the world (Blake and Karr 1984; Warburton 1997; Stratford and Stouffer 1999). However, as in the Australian eucalypt forests, extinction filtering has limited the number of habitat specialists and depressed the species-area relationship ($z = 0.15$, Warburton 1997).

The Limpopo Province Drakensberg z -value is, however, steeper than those for South African Afrotropical forests in the Karkloof and Amatola regions ($z = 0.05$ for both regions, Castley 1997; Wethered and Lawes in prep). The Limpopo Province, Karkloof and Amatola forests all have comparable regional species pools so the differences in slopes cannot be explained by differences in landscape species richness. The main differences lie in the species richness of small forest patches where small forests in the Limpopo Province held comparatively fewer species, thus increasing the slope of the species-area relationship. The most likely processes in reducing small patch species richness are landscape and patch disturbance effects including cattle grazing, wood collection, damage to the forest edge, dumping of wastes and agricultural practices in the matrix (Rodewald and Yahner 2001). Anthropogenic disturbance of patches would reduce the number of species in small patches while also reducing the diversity of habitats within patches (creating overall species-area and species-habitat effects)(Martin 1984; Castley 1997; Rodewald and Yahner 2001). The restrictions on species richness in small patches in the Limpopo Province Drakensberg may account for the differences with the Soutpansberg in

species-area relationship; where the small patches sampled were relatively untouched and protected within forestry estates. The reduced species area relationship in the Soutpansberg (compared to the Limpopo Province Drakensberg) can also be explained by greater extinction filtering of these faunas (Chapter 2). Although matrix effects may also affect species-area slopes (Wethered 2001), the forests sampled in both the Limpopo Province archipelagos were in a matrix of pine plantations, thus diminishing the importance of matrix effects in explaining these species-area trends.

Forests above about 137.5ha (the MCPS) represent assemblages that are the ecological equivalents of 'mainland' assemblages in the Limpopo Province Drakensberg (Wethered 2001). This MCPS is smaller than estimates for the Karkloof (302 ha), Amatola (352 ha) and Outeniqua regions (539 ha)(Wethered and Lawes in prep), primarily because of the steeper species-area relationship associated with the Limpopo Province Drakensberg forests. Thus, smaller forests are required in the Limpopo Province (compared to other South African Afrotropical forest regions) to ensure the preservation and conservation of pristine forest bird assemblages.

The effect of habitat heterogeneity on assemblage composition

Habitat structural heterogeneity is an important determinant of the bird species richness and assemblage composition in the Limpopo Province Drakensberg forests. The habitat classification scheme (Table 1) was designed to be sensitive to changes in the vertical structure of the forest. As a result, the analysis reflected the changes in assemblage composition associated with the vertical stratification of bird species in South African forests (Cody 1983; Koen 1988b; Earlé 1989). Habitat heterogeneity is well-known to have an important influence on forest bird assemblages (MacArthur and MacArthur 1961; MacArthur *et al.* 1962; Cody 1985; Gentilli 1992) for if this heterogeneity exists on a small spatial scale (as with habitats) then bird diversity would be enhanced because of subtly different habitat preferences between species (Roth 1976; Cody 1985).

The use of diversity indices in the classification of communities has drawn some criticism (Hurlbert 1971; Peet 1974) and Simpson's diversity measure, used with the habitat data, appears to be insensitive to changes in bird species richness and habitat heterogeneity (as measured by the number of habitats)(this study, Wethered 2001). Simpson's diversity index is heavily weighted towards the most

abundant habitat (Magurran 1988) and would thus have been insensitive to the relatively minor levels of additional habitats needed in order for effects to be noted in the bird assemblages.

Forest bird assemblages in the Soutpansberg were not significantly affected by forest sub-type or habitat heterogeneity and thus appear to have broader habitat tolerances than assemblages in the Limpopo Province Drakensberg. This suggests that the past filtering of bird assemblages in the Soutpansberg has resulted in resilient and robust assemblages, dominated by eurytopic bird species (Koen and Crowe 1987) with a greater proportion of generalist, forest associated species. These species would be less restricted in their habitat choice and may use alternative habitats (or habitats) when access to the preferred habitat is restricted (habitat compensation, Norton *et al.* 2000). A similar result in the Knysna forests led Koen and Crowe (1987) to suggest that floristics and vegetation structure have, at best, a minor influence on bird community structure, and that historical and biogeographic factors may be the causes of low forest bird density and diversity.

