

# Avifaunal responses to environmental conditions and land-use changes in South Africa: diversity, composition and body size

by

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## Declaration

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I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: \_\_\_\_\_

Date: \_\_\_\_\_

## Abstract

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In macroecology, body sizes in animal assemblages have traditionally been investigated from two perspectives: body size frequency distributions (BSFDs) and geographic variation in body size. Neither of these has been investigated for the South African avifauna; one objective of this study was therefore to explore these. The regional BSFD of South African birds was found to be right-skewed, as is usually found for assemblages at large scales. This suggests that mechanisms driving the shape of BSFDs elsewhere are also acting for the South African avifauna. The Southern African Bird Atlas database was used to calculate median body sizes of avian assemblages in quarter degree grid cells. Median sizes were then used to investigate geographic variation in body size across the country. Of the mechanisms previously proposed to explain geographic variation in body size, only the starvation resistance hypothesis, which states that large size confers starvation resistance during seasonally resource shortages, was supported, though weakly, as median body size decreased with increasing productivity. The ability of null models to predict the variation in body size was subsequently explored, and it was found that much of the variation in median size of assemblages could be predicted by randomly drawing species from the regional BSFD, particularly at high species richness values. This provides empirical support for a continuum between the dominance of niche-based processes (where assemblages are a product of organisms' response to their environment) at low richness and neutral processes (where organisms assemble at random) at higher richness. In addition, it emphasizes the need to consider null expectations in investigations of the geographic variation in size. The importance of the regional BSFD and species richness for body sizes of local assemblages is highlighted.

Body size is one of several life history and community characteristics of animals that may be affected by anthropogenic disturbance to the environment. World-wide, landscapes are increasingly being altered by people, though few studies have investigated the effect of such disturbances on the avifauna of South Africa. The consequence of land-use changes on avian assemblages was therefore assessed in three South African regions which experience different environmental conditions and are threatened by different land-use changes. Birds were recorded in transects in undisturbed protected areas and the disturbed landscape outside the protected areas in the three regions. The effect of land-use change on avian assemblages varied between regions, and avian assemblages were most affected where disturbance was most intense. While species richness was not affected in a consistent manner across regions, species composition always changed in response to disturbance. This led to higher regional species richness as natural and disturbed areas supported different avian assemblages, and heterogeneity of assemblages between vegetation types usually became less pronounced in disturbed areas. Functional diversity was also compromised by land-use changes: the relative proportion of feeding guilds was altered, indicating that changes in food availability affect composition of assemblages. In contrast, mean body size of birds did not change in disturbed landscapes, which suggests that habitat architecture has little effect on body size. This study therefore highlights the importance of natural and protected areas for conserving species, assemblages and ecosystem processes.



## Opsomming

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In makro-ekologie is liggaamsgrootte van diergemeenskappe tradisioneel uit twee oogpunte ondersoek: liggaamsgrootte-frekwensieverspreidings (LGFVs) en geografiese variasie in liggaamsgrootte. Nie een van hierdie twee is al vir Suid-Afrikaanse voëls bepaal nie, en dit is dus 'n doel van hierdie studie om dit te ondersoek. Daar is gevind dat die land-wye LGFV 'n patroon van skuins na regs gewys het, soos gewoonlik die geval is vir diergemeenskappe op groot skaal. Prosesse wat die LGFV elders bepaal, is dus waarskynlik ook belangrik vir die LGFV van Suid-Afrikaanse voëls. Die Suider Afrikaanse Voël Atlas is gebruik om die mediaan van die liggaamsgrootte van voëlspesies in elke 15' x 15' vierkant te bepaal. Die waardes is gebruik om die geografiese variasie in liggaamsgrootte oor die hele land te ondersoek. Daar is al verskeie meganismes voorgestel wat geografiese variasie in liggaamsgrootte kan beïnvloed. Hier is ondersteuning, alhoewel swak, gevind (liggaamsgrootte neem toe soos produktiwiteit afneem) vir die verhongering-weerstand hipotese, wat sê dat groot liggaamsgrootte weerstand teen verhongering bied tydens tydperke van seisoenale tekortkominge. Daar is ook ondersoek hoe nul-modelle variasie in liggaamsgrootte kan voorspel, en daar is gevind dat baie van die variasie in liggaamsgrootte voorspel kon word deur spesies willekeurig vanuit die land-wye LGFV te kies. Dit was veral die geval vir gemeenskappe met hoë spesierikheid. Dít resultate verskaf empiriese steun vir 'n kontinuum tussen nis-gebaseerde prosesse (waar gemeenskappe ontstaan as gevolg van die manier hoe organismes op hulle omgewing reageer) wat by lae spesierikheid domineer, en neutrale prosesse (waar gemeenskappe willekeurig saamgestel word) wat by hoër spesierikheid domineer. Dít beklemtoon ook die noodsaaklikheid van nul-modelle in die ondersoek van geografiese variasie in liggaamsgrootte, sowel as die

belangrikheid van spesierykheid en die grootskaalse LGFV vir liggaamsgroottes in plaaslike gemeenskappe.

Liggaamsgrootte en ander kenmerke van dieregemeenskappe kan beïnvloed word deur menslike steuringe aan die omgewing. Landskappe word wêreldwyd al hoe meer deur mense verander. Daar bestaan tans min studies wat die invloed van hierdie antropogeniese steuringe op voëls in Suid-Afrika bestudeer het. Die gevolge van landskapveranderinge vir voëlgemeenskappe in drie Suid-Afrikaanse streke wat van mekaar verskil op grond van die omgewing en van landskapveranderinge is dus hier ondersoek. Voëls is getel in natuurlike bewaarde gebiede en in versteurde areas buite die bewaringsgebiede. Die invloed van landskapveranderinge op voëlgemeenskappe was verskillend in die drie streke, en die voëlgemeenskappe is meeste geaffekter waar die landskapsteuring die meeste intens was. Terwyl spesierykheid nie op 'n konsekwente manier deur landskapveranderinge beïnvloed is nie, het die samestelling van die gemeenskappe altyd verander. Die gemeenskappe in natuurlike en versteurde gebiede besit dus verskillende spesiesamestellings, wat tot hoër spesierykheid in die streke lei. Heterogeniteit in voëlgemeenskappe tussen verskillende soorte vegetasie was meestal ook minder in versteurde as in natuurlike gebiede. Die funksionele diversiteit van voëlgemeenskappe word boonop bedreig deur landskapveranderinge: in versteurde gebiede het die relatiewe proporsies van voedinggildes verander, wat aandui dat voedselbesikbaarheid die samestelling van gemeenskappe affekteer, maar die gemiddelde grootte van voëls het nie verander nie; die argitektuur van die omgewing het dus min invloed op die voëls se liggaamsgrootte. Die studie beklemtoon dus dat ongesteurde en bewaarde gebiede belangrik is om spesies, gemeenskappe en ekosisteemprosesse te bewaar.

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# Chapter 1

## General Introduction

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### **The importance of protected areas and the effect of land-use changes**

Habitat destruction and transformation are among the largest threats faced by birds (e.g. Stratford and Stouffer 1999, Castelletta et al. 2000, Wardell-Johnson and Williams 2000, Dean et al. 2002, Gaston et al. 2003, BirdLife International 2004). Given current trends in land-use practices and human population growth, there is ample reason to be concerned about the world's avifauna (Vitousek et al. 1997, Balmford et al. 2001, McKee et al. 2003, BirdLife International 2004, Gaston 2005, Davies et al. 2006). In the last three centuries, areas with the highest concentrations of endemic bird species have been disproportionately targeted for agriculture (Scharlemann et al. 2004a), the land use practice posing the largest threat to birds (Scharlemann et al. 2004b). In addition, the majority of the world's threatened species are found in developing countries (Scharlemann et al. 2004c), which are generally those that possess inadequate resources and funds to invest in conservation (Brooks and Thompson 2001, BirdLife International 2004). In South Africa (Chown et al. 2003, Evans et al. 2006b), as elsewhere in Africa (Balmford et al. 2001, Burgess et al. 2007) and the world (Gaston 2005), a positive relationship between avian species richness and human population densities exists. Given that demographic pressures constitute one of the most serious threats to the world's biota (BirdLife International 2004, Davies et al. 2006), the fact that humans have aggregated in areas that also support the highest diversity of birds is alarming.

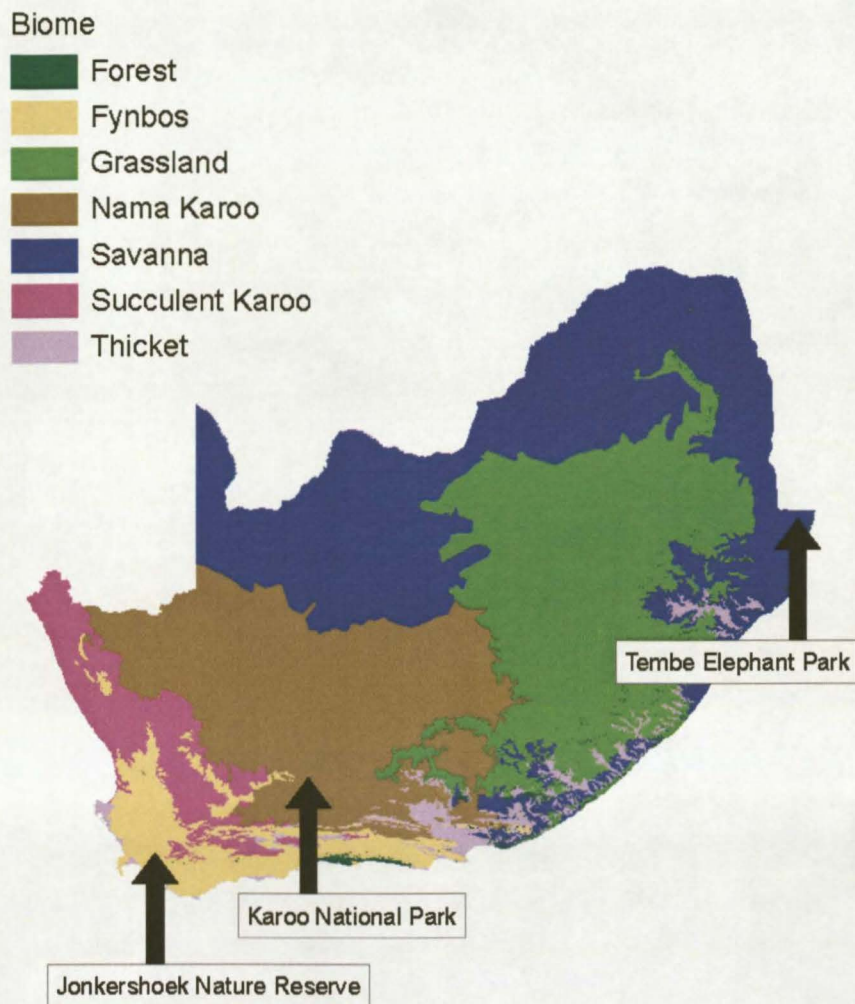
Globally, agriculture is the main source of landscape transformation (Vitousek et al. 1997, BirdLife International 2004, Foley et al. 2005). South Africa follows this world-wide trend, with the main sources of landscape transformation, in decreasing

order of importance, being cultivation, afforestation and urbanization (Fairbanks et al. 2000, Biggs and Scholes 2002). While grazing does not directly transform landscapes *per se*, it can have detrimental affects on the environment (sometimes resulting in vegetation changes) and the avifauna inhabiting it (e.g. Macdonald 1989, Herremans 1998, Hoffman et al. 1999, Zalba and Cozzani 2004). Much of South Africa's landscape is used for livestock grazing, the extent of which has been estimated to be about two-thirds of South Africa's surface (Macdonald 1989). Dense stands of invasive plants have also modified South Africa's environment considerably (see e.g. Rouget et al. 2003, Latimer et al. 2004, Richardson and van Wilgen 2004), and may pose a threat to avian diversity (Dean et al. 2002, BirdLife International 2004, Flanders et al. 2006, Ortega et al. 2006).

Few studies have assessed the effects of landscape transformation or land-use changes on South African avifauna at local scales (Armstrong and Vanhensbergen 1994, Little and Crowe 1994, Jansen et al. 1999, Dean et al. 2002, Mangnall and Crowe 2003, Schwarzenberger and Dean 2003, Little et al. 2005, Wethered and Lawes 2005), and there is a paucity of studies that compares the effects of land use on avifauna at small and large scales (Fairbanks 2004). At regional (quarter-degree grid) scale, Van Rensburg et al. (2004b) established that boundaries between transformed and untransformed landscapes are not associated with spatial turnover of avifauna. At this same scale, areas with the greatest degree of transformation or human disturbance tend to possess the lowest evenness and, contrary to expectations, the highest diversity of avifauna (Fairbanks et al. 2002, Fairbanks 2004). The increase in diversity may be a scaling effect. At small scales, heavily transformed and untransformed areas may support different bird assemblages. At the larger, quarter-degree grid cell-scale, heavily transformed areas which are interspersed with pockets of natural vegetation are classified as transformed, yet they



support birds associated with both transformed and natural landscapes (Chown et al. 2003, Fairbanks 2004).



**Figure 1.** The positions of Jonkershoek Nature Reserve, the Karoo National Park and Tembe Elephant Park and the biomes (after Low and Rebelo 1996) in which they are located.

Because species are increasingly being threatened by changes in land use, interest has grown in the success of untransformed, and, especially, protected areas at conserving ecosystems and the organisms inhabiting them (Siegfried 1989, Howard et al. 1998, Margules and Pressey 2000, Balmford et al. 2001, Bruner et al. 2001, Lovejoy 2006). While parks were historically not necessarily selected to



maximise the species conserved and have, in some instances, failed to conserve a representative proportion of the biodiversity of an area (Siegfried 1989, Wright and Mattson 1996, Margules and Pressey 2000, Yip et al. 2004), they have been valuable in maintaining viable populations of several species in areas where the landscape is otherwise much transformed or disturbed (Brooks 1999, Sánchez-Azofeifa et al. 1999, Bruner et al. 2001, Sánchez-Azofeifa et al. 2003, Evans et al. 2006a). Evans et al. (2006a) used the Southern African Bird Atlas Project (SABAP) data (Harrison et al. 1997) to assess how well South Africa's protected areas perform in conserving avian species richness. After controlling for NDVI (Normalized Difference Vegetation Index - a measure of productivity, Kerr and Ostrovsky 2003), percentage protected area was positively related to species richness of all species and of threatened species, suggesting that protected areas are important in preserving species richness.

Findings by Fairbanks (2002, 2004) and van Rensburg et al. (2004b) are contrary to those of Evans et al. (2006a): the former found that anthropogenic activities had little or a positive effect on avian species richness, while the latter suggested that richness was adversely affected by human activities. It is thus necessary to examine how land-use changes and protected areas affect the South African avifauna at smaller spatial scales (Blackburn and Gaston 2002, Cushman and McGarigal 2004). Therefore, the first major aim of this study is to ascertain how essential three very different reserves (Fig. 1) are for the protection of the avifauna of the regions within which they are embedded. One (Jonkershoek Nature Reserve) is situated in a winter rainfall, high productivity area, another (Karoo National Park) in a summer rainfall, low productivity area, and the third (Tembe Elephant Park) in a summer rainfall, high productivity region. The three regions also differ from one another in terms of the land-use changes that have taken place outside the boundaries of the reserve.

Outside Jonkershoek, *Pinus* plantations dominate; cattle, sheep and game farms (often characterized by overgrazing in the latter case) surround the Karoo National Park. Areas outside Tembe Elephant Park have mainly been transformed by subsistence farming.

### **Avian body size**

Land-use change is likely not only to influence species richness and abundance, but also the body size of birds in local assemblages (Gaston and Blackburn 1995, Cardillo and Bromham 2001). To comprehend the full extent of such changes and what might be responsible for them, it is necessary to understand what is driving body size patterns more broadly in the region. Therefore, a second major aim of this study is to investigate mechanisms that may be affecting body sizes of assemblages of South African birds.

Body size is one of the best-studied attributes of animals, and it influences or is influenced by processes at all levels of organisation (Peters 1983, Schmidt-Nielsen 1984, Blackburn and Gaston 1994, Kozłowski and Weiner 1997, Smith et al. 2004). In addition to affecting the biology of organisms, e.g. metabolic rate, transport mechanisms, organ design and functioning, and locomotion (Peters 1983, Schmidt-Nielsen 1984), body size also influences the manner in which organisms interact with their environment, perhaps most notably their energy consumption (Brown and Maurer 1989, Currie and Fritz 1993, Blackburn and Gaston 2001). Moreover, community characteristics such as abundance and diversity are also affected by body size (Griffiths 1986, Cardillo 2002). Indeed, it has been proposed that life history attributes, population interactions and ecosystem processes can all be quantitatively predicted from the 0.75 size scaling exponent of metabolic rate (Metabolic Theory of Ecology [MTE], Brown et al. 2004) – though the MTE has been

criticized on several grounds (see Cyr and Walker 2004, Tilman et al. 2004, Clarke 2006, van der Meer 2006).

Over short time periods, size-dependent behavioural responses or extinction in reaction to environmental change may affect the body sizes of species in assemblages. In terrestrial vertebrates, large species are likely to be the first species to disappear when anthropogenic pressures arise (Gaston and Blackburn 1995, McKinney 1997, Cardillo and Bromham 2001, Gaston and Evans 2004), although it has been reported that large birds are mainly threatened by human-related hunting and predation, while habitat destruction is posing the greatest threat to small species (Owens and Bennett 2000). Unfortunately, size-selective disappearance of species does not only affect these species, but may result in cascading effects on other components of communities as food web construction is perturbed (Woodward et al. 2005).

Over longer time periods, body sizes may evolve in response to the conditions species experience (McKinney 1990). Larger animals generally possess a smaller surface-area volume ratio, through which heat or water is lost and gained slower than for large animals (Schmidt-Nielsen 1984). It has therefore long been suggested that the size of animals, especially homeotherms, evolves in response to the climatic conditions they experience (Bergmann 1847, James 1970, Ashton et al. 2000). Selection on body size also takes place as a consequence of the quality and predictability of food supplies and extent of seasonal variation (McKinney 1990). In addition, avian body size may be associated with habitat structure. In benthic ecosystems, the correlation between habitat architecture and body sizes has been relatively well explored (Robson et al. 2005), while the relationship between body size and habitat preference in vertebrates has been poorly researched. In Mediterranean woods, average body mass of birds increased in thinned forest stands

(De la Montaña et al. 2006). Body mass frequency distributions (Bakker and Kelt 2000), gaps in distributions (Holling 1992, but see Siemann and Brown 1999, Leaper et al. 2001) and mean sizes (Tellería and Carrascal 1994, Polo and Carrascal 1999) of organisms living in differently structured environments have been explained by environmental architecture. However, based on analyses conducted at the biome scale, Siemann and Brown (1999) contested the idea that vegetation structure affects body size structure, and suggested that instead size is influenced by continental-scale processes.