Bird density and saturation effects

The total density of forest birds in the large forests of the Limpopo Province (Woodbush = 10.87 ind.ha⁻¹ and Matiwe = 12.93 ind.ha⁻¹) was comparable with large forest estimates from Knysna (7.5-8.8 ind.ha⁻¹, Koen and Crowe 1987), the Amatolas (8.49-12.08 ind.ha⁻¹, Castley 1997), Alexandria (12.73 ind.ha⁻¹, Castley 1997) and the Karkloof (8.87 ind.ha⁻¹, Wethered 2001). South African forest bird density estimates are distinctly lower than estimates from Australia (22.5 ind.ha⁻¹, Ford and Bell 1981; 20-24 ind.ha⁻¹, Recher *et al.* 1983; 40-44 ind.ha⁻¹, Pyke and Recher 1985), New Guinea (69 ind.ha⁻¹, Bell 1980) and Kenya (69 ind.ha⁻¹, Zimmerman 1972) but similar to those for North American broad-leaved forests (10-15 ind.ha⁻¹, Udvardy 1957; cited in Pyke and Recher 1985). The low density of forest birds in South African Afrotropical forests has been attributed to irregular periods of low food production (Koen 1992) but this probably acts in conjunction with historical and biogeographic factors that continue to limit forest bird diversity and density (Koen and Crowe 1987). One consequence of these historical processes may be the coarser niche partitioning of forest bird species in South Africa, compared to other forest regions, thus limiting total bird densities in South African forests (Koen 1988b).

Weak density compensation was shown in both Limpopo Province forest archipelagos (Figure 5) and is indicative of some degree of competitive release in species-poor assemblages (McGrady-Steed and Morin 2000). More importantly, density compensation effects were more prominent in the Limpopo Province Drakensberg than in the Soutpansberg, suggesting that assemblages in the former region are more interactive and local ecological processes play a relatively greater role in the determination of assemblage composition. By inference, historical and regional processes have played a relatively greater role in determining assemblage composition in the Soutpansberg (Chapter 2).

Wethered (2001) showed significant density compensation for forest birds in the Karkloof while total bird density remained relatively constant in the Western Cape, despite a three-fold difference species richness (Cody 1983). In explanation, Cody (1983) suggests that not all species in low-diversity assemblages are involved in density compensation but that a few species (most notably the Cape White-eye) had significantly greater densities in species-poor forests. The Cape White-eye showed significant density compensation in the Limpopo Province Drakensberg but not in the Soutpansberg, further suggesting that assemblages in the Limpopo Province Drakensberg are more interactive and are more affected by local determinants of assemblage composition.

The density compensation regression (Figure 5) superficially appears to be unreliable as the estimation of mean family density had a high dispersion (SE), particularly in species-poor forests (Zar 1984; Mead *et al.* 1993). This was because while many families had higher densities in species-poor assemblages, uncommon species were still found in these assemblages, thus increasing the estimate of dispersion. However, this limitation of the statistical scope of the regression does not make the detection of density compensation any less biologically meaningful.

Total bird density was significantly greater near the forest edge than in the forest core (of Woodbush Forest 4952 ha). Because the diversity and density of taxa is increased by edge effects (Kroodsma 1984; Yahner 1988; Longman and Jenik 1992), the increase in bird density in small forest patches is, at least in part, because their ecology is dominated by edge effects. This implies that edge effects and competition are confounded and their effects on density compensation cannot be clearly separated. As a result, the insight gained from the analysis of density

compensation needs to be viewed in the context of strong evidence for unsaturated assemblages (Chapter 2) and the relatively minor role of local processes, particularly in the Soutpansberg (this chapter).

Conclusion

Local ecological processes affected forest bird assemblages in the Limpopo Province Drakensberg where species assemblages responded to forest area and habitat heterogeneity. Forest bird assemblages in the Soutpansberg were independent of all local-scale predictors tested and have been primarily determined by regional and historical processes. Weak density compensation in both archipelagos suggested some level of assemblage interaction but saturation effects were inseparable from edge effects. On balance, local processes appear to have been relatively more important for forest bird assemblages in the Limpopo Province Drakensberg than for those in the Soutpansberg. I suggest that this is a combination of greater historical filtering of Soutpansberg forest bird assemblages and anthropogenic impacts on small forests in the Limpopo Province Drakensberg, reducing the number of bird species in small forest fragments and creating area and habitat heterogeneity effects.

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Appendix 1: Geographical coordinates for forest patches sampled in the Limpopo Province Drakensberg and Soutpansberg.

	Grid reference	1:50 000 map
Drakensberg		
Tea	23°54S 30°01E	2330CC
Ducklands	23°51S 29°59E	2329DD
Magic	23°55S 29°58E	2329DD
Forbidden	23°54S 29°57E	2330CC
Crystal Valley	23°53S 29°58E	2330CC
Ravine	23°59S 30°04E	2329DD
Brown Robin Road	23°59S 30°04E	2330CC
Swartbos	23°53S 29°59E	2330CC
Forest Glens	23°58S 29°55E	2329DD
Samangobos	23°48S 29°58E	2329DD
Essenhout	23°52S 29°59E	2329DD
Baccarat	23°53S 30°01E	2329DD
Woodbush	23°50S 30°00E	2330CC
Soutpansberg		
Mahogany	23°02S 30°14E	2330AA
Spot	22°59S 30°16E	2230CD
Small Ratombo	23°02S 30°12E	2330AA
Corridor	22°59S 30°16E	2230CD
Wonderland	23°00S 30°14E	2330AA
Big Ratombo	23°02S 30°12E	2330AA
Hanglip	22°59S 29°53E	2329BB
Tathe Vondo	22°52S 30°20E	2330AA
Matiwe	22°59S 30°17E	2230CD

Chapter 4

Summary and conservation recommendations

This study investigated the relative importance of local and regional processes on forest vertebrate assemblage composition in the Limpopo Province. The Limpopo Province is a region of great biogeographical interest as the Limpopo River, to the north, acted as a significant barrier to the southward dispersal of forest vertebrates from the tropics (Poynton 1961, 1989; Clancey 1994). The study focussed primarily on birds but the regional distribution and biogeography of frogs was also considered. In addition, the conservation importance of the Limpopo Province forests in terms of all vertebrates is considered below.

Local and regional determination of assemblage composition – which is more important?

While regional (historical) processes act over large scales and determine the landscape species pool, local ecological processes determine what species are drawn from the species pool and included in assemblages (Schluter and Ricklefs 1993; Caley and Schluter 1997). To examine the relative importance of local and regional processes on assemblage composition, I tested for assemblage saturation for without assemblage saturation the role of local processes in limiting species richness in forests is diminished (Cornell 1993). Limpopo Province forest bird and frog assemblages are likely to be a consequence of regional (historical) processes as they appear to be unsaturated.

- In South African Afrotropical forests, local bird species richness is linearly dependent on regional species richness and suggests that assemblages are unsaturated (Cornell and Lawton 1992; Cornell 1993; Srivastava 1999)(Chapter 2).
- A large proportion of species in southern African forest frog and bird assemblages are matrix species, implying that empty niches in the forests have allowed generalist, matrix species to establish in forests (Begon *et al.* 1996; Beier *et al.* 2002)(Chapter 2).

- Forest frog and bird assemblages appear to hold a number of empty niches with a paucity of tree frogs, leaf litter frogs and forest floor birds (unpubl. data, Clancey 1975)(Chapter 2).
- However, weak density compensation was detected in the Limpopo Province forest bird assemblages but competition effects in density compensation could not be separated from edge effects (Chapter 3).

Forest history and faunal radiation in southern Africa – major findings

- Afrotemperate forest assemblages established in southern Africa prior to the last glacial maximum (LGM, hypothermal)(Eeley *et al.* 1999). However, major climatic changes over the last 18 000 years have been most influential in determining contemporary vertebrate assemblage structure (Lawes 1990; Eeley *et al.* 1999). The LGM resulted in extinction filtering of forest vertebrate species assemblages (Lawes 1990).
- The contemporary distribution of forest vertebrates has been primarily determined by two major radiation events in the last 18 000 years (Lawes 1990; Eeley *et al.* 1999). The first is associated with the radiation of Afrotemperate faunas out of South African LGM forest refugia. The second radiation brought Afrotropical faunas into South Africa about 8000 years ago and is associated with the southward spread of Indian Ocean coastal belt forests from East African refugia (Lawes 1990; Eeley *et al.* 1999).
- Forest faunal assemblages in the Limpopo Province have been primarily derived from Afrotemperate refugia within South Africa, particularly the KwaZulu-Natal scarp forests (Chapter 2). While of little importance to Limpopo Province forest vertebrate assemblages, other LGM refugia – of importance to South African forest assemblages – persisted in the Eastern Cape escarpment (birds, mammals and frogs), Knysna (frogs) and, the Cape Peninsula (frogs).
- Afrotropical birds and mammals have dispersed into the Limpopo Province forests from the Mozambican coastal plain (moving up forested riparian zones) and via Maputaland and the Mpumalanga escarpment forests (Lawes 1990).
- Local faunas from the matrix have also made a significant contribution to forest faunal assemblage composition in the Limpopo Province.