Species-body size frequency distributions are one of a number of measures related to animal body size that have enjoyed considerable attention in the literature (e.g. Lindsey 1966, van Valen 1972, May 1978, Brown and Maurer 1989, Brown and Nicoletto 1991, Chown and Gaston 1997, Polo and Carrascal 1999, Bakker and Kelt 2000, Kozłowski and Gawelczyk 2002, Smith et al. 2004, Allen et al. 2006). They quantify how many species of different body size classes comprise an assemblage. The shape of the species-body size distribution seems to depend on the scale at which studies are conducted. Analyses of a wide variety of taxa have indicated that, at global or continental scales, body size distributions are right-skewed, i.e. most species are small, but not of the smallest body size class (May 1978, 1988, Brown and Maurer 1989, Blackburn and Gaston 1994, Gaston and Blackburn 2000, Smith et al. 2004, Storch and Gaston 2004). At regional or local spatial scales, however, the distribution of species-body size is very variable. In many cases (see Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000 for exceptions) they differ from what would be expected if the species were a random draw from the broader-scale species pool (Gaston and Blackburn 2000). While some local- or regional-scale distributions simply exhibit less right skew than larger scale distributions (Bakker and Kelt 2000, Cardillo 2002), others show no modality (Brown

and Nicoletto 1991, Bakker and Kelt 2000, Aava 2001), are bimodal (Griffiths 1986, Gaston and Blackburn 2000), left-skewed (Bakker and Kelt 2000), or unimodal without skew (Maurer et al. 1992, Arita and Figueroa 1999, Bakker and Kelt 2000).

Because there is no consistent manner in which species-body size distributions change when examined at increasingly smaller scales, it is difficult to determine what generates these changes (Gaston and Blackburn 2000), although some hypotheses have been proposed. Brown and Nicoletto (1991), for example, speculated about the cause of the dissimilarities in body size distributions they obtained at different scales (right-skewed at continental-scale, uniform at patch-scale and intermediate at biome-scale). They suggested that three mechanisms act to generate these body size distributions. 1) Competition between similar-sized organisms prevents them from co-existing in the same local environment. Body size distributions at small scales are thus more uniform than expected by chance. 2) The likelihood of extinction is great for large species occupying small ranges: because large species have high energy requirements, they forage more extensively and thus occur at low densities. 3) Animals of the modal size class have undergone specialization. The animals in these size classes have small range sizes and exhibit high species turnover, which, the authors propose, is a factor of size-specific constraints on physiology and energetics: smaller organisms possess higher mass-specific nutritional demands and require better quality food than larger animals due to their lower mass-specific gut capacity and gut retention time. Therefore, small animals are required to specialise on high quality food, which constrains them to forage only within a small area where the food they have specialized on is located. The mode of the species body size distributions is always situated at small size categories at a regional scale, while at a local scale there is little overlap of ranges of specialized species, resulting in a uniform size distribution. One of the criticisms of this model is that distributions at smaller spatial

scales are not always different from what would be expected from a random draw from a larger species pool (Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000). In addition, the model fails to explain the decrease in the frequency of the smallest body size values (Brown and Nicoletto 1991).

Several other hypotheses have been proposed to explain right-skewed body size frequency distributions (Gaston and Blackburn 2000, Allen et al. 2006). Brown et al. (1993) suggested that 'reproductive power', the rate at which resources are turned into reproduction, drives body size evolution, and that an optimum body mass exists at which reproductive power is maximized. It is this body mass which is the modal size in body size frequency distributions. This model has been criticized on several grounds (see Blackburn and Gaston 1996, Chown and Gaston 1997, Gaston and Blackburn 2000, Kozłowski 2002), including the absence of the effect of mortality on life history evolution (Kozłowski and Weiner 1997), the questionability of the existence of an optimum size (Blackburn and Gaston 1996, Gaston and Blackburn 2000), and the inability to predict the shape of the distribution of sizes around the so-called optimum (Blackburn and Gaston 1996).

By contrast, Kozłowski and colleagues (Kozłowski and Weiner 1997, Kozłowski and Gawelczyk 2002) proposed that a range of optimum body sizes exists. Optimal size depends not only on energy requirements for investing in growth and reproduction, but also on size-dependent mortality. A trade-off exists between 1) being small, investing little energy into growth and much energy into reproduction, but possessing high mortality, and 2) investing much energy into growth, reproducing less frequently, but possessing lower mortality. The variation that exists in organisms' energy requirements and mortality rates generates a right-skewed species-body size distribution in large assemblages, and, as the variation in body size decreases, distributions become more log-normal (Kozłowski and Weiner 1997, Kozłowski and

Gawelczyk 2002). For tests of this (and the previous) model, assumptions are made about the values of constants used in the simulations, which may have affected the results obtained. A further problem with model is the lack of explanation offered for size distributions of small assemblages, which are frequently non-random samples of distributions at larger scales (Gaston and Blackburn 2000).

The fractal nature of the environment, providing more space for smaller organisms to inhabit and allowing more small than large species to co-exist (Hutchinson and MacArthur 1959, Morse et al. 1985), size-biased extinctions (Maurer et al. 1992), and constraint on the evolution of small species (McKinney 1990, McShea 1994) have also been implicated in the development of right-skewed body size frequency distributions, although these hypotheses have also been questioned on a variety of grounds (Maurer 1998, Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002, Allen et al. 2006).

In the second chapter I therefore investigate the factors that may be influencing median size and, in less detail, other size variables of bird assemblages in South Africa at the regional scale. Initially, only the effects of environmental factors which have traditionally been thought to be major determinants of body size (e.g. Bergmann 1847, James 1970, Lindstedt and Boyce 1985, Blackburn et al. 1999, Blackburn and Hawkins 2004, Jones et al. 2005) on median size are investigated. Subsequently, the ability of null models to predict body size patterns is examined. This provides an indication of the contribution of the regional body size frequency distribution to the local size frequency distribution.

## **Birds and Landscapes**

South Africa has shown to be a useful location for testing ideas in ecology. In addition to the above-mentioned studies (Fairbanks et al. 2002, Fairbanks 2004,



Evans et al. 2006a), several other investigations of South Africa's avifauna have been undertaken to evaluate ideas or patterns that have relevance for other regions or other taxa. For example, the effectiveness of data from different levels of sampling intensity for reserve selection based on complementarity was assessed using the South African avifauna (Gaston and Rodrigues 2003) – reserve selection was found to be effective even when sampling intensity was poor. In light of the fact that conservation prioritization is frequently based on certain groups of species or taxa, Bonn et al. (2002) assessed the efficacy of endemic and threatened for predicting the biodiversity of all birds. Although areas selected on the basis of endemic or threatened species perform better than areas selected at random, they fail to capture some patterns of overall biodiversity. The effects of expected climate change on the geographic ranges of several species, including birds, have been investigated with climate envelope models, which predict that a general eastward shift of species ranges (Erasmus et al. 2002), but also range contractions (Simmons et al. 2004) will occur. A further study found that selected environmental variables, particularly temperature seasonality and variability, explained a considerable amount of the variation in the distribution and abundance of bird species in the arid Karoo of South Africa (Githaiga-Mwicigi et al. 2002). In a similar vein, Van Rensburg et al. (2002) investigated the contribution of several climatic variables and habitat heterogeneity to the variability in avian species richness at different spatial scales. They concluded that richness is probably a function of several variables, the importance of which varies at different spatial scales. In addition, a positive relationship between avian species richness and human population density has been observed (Chown et al. 2003), though change in population size over a five-year period was unrelated to avian species richness (Evans et al. 2006b). Based on data of the South African



avifauna, methods to estimate bird abundances (Kemp et al. 2001) and predicting species occurrence (Osborne and Tigar 1992) have also been developed.

It has been suggested that vegetation is the major driver of avian distributions in South Africa (Winterbottom 1978, van Rensburg et al. 2004b), and vicariance events have had little effect on the distribution of the South African avifauna (Hockey et al. 2005). South Africa has indeed experienced a relatively stable geological and climatic history (Hockey et al. 2005). However, the current climate and vegetation vary considerably across the country (see Figure 1, Rutherford and Westfall 1986, Low and Rebelo 1996, Schulze 1997), and much of the distribution of the vegetation is determined by climatic conditions, particularly rainfall seasonality and summer aridity (Rutherford and Westfall 1986). The central and western parts of the region receive little and unpredictable rainfall and the vegetation lacks structural complexity, while the eastern areas of the country predominantly comprise grasslands and savannas (Rutherford and Westfall 1986, Low and Rebelo 1996, Schulze 1997). The Mediterranean-type Fynbos biome, dominated by shrubs, is mainly situated in the south-western parts of the country, where it receives winter rainfall, and thus experience hot, dry summers (Cowling and Richardson 1995, Low and Rebelo 1996). Some small forest pockets are found in the southern and eastern regions, and subtropical thicket, which is dominated by succulent and sclerophyllous trees and lacks a grassy understory, occupies parts of the southern and eastern parts of the country (Low and Rebelo 1996).

Within the context of their environment, birds perform a variety of ecological functions (Şekercioğlu 2006). They act as pollinators (Anderson et al. 2005, Ortega-Olivencia et al. 2005, Wester and Claßen-Bockhoff 2006) and seed dispersers (Bas et al. 2006, Dennis and Westcott 2006, McEuen and Curran 2006), and perform vital roles in nutrient cycling (Lindeboom 1984, Post et al. 1998). They form important

links between trophic processes (Şekercioğlu 2006) – e.g. raptors as top predators (Korpimäki and Norrdahl 1998, Mitani et al. 2001), insectivores as regulators of insect populations (Mols and Visser 2002, Van Bael and Brawn 2005) and scavengers as recyclers of carcasses (Dean and Milton 2003, DeVault et al. 2003). Some bird species also function as ecosystem engineers, generating biotic or abiotic modifications in their environment which affect the resource availability of other organisms (Casas-Crivillé and Valera 2005, Sinclair and Chown 2006).

These and other factors make birds popular environmental indicators: they are also an easily identified and well-studied taxon, and their mobility enables comparative studies to be conducted at relatively large scales (Furness et al. 1993, but see Hilty and Merenlender 2000, Moore et al. 2003). Multi-species studies are especially effective at establishing how communities are impacted by their environment (Hilty and Merenlender 2000), and it has been predicted that bird declines will have significant ecological repercussions due to the loss of ecological functions (Bond 1994, Şekercioğlu et al. 2004).

For the southern African avifauna, the Southern African Bird Atlas (Harrison et al. 1997) provides detailed information about the distribution of the region's avifauna. It was compiled from data collected from 1987-1992. Voluntary observers used score cards to record the bird species they detected within a month in quarter-degree grid cells of South Africa. Several large-scale studies have been conducted using the SABAP data (e.g. Osborne and Tigar 1992, Berruti et al. 1994, Allan et al. 1997, Wessels et al. 2000, Bonn et al. 2002, Erasmus et al. 2002, Fairbanks et al. 2002, Githaiga-Mwicigi et al. 2002, van Rensburg et al. 2002, Chown et al. 2003, Gaston and Rodrigues 2003, Fairbanks 2004, van Rensburg et al. 2004a, van Rensburg et al. 2004b, Evans et al. 2006a, Evans et al. 2006b). Given all these factors, the South African avifauna makes an appropriate taxon to examine the subjects set out above.

## References

- Aava, B. 2001. Primary productivity can affect mammalian body size frequency distributions. *Oikos* **93**:205-212.
- Allan, D. G., J. A. Harrison, R. A. Navarro, B. W. van Wilgen, and M. W. Thompson. 1997. The impact of commercial afforestation on bird populations in Mpumalanga Province, South Africa - insights from bird-atlas data. *Biological Conservation* **79**:173-185.
- Allen, C. R., A. S. Garmestani, T. D. Havlicek, P. A. Marquet, G. D. Peterson, C. Restrepo, C. A. Stow, and B. E. Weeks. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* **9**:630-643.
- Anderson, B., W. W. Cole, and S. C. H. Barrett. 2005. Specialized bird perch aids cross-pollination. *Nature* **435**:41-42.
- Arita, H. T., and F. Figueroa. 1999. Geographic patterns of body-mass diversity in Mexican mammals. *Oikos* **85**:310-319.
- Armstrong, A. J., and H. J. Vanhensbergen. 1994. Comparison of avifaunas in *Pinus radiata* habitats and indigenous riparian habitat at Jonkershoek, Stellenbosch. *South African Journal of Wildlife Research* **24**:48-55.
- Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? *American Naturalist* **156**:390-415.
- Bakker, V. J., and D. A. Kelt. 2000. Scale-dependent patterns in body size distributions of neotropical mammals. *Ecology* **81**:3530-3547.
- Balmford, A., J. L. Moore, T. Brooks, N. Burgess, L. A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. *Science* **291**:2616-2619.
- Bas, J. M., P. Pons, and C. Gómez. 2006. Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season. *Plant Ecology* **183**:77-89.

- Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* **3**:595-708.
- Berruti, A., J. A. Harrison, and R. A. Navarro. 1994. Seasonal migration of terrestrial birds along the southern and eastern coasts of southern Africa. *Ostrich* **65**:54-65.
- Biggs, R., and R. J. Scholes. 2002. Land-cover changes in South Africa 1911-1993. *South African Journal of Science* **98**:420-424.
- BirdLife International. 2004. State of the world's birds 2004: indicators for our changing world, 1st edition. BirdLife International, Cambridge, U.K.
- Blackburn, T. M., and K. J. Gaston. 1994. Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution* **9**:471-474.
- Blackburn, T. M., and K. J. Gaston. 1996. On being the right size: different definitions of 'right'. *Oikos* **75**:551-557.
- Blackburn, T. M., and K. J. Gaston. 2001. Linking patterns in macroecology. *Journal of Animal Ecology* **70**:338-352.
- Blackburn, T. M., and K. J. Gaston. 2002. Scale in macroecology. *Global Ecology and Biogeography* **11**:185-189.
- Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* **5**:165-174.
- Blackburn, T. M., and B. A. Hawkins. 2004. Bergmann's rule and the mammal fauna of northern North America. *Ecography* **27**:715-724.
- Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London B* **344**:83-90.

- Bonn, A., A. S. L. Rodrigues, and K. J. Gaston. 2002. Threatened and endemic species: are they good indicators of patterns of biodiversity on a national scale? *Ecology Letters* **5**:733-741.
- Brooks, M. 1999. Effects of protective fencing on birds, lizards, and black-tailed hares in the western Mojave Desert. *Environmental Management* **23**:387-400.
- Brooks, T., and H. S. Thompson. 2001. Current bird conservation issues in Africa. *The Auk* **118**:575.
- Brown, J. H., J. F. Gilgooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* **85**:1771-1789.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* **142**:573-584.
- Brown, J. H., and B. A. Maurer. 1989. Macroecology: The division of food and space among species on continents. *Science* **243**:1145-1150.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist* **138**:1478-1512.
- Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. d. Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* **291**:125.
- Burgess, N. D., A. Balmford, N. J. Cordeiro, J. Fjelds , W. K per, C. Rahbek, E. W. Sanderson, J. P. W. Scharlemann, J. H. Sommer, and P. H. Williams. 2007. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation* **134**:164-177.
- Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecology and Biogeography* **11**:59-65.

- Cardillo, M., and L. Bromham. 2001. Body size and risk of extinction in Australian mammals. *Conservation Biology* **15**:1435-1440.
- Casas-Crivillé, A., and F. Valera. 2005. The European bee-eater (*Merops apiaster*) as an ecosystem engineer in arid environments. *Journal of Arid Environments* **60**:227-238.
- Castelletta, M., N. S. Sodhi, and R. Subaraj. 2000. Heavy extinctions of forest avifauna in Singapore: lessons for biodiversity conservation in Southeast Asia. *Conservation Biology* **14**:1870-1880.
- Chown, S. L., and K. J. Gaston. 1997. The species-body size distribution: energy, fitness and optimality. *Functional Ecology* **11**:365-375.
- Chown, S. L., B. J. van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13**:1233-1241.
- Clarke, A. 2006. Temperature and the metabolic theory of ecology. *Functional Ecology* **20**:405-412.
- Cowling, R. M., and D. M. Richardson. 1995. Fynbos. South Africa's Unique Floral Kingdom, 1st edition. Fernwood Press, Vlaeberg.
- Currie, D. J., and J. T. Fritz. 1993. Global patterns of animal abundance and species energy use. *Oikos* **67**:56-68.
- Cushman, S. A., and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* **14**:1090-1105.
- Cyr, H., and S. C. Walker. 2004. An illusion of mechanistic understanding. *Ecology* **85**:1802-1804.

- Davies, R. G., C. D. L. Orme, V. Olson, G. H. Thomas, S. G. Ross, T.-S. Ding, P. C. Rasmussen, A. J. Stattersfield, P. M. Bennett, T. M. Blackburn, I. P. F. Owens, and K. J. Gaston. 2006. Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society B* **273**:2127-2133.
- De la Montaña, E., J. M. Rey-Benayas, and L. M. Carrascal. 2006. Response of bird communities to silvicultural thinning of Mediterranean maquis. *Journal of Applied Ecology* **43**:651-659.
- Dean, W. R. J., M. D. Anderson, S. J. Milton, and T. A. Anderson. 2002. Avian assemblages in native *Acacia* and alien *Prosopis* drainage line woodland in the Kalahari, South Africa. *Journal of Arid Environments* **51**:1-19.
- Dean, W. R. J., and S. Milton. 2003. The importance of roads and road verges for raptors and crows in the Succulent and Nama-Karoo, South Africa. *Ostrich* **74**:181-186.
- Dennis, A. J., and D. A. Westcott. 2006. Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia* **149**:620-634.
- DeVault, T. L., O. E. J. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**:225-234.
- Erasmus, B. F. N., A. S. van Jaarsveld, S. L. Chown, M. Kshatriya, and K. J. Wessels. 2002. Vulnerability of South African animal taxa to climate change. *Global Change Biology* **8**:679-693.
- Evans, K. L., A. S. L. Rodrigues, S. L. Chown, and K. J. Gaston. 2006a. Protected areas and regional avian species richness in South Africa. *Biology Letters* **2**:184-188.