- Thus, regional processes have had a significant effect on the forest vertebrate assemblages in the Limpopo Province.

Local determinants of assemblage composition – major findings

- Local processes affect forest bird assemblage composition in the Limpopo Province Drakensberg where assemblage composition is affected by both forest area and habitat heterogeneity. This is most likely a consequence of the anthropogenic disturbance of small forest patches (Chapter 3).
- Local processes appear to have had little influence on forest bird assemblage composition in the Soutpansberg and none of the ecological variables tested had a significant effect on assemblage composition.
- On balance, regional and historical processes appear to have been relatively more important for forest assemblages in the Soutpansberg than for those in the Limpopo Province Drakensberg and, faunal assemblages in the Soutpansberg are characterised by more robust and resilient taxa than in the Limpopo Province Drakensberg.
- Thus, regional processes dominate vertebrate assemblage composition in the Limpopo Province while local processes play a minor role. However, the importance of local processes is likely to increase with increasing anthropogenic disturbance.

Conservation and management recommendations

Scientific management policies have traditionally focused on particular species and the local-scale processes affecting habitat patches (Pullin 2002). This is because conservation threats are more easily recognized, isolated and interpreted when acting on population or habitat levels than at landscape and regional levels. In addition, identifying and understanding local processes can lead to implementable management options. However, the effective long-term conservation of forest vertebrate assemblages requires conservation initiatives at all spatial scales and must take into account landscape and regional processes (Noss 1983; Boutin and Herbert 2002; Noss 2002; Pullin 2002). The landscape approach emphasises the conservation of habitat patches so that a mosaic of patches of different sizes, shapes and habitat features are conserved in the maintenance of a heterogeneous landscape (Noss 1983; Recher *et al.* 1987). The conservation of regional processes

requires the maintenance of evolutionary processes and radiation routes (Ricklefs and Schluter 1993; Pullin 2002).

Species level conservation considerations

Is it important to conserve the Limpopo Province forests?

The Soutpansberg and Limpopo Province Drakensberg hold a large number of endemic, geographically restricted and unusual plant species and represent botanically interesting regions (Hahn 1994; Geldenhuys and Venter 2002). Forests hold the greatest per-area diversity of threatened vertebrates of any habitat in South Africa (Castley 1997) and 10% of South Africa's threatened bird species are reliant on forests (Barnes 2000). The Soutpansberg and Limpopo Province Drakensberg constitute two of South Africa's seven regions that are most sensitive to the loss of amphibian and reptile diversity (Smithers 1986). The conservation value of the Limpopo Province forests is undeniable.

While this study has concentrated on the processes affecting bird and amphibian assemblages, the following section examines the species-level conservation importance of the Limpopo Province forests in terms of all terrestrial vertebrates. The Limpopo Province forests support a variety of threatened vertebrates (Table 1). In terms of threatened mammals, the conservation of forests in the Limpopo Province is of greatest importance to the Red Duiker and Gunning's Golden Mole (Smithers 1986; IUCN 2002), the latter of which has only been found in the forests of the Limpopo Province Drakensberg (and adjacent grasslands, IUCN 2002). The Red Duiker is common in the forests of the Soutpansberg (Stuart and Stuart 2001) but rare in the Limpopo Province Drakensberg (unpubl. data). The survival of the species in these forests (and globally) is dependent on the forests being protected from poaching, habitat alteration and habitat destruction (IUCN 2002).

While no threatened frogs or reptiles are restricted to forest in the Limpopo Province, at least five threatened reptiles are found in the immediate vicinity of the forests (Branch 1988). In addition, the forests of the Limpopo Province support large populations of the Transvaal Forest Rain Frog and the Transvaal Dwarf Chameleon

Table 1: Status of threatened vertebrates in the Limpopo Province forests (Branch 1988; Barnes 2000; IUCN 2002). Asterisks denote forest dependent species.

	Status	Species	Comments
Mammals	Vulnerable	Gunning's Golden Mole <i>Amblysomus gunningi</i>	Endemic to the LP Drakensberg
	Dependent on conservation	* Red Duiker <i>Cephalophus natalensis</i>	Common in forests and woodlands of the Soutpansberg
Frogs		No Red Data Book species	
	Of interest	Transvaal Forest Rain Frog <i>Breviceps sylvestris</i>	Common in forests and grasslands in both regions
Reptiles		No Red Data Book species	
	In the area	Woodbush Legless Skink <i>Acontophiops lineatus</i>	Endemic to the LP Drakensberg
		Woodbush Flat Gecko <i>Afroedura pondolia multiporis</i>	Endemic to the LP Drakensberg
		Soutpansberg Rock Lizard <i>Lacerta rupicola</i>	Endemic to the Soutpansberg
		Soutpansberg Flat Lizard <i>Platysaurus relictus</i>	Endemic to the Soutpansberg
		Black Whitelipped Snake <i>Amblyodipsas microphthalmalma nigra</i>	Endemic to the Soutpansberg
	Of interest	* Transvaal Dwarf Chameleon <i>Bradypodion transvaalense</i>	A common SA endemic in the Magoebaskloof area
	Birds	Endangered	* Cape Parrot <i>Poicephalus robustus</i>
Vulnerable		* Delegorgues Pigeon <i>Aplopelia larvata</i>	One record from Lekgalameetse in 1974 (Clancey 1975)
Near threatened		* African Broadbill <i>Smithornis capensis</i>	Fairly common in broadleaved woodland and riparian bushveld in the Soutpansberg
		* Orange Thrush <i>Zoothera gurneyii</i>	Fairly common in forests of both regions
		* Crowned Eagle <i>Stephanoaetus coronatus</i>	Uncommon in both regions
		Bat Hawk <i>Macheiramphus alcinus</i>	Hunts over forests of both regions
		Peregrine Falcon <i>Falco peregrinus</i>	Hunts over forests of both regions
		Lanner Falcon <i>Falco biarmicus</i>	Hunts over forests of both regions
In the area		Blue Swallow <i>Hirundo atrocaerulea</i>	A few relict pairs in the Haenertzburg grasslands
Of interest		* Blackfronted Bushshrike <i>Telophorus nigrifrons</i>	SA distribution almost entirely restricted to LP Drakensberg
		Bluespotted Dove <i>Turtur afer</i>	SA distribution restricted to the Soutpansberg (most common in Matiwe)

(unpubl. data), species that, while not threatened, may be vulnerable to habitat destruction and transformation.

Five threatened forest dependent bird species have been recorded in the Limpopo Province forests (Table 1)(Barnes 2000). A small population of the endemic Cape Parrot persists in the Limpopo Province Drakensberg. This population represents an isolate in that the closest regular population is in Karkloof, KwaZulu-Natal (Wirminghaus *et al.* 2000). No more than about 50 individuals survive in the Limpopo Province but this represents about 10% of the entire population of Cape Parrots (Wirminghaus *et al.* 2000). The conservation of Baccarat, Woodbush and Swartbos forests is essential to the survival of the Cape Parrot in the region. The illegal capture of the Cape Parrot is also a major threat to the species (Wirminghaus *et al.* 1999) and effective policing is of critical importance to the persistence of this population. The African Broadbill is fairly common in the broadleaved woodlands and riparian zones in the bushveld of the Soutpansberg. Habitat destruction is likely to be the only major threat to the persistence of this species in the Soutpansberg (Symes and Perrin 2000). The Orange Thrush requires pristine forest and is fairly common in the forests of both the Soutpansberg and Limpopo Province Drakensberg. The Orange Thrush was most abundant in Entabeni, Goedehoop, Woodbush, Swartbos and Baccarat Forests and the protection of these forests is needed to ensure its continued survival in the region. Population numbers of the Crowned Eagle appear to be low in the Limpopo Province, despite the apparent abundance of prey animals in both forest archipelagos. This may be due to persecution, but the disturbance and destruction of nest sites may be a contributing factor. The Bat Hawk, Peregrine Falcon and Lanner Falcon all nest in the vicinity of the forests and hunt over the forests (pers. obs.). The protection of these species requires a conservation effort (and ethos) that incorporates the entire region. While not threatened, the South African distributions of the Bluespotted Dove and Blackfronted Bushshrike are restricted to the Limpopo Province.