- Evans, K. L., B. J. van Rensburg, K. J. Gaston, and S. L. Chown. 2006b. People, species richness and human population growth. *Global Ecology and Biogeography* **15**:625-636.
- Fairbanks, D. H. K. 2004. Regional land-use impacts affecting avian richness patterns in Southern Africa - insights from historical avian atlas data. *Agriculture, Ecosystems and Environment* **101**:269-288.
- Fairbanks, D. H. K., M. Kshatriya, A. S. van Jaarsveld, and L. G. Underhill. 2002. Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* **5**:61-74.
- Fairbanks, D. H. K., M. W. Thompson, D. E. Vink, T. S. Newby, H. M. van den Berg, and D. A. Everard. 2000. The South African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science* **96**:69-82.
- Flanders, A. A., W. P. Kuvlesky, D. C. Ruthven, III, R. E. Zaiglin, R. L. Bingham, T. E. Fulbright, F. Hernández, and L. A. Brennan. 2006. Effects of invasive exotic grasses on South Texas rangeland breeding birds. *Auk* **123**:171-182.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. *Science* **309**:570-574.
- Furness, R. W., J. J. D. Greenwood, and P. J. Jarvis. 1993. Can birds be used to monitor the environment? Pages 1-41 *in* R. W. Furness and J. J. D. Greenwood, editors. *Birds as Monitors of Environmental Change*. Chapman & Hall, London.



- Gaston, K. J. 2005. Biodiversity and extinction: species and people. *Progress in Physical Geography* **29**:239-247.
- Gaston, K. J., and T. M. Blackburn. 1995. Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society of London B* **347**:205-212.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and Process in Macroecology*, 1st edition. Blackwell Science, Oxford.
- Gaston, K. J., T. M. Blackburn, and K. Klein Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. *Proceedings of the Royal Society of London B* **270**:1293-1300.
- Gaston, K. J., and K. L. Evans. 2004. Birds and people in Europe. *Proceedings of the Royal Society of London B* **271**:1649-1655.
- Gaston, K. J., and A. S. L. Rodrigues. 2003. Reserve selection in regions with poor biological data. *Conservation Biology* **17**:188-195.
- Githaiga-Mwicigi, J. M. W., D. H. K. Fairbanks, and G. Midgley. 2002. Hierarchical processes define spatial pattern of avian assemblages restricted and endemic to the arid Karoo, South Africa. *Journal of Biogeography* **29**:1067-1087.
- Griffiths, D. 1986. Size-abundance relations in communities. *American Naturalist* **127**:140-166.
- Harrison, J. A., D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker, and C. J. Brown, editors. 1997. *The Atlas of Southern African Birds*, 1st edition. BirdLife South Africa, Johannesburg.
- Herremans, M. 1998. Conservation status of birds in Botswana in relation to land use. *Biological Conservation* **86**:139-160.
- Hilty, J., and A. Merenlender. 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation* **92**:185-197.

- Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. 2005. Roberts Birds of Southern Africa, 7th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hoffman, M. T., B. Cousins, T. Meyer, A. Petersen, and H. Hendricks. 1999. Historical and contemporary land use and the desertification of the Karoo. Pages 257-273 in W. R. J. Dean and S. J. Milton, editors. The Karoo. Ecological Patterns and Processes. Cambridge University Press, Cambridge.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* **62**:447-502.
- Howard, P. C., P. Viskanic, T. R. B. Davenport, F. W. Kigenyi, M. Baltzer, C. J. Dickinson, J. S. Lwanga, R. A. Matthews, and A. Balmford. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**:472-475.
- Hutchinson, G. E., and R. H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. *American Naturalist* **93**:117-125.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* **51**:365-390.
- Jansen, R., R. M. Little, and T. M. Crowe. 1999. Implications of grazing and burning of grasslands on the sustainable use of francolins (*Francolinus* spp.) and on overall bird conservation in the highlands of Mpumalanga province, South Africa. *Biodiversity and Conservation* **8**:587-602.
- Jones, J., C. E. Gibb, S. C. Millard, J. J. Barg, M. K. Girvan, M. L. Veit, V. L. Friesen, and R. J. Robertson. 2005. Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. *Journal of Biogeography* **32**:1827-1833.

- Kemp, A. C., J. J. Herholdt, I. Whyte, and J. Harrison. 2001. Birds of the two largest national parks in South Africa: a method to generate estimates of population size for all species and assess their conservation ecology. *South African Journal of Science* **97**:393-403.
- Kerr, J. T., and M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution* **18**:299-305.
- Korpimäki, E., and K. Norrdahl. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* **79**:2448-2455.
- Kozłowski, J. 2002. Theoretical and empirical status of Brown, Marquet and Taper's model of species-size distribution. *Functional Ecology* **16**:540-542.
- Kozłowski, J., and A. T. Gawelczyk. 2002. Why are species' body size distributions usually skewed to the right? *Functional Ecology* **16**:419-432.
- Kozłowski, J., and J. Weiner. 1997. Interspecific allometries are by-products of body size optimization. *American Naturalist* **149**:352-380.
- Latimer, A. M., J. A. Silander, A. E. Gelfand, A. G. Rebelo, and D. M. Richardson. 2004. Quantifying threats to biodiversity from invasive alien plants and other factors: a case study from the Cape Floristic Region. *South African Journal of Science* **100**:81-86.
- Leaper, R., D. Raffaelli, C. Emes, and B. Manly. 2001. Constraints on body-size distributions: an experimental test of the habitat architecture hypothesis. *Journal of Animal Ecology* **70**:248-259.
- Lindeboom, H. J. 1984. The nitrogen pathway in a penguin rookery. *Ecology* **65**:269-277.
- Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* **20**:456-465.

- Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* **125**:873-878.
- Little, I. T., R. M. Little, R. Jansen, and T. M. Crowe. 2005. Winter bird assemblages, species richness and relative abundance at a re-vegetated coal mine in the Middelburg district, Mpumalanga province, South Africa. *South African Journal of Wildlife Research* **35**:13-22.
- Little, R. M., and T. M. Crowe. 1994. Conservation implications of deciduous fruit farming on birds in the Elgin district, Western Cape Province, South Africa. *Transactions of the Royal Society of South Africa* **49**:185-198.
- Lovejoy, T. E. 2006. Protected areas: a prism for a changing world. *Trends in Ecology and Evolution* **21**:329-333.
- Low, A. B., and A. G. Rebelo, editors. 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- Macdonald, I. A. W. 1989. Man's role in changing the face of southern Africa. Pages 51-77 *in* B. J. Huntley, editor. *Biotic Diversity in Southern Africa*. Oxford University Press, Oxford.
- Mangnall, M. J., and T. M. Crowe. 2003. The effects of agriculture on farmland bird assemblages on the Agulhas Plain, Western Cape, South Africa. *African Journal of Ecology* **41**:266-276.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-253.
- Marquet, P. A., and H. Cofré. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos* **85**:299-309.
- Maurer, B. A. 1998. The evolution of body size in birds. I. Evidence for non-random diversification. *Evolutionary Ecology* **12**:925-934.

- Maurer, B. A., J. H. Brown, and R. D. Rusler. 1992. The micro and macro in body size evolution. *Evolution* **46**:939-953.
- May, R. M. 1978. The dynamics and diversity of insect faunas. Pages 188-204 *in* L. A. Mound and N. Waloff, editors. *Diversity of Insect Faunas*. Blackwell Scientific Publications, Oxford.
- May, R. M. 1988. How many species are there on earth? *Science* **241**:1441.
- McEuen, A. B., and L. M. Curran. 2006. Plant recruitment bottlenecks in temperate forest fragments: seed limitation and insect herbivory. *Plant Ecology* **184**:297-309.
- McKee, J. K., P. W. Sciulli, C. D. Foose, and T. A. Waite. 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* **115**:161-164.
- McKinney, M. L. 1990. Trends in body-size evolution. Pages 75-118 *in* K. J. McNamara, editor. *Evolutionary Trends*. The University of Arizona Press, Tucson.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics* **28**:495-516.
- McShea, D. W. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* **48**:1747-1763.
- Mitani, J. C., W. J. Sanders, J. S. Lwanga, and T. L. Windfelder. 2001. Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* **49**:187-195.
- Mols, C. M. M., and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology* **39**:888-899.

- Moore, J. L., A. Balmford, T. Brooks, N. D. Burgess, L. A. Hansen, C. Rahbek, and P. H. Williams. 2003. Performance of sub-Saharan vertebrates as indicator groups for identifying priority areas for conservation. *Conservation Biology* **17**:207-218.
- Morse, D. R., J. H. Lawton, M. M. Dodson, and M. H. Williamson. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* **314**:731-733.
- Ortega, Y. K., K. S. McKelvey, and D. L. Six. 2006. Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird. *Oecologia* **149**:340-351.
- Ortega-Olivencia, A., T. Rodriguez-Riaño, F. J. Valtueña, J. López, and J. A. Devesa. 2005. First confirmation of a native bird-pollinated plant in Europe. *Oikos* **110**:578-590.
- Osborne, P. E., and B. J. Tigar. 1992. Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *Journal of Applied Ecology* **29**:55-62.
- Owens, I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences of the United States of America* **97**:12144-12148.
- Peters, R. H. 1983. *The Ecological Implications of Body Size*, 1st edition. Cambridge University Press, New York.
- Polo, V., and L. M. Carrascal. 1999. Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related. *Journal of Animal Ecology* **68**:324-337.

- Post, D. M., J. P. Taylor, J. F. Kitchell, M. H. Olson, D. E. Schindler, and B. R. Herwig. 1998. The role of migratory waterfowl as nutrient vectors in a managed wetland. *Conservation Biology* **12**:910-920.
- Richardson, D. M., and B. W. van Wilgen. 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? *South African Journal of Science* **100**:45-52.
- Robson, B. J., L. A. Barmuta, and P. G. Fairweather. 2005. Methodological and conceptual issues in the search for a relationship between animal body-size distributions and benthic habitat architecture. *Marine and Freshwater Research* **56**:1-11.
- Rouget, M., D. M. Richardson, R. M. Cowling, J. W. Lloyd, and A. T. Lombard. 2003. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* **112**:63-85.
- Rutherford, M. C., and R. H. Westfall. 1986. The biomes of southern Africa - an objective categorization. *Memoirs of the Botanical Survey of South Africa* **54**.
- Sánchez-Azofeifa, G. A., G. C. Daily, A. S. P. Pfaff, and C. Busch. 2003. Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. *Biological Conservation* **109**:123-135.
- Sánchez-Azofeifa, G. A., C. Quesada-Mateo, P. Gonzalez-Quesada, S. Dayanandan, and K. S. Bawa. 1999. Protected areas and conservation of biodiversity in the tropics. *Conservation Biology* **13**:407-411.
- Scharlemann, J. P. W., R. E. Green, and A. Balmford. 2004a. Agricultural land has expanded six-fold since 1700 and Endemic Bird Areas have suffered disproportionately. Page 32 *in* BirdLife International, editor. State of the

World's Birds 2004: Indicators for our Changing World. BirdLife International, Cambridge.

Scharlemann, J. P. W., R. E. Green, and A. Balmford. 2004b. Agricultural expansion is a major threat to birds, and appears to be increasing in importance. Page 33 *in* BirdLife International, editor. State of the World's Birds 2004: Indicators for our Changing World. BirdLife International, Cambridge.

Scharlemann, J. P. W., R. E. Green, and A. Balmford. 2004c. More species are threatened in the developing world than in the developed world. Page 50 *in* BirdLife International, editor. State of the World's Birds 2004: Indicators for our Changing World. BirdLife International, Cambridge.

Schmidt-Nielsen, K. 1984. Scaling. Why is Animal Size so Important?, 1st edition. Cambridge University Press, New York.

Schulze, R. E. 1997. South African Atlas of Agrohydrology and -Climatology. Report TT82/96, Water Research Commission, Pretoria.

Schwarzenberger, A., and W. R. J. Dean. 2003. The influence of vegetation structure on bird communities in a Karoo village, South Africa. *Ostrich* **74**:209-216.

Şekercioğlu, Ç. H. 2006. Increasing awareness of avian ecological function. *Trends in Ecology and Evolution* **21**:464-471.

Şekercioğlu, Ç. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* **101**:18042-18047.

Siegfried, W. R. 1989. Preservation of species in southern African nature reserves. Pages 186-201 *in* B. J. Huntley, editor. *Biotic Diversity in Southern Africa*. Oxford University Press, Oxford.

Siemann, E., and J. H. Brown. 1999. Gaps in mammalian body size distributions reexamined. *Ecology* **80**:2788-2792.



- Simmons, R. E., P. Barnard, W. R. J. Dean, G. F. Midgley, W. Thuiller, and G. Hughes. 2004. Climate change and birds: perspectives and prospects from southern Africa. *Ostrich* **75**:295-308.
- Sinclair, B. J., and S. L. Chown. 2006. Caterpillars benefit from thermal ecosystem engineering by wandering albatrosses on sub-Antarctic Marion Island. *Biology Letters* **2**:51-54.
- Smith, F. A., J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, E. A. Hadly, K. E. Jones, D. M. Kaufman, P. A. Marquet, B. A. Maurer, K. J. Niklas, W. P. Porter, B. Tiffney, and M. R. Willig. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *American Naturalist* **163**:672-691.
- Storch, D., and K. J. Gaston. 2004. Untangling ecological complexity on different scales of space and time. *Basic and Applied Ecology* **5**:389-400.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* **13**:1416-1423.
- Tellería, J. L., and L. M. Carrascal. 1994. Weight-density relationships between and within bird communities: implications of niche space and vegetation structure. *American Naturalist* **143**:1083-1092.
- Tilman, D., J. Hillerislambers, S. Harpole, R. Dybzinski, J. Fargione, C. Clark, and C. Lehman. 2004. Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology* **85**:1797-1799.
- Van Bael, S. A., and J. D. Brawn. 2005. The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests. *Oecologia* **143**:106-116.

- van der Meer, J. 2006. Metabolic theories in ecology. *Trends in Ecology and Evolution* **21**:136-140.
- van Rensburg, B. J., S. L. Chown, and K. J. Gaston. 2002. Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist* **159**:566-577.
- van Rensburg, B. J., B. F. N. Erasmus, A. S. van Jaarsveld, K. J. Gaston, and S. L. Chown. 2004a. Conservation during times of change: correlations between birds, climate and people in South Africa. *South African Journal of Science* **100**:266-272.
- van Rensburg, B. J., P. Koleff, K. J. Gaston, and S. L. Chown. 2004b. Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* **31**:843-854.
- van Valen, L. 1972. Body size and number of plants and animals. *Evolution* **27**:27-35.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494-499.
- Wardell-Johnson, G., and M. Williams. 2000. Edges and gaps in mature karri forest, south-western Australia: logging effects on bird species abundance and diversity. *Forest Ecology and Management* **131**:1-21.
- Wessels, K. J., B. Reyers, and A. S. van Jaarsveld. 2000. Incorporating land cover information into regional biodiversity assessments in South Africa. *Animal Conservation* **3**:67-79.
- Wester, P., and R. Claßen-Bockhoff. 2006. Bird pollination in South African *Salvia* species. *Flora* **201**:396-406.
- Wethered, R., and M. J. Lawes. 2005. Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. *Biological Conservation* **123**:125-137.

- Winterbottom, J. M. 1978. Birds. Pages 949-979 *in* M. J. A. Werger, editor. Biogeography and Ecology of Southern Africa. Dr W. Junk bv Publishers, The Hague.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* **20**:402-409.
- Wright, R. G., and D. J. Mattson. 1996. The origin and purpose of national parks and protected areas. Pages 1-14 *in* R. G. Wright and J. Lemons, editors. National Parks and Protected Areas: Their Role in Environmental Protection. Blackwell Science, Massachusetts.
- Yip, J. Y., R. T. Corlett, and D. Dudgeon. 2004. A fine-scale gap analysis of the existing protected area system in Hong Kong, China. *Biodiversity and Conservation* **13**:943-957.
- Zalba, S. M., and N. C. Cozzani. 2004. The impact of feral horses on grassland bird communities in Argentina. *Animal Conservation* **7**:35-44.

## Chapter 2

### Geographic variation in body size of the South African avifauna, and the use of deterministic and neutral models in assessing this variation

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#### Introduction

Body size variation has traditionally been investigated from two perspectives: body size frequency distributions (BSFDs) and geographic variation in body size. At large geographic scales, BSFDs of terrestrial vertebrates tend to be right log-skewed (Brown and Nicoletto 1991, Gaston and Blackburn 1995, Marquet and Cofré 1999, Gaston and Blackburn 2000), while at smaller spatial scales they are more variable, ranging from right-skewed to log-normal and bimodal (Brown and Nicoletto 1991, Maurer et al. 1992, Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000, Gaston and Blackburn 2000, Aava 2001). BSFDs also become more variable at lower taxonomic levels (Chown and Gaston 1997, Maurer 1998, Kozłowski and Gawelczyk 2002). Several studies have investigated how well random draws from regional species body size distributions predict patterns in local BSFDs (Brown and Nicoletto 1991, Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000). Whilst BSFDs of some assemblages can be predicted by a random draw from the regional body size distribution (Brown and Nicoletto 1991, Arita and Figueroa 1999, Marquet and Cofré 1999), in other assemblages BSFDs are less right-skewed than expected from regional distributions (Brown and Nicoletto 1991, Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000).