Patch level conservation considerations

Does forest area affect a forest's conservation value?

Forest area is the most important local determinant of bird assemblage composition and structure in the Limpopo Province Drakensberg and large forests (with the most species) have the greatest conservation importance and should be given the highest priority for protection (Lindenmayer *et al.* 2002). Forests above about 137.5 ha (the MCPS) represent assemblages that are the ecological equivalents of 'mainland' assemblages in the Limpopo Province Drakensberg (Wethered and Lawes in prep). In other words, forests above 137.5 ha are essential for the preservation and conservation of pristine forest bird assemblages. Other studies have shown that assemblages of smaller habitat patches are generally subsets of larger patches (Patterson and Atmar 1986; Patterson 1987; Wethered 2001). In addition, the larger forests in the Limpopo Province had more forest dependent bird species. Large forests (i.e. above the MCPS) are essential for the conservation of the full forest bird fauna of the Limpopo Province Drakensberg.

- Any reduction in forest area (through anthropogenic influences) is likely to negatively impact forest bird assemblage composition (Chapter 3).
- In the Limpopo Province Drakensberg, the conservation of all forests above the minimum critical patch size (137.5 ha) is of utmost importance. This includes Woodbush (4952 ha), Baccarat (309 ha), Kolbos (190 ha) and Helpmekaarbos (149 ha) with Essenhoutbos (129 ha), Black Forest (118 ha) and Samangobos (108 ha) approaching this size.
- Because of its large size, Woodbush Forest acts as a 'mainland' habitat in that it supports large populations of species, allowing individuals to move out to supplement and re-establish populations in other forests in the area. The physical and legislative protection of Woodbush Forest cannot be overemphasized.
- The protection of Baccarat, Swartbos and Woodbush Forests should be a priority for the conservation of the Cape Parrot, Orange Thrush, Blackfronted Bushshrike and Samango Monkey.

- No area effect was found in the Soutpansberg. However, the large forest complexes of Entabeni and Tathe Vondo should be afforded the greatest protection as these complexes support large populations of forest species.

Landscape level conservation considerations

Are small forests of any conservation value?

Lindenmayer (2000) warns that the inappropriate application of concepts such as indicator species and species-area relationships could result in poor land-use planning such as the clearing of small vegetation remnants. Small forest patches (<10ha) in the Limpopo Province still hold substantial biodiversity (Table 2 of Chapter 3) with forest fragments of 4ha holding as many as 76% of the species recorded in Woodbush Forest (Figure 4 of Chapter 3). In addition, because of density compensation, small forest fragments may support some forest bird species at greater densities than larger forests (Lindenmayer 2000; Lindenmayer *et al.* 2002). A similar finding in Australian eucalypt forests led Lindenmayer (2000, p. 37) to suggest that forest patches 'as small as 0.5 ha can have considerable value for biodiversity' and should not be cleared.

The protection of small forest fragments would provide greater landscape heterogeneity (Forman 1995) than a completely 'inhospitable sea' of matrix habitat (Armstrong 1993) and provide greater forest connectivity (Recher *et al.* 1987; Lindenmayer *et al.* 2002). Small patches acting as 'stepping-stones' or corridors would promote the recolonization and maintenance of populations in suitable habitat patches (Hobbs 1992; Simberloff *et al.* 1992; Warburton 1997; Lindenmayer 2000). This would promote the existence of a functioning meta-population as opposed to relaxing, fragmented populations (Simberloff *et al.* 1992; Hanski and Simberloff 1997). So, while the preservation of Australian eucalypt forest patches of 50-100ha (similar to Limpopo Province MCPS estimates) was essential to ensure the short to medium-term survival (40-50 years) of all species, larger forests are also essential for the continued persistence and viability of forest bird assemblages (Kavanagh *et al.* 1985).

- Forests smaller than the MCPS should not be ignored as they increase landscape connectivity by acting as potential "stepping-stones" for animal movement.

- Small forests also act as repositories of biodiversity of invertebrate and plant orders.
- Small patches probably provide important ecosystem services in both the forest and the matrix and these small patches may serve as nuclei for future ecosystem recovery (Beier *et al.* 2002).

Would the establishment of corridors be of conservation benefit?