Geographic variation in body size is typically investigated by exploring the existence and form of such variation and then by testing the underlying mechanisms

that have been proposed to explain it. Although the identification of geographic patterns in body size and the subsequent exploration of mechanisms underlying that variation are interlinked, as are pattern and process investigations in all macroecological investigations, distinguishing the two remains important (Lomolino et al. 2006), especially in the context of spatial variation in body size (Blackburn et al. 1999). Bergmann's rule (Bergmann 1847), or the increase of body size with latitude, is probably the most commonly tested ecological 'rule' relating body size to geographic variation in the environment (see Blackburn et al. 1999, Ashton et al. 2000, Meiri and Dayan 2003). Debate about the precise definition of the rule is common for several reasons. A failure to distinguish pattern from process is one of the most significant causes of the debate (James 1970, Blackburn et al. 1999). Bergmann attributed the latitudinal body size cline to a decrease of temperature with increasing body size. Some authors have thus interpreted Bergmann's rule as an increase in body size with decreasing temperature (Wigginton and Dobson 1999, Ashton et al. 2000, Freckleton et al. 2003, Meiri and Dayan 2003, Rodríguez et al. 2006), which really describes one potential mechanism underlying the pattern. Another source of contention surrounding Bergmann's rule is the taxonomic level at which latitudinal body size variation is measured (James 1970, Blackburn et al. 1999). Although Bergmann was referring to interspecific differences in body size between closely related species when he formulated his hypothesis (James 1970), tests of latitudinal body size clines have been extended to various other taxonomic levels (see Blackburn et al. 1999 for a discussion thereof).

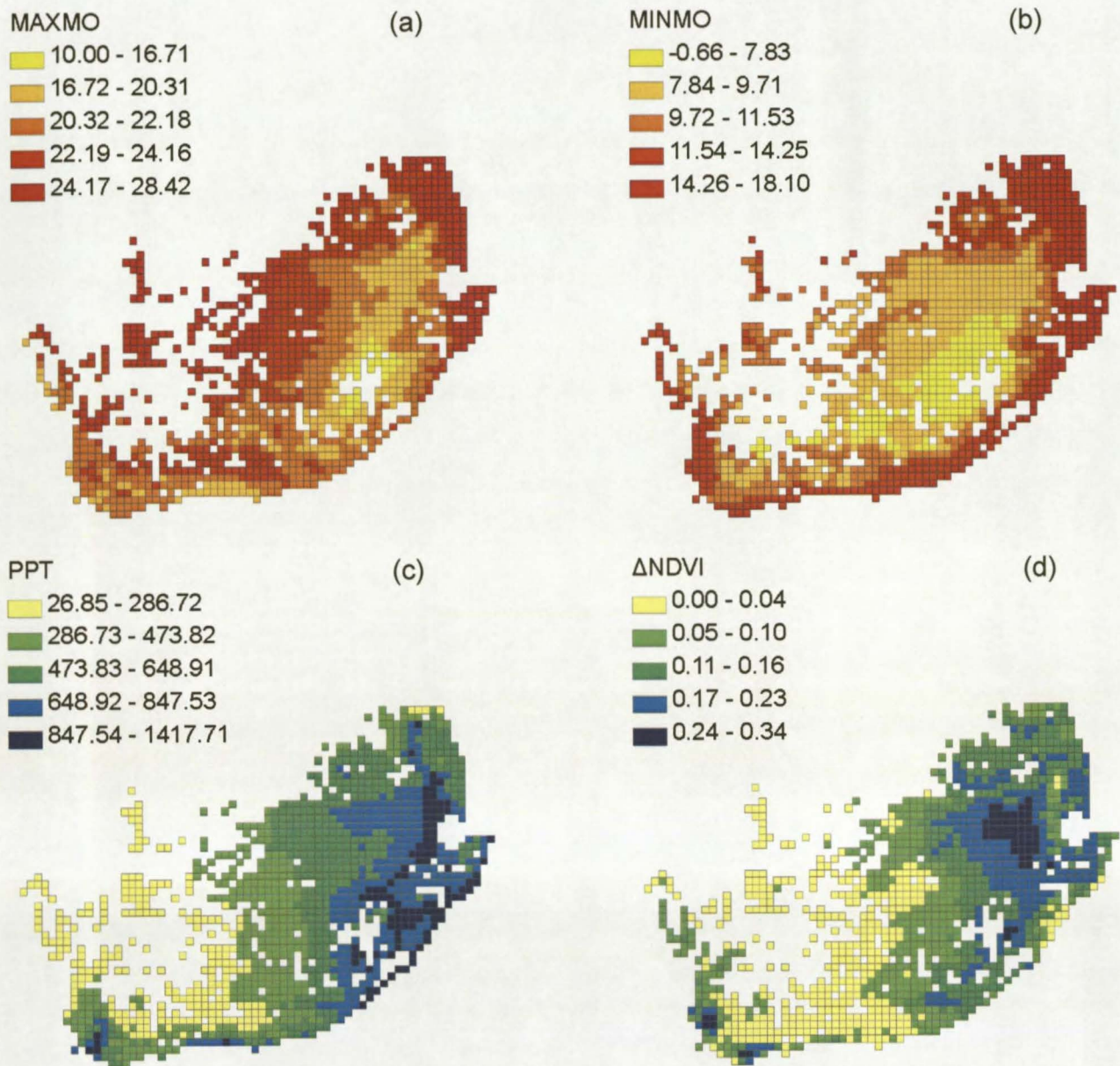
In terms of a mechanistic explanation for the interspecific increase of size with latitude, Bergmann (1847) suggested that animals were larger at high latitudes to prevent heat loss in these cold areas (heat conservation hypothesis). Several alternative biological hypotheses have subsequently been proposed: small size is



favoured in hot, humid environments to facilitate evaporative cooling (evaporative cooling hypothesis, James 1970); more large species have managed to colonize areas that were previously glaciated/inaccessible because they have better dispersal capabilities over greater distances (glaciation hypothesis, Blackburn and Hawkins 2004); large body size confers starvation resistance in environments that experience seasonal resource shortages (starvation resistance hypothesis, Rosenzweig 1968, Lindstedt and Boyce 1985). Given suggestions that pattern should be separated from process during investigations of Bergmann's rule, many studies have recently adopted such an approach. First, a pattern is examined, often from a latitudinal perspective (Rosenzweig 1968, McNab 1971, Cushman et al. 1993, Blackburn and Gaston 1996b, Ashton and Feldman 2003, Jones et al. 2005), or, especially more recently, in two dimensions (James 1970, Wigginton and Dobson 1999, Blackburn and Ruggiero 2001, Blackburn and Hawkins 2004, Meiri et al. 2005, Olalla-Tárraga et al. 2006), with maps of spatial variation being identified as useful for interpretation of the patterns (Ruggiero and Hawkins 2006). Thereafter, if spatial variation is significant (Blackburn and Gaston 2006), which typically means an increase of body size with latitude, the mechanisms underlying such variation are investigated. Usually, the percentage variation in body size explained by one or more environmental variable that relates to the hypotheses being tested is determined, using either univariate methods (Zaveloff and Boyce 1988, Blackburn and Gaston 1996b, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006) or a multivariate model-selection process, such as minimum adequate regression models, which consider the model explaining most of the variation of the dependent variable (Zaveloff and Boyce 1988, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006). The variable(s) explaining most of the

variation are then assumed to be indicators of the primary mechanism underlying the pattern observed.

However, little has been done to assess how much of the geographic variation in local body size is explained by sampling from the regional body size frequency distribution. If BSFDs of local assemblages represent a random sample of a regional frequency distribution, as has been shown in several studies (Arita and Figueroa 1999, Marquet and Cofré 1999, Blackburn and Gaston 2001), geographic variation in body sizes of assemblages might be a consequence of random sampling at various species richness values. Although such a sampling effect has been poorly explored in the literature (Cardillo 2002, Rodríguez et al. 2006), it has been suggested that variation in biological traits such as body size should be well predicted by random sampling (neutrality, *sensu* Hubbell 1997, 2001) at higher species richness as all available niches become occupied (Gravel et al. 2006, Holt 2006, Scheffer and van Nes 2006). Moreover, as richness increases and approaches the overall richness of the regional distribution, possible values of body size become increasingly constrained as they tend towards the size statistic of the regional BSFD (Cardillo 2002). If this is not taken into consideration when examining the extent to which variation in parameters such as mean body size can be predicted by environmental predictors, relationships between size and the environment may be detected merely as a feature of a relationship between the environment and species richness. Indeed, much of the variation in species richness is typically explained by the same environmental variables that are thought to influence body size variation (Blackburn and Gaston 1996a, Chown and Gaston 1999, van Rensburg et al. 2002, Bailey et al. 2004, Bonn et al. 2004, Evans et al. 2005).



**Figure 1.** (a) Maximum monthly temperatures ( $^{\circ}\text{C}$ ) of the hottest months of the year, (b) minimum monthly temperatures ( $^{\circ}\text{C}$ ) of the coldest months of the year, (c) annual precipitation (mm), and (d) the absolute difference between the January and July normalized difference vegetation indices across South Africa and Lesotho at quarter degree grid cell-resolution. Only grid cells used in the study are shown.



Therefore, my aims here are to

1. Investigate the species body size frequency distribution of the South African avifauna. Although regional-scale spatial variability of many aspects of this group has been investigated (Harrison and Martinez 1995, Fairbanks et al. 2002, van Rensburg et al. 2002, Chown et al. 2003, Bonn et al. 2004, Fairbanks 2004, van Rensburg et al. 2004, Evans et al. 2006a, Evans et al. 2006b), body size is conspicuously absent from most of these studies. The South African avifauna constitutes an appropriate test case for exploring variation between body size and environmental variables for several reasons. First, the country supports over 700 bird species, the body sizes of which vary quite considerably (ranging from 5.9 to 68 700 g). Second, the distributions of birds in the region were well-mapped between 1987 and 1993 at quarter degree grid cell (QDGC) grain for the Southern African Bird Atlas Project (SABAP, Harrison et al. 1997). For the SABAP, observers created monthly records of the species they observed within a QDGC, from which the distribution of species was mapped. Third, South Africa experiences a range of geographically structured climatic conditions (Schulze 1997a, b).
2. Examine whether spatial variation in body size exists in the South African avifauna. The heat conservation hypothesis (Bergmann 1847) predicts that the variation in temperature experienced across the country may explain much of the body size variation. South Africa's north-south temperature gradient is interrupted by the effect of topography on temperature (Figs 1a & b, Schulze 1997a). The Great Escarpment, which stretches approximately 200-300 km inland from the south to the east coast of the country, and the easterly increase in elevation, result in lowered temperatures of the interior, while the ocean buffers temperatures along the coast. Humidity is most

marked along the coast, especially the southern and the eastern coast, and displays a general declining east-west gradient (Schulze 1997b). James' (1970) evaporative cooling hypothesis thus predicts a west to east decline in bird sizes associated with the precipitation. The starvation resistance hypothesis (Rosenzweig 1968) predicts a relatively strong east to west decline in body size, associated with the seasonality of productivity, as seasonality is most marked in the eastern parts of the country, particularly the high-lying areas that are some distance away from the ocean (Fig. 1d). Likewise, it might be expected that a complex pattern should be present owing to the interaction of several of the above-mentioned factors on avian body sizes.

3. Explore the extent to which the variation in median body size of avian assemblages can be predicted by random draws from the regional BSFD. Although the regional BSFD constrains the range of size variation that can be obtained for a given richness (Cardillo 2002, Makarieva et al. 2005), median (or mean) body sizes may still differ considerably from what would be expected from random sampling (e.g. Bakker and Kelt 2000, Rodríguez et al. 2006). If the regional BSFD predicts much of the variation in median body size, then geographic variation in size must be considered in the context of processes that determine the regional BSFD, which ultimately result from the interplay between regional and local processes. In addition, richness constrains median body sizes that can be obtained from the regional BSFD (Cardillo 2002). I therefore also examined how much of the variation in body size can be explained by species richness. Richness may also be influenced by the same factors driving body size variation (Cardillo 2002, Evans et al. 2005), and is thought to impact on body size (Blackburn and Gaston 1996b,

c, Cardillo 2002). Including species richness as a covariate in statistical models (e.g. Cardillo 2002) may therefore factor out the environmental variation acting on species richness rather than body size.

## Methods

Body size measures for bird assemblages of QDGCs in South Africa and Lesotho were calculated. Bird distributions were obtained from the SABAP (Harrison et al. 1997). Adult body mass (in grams) was used as a measure of bird body size. Although body mass can be a variable trait, dependent on aspects such as season, sex, and the condition of the bird, it is not as variable as other body size measures, and it is comparable across all species (Gaston and Blackburn 2000). Roberts Birds of Southern Africa (VIIth edition, Hockey et al. 2005) was used as the primary source for obtaining avian body sizes. Where the mean male and mean female body masses of a species were available, their arithmetic mean was calculated and used as body mass for the species. Otherwise the mean of unsexed individuals was used. If the mean size of one sex was obtained from less than 10 individuals, and a mean from a large sample size of unsexed individuals was given, the latter was used instead of the male-female mean. If means from different locations and/or seasons were given, their arithmetic mean was used. If only a range of sizes was provided, the mid-point of the range was used instead of the mean. For species whose sizes were unavailable or unreliable (e.g. small sample sizes, approximated weights, juvenile weights), other sources were used (Brown et al. 1982, Urban et al. 1986, Fry et al. 1988, Keith et al. 1992, Maclean 1993, Urban et al. 1997, Fry et al. 2000, Fry and Keith 2001). Seabirds were removed from the analyses because their distribution is dependent on oceanic conditions rather than environmental characteristics of the terrestrial landscape. Body sizes were  $\log_{10}$  transformed.

Only QDGCs with 50% or more of their surface area on South African and/or Lesotho ground were considered in this study. QDGCs with a reporting rate smaller than 11 (i.e. QDGCs for which less than 11 reporting cards were collected) were discarded because they were inadequately sampled. The midpoints of QDGCs used in this study lie between 22°13.5' S and 34°22.5' S, and between 16°13.5 E and 32°52.5 E. The body size frequency distribution of the birds that were recorded in the QDGCs included in the study was plotted. Shapiro-Wilk's *W* test for normality was conducted to determine whether the distribution differed significantly from normality.

For each QDGC, the median, skewness, kurtosis, the coefficient of variation, 25% and 75% quartiles, and the interquartile range of body sizes were calculated. Because minimum and maximum body size values could represent outliers or extreme values, quartiles were used (Blackburn and Hawkins 2004).

#### GEOGRAPHIC VARIATION IN BODY SIZE

Each of the mechanisms proposed to underlie spatial variation in body size makes specific predictions regarding the relationship between one or more environmental variables and body size. Therefore, the following environmental variables were examined: 1.) Temperature (maximum [MAXMO] and minimum [MINMO] monthly temperatures of the hottest and coldest months of the year respectively) was used to test the heat conservation hypothesis. In cooler areas animals would be expected to be larger to minimize the surface area-volume ratio and therefore also heat loss. 2.) In conjunction with temperature, mean annual precipitation (PPT) was used to test the evaporative cooling hypothesis. In humid (warm, moist) areas species should be smaller to facilitate evaporative heat loss through their small surface area-volume ratio. 3.) To test the starvation resistance hypothesis, the absolute differences between the mean January and July normalized difference vegetation indices

( $\Delta$ NDVI), a measure of primary productivity, were used. This seasonal variation in NDVI provides one measure of the likelihood that starvation resistance increases survival during periods of low resource availability. Mean January and July NDVI measures (obtained from the African Real Time Environmental Monitoring using the Meteorological Satellites program [Artemis] of the Food and Agriculture Organization [FAO, see <http://metart.fao.org/default.htm>]) were calculated from 1982 – 1999 values. Because the only glaciation South Africa has experienced since the start of the Quaternary encompasses a very restricted area (the Drakensberg, Young and Hastenrath 1991), the glaciation hypothesis is irrelevant. The square of all predictors were also included in models to detect curvilinear relationships (van Rensburg et al. 2002, Blackburn and Hawkins 2004).

General linear models (PROC MIXED, SAS 9.1) were used to examine body size variation. First, models were constructed to determine whether latitude or longitude, or an interaction between the two, might explain variation among QDGCs in avian median body size. Initially, either latitude or longitude was the only predictor in models to test the existence and strength of north-south and east-west median size gradients respectively. Polynomial regressions detect non-linear relationships between a response variable and predictors, and tend to increase model fit (Legendre and Legendre 1998). A third-order polynomial regression detects linear relationships, but also patches or gaps in data (Borcard et al. 1992). To identify which combination of the nine spatial terms of a third-order polynomial best describe variability in median size, the Akaike information criterion (AIC) was used. Models with all combinations of the nine terms were constructed and analysed using PROC MIXED. The model with the lowest AIC value represents the best-fit model and should be reported (Burnham and Anderson 1998).



A similar procedure was followed to determine how well the environmental variables explain variation in median body size. Models with all combinations of the four predictors and their squares were constructed, and the model with the lowest AIC value selected and reported. Akaike weights, which quantify how well each of the model fits the data, were calculated from AIC values. The best-fit models with the lowest AIC values possess the highest AIC weights. If the AIC weight is larger than 0.1, the model is considered to fit data well (Westphal et al. 2003). Spatial data, especially if presented in a spatial lattice (such as the environmental variables used here), is usually spatially autocorrelated (Lennon 2000). Conducting simple statistical tests on such data without factoring out spatial autocorrelation can lead to inflation of Type I errors (Borcard et al. 1992, Diniz-Filho et al. 2003), and an inflated likelihood that spatially autocorrelated predictors explain variation in the dependent variable (Lennon 2000). To compensate for the spatial structure in the variation in environmental variables, all models, except those already containing spatial terms (latitude and longitude) were therefore also run with the PROC MIXED procedure. Models with no predictors were run with different spatial covariance structures (exponential, power, spatial, Gaussian, log and log-linear), and the structure that produced the lowest AIC value (exponential in this case) was used to run the full models.

From the random draw models (see next section) it was apparent that median size behaved differently at low and at higher species richness values. This suggests that different mechanisms may be impacting median body size in more species-rich and less species-rich assemblages. Therefore, the above analyses were repeated for QDGCs with species richness values lower than 105, and with those greater than or equal to 105.

## NULL MODELS

Null models were used to determine how bird assemblages in QDGCs differ from random expectation. Random assemblages were generated to predict body size variables of QDGCs with different species richness values given the regional BSFD. Random draws were conducted in R (v. 2.3.1). Species richness values in QDGCs included in the analyses ranged from 35 to 403. For each species richness value, 1000 random assemblages were created from the regional body size frequency distribution (which comprised all species present in the QDGCs used for this study). For each random assemblage, species were sampled without replacement. These “unweighted randomizations” are based on the assumption that all species are demographically identical. Such neutrality may be an acceptable assumption for trophically similar groups that compete with one another (Hubbell 1997). However, the bird species of South Africa are not trophically similar. Therefore, because assumptions made by the models are not met for the South African avifauna, a second set of random assemblages was generated in which species were selected with a probability proportional to their geographical distribution in the region (Preston 1948, Stone et al. 1996, Gotelli 2000), i.e. the number of QDGCs in which a given species was recorded in (‘partial range size’, Blackburn and Gaston 1996b, which therefore does not encompass the entire distribution), rather than their entire distribution. Blackburn and Gaston (2001) found that such randomizations were the best predictors of several body size statistics of a deciduous wood bird community. Randomizations weighted by species range size are henceforth referred to as “range-weighted randomizations”.

To determine how well random sampling from the regional BSFD predicts body size statistics of the actual assemblages, each QDGC was classified according to whether its median size was smaller or larger than the median of random median

sizes at the corresponding species richness value. To determine whether the degree to which random values predicted real values changed with species richness, QDGCs were then assigned to categories according to their species richness values; each category contained 20 species richness values (30-49, 50-69..., 390-409). Two-tailed Fisher exact tests (Siegel 1956) were conducted to determine whether the proportion of QDGCs with median sizes smaller and sizes larger than the median of the randomizations were equal in each species richness category. Size categories 30-49, 370-389 and 390-409 contained few (three or four) grid cells – Fisher exact tests were thus not conducted for these. When conducting several tests, the likelihood of type I errors is inflated (García 2003, 2004). Therefore, step-up false discovery rates (FDR, Benjamini and Hochberg 1995) were applied to the p-values from Fisher exact tests. This analysis was repeated for the other six body size variables too. QDGCs with median size values which fell outside 95 % of the random size values for the respective species richness value were also assigned to species richness categories and plotted against species richness.

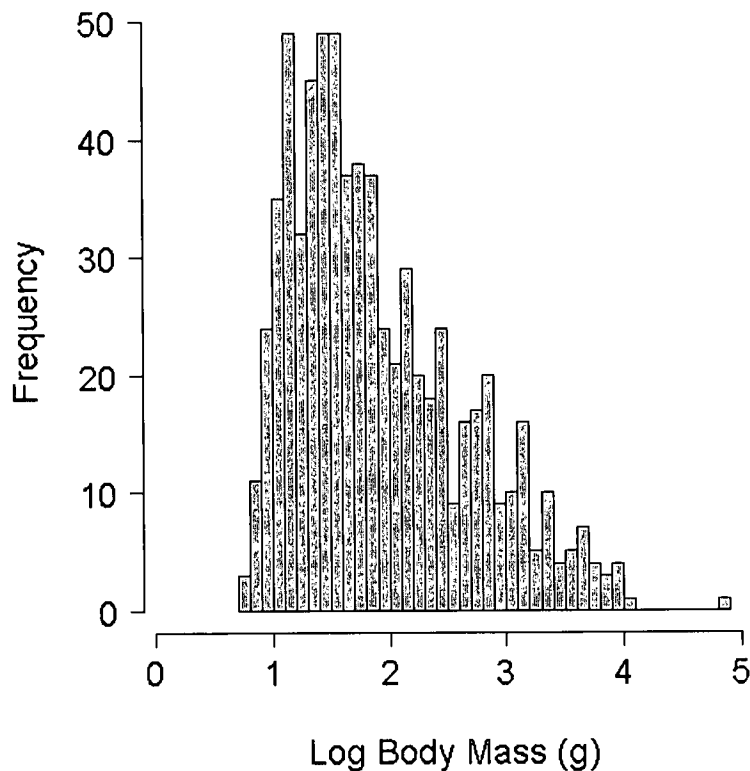
## Results

The BSFD of South African birds is right-log skewed (skewness = 0.8291, Shapiro-Wilk's  $W = 0.93520$ ,  $p < 0.0001$ ), with the highest number of species occurring in small, but not the smallest, size categories (Fig. 2).

Contrary to Bergmann's rule, no latitudinal body size gradient exists (Fig. 3, Table 1a). Longitude also explained little of the variation in median body size. The minimum adequate model of the terms from the third-order polynomial equation for latitude and longitude retained both latitudinal and longitudinal terms (Table 1a). The model indicated that patches exist where adjacent QDGCs possess similar median size values, which is also evident from Fig. 3a. Median body sizes are especially large in



the north-east of the country in the savanna biome (particularly in the Kruger National Park, the largest protected area in the country), the central north-eastern areas of the country in the grassland biome (areas of which support the highest human population densities in the country, Chown et al. 2003, van Rensburg et al. 2004), and the south-western Cape in the fynbos biome. In the semi-arid Kalahari and Karoo median sizes tend to be small.

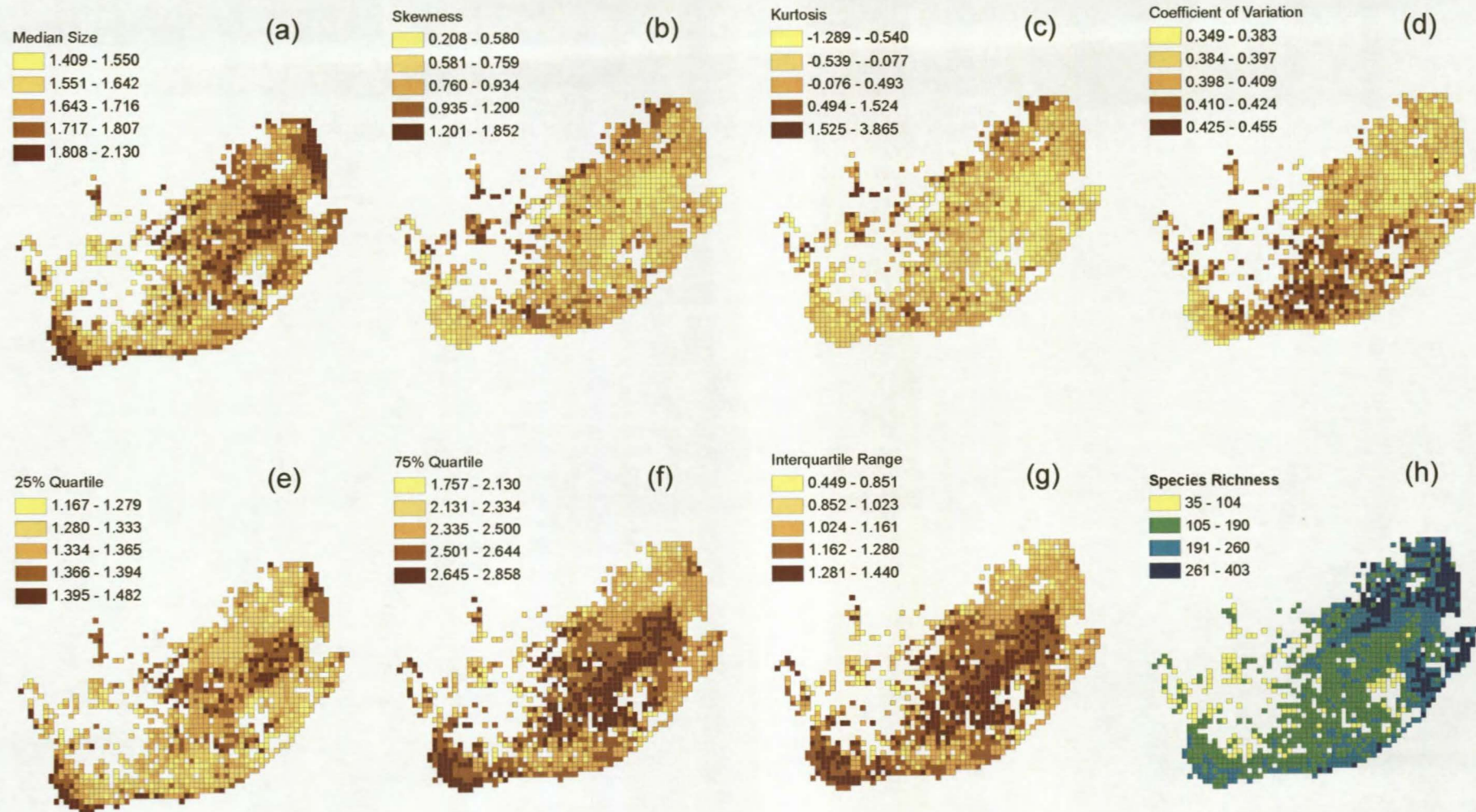


**Figure 2.** Frequency distribution of log body mass of the birds of South Africa and Lesotho (686 species, excluding sea birds).

Because environmental variables show strong spatial autocorrelation (Fig. 1), results from the spatial models will mainly be considered here. Because no  $r^2$  value can be obtained for the spatial models (K. L. Evans, pers. comm.), non-spatial results are also shown to give an indication of the percentage variability explained by the environmental models. If minimum adequate models alone are used to ascertain how

environmental variables explain geographic variation in median body size, as is done in most such studies (e.g. Zeveloff and Boyce 1988, Blackburn and Gaston 1996b, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006), some of the variation in median body size of the complete dataset could be explained by environmental factors (Table 1). All predictors co-varied (Table 2), therefore the explanatory power assigned to one variable in regression models may be affected by the other predictors.  $\Delta$ NDVI was the only significant predictor of median size – the relationship between median size and  $\Delta$ NDVI could be explained by a positive linear function (Table 1b). However, species richness, which was related to median size by a quadratic relationship (hump-shaped), alone explained almost as much of the variation in size as the best-fit environmental model (Table 1c). If species richness was included as predictor in the environmental models, model fit increased, and, in the spatial model, richness remained the only significant predictor of median body size (Table 1d).

Because at low species richness median size always fell within the lower range of values expected from randomizations (see below), general linear models were also run for median size at species richness smaller than 105, and greater or equal than 105 (see Fig. 3h for the geographic locations of the respective QDGCs). This provided an opportunity to determine whether different environmental variables are driving body size at high and low species richness. At low species richness ( $< 105$ ), none of the environmental variables predicted body size variation (Table 3a[2]), while species richness increased with median size (Table 3a[3]; see also Figs 2a & 3a). When species richness was included in environmental models, it again remained the only significant explanatory variable (Table 3a[4]). Model fit for all non-spatial models was relatively low ( $r^2 < 19\%$ ).



**Figure 3.** Statistics of log body sizes (a-g) and species richness (h) of birds (excluding sea birds) in South Africa and Lesotho in quarter degree grid cells with a reporting rate greater than 10.

**Table 1.** Minimum adequate models of the relationship between median avian log body size in quarter degree grid cells and various predictors. Models were selected on account of model fit as indicated by the Akaike information criterion (AIC); lower AIC-values, which result in higher AIC-weights, indicate a better fit. Results from non-spatial general linear models (GLM) and spatial models with exponential covariance structure (Spatial [Exp]) are shown. In (a), results of models containing only either latitude or longitude as predictor, and the best subset model of a third-order polynomial of latitude and longitude are shown; (b) represents the best-fit model from models with all combinations of environmental variables; in (c) only species richness was included in the model; (d) is as (b), except species richness was included as covariate in all models. Lat = latitude, Long = longitude,  $\Delta$ NDVI = absolute difference between January and July NDVI, MAXMO and MINMO = maximum and minimum monthly temperatures of the hottest and coldest months of the year respectively, PPT = annual precipitation, SppRich = species richness. (<sup>ns</sup> = not significant; + =  $p < 0.05$ , positive effect; ++ =  $p < 0.01$ , positive effect; +++ =  $p < 0.0001$ , positive effect; --- =  $p < 0.0001$ , negative effect)

Model Type	Variables in model	AIC value (model weight)	Model Fit ( $r^2$ )
<b>(a) Latitude &amp; Longitude</b>			
GLM	Lat ( $F_{1,1296} = 41.30^{++++}$ )	-2288.9	3.09%
GLM	Long ( $F_{1,1296} = 61.09^{++++}$ )	-2307.5	4.50%
GLM	Lat ( $F_{1,1290} = 43.7^{++++}$ ), Long ( $F_{1,1290} = 83.3^{--}$ ), Lat <sup>2</sup> ( $F_{1,1290} = 52.71^{++++}$ ), Lat*Long ( $F_{1,1290} = 52.55^{--}$ ), Long <sup>2</sup> ( $F_{1,1290} =$	-2375.7 (0.688)	15.5%
(best subset)	44.09 <sup>++++</sup> ), Lat <sup>2</sup> *Long ( $F_{1,1290} = 62.74^{--}$ ), Long <sup>3</sup> ( $F_{1,1290} = 44.64^{--}$ )		

Table 1 (continued)

Model Type	Variables in model	AIC value (model weight)	Model Fit ( $r^2$ )
<b>(b) Environmental Variables</b>			
GLM	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1294}=47.99^{****}$ ), PPT ( $F_{1,1294}=114.47^{****}$ ), PPT <sup>2</sup> ( $F_{1,1294}=102.28^{--}$ )	-2465.3 (0.473)	18.03%
Spatial (Exp)	$\Delta$ NDVI ( $F_{1,1295}=6.7^{++}$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,1295}=0.07^{ns}$ )	-2931.8 (0.530)	n/a
<b>(c) Species Richness</b>			
GLM	SppRich ( $F_{1,1295}=134.22^{****}$ ), SppRich <sup>2</sup> ( $F_{1,1295}=78.31^{--}$ )	-2469.7	17.87%
Spatial (Exp)	SppRich ( $F_{1,1295}=110.46^{****}$ ), SppRich <sup>2</sup> ( $F_{1,1295}=48.09^{--}$ )	-3110.1	n/a
<b>(d) Environmental Variables + Species Richness</b>			
GLM	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1291}=68.03^{****}$ ), MAXMO ( $F_{1,1291}=18.30^{****}$ ), MINMO ( $F_{1,1291}=31.41^{--}$ ), MINMO <sup>2</sup> ( $F_{1,1291}=21.82^{****}$ ), SppRich ( $F_{1,1291}=127.41^{****}$ ), SppRich <sup>2</sup> ( $F_{1,1291}=77.02^{--}$ )	-2530.9 (0.465)	23.91%
Spatial (Exp)	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1294}=1.63^{ns}$ ), SppRich ( $F_{1,1294}=108.14^{****}$ ), SppRich <sup>2</sup> ( $F_{1,1294}=47.35^{--}$ )	-3112.9 (0.430)	n/a

**Table 2.** r-values from the correlation matrix of the predictor variables used in minimum adequate models. All correlations are significant ( $p < 0.05$ ). See Table 1 for abbreviations.

	$\Delta$ NDVI	MAXMO temperature	MINMO temperature	Precipitation
$\Delta$ NDVI	1			
MAXMO temperature	-0.353	1		
MINMO temperature	0.143	0.569	1	
Precipitation	0.673	-0.428	0.145	1



**Table 3.** Minimum adequate models of the relationship between median avian log body size in quarter degree grid cells and various predictors. QDGCs were divided into those with species richness smaller than 105 (a), and with species richness equal or greater than 105 (b). Models were selected on account of model fit as indicated by the Akaike information criterion (AIC); lower AIC-values, which result in higher AIC-weights, indicate a better fit. Results from non-spatial general linear models (GLM) and spatial models with exponential covariance structure (Spatial [Exp]) are shown. In (1), results of models containing only either latitude or longitude as predictor, and the best subset model of a third-order polynomial of latitude and longitude are shown; (2) represents the best-fit model from models with all combinations of environmental variables; in (3) only species richness was included in the model; (4) is as (2), except species richness was included as covariate in all models. See Table 1 for abbreviations. (<sup>ns</sup> = not significant; <sup>+</sup> =  $p < 0.05$ , positive effect; <sup>++</sup> =  $p < 0.01$ , positive effect; <sup>+++</sup> =  $p < 0.001$ , positive effect; <sup>++++</sup> =  $p < 0.0001$ , positive effect; <sup>---</sup> =  $p < 0.0001$ , negative effect)

(a) Quarter degree grid cells with a species richness less than 105.