Persuasive evidence exists that corridors can provide sufficient connectivity to improve the viability of populations in patches (Beier and Noss 1998). However, some authors have questioned the efficacy and value of corridors and have suggested various negative impacts that corridors could have on populations (Simberloff and Cox 1987; Hobbs 1992; Simberloff *et al.* 1992). One potential disadvantage is that corridors may lure individuals away from prime habitat to edge habitat where the predation and mortality risk is higher (Henien and Merriam 1990; Soulé and Gilpin 1991). However, there does not appear to be any empirical evidence for the negative impacts of corridors preserved for conservation purposes (Beier and Noss 1998).

- Riparian forests are particularly important as habitat corridors and should be at least 40 m wide (Lindenmayer 2000). However, the conservation of at least 50 m of natural bush on either side of the drainage line may be necessary as smaller reserves may be too narrow to provide the resources required by wildlife and, the vegetation is detrimentally affected by edge-effects (Recher *et al.* 1987).
- In the Limpopo Province Drakensberg, the rehabilitation of riparian zones in the Helpmekaar and Debegeni catchments should be a conservation priority.
- In the Soutpansberg, the rehabilitation of the riparian zones that connect with Matiwe, Tathe Vondo or Wonderland Forests (23°00'S 30°14.5'E) is of greatest importance as these represent the most pristine forest vertebrate assemblages.

What are the greatest threats to forest faunas?

The greatest direct threats to forest faunas in the Limpopo Province are anthropogenic in origin. Because of the large number of people in the Soutpansberg, and the past and present economic climates, some of the forests in the Soutpansberg are severely threatened by human exploitation. Common issues include the destruction of forests, the alteration of the habitat (removal of plants, bark and wood), overgrazing and poaching. Gaba, Phiphidi and Mafela Forests appear to be under the greatest pressure.

A large amount of forest persists on private land in the Limpopo Province Drakensberg (e.g. Boterfontein, Crown Mount and Goedehoop). These private forests are important for the landscape conservation of forest faunas and their destruction and alteration would pose the greatest threat to faunal assemblages in the Limpopo Province Drakensberg. The active involvement of the government (at various levels) and landowners could help stimulate a strong conservation ethos among the people of the area and would provide immeasurable conservation benefits in the development of a holistic conservation programme.

Most of the large forests in the Limpopo Province are controlled by the Department of Water Affairs and Forestry and are afforded some degree of legislative protection. However, it is important that DWAF works with private landowners to protect smaller forests in the matrix and, re-establish riparian and drainage line vegetation.

Regional conservation considerations

Can we conserve regional processes?

This study has shown that regional and historical processes have been fundamental in the determination of vertebrate assemblage composition in the Limpopo Province forests. As a result, the long-term conservation of forest assemblages must take into account these regional processes; particularly continued speciation, landscape connectivity and faunal radiation routes.

- The conservation of large forests would help ensure the persistence and long-term evolution of forest taxa.

- Keeping the major south-north radiation route from KwaZulu-Natal open would require the conservation of a complex series of Afrotropical forests along the entire northern Drakensberg escarpment. Any removal of forests along the escarpment would create unnatural, and potentially impassable, barriers to dispersal.
- In order to maintain the natural dispersal of taxa associated with the regional radiations (Figure 8 of Chapter 2), it is critically important that LGM forest refugia are protected. Of greatest importance to forest vertebrate assemblages in the Limpopo Province is the conservation of KwaZulu-Natal scarp forests while, for South African forest assemblages as a whole, forests need to be protected on the Eastern Cape escarpment, Knsyna and the Cape Peninsula.
- For assemblages in the Soutpansberg, in particular, it is important that riparian zones are protected along the Limpopo and Luvuvhu Rivers (and their tributaries). This would aid the continued radiation of Afrotropical faunas from Mozambican Indian Ocean coastal belt forests into the Limpopo Province forests. This dispersal is obviously also reliant on the protection of forests and forest faunas within Mozambique.

Conclusion

The protection and conservation of vertebrate assemblages in the Limpopo Province forests is reliant on the protection of a complex series of forests within each archipelago, representing both large (mainland) and smaller forests. Such an array would be important for the short- and medium-term conservation of biological diversity by maximising the connectivity of forests and increasing the landscape heterogeneity. In the long-term, forests along the entire northern Drakensberg escarpment and, riparian zones in the Limpopo River catchment need to be conserved in order to maintain historical dispersal routes. Conservation actions taken at the landscape and regional levels would help maintain those regional-scale processes that have been so fundamental to the determination of forest vertebrate assemblages in the Limpopo Province.

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