Model Type	Variables in model	AIC value (model weight)	Model Fit ( $r^2$ )
<b>(1) Latitude &amp; Longitude</b>			
GLM	Lat ( $F_{1,131} = 5.24^+$ )	-175.4	3.85%
GLM	Long ( $F_{1,131} = 3.48^{ns}$ )	-172.4	ns
GLM	Lat ( $F_{1,131} = 5.24^+$ )	-175.4	3.85%
(best subset)			

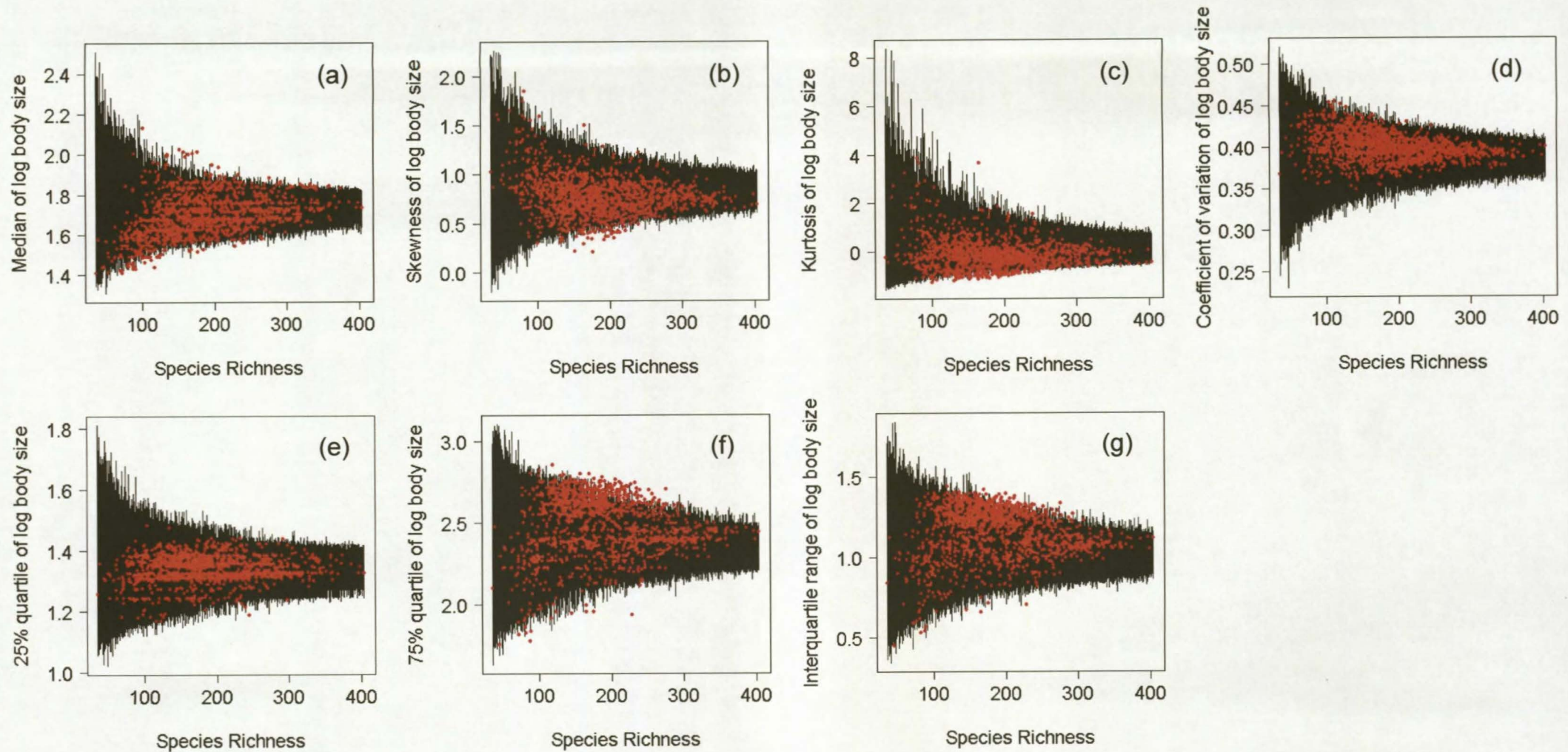
Table 3(a) (continued)

Model Type	Variables in model	AIC value (model weight)	Model Fit ( $r^2$ )
<b>(2) Environmental Variables</b>			
GLM	$\Delta$ NDVI ( $F_{1,130}=3.7^{ns}$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,130}=1.04^{ns}$ )	-190.4 (0.711)	ns
Spatial (Exp)	$\Delta$ NDVI ( $F_{1,130}=0.22^{ns}$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,130}=0.24^{ns}$ )	-228.6 (0.739)	n/a
<b>(3) Species Richness</b>			
GLM	SppRich ( $F_{1,131}=22.81^{****}$ )	-187.0	14.83%
Spatial (Exp)	SppRich ( $F_{1,131}=21.73^{****}$ )	-226.8	n/a
<b>(4) Environmental Variables + Species Richness</b>			
GLM	$\Delta$ NDVI ( $F_{1,129}=2.43^{ns}$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,129}=0.72^{ns}$ ), SppRich ( $F_{1,129}=18.67^{****}$ )	-195.1 (0.301)	18.53%
Spatial (Exp)	$\Delta$ NDVI ( $F_{1,129}=0.16^{ns}$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,129}=1.74^{ns}$ ), SppRich ( $F_{1,129}=21.97^{****}$ )	-235.8 (0.747)	n/a



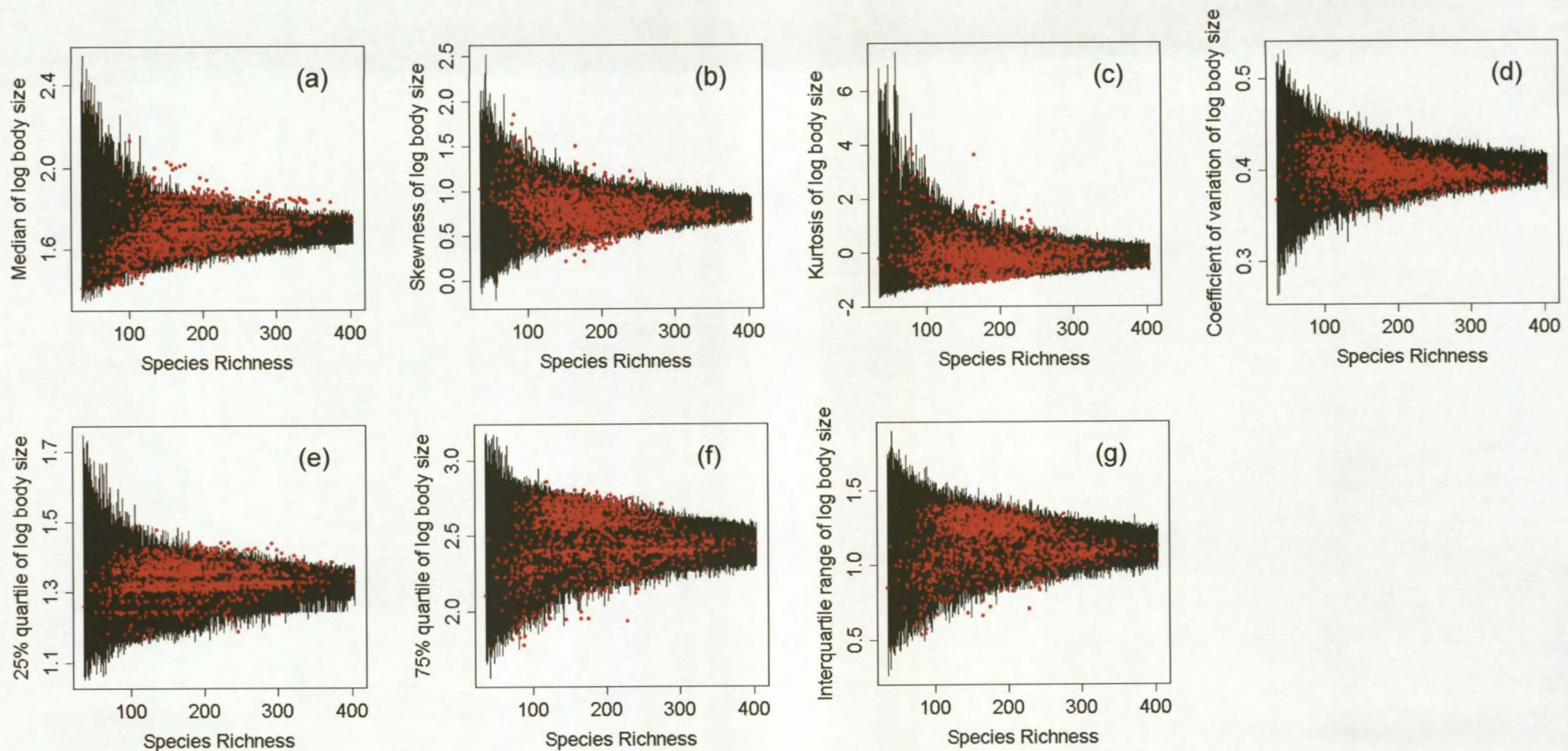
Table 3(b) Quarter degree grid cells with a species richness equal or greater than 105.

Model Type	Variables in model	AIC value (model weight)	Model Fit ( $r^2$ )
<b>(1) Latitude &amp; Longitude</b>			
GLM	Lat ( $F_{1,1163} = 30.19^{****}$ )	-2300.4	2.53%
GLM	Long ( $F_{1,1163} = 8.81^{**}$ )	-2279.2	0.75%
GLM	Lat ( $F_{1,1157} = 33.87^{---}$ ), Long ( $F_{1,1157} = 30.25^{---}$ ), Lat <sup>2</sup> ( $F_{1,1157} = 27.17^{---}$ ), Lat*Long ( $F_{1,1157} = 27.43^{****}$ ),	-2322.6 (0.481)	11.5%
(best subset)	Long <sup>2</sup> ( $F_{1,1157} = 38.49^{****}$ ), Lat <sup>3</sup> ( $F_{1,1157} = 24.42^{---}$ ), Long <sup>3</sup> ( $F_{1,1157} = 37.43^{---}$ )		
<b>(2) Environmental Variables</b>			
GLM	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1163}=116.83^{****}$ )	-2394.6 ( 0.413)	9.13%
Spatial (Exp)	$\Delta$ NDVI ( $F_{1,1162}=4.65^+$ ), $\Delta$ NDVI <sup>2</sup> ( $F_{1,1162}=0.01^{ns}$ )	-2788.0 (0.694)	n/a
<b>(3) Species Richness</b>			
GLM	SppRich ( $F_{1,1163}=59.74^{****}$ )	-2323.0	4.89%
Spatial (Exp)	SppRich ( $F_{1,1163}=139.07^{****}$ )	-2394.6	n/a
<b>(4) Environmental Variables + Species Richness</b>			
GLM	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1159}=86.44^{****}$ ), MAXMO ( $F_{1,1159}=13.07^{***}$ ), MINMO ( $F_{1,1159}=30.22^{---}$ ), MINMO <sup>2</sup> ( $F_{1,1159}=21.84^{****}$ ), SppRich ( $F_{1,1159}=27.17^{****}$ )	-2399.8 (0.276)	13.80%
Spatial (Exp)	$\Delta$ NDVI <sup>2</sup> ( $F_{1,1162}=1.96^{ns}$ ), SppRich ( $F_{1,11629}=134.17^{****}$ )	-2892.4 (0.393)	n/a



**Figure 4.** Log body size variables of birds in South African quarter-degree grid cells (red) and in random assemblages (black) at different species richness values. For each random assemblage, species were randomly selected without replacement from the pool of South African species.





**Figure 5.** Log body size variables of birds in South African quarter-degree grid cells (red) and in random assemblages (black) at different species richness values. For each random assemblage, species were randomly selected without replacement from the pool of South African species with a probability proportional to the extent of the geographical distribution of the species.

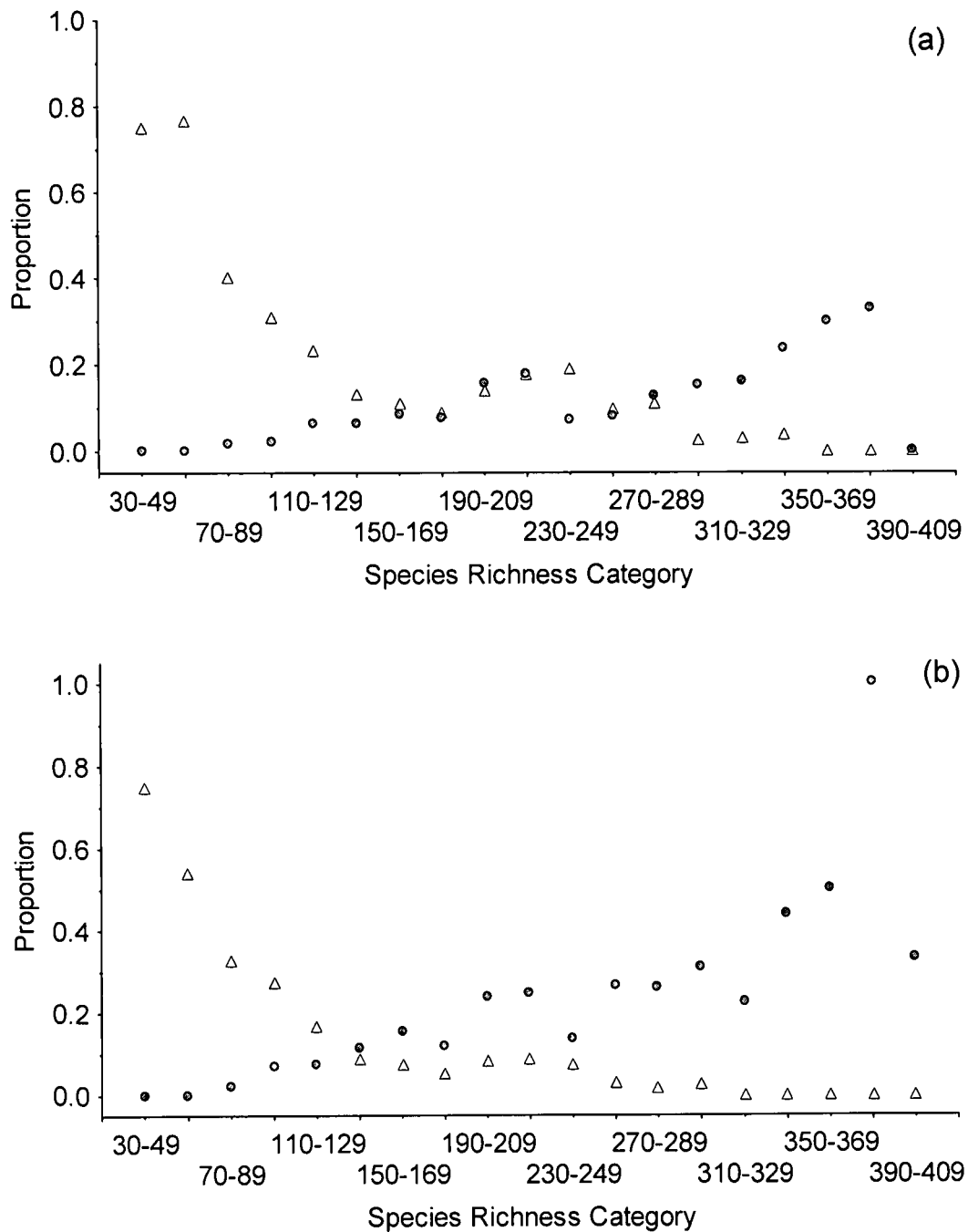
**Table 4.** Number of quarter degree grid cells with median avian body size smaller:larger than expected from 1000 unweighted randomizations and 1000 randomizations weighted by species range sizes (see text for details) conducted for each species richness value. Grid cells were grouped into species richness categories. Two-tailed Fisher exact tests were performed to determine whether the proportion of grid cells with the ratio smaller:larger size was significantly different from 1:1. \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . (\*) represents values that were not significant after controlling for false discovery rate.

Species Richness Category	Unweighted	Weighted
50-69	13:0**	13:0**
70-89	48:4***	47:5***
90-109	73:11***	69:15***
110-129	83:24***	73:34**
130-149	103:47**	86:65
150-169	94:55(*)	68:78
170-189	109:58**	75:92
190-209	70:64	58:77
210-229	55:46	41:60
230-249	61:34	47:48
250-269	40:31	23:48(*)
270-289	31:20	10:41**
290-309	19:19	10:27
310-329	16:14	8:22
330-349	9:16	1:24***
350-369	2:8	1:9

The results for QDGCs with high species richness ( $\geq 105$ , Table 3b) were similar to those of the complete dataset.  $\Delta$ NDVI remained the only significant variable in the environmental models, increasing with median size whether models were run with or without considering spatial autocorrelation (Table 3b[2]). Species richness also increased with median size, but it predicted very little of the variation in median size (Table 3b[3]). When species richness was included as predictor in the environmental models, it remained the only significant variable in spatial models (Table 3b[4]). Model fit of non-spatial models was poor ( $r^2 < 14\%$ ) in all cases.

For a given species richness value, body size variables of actual assemblages displayed a fair amount of similarity with assemblages expected from randomizations (Figs 4 & 5, Appendix 1). If the median body sizes of QDGCs with different species richness values are overlaid on the median sizes from both weighted (Fig. 4a) and unweighted (Fig. 5a) randomizations, much of the variation seems to be explained by random sampling alone. Only at low species richness does median size continuously fall within the lower values that would be expected from randomizations (see also Table 4). At low richness values, more QDGCs had median size values significantly lower than expected from random (Fig. 6a). Unweighted randomizations predicted real median body size in South African QDGCs better than weighted randomizations did (Table 4, Fig. 6). For example, the number of QDGCs with median size values larger than expected from random increased with richness for the weighted randomizations (Fig. 6b). From Figs 4 and 5 it is apparent that all body size variables were not always as well predicted by the randomizations as median size was. Although the empirical data mostly fell within the boundaries of the unweighted randomizations, they were usually biased towards either the upper or the lower random values – with the exception of 25% quartiles (Fig. 4, Appendix 1). Range-weighted randomizations were better predictors of the actual data for skewness,

coefficients of variation, 75% quartiles and interquartile ranges of body size (Fig 5, Appendix 1).



**Fig. 6.**

**Figure 6.** Proportion of quarter degree grid cells with median sizes larger (●) and smaller (Δ) than 95 % of the median sizes of (a) unweighted and (b) weighted randomizations (see text).

## Discussion

The body size frequency distribution of the birds of South Africa and Lesotho is strongly right-skewed, as has been shown for various regional assemblages and taxa (May 1978, Brown and Nicoletto 1991, Marquet and Cofré 1999, Bakker and Kelt 2000, Gaston and Blackburn 2000), and for the global avian BSFD (Blackburn and Gaston 1994). This suggests that the mechanisms generating right-skewed BSFDs elsewhere may also be operating here. Compared to the global avian BSFD (Blackburn and Gaston 1994), birds in the smallest size classes, e.g. hummingbirds (Dunning 1993), are missing from the South African BSFD, while the upper limits of the South African and global avian BSFDs are similar. The modes of the global and South African avian BSFDs are similar, and the median size of South African birds (53.45 g) is somewhat higher than that of the birds as a whole (37.6 g).

If, as in most studies, only the relationship between the geographic variation in body size and possible predictors of median body size are considered for the South African avifauna, several patterns are observed. No latitudinal body size cline, as predicted by Bergmann (1847), exists for South African avifaunal assemblages. Longitude alone also explains little of the variation in median size. However, median body size variation is not randomly distributed across the landscape – patches of assemblages with similar median sizes exist. Given features of South Africa's topography and climate that interrupt latitudinal and longitudinal climatic gradients, this is, perhaps, not unexpected. The gradual west-east increase in altitude across the country is, for example, interrupted by a sudden drop in altitude at the escarpment, which influences rainfall and temperature, while the eastern escarpment interrupts the south-north temperature gradient (Schulze 1997b). As mentioned previously, temperatures around the coast are also buffered and display relatively low variability, while humidity in coastal regions is raised due to the effect of the



ocean (Schulze 1997b). All of these factors result in 'patches', rather than absolute gradients, in the environment that are climatically or environmentally similar and could possess avian assemblages with similar body sizes. In addition, median body sizes of adjacent QDGCs in this study are not independent – overlap in the ranges of species, but also populations and individual birds will exist between adjacent QDGCs, which may further promote the occurrence of areas with similar median body sizes (Diniz-Filho et al. 2003).

Despite the absence of a latitudinal or longitudinal body size cline, environmental variables alone do explain some variability in body size, suggesting that the mechanisms driving latitudinal body size clines elsewhere (Zaveloff and Boyce 1988, Cotgreave and Stockley 1994, Blackburn and Gaston 1996b, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006) could be affecting body size patterns of South African avifaunal assemblages. The percentage variability explained by environmental models is not high, however ( $r^2 < 20\%$ ). In other investigations of Bergmann's rule in vertebrate assemblages the amount of variability explained by the environment is often considerably higher than that found here (Zaveloff and Boyce 1988, Blackburn and Gaston 1996b, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006), with the exception of the lizard and snake fauna of North America ( $r^2 < 20\%$ , Olalla-Tárraga et al. 2006) and the mammal fauna of southern Europe ( $r^2 = 18\%$ , Rodríguez et al. 2006).

Nevertheless, of the environmental variables considered in this study, seasonality in NDVI alone remains as predictor of median body size. The South African landscape varies quite considerably in terms of seasonality (Schulze 1997a). For example, temperatures along the coastal areas are buffered by the ocean, creating an environment with relatively small temperature variation between seasons, while the continental interior displays more variability in temperature, resulting in higher



distinctions between seasons. Seasonal variation in solar radiation is affected by the timing of the rainy season, day length, which varies from the northern to the southern parts of the country, and proximity to the ocean, where weather systems often originate (Schulze 1997b). For the South African avifauna, median body size increases with seasonality in NDVI (when species richness is not included in minimum adequate models). This is in agreement with the starvation resistance hypothesis, which predicts that size increases in more variable environments, allowing larger animals to better survive periods of resource shortage because of their ability to store greater quantities of fat per unit body mass (Lindstedt and Boyce 1985). Although it has been suggested that small animals should be able to survive unfavourable periods due to their ability to better exploit microclimates or employ physiological compensatory mechanisms such as torpor (Dunbrack and Ramsay 1993), this mechanism does not appear to be operating within the avifauna of South Africa (see also Zeweloff and Boyce 1988, Blackburn and Hawkins 2004, Rodríguez et al. 2006). The South African avifauna also supports several migratory species (Hockey et al. 2005), which are therefore not exposed to seasonality. It has indeed been shown that migrants are less likely to conform to Bergmann's rule than sedentary species are (Meiri and Dayan 2003). Because migratory species were included in analyses, the strength of the body size-NDVI seasonality relationship presented in the results may be a conservative representation of the effect of seasonality on avian body size of South Africa assemblages.

In South Africa, annual variation in environmental variables follows a different pattern to seasonal variation though: areas displaying high seasonal variability often show low annual variability, and vice versa (Schulze 1997a, b). The response of median body size to annual variation in the environment may therefore differ from the response to seasonal variation (see Rosenzweig 1968). However, in North America,

annual variation in climatic variables does correlate positively with mean body size, although not as strongly as seasonal variation (Zaveloff and Boyce 1988). Therefore, large body size may increase the ability to survive high annual resource variability too (Zaveloff and Boyce 1988). Given that resource availability in regions with high annual variation is often patchy (e.g. Desmet and Cowling 1999), large animals could also possess the ability to travel to such patches over larger distances to obtain food, which would result in a positive relationship between annual environmental variation and body size too. Alternatively, in highly variable regions with patchy resource availability, smaller species may be favoured due to their ability to exploit smaller patches of resources because of their lower individual energy requirements. Whether a relationship between inter-annual variation in environmental variables and median body size exists in South African birds remains to be determined.

Temperature has been shown to be an important predictor of body size in several studies (Zaveloff and Boyce 1988, Blackburn and Gaston 1996b, Blackburn and Hawkins 2004, Rodríguez et al. 2006), but explained little of the variation here. In a study of European mammals it was found that temperature was an important predictor of body size in the cold northern areas of the region, but that this relationship virtually disappeared above a certain temperature threshold (Rodríguez et al. 2006). As for the South African avifauna, seasonality (in plant production) was the best predictor of body size variation in the warm southern region, and also explained only a small percentage (18%) of the variation. Rodríguez et al. (2006) suggested that temperature-body size relationships may be non-linear, increasing in colder areas, but becoming non-significant in warmer environments. In terms of temperature, South Africa's climate is more similar to that of southern than northern Europe (Lockwood 1985). If the non-linear temperature-body size relationship

proposed by Rodriguez et al. (2006) is indeed operating, South Africa's temperature range may fall within the horizontal portion of the relationship.

In multi-species investigations of Bergmann's rule, only the relationship between body size and some environmental predictor(s) associated with a mechanism that could generate body size clines are typically investigated. Few studies (Cardillo 2002, Rodríguez et al. 2006) have considered the contribution of random sampling from a regional species pool on variation in body size. While results from the minimum adequate models can be used to hypothesize what mechanisms might be responsible for the geographic variation of body size in avian assemblages, the correspondence between real and random median sizes seen here indicates that much of the variation in body size can be predicted by random sampling from the regional BSFD. Null models have increasingly been used to ascertain how closely community characteristics correspond to what would be expected from randomizations from a known or imagined distribution (Gotelli and Graves 1996, see e.g. Stone et al. 1996, Marquet and Cofré 1999, Blackburn and Gaston 2001, Cardillo 2002, Diniz-Filho et al. 2002, Bell 2003, Smith et al. 2004, Sfenthourakis et al. 2006). Here, bird assemblages at higher species richness in South Africa possess median body sizes that may be expected from unweighted randomizations. While there is general agreement that all individuals and species are unlikely to be identical (Hubbell 1997, Chave 2004), as is assumed by the null models conducted here, it is none the less noteworthy that randomizations predicted assemblage body size relatively effectively.

Recent work has attempted to reconcile niche and neutral theory (Etienne and Olf 2004, Gravel et al. 2006, Holt 2006, Leibold and McPeck 2006, Scheffer and van Nes 2006). Gravel et al. (2006) proposed that niche and neutral theories form two extremes of a continuum. In a model of this continuum, the probability of a species

establishing is proportional to its abundance in the source pool (as in neutral theory), while propagules possess species-specific survival rates (as in niche theory). Under a range of conditions, increasing species richness results in increasing neutrality because higher niche overlap is required for species to co-exist (i.e. more similar species have to co-exist as all possible niches became occupied). In addition, assemblages tend towards neutrality if there is high local dispersal, because immigration balances out the effect of competition, and because species richness increases, which again results in all possible niches being occupied. A model by Scheffer and van Nes (2006) also predicted increased neutrality at higher species richness. The model assumed that similar-sized species occupied the same niche and were thus strong competitors. As many different-sized species were placed along a niche axis at high abundances, similar-sized species formed aggregations on the niche axis, and such aggregations of similar-sized species were separated from one another by strong competition. Therefore, as neutral theory predicts, species that are strong competitors were found to co-exist at high richness.

South African avifaunal assemblages support predictions of Gravel et al.'s (2006) continuum hypothesis: randomizations were better predictors of median size as species richness increased, while environmental factors, which represent the niche-based end of the continuum, were poor predictors of body size variation. Stochastic neutral processes may thus indeed be more important than niche processes at high richness.

In conclusion, this work has provided support for the general pattern of log right-skewed body size frequency distributions at regional scales. Moreover, it has shown that the factors which give rise to the regional BSFD (see e.g. Hutchinson and MacArthur 1959, Brown and Nicoletto 1991, Maurer et al. 1992, Brown et al. 1993, Kozłowski and Weiner 1997) play a primary role in generating patterns of geographic



variation in size, especially in areas of high richness. In consequence, this study demonstrates that future investigations of geographic variation in size should take stochastic processes into account before attributing variation entirely to deterministic responses to environmental variation.

## References

- Aava, B. 2001. Primary productivity can affect mammalian body size frequency distributions. *Oikos* **93**:205-212.
- Arita, H. T., and F. Figueroa. 1999. Geographic patterns of body-mass diversity in Mexican mammals. *Oikos* **85**:310-319.
- Ashton, K. G., and C. R. Feldman. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* **57**:1151-1163.
- Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? *American Naturalist* **156**:390-415.
- Bailey, S. A., M. C. Horner-Devine, G. Luck, L. A. Moore, K. M. Carney, S. Anderson, C. Betrus, and E. Fleishman. 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. *Ecography* **27**:207-217.
- Bakker, V. J., and D. A. Kelt. 2000. Scale-dependent patterns in body size distributions of neotropical mammals. *Ecology* **81**:3530-3547.
- Bell, G. 2003. The interpretation of biological surveys. *Proceedings of the Royal Society of London B* **270**:2531-2542.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B* **57**:289-300.

- Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* **3**:595-708.
- Blackburn, T. M., and K. J. Gaston. 1994. The distribution of body sizes of the world's bird species. *Oikos* **70**:127-130.
- Blackburn, T. M., and K. J. Gaston. 1996a. A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Letters* **3**:44-53.
- Blackburn, T. M., and K. J. Gaston. 1996b. Spatial patterns in the body sizes of bird species in the New World. *Oikos* **77**:436-446.
- Blackburn, T. M., and K. J. Gaston. 1996c. Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society of London B* **351**:897-912.
- Blackburn, T. M., and K. J. Gaston. 2001. Local avian assemblages as random draws from regional pools. *Ecography* **24**:50-58.
- Blackburn, T. M., and K. J. Gaston. 2006. There's more to macroecology than meets the eye. *Global Ecology and Biogeography* **15**:537-540.
- Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* **5**:165-174.
- Blackburn, T. M., and B. A. Hawkins. 2004. Bergmann's rule and the mammal fauna of northern North America. *Ecography* **27**:715-724.
- Blackburn, T. M., and A. Ruggiero. 2001. Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecology and Biogeography* **10**:245-259.
- Bonn, A., D. Storch, and K. Gaston. 2004. Structure of the species-energy relationship. *Proceedings of the Royal Society of London B* **271**:1685-1691.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045-1055.

- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* **142**:573-584.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist* **138**:1478-1512.
- Brown, L. H., E. K. Urban, and K. Newman. 1982. *The Birds of Africa Volume I*, 1st edition. Academic Press, London.
- Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Multimodel Inference*, 2nd edition. Springer-Verlag, New York.
- Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecology and Biogeography* **11**:59-65.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* **7**:241-253.
- Chown, S. L., and K. J. Gaston. 1997. The species-body size distribution: energy, fitness and optimality. *Functional Ecology* **11**:365-375.
- Chown, S. L., and K. J. Gaston. 1999. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evolutionary Ecology Research* **1**:365-373.
- Chown, S. L., B. J. van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13**:1233-1241.
- Cotgreave, P., and P. Stockley. 1994. Body size, insectivory and abundance in assemblages of small mammals. *Oikos* **71**:89-96.



- Cushman, J. H., J. H. Lawton, and B. F. J. Manly. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* **95**:30-37.
- Desmet, P. G., and R. M. Cowling. 1999. The climate of the Karoo - a functional approach. Pages 3-16 *in* W. R. J. Dean and S. Milton, editors. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* **12**:53-64.
- Diniz-Filho, J. A. F., C. E. R. de Sant'Ana, M. C. de Souza, and T. F. L. V. B. Rangel. 2002. Null models and spatial patterns of species richness in South American birds of prey. *Ecology Letters* **5**:47-55.
- Dunbrack, R. L., and M. A. Ramsay. 1993. The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos* **66**:336-342.
- Dunning, J. B., Jr., editor. 1993. *CRC Handbook of Avian Body Masses*, 1st edition. CRC Press, Inc., Florida.
- Etienne, R. S., and H. Olf. 2004. How dispersal limitation shapes species-body size distributions in local communities. *American Naturalist* **163**:69-83.
- Evans, K. L., J. J. D. Greenwood, and K. J. Gaston. 2005. Dissecting the species-energy relationship. *Proceedings of the Royal Society B* **272**:2155-2163.
- Evans, K. L., A. S. L. Rodrigues, S. L. Chown, and K. J. Gaston. 2006a. Protected areas and regional avian species richness in South Africa. *Biology Letters* **2**:184-188.

- Evans, K. L., B. J. van Rensburg, K. J. Gaston, and S. L. Chown. 2006b. People, species richness and human population growth. *Global Ecology and Biogeography* **15**:625-636.
- Fairbanks, D. H. K. 2004. Regional land-use impacts affecting avian richness patterns in Southern Africa - insights from historical avian atlas data. *Agriculture, Ecosystems and Environment* **101**:269-288.
- Fairbanks, D. H. K., M. Kshatriya, A. S. van Jaarsveld, and L. G. Underhill. 2002. Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* **5**:61-74.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2003. Bergmann's rule and body size in mammals. *American Naturalist* **161**:821-825.
- Fry, C. H., and S. Keith. 2001. *The Birds of Africa Volume VII*, 1st edition. Academic Press, London.
- Fry, C. H., S. Keith, and E. K. Urban. 1988. *The Birds of Africa Volume III*, 1st edition. Academic Press, London.
- Fry, C. H., S. Keith, and E. K. Urban. 2000. *The Birds of Africa Volume VI*, 1st edition. Academic Press, Cape Town.
- García, L. V. 2003. Controlling the false discovery rate in ecological research. *Trends in Ecology and Evolution* **18**:553-554.
- García, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**:657-663.
- Gaston, K. J., and T. M. Blackburn. 1995. The frequency-distribution of bird body weights: aquatic and terrestrial species. *Ibis* **137**:237-240.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and Process in Macroecology*, 1st edition. Blackwell Science, Oxford.

- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**:2606-2621.
- Gotelli, N. J., and G. R. Graves. 1996. *Null Models in Ecology*, 1st edition. Smithsonian Institution Press, Washington.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* **9**:399-409.
- Harrison, J. A., D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker, and C. J. Brown, editors. 1997. *The Atlas of Southern African Birds*, 1st edition. BirdLife South Africa, Johannesburg.
- Harrison, J. A., and P. Martinez. 1995. Measurement and mapping of avian diversity in Southern Africa: implications for conservation planning. *Ibis* **137**:410-417.
- Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. 2005. *Roberts Birds of Southern Africa*, 7th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Holt, R. D. 2006. Emergent neutrality. *Trends in Ecology and Evolution* **21**:531-533.
- Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* **16**:S9-S21.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, 1st edition. Princeton University Press, Princeton.
- Hutchinson, G. E., and R. H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. *American Naturalist* **93**:117-125.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* **51**:365-390.
- Jones, J., C. E. Gibb, S. C. Millard, J. J. Barg, M. K. Girvan, M. L. Veit, V. L. Friesen, and R. J. Robertson. 2005. Multiple selection pressures generate adherence

- to Bergmann's rule in a Neotropical migratory songbird. *Journal of Biogeography* **32**:1827-1833.
- Keith, S. K., E. K. Urban, and C. H. Fry. 1992. *The Birds of Africa Volume IV*, 1st edition. Academic Press, London.
- Kozłowski, J., and A. T. Gawelczyk. 2002. Why are species' body size distributions usually skewed to the right? *Functional Ecology* **16**:419-432.
- Kozłowski, J., and J. Weiner. 1997. Interspecific allometries are by-products of body size optimization. *American Naturalist* **149**:352-380.
- Legendre, L., and P. Legendre. 1998. *Numerical Ecology*, 1st edition. Elsevier, Amsterdam.
- Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* **87**:1399-1410.
- Lennon, J. J. 2000. Red shifts and red herrings in geographical ecology. *Ecography* **23**:101-113.
- Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* **125**:873-878.
- Lockwood, J. G. 1985. *World Climatic Systems*, 1st edition. Edward Arnold, London.
- Lomolino, M. V., D. F. Sax, B. R. Riddle, and J. H. Brown. 2006. The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography* **33**:1503-1510.
- Maclean, G. L. 1993. *Roberts' Birds of Southern Africa*, 6th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Makarieva, A. M., V. G. Gorshkov, and B. L. Li. 2005. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos* **111**:425-436.

- Marquet, P. A., and H. Cofré. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos* **85**:299-309.
- Maurer, B. A. 1998. The evolution of body size in birds. I. Evidence for non-random diversification. *Evolutionary Ecology* **12**:925-934.
- Maurer, B. A., J. H. Brown, and R. D. Rusler. 1992. The micro and macro in body size evolution. *Evolution* **46**:939-953.
- May, R. M. 1978. The dynamics and diversity of insect faunas. Pages 188-204 in L. A. Mound and N. Waloff, editors. *Diversity of Insect Faunas*. Blackwell Scientific Publications, Oxford.
- McNab, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology* **52**:845-854.
- Meiri, S., and T. Dayan. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* **30**:331-351.
- Meiri, S., T. Dayan, and D. Simberloff. 2005. Biogeographical patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule. *Journal of Biogeography* **32**:369-375.
- Olalla-Tárraga, M. Á., M. Á. Rodríguez, and B. A. Hawkins. 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* **33**:781-793.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* **29**:254-283.
- Rodríguez, M. Á., I. L. López-Sañudo, and B. A. Hawkins. 2006. The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography* **15**:173-181.
- Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. *The American Midland Naturalist* **80**:299-315.

- Ruggiero, A., and B. A. Hawkins. 2006. Mapping macroecology. *Global Ecology and Biogeography* **15**:433-437.
- Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences of the United States of America* **103**:6230-6235.
- Schulze, R. E. 1997a. Climate. Pages 21-41 *in* S. M. Pierce, editor. *Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Schulze, R. E. 1997b. *South African Atlas of Agrohydrology and -Climatology*. Report TT82/96, Water Research Commission, Pretoria.
- Sfenthourakis, S., E. Tzanatos, and S. Giokas. 2006. Species co-occurrence: the case of congeneric species and a causal approach to patterns of species association. *Global Ecology and Biogeography* **15**:39-49.
- Siegel, S. 1956. *Nonparametric Statistics*, 1st edition. McGraw-Hill Book Company, Inc., New York.
- Smith, F. A., J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, E. A. Hadly, K. E. Jones, D. M. Kaufman, P. A. Marquet, B. A. Maurer, K. J. Niklas, W. P. Porter, B. Tiffney, and M. R. Willig. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *American Naturalist* **163**:672-691.
- Stone, L., T. Dayan, and D. Simberloff. 1996. Community-wide assembly patterns unmasked: the importance of species' differing geographical ranges. *American Naturalist* **148**:997-1015.
- Urban, E. K., C. H. Fry, and S. Keith. 1986. *The Birds of Africa Volume II*, 1st edition. Academic Press, London.

- Urban, E. K., C. H. Fry, and S. Keith. 1997. *The Birds of Africa Volume V*, 1st edition. Academic Press, London.
- van Rensburg, B. J., S. L. Chown, and K. J. Gaston. 2002. Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist* **159**:566-577.
- van Rensburg, B. J., B. F. N. Erasmus, A. S. van Jaarsveld, K. J. Gaston, and S. L. Chown. 2004. Conservation during times of change: correlations between birds, climate and people in South Africa. *South African Journal of Science* **100**:266-272.
- Westphal, M. I., S. A. Field, A. J. Tyre, D. Paton, and H. P. Possingham. 2003. Effects of landscape pattern on bird species distribution in the Mt. Lofty Ranges, South Australia. *Landscape Ecology* **18**:413-426.
- Wigginton, J. D., and F. S. Dobson. 1999. Environmental influences on geographic variation in body size of western bobcats. *Canadian Journal of Zoology* **77**:802-813.
- Young, J. A. T., and S. Hastenrath, editors. 1991. *Glaciers of the Middle East and Africa - Glaciers of Africa*, edition 1.0. U.S. Geological Survey.
- Zeveloff, S. I., and M. S. Boyce. 1988. Body size patterns in North American mammal faunas. Pages 123-146 *in* M. S. Boyce, editor. *Evolution of Life Histories of Mammals: Theory and Pattern*. Yale University Press, New Haven.



## Appendix

**Appendix 1.** Number of quarter degree grid cells with body size measures smaller:larger than expected from 1000 unweighted ("Unweight") randomizations and 1000 randomizations weighted by species range sizes ("Weight", see text for details) conducted for each species richness value. Grid cells were grouped into species richness categories. Two-tailed Fisher exact tests were performed to determine whether the proportion of grid cells with the ratio of smaller:larger sizes was significantly different from 1:1. \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . (\*) represents values that were insignificant after controlling for false discovery rate.

(a)

Spp. Rich. Category	Skewness		Kurtosis		Coefficient of Variation		First Quartile		Third Quartile		Interquartile Range	
	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight
50-69	0:13**	0:13**	3:10	0:13**	2:11	13:0**	10:30	11:2	10:3	13:0**	9:4	13:0**
70-89	9:43***	7:45***	22:30	11:41**	9:43***	41:11**	34:18	34:18	33:18	41:11**	34:18	40:12**
90-109	29:55	26:58(*)	42:42	32:52	12:72***	48:36	50:33	50:33	36:48	48:36	32:52	46:38
110-129	55:52	47:60	49:58	35:72*	16:91***	43:64	44:63	43:64	24:83***	43:64	21:86***	42:65
130-149	85:66	76:75	89:62	62:89	25:126***	41:110***	64:87	58:88	22:129***	41:110***	16:135***	38:113***
150-169	94:57(*)	88:63	89:62	65:86	34:117***	38:113***	51:100(**)	48:101**	21:128***	38:113***	18:133***	37:114***
170-189	119:49***	105:63(*)	118:50***	87:81	31:137***	39:129***	66:102	60:106(*)	21:146***	39:129***	18:150***	35:133***
190-209	90:45**	88:47(*)	94:41**	82:53	38:97***	40:93**	55:80	50:82(*)	28:106***	40:93**	26:109***	39:96***

## Appendix 1 (continued)

Spp. Rich. Category	Skewness		Kurtosis		Coefficient of Variation		First Quartile		Third Quartile		Interquartile Range	
	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight	Unweight	Weight
210-229	66:35*	62:39	76:25**	69:32*	31:70**	43:57	52:49	46:52	23:77***	43:57	20:81***	42:59
230-249	57:38	56:39	68:27**	65:30*	28:67**	49:45	59:35	49:41	24:71***	49:45	20:75***	45:50
250-269	50:22*	48:24	53:19	51:21*	19:53**	32:38	35:37	23:47(*)	12:60***	32:38	15:57***	33:39
270-289	38:16 <sup>(*)</sup>	32:22	35:19	28:26	9:45**	34:20	29:24	18:29	7:46***	34:20	9:45***	33:21
290-309	28:11	27:12	27:12	21:18	10:29*	22:16	24:15	9:27(*)	5:33***	22:16	5:34***	26:13
310-329	21:10	21:10	20:11	18:13	8:23	23:7(*)	21:10	8:17	5:25**	23:7(*)	4:27**	26:5**
330-349	24:1***	24:1***	22:3**	19:6	5:20*	7:18	10:14	1:24***	1:24***	7:18	1:24***	16:9
350-369	9:1	9:1	8:2	6:4	3:7	4:5	5:4	1:8	1:9	4:5	0:10*	8:2

## Chapter 3

### The effects of human disturbance on avian assemblages in three South African regions: species richness, composition and functional diversity

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#### Introduction

Conflict between humans and biodiversity exists globally, and is predicted to increase in the future (Kerr and Currie 1995, Balmford et al. 2001, McKee et al. 2003, Scharlemann et al. 2004). Although regions that are not under formal protection are of considerable significance for biodiversity conservation (Knight 1999, Norton 2000, Dudley et al. 2005), they are increasingly being fragmented and placed under mounting threat by land-use changes (Sánchez-Azofeifa et al. 2003, Gutiérrez 2005, Gaston et al. 2006, Sigel et al. 2006, Young et al. 2006). Protected areas are therefore playing an increasingly important role in protecting indigenous biodiversity as anthropogenic pressures increase outside the borders of these conservation areas (e.g. Bruner et al. 2001, Lamprey and Reid 2004).

Species richness comprises one possible measure of the effect of land-use change on biodiversity, although interpretations of changes in richness necessarily depend on spatial scale (Sax and Gaines 2003). At the global scale, richness is decreasing because the global rate of extinction is outweighing that of speciation (Sax and Gaines 2003). At regional and local scales species richness often shows temporal increases owing to the introduction of exotics and changes in patch heterogeneity. Landscapes classified as transformed can therefore have higher species richness values than natural landscapes because they are often interspersed with small patches of natural vegetation that support different assemblages (Rosenzweig 2001, Sax and Gaines 2003, Fairbanks 2004). At the patch scale, the

richness of a transect with a single land use is usually measured, therefore this scale often reveals local extinctions, invasions, or both, frequently as a consequence of land-use changes (e.g. Little and Crowe 1994, Wardell-Johnson and Williams 2000, Dean et al. 2002, Watson 2003, Didham et al. 2005, Smart et al. 2005).

However, losses or changes in biodiversity cannot simply be assessed in terms of species richness, because richness does not describe assemblage compositional change, i.e. the identity of the species lost or gained (Dufrêne and Legendre 1997, Whitford 1997, Margules and Pressey 2000). Ecological effects of disturbances should rather be considered in the context of impacts on richness, identity and abundance, i.e. the community and environment within which species exist, and the ecological roles such species fulfill (Cardinale et al. 2006). Extinction of species may result in the loss of the ecological functions they fulfill in their habitat (Petchey and Gaston 2002a), while the addition of species may create new ecological roles in the ecosystem (e.g. Huyser et al. 2000, Coomes et al. 2003, Wiles et al. 2003). Because individuals and species do not exist in isolation, but interact with other organisms (see Begon et al. 1996), factors that directly affect one taxon may indirectly impact other taxa through the breakdown or alteration of such interactions and of ecosystem functions (Paine 1969, Bond 1994, Vitousek et al. 1996, Berlow 1999, Knops et al. 1999, Huyser et al. 2000, Loreau et al. 2001, Koh et al. 2004, Şekercioğlu et al. 2004, Knight et al. 2005, Cardinale et al. 2006).

One process by which community interactions are disrupted is through alterations to the existing food web. Indeed, changes in land use have been shown to affect bird assemblages by altering their food availability (Söderström et al. 2001, Benton et al. 2002, Newton 2004, Maron and Lill 2005). Much attention has been directed at drastic declines of farmland birds in Europe, which have largely been attributed to reductions in components of the birds' diets (Beecher et al. 2002, Benton et al. 2002,

Barker 2004, Moreby 2004, Newton 2004, Britschgi et al. 2006). For example, negative effects of land use on insects seem to be leading to lower abundances and local extinction of insectivorous birds. Declines in insect abundance and diversity in response to vegetation changes associated with agricultural practices, and as a consequence of pesticide and herbicide use have been recorded (Herremans 1998, Clapperton et al. 2002, Sinclair et al. 2002, Gebeyehu and Samways 2003, Barker 2004, Newton 2004, Stefanescu et al. 2004, Botes et al. 2006, Britschgi et al. 2006, Chacoff and Aizen 2006, Cleary and Mooers 2006), and land-use changes have often been shown to result in lowered abundance and species richness of insectivorous birds (Fjeldså 1999, Stratford and Stouffer 1999, Dean et al. 2002, Raman and Sukumar 2002, Lim and Sodhi 2004, Little et al. 2005, Waltert et al. 2005, Newmark 2006). Indeed, several studies have directly linked declines in insectivore abundance to decreases in insect diversity (Benton et al. 2002, Sinclair et al. 2002, Britschgi et al. 2006).

Gaston et al. (2006) recently highlighted the need for, but also the lack of, studies investigating the effectiveness of conservation areas for representing and protecting biodiversity. Protected areas can serve as benchmarks to evaluate the effects of anthropogenic activities on biodiversity (Sinclair et al. 2002, Sigel et al. 2006), and make important contributions to the conservation of the organisms inhabiting them, whose diversity is otherwise adversely affected in surrounding landscapes. Conservation areas have indeed been shown to be valuable for conserving bird (Brooks 1999, Sinclair et al. 2002, Sigel et al. 2006), reptile (Brooks 1999, though see Smart et al. 2005) and insect (Rivers-Moore and Samways 1996, Gebeyehu and Samways 2002, Sinclair et al. 2002, Botes et al. 2006) assemblages.

In South Africa, as is the case elsewhere, humans and other species are competing for available land and resources (Macdonald 1989, Wessels et al. 2000,

Chown et al. 2003, Wessels et al. 2003). Human effects on biodiversity have been detected at several levels and for a variety of taxa (for reviews see Huntley 1989, Driver et al. 2005). At a regional scale, for example, these effects are reflected by increasing avian species richness with an increase in percentage of area protected (Evans et al. 2006), although it has also been found that landscape transformation has little effect on species turnover at this scale (van Rensburg et al. 2004). Moreover, it also appears that at this scale richness increases with human disturbance – possibly due to the addition of synantropic species to the already existing species pool remaining in fragments of natural vegetation (Fairbanks 2004).

At local scales, few investigations have quantitatively investigated the contribution of protected areas to the conservation of birds in South Africa (Little and Crowe 1994, Little et al. 2005, Fox 2006), or the effects of land-use changes on the avifauna (Armstrong and Vanhensbergen 1994, Little and Crowe 1994, Jansen et al. 1999, Dean et al. 2002, Mangnall and Crowe 2003, Schwarzenberger and Dean 2003, Little et al. 2005, Wethered and Lawes 2005, Fox 2006). At local scales, species richness has been shown to be both higher (Armstrong and Vanhensbergen 1994, Jansen et al. 1999, Dean et al. 2002, Mangnall and Crowe 2003, Little et al. 2005) and lower (Little and Crowe 1994, Schwarzenberger and Dean 2003, Fox 2006) in natural than in disturbed landscapes, although differences are often small. This suggests that at local scale the effect of land-use changes on avian richness may be dependent on factors such as locality and the type of land-use change. However, several of these studies were not conducted with the purpose of directly assessing the effect of land-use changes on avian assemblages. Therefore, other factors may have influenced their outcomes. For example, sampling effort in different land-use types was not always equivalent (e.g. Little and Crowe 1994), the disturbed landscape did not support the same vegetation type prior to its transformation as the natural landscape

with which it was being compared (Armstrong and Vanhensbergen 1994), and differences in richness could be attributed to factors other than land-use changes, such as the presence or absence of planted trees (Little et al. 2005). In some instances, increases in richness with disturbance were also a consequence of artificial water bodies which allowed water birds to occupy areas previously not available to them (e.g. Little and Crowe 1994, Fox 2006). In consequence, few studies have offered conclusive evidence for the contribution of reserves to avian conservation in South Africa, and the effects of landscape change on avian assemblages.

The aim of the present study is therefore to provide a quantitative evaluation of the contribution of three South African reserves to the conservation of the avifauna of three very different regions. More specifically, I will test Fairbanks' (2004), van Rensburg et al.'s (2004) and Evans et al.'s (2006) conflicting conclusions about the effect of protected/natural land on the species richness of South African birds at a finer spatial scale than the one used in each of those studies. That is, I will determine whether richness in pristine areas inside reserves differs from richness in disturbed areas outside reserves and how species turnover between areas inside and outside the reserve contribute to the overall species richness of a region. I will also examine how the functional diversity (in particular feeding guilds and body size) is affected by land-use changes. In two of the three regions investigated, insect numbers are known to decrease in response to agricultural practices (Witt and Samways 2004, Botes et al. 2006), and these declines in insect abundance may be reflected in the avian communities.



## Methods

### STUDY AREA

Three regions in South Africa were selected for this study (see Fig. 1 in Chapter 1). Each region consisted of a protected area (Jonkershoek Nature Reserve [33°57' S, 18°55' E] in the south-western Cape, the Karoo National Park in the southern-central area of South Africa [32°17' S, 22°25' E] and Tembe Elephant Park [27°01' S, 32°24' E] in northern KwaZulu-Natal), and land adjacent to each of the protected areas that has been modified by human activities. The vegetation and biota of the latter was similar to those of the adjacent reserves prior to land-use changes. Protected areas will also be referred to as 'natural' areas in the text, and unprotected areas which have undergone land-use changes as 'disturbed' areas.

Jonkershoek Nature Reserve and Assegaibos Nature Reserve (henceforth Jonkershoek) lie in the Jonkershoek valley, one of the highest rainfall regions in South Africa (Schulze 1997). Most precipitation is recorded in winter, and summers are hot and dry. Jonkershoek forms part of the larger Hottentots-Holland Nature Reserve, which is situated in the Fynbos biome. Fynbos is a component of the Cape Floral Kingdom – the smallest, but richest floral kingdom of the world, and its vegetation is characterized by a high diversity of three plant families: the Restionaceae, Proteaceae and Ericaceae, of which a large proportion are endemic to the region (Cowling and Richardson 1995). Despite its high floral diversity, Fynbos is not home to a large variety of vertebrates, primarily because the region is nutrient-poor and structurally simple (Cowling and Richardson 1995). In addition, many of the large game species that roamed the area are now extinct in the biome (Cowling and Richardson 1995). Fire is an integral part of Fynbos; fires naturally recur every 12 to 15 years. The region in which this study was conducted is situated at the foot of the Hottentots Holland Mountains in the Eerste River valley. The vegetation here has

been classified as mesic mountain fynbos, characterized by seasonally waterlogged, mesic soils, and is interspersed with forests and riparian vegetation on the banks of rivers and streams (Moll et al. 1984, McDonald 1985). Because of its low nutrient quality, Fynbos is unsuitable for intensive grazing; therefore, land-use activities usually result in complete transformation of the landscape. Areas directly adjacent to the reserve have been afforested by *Pinus radiata*. Because (as the name suggests) mountain fynbos is mainly restricted to mountainous terrain, it is not as threatened as lowland fynbos and renosterveld of the low-lying areas of the south-western Cape, which have been extensively transformed by agricultural activities (Hockey et al. 1989, Cowling and Richardson 1995). Even so, tracts of Fynbos, including those adjacent to Jonkershoek, have been replaced by vineyards and plantations of fast-growing exotics such as *Pinus*, *Eucalyptus* and *Acacia* species (Hockey et al. 1989). In addition, alien invasives are a major threat to the biome (Cowling and Richardson 1995).

The Karoo National Park (henceforth Karoo) lies in the semi-arid Nama Karoo biome (Desmet and Cowling 1999), the vertebrate fauna of which is relatively species-poor and supports few endemics (Vernon 1999). Due to seasonal and unpredictable climatic conditions, the area was historically characterized by migrating species. The region supports the highest proportion of nomadic bird species in the country, which take advantage of seasonally unfavourable conditions which other species cannot endure (Dean 1997). The erection of fences and hunting have greatly reduced numbers of migrating mammals and have effectively caused the disintegration of their movement patterns (Hoffman et al. 1999, Siegfried 1999). The vegetation of the Nama Karoo is dominated by grasses and shrubs (Midgley and van der Heyden 1999), and the greatest limiting factor of the region is moisture (Cowling and Hilton-Taylor 1999). The Karoo National Park was proclaimed in 1979, and

further farms, previously used for stock farming, have been added to the reserve since the 1990s (Rubin et al. 2001, South African National Parks 2005). Several game species that once occupied the region have been reintroduced to the park over the past years (South African National Parks 2005). A segment of the Nuweveld Mountains falls within the boundaries of the Karoo National Park, where they form part of the escarpment that divides South Africa's central plateau and coastal areas (Rubin et al. 2001). Two veld types, as defined by Acocks (1988), are represented in the Karoo, namely Karroid Broken Veld and Karroid *Merxmuellera* Mountain Veld replaced by Karoo vegetation (Rubin et al. 2001). The former is associated with the middle, and the latter with the upper plateau of the Karoo (Rubin et al. 2001) The major threats to the region are associated with farming activities, specifically pastoralism. Overgrazing and trampling by livestock (mainly sheep, goats, some cattle, and more recently, game), and the imposition of perennial grazing regimes in highly seasonal or periodic landscapes is having negative effects on the landscape (Werger 1978, Hoffman et al. 1999, Vernon 1999, G. Pretorius pers. comm.).

Tembe Elephant Park (hereafter Tembe) was proclaimed in 1983, prior to which it was sparsely populated communal land. The park lies in the Maputaland Centre, which is part of the Maputaland-Pondoland-Albany biodiversity hotspot and is home to many endemic species and subspecies (Matthews et al. 2001, [www.biodiversityhotspots.org](http://www.biodiversityhotspots.org)) and is a region with a relatively high turnover in vegetation (Moll 1980, Kirkwood and Midgley 2003). The fauna and flora of the region possess a distinctive tropical element (Poynton 1961). The area in and around the Tembe consists of a matrix of woodland, grassland and sand forest patches, of which the latter is considered to be of particularly high conservation value (Matthews et al. 2001). Sand forest distributions are thought to be determined mainly by historic plant dynamics, rather than current environmental factors, and it is thus thought that

they do not re-grow once they have been disturbed (Matthews et al. 2001). Vegetation plays an important role in the distribution of birds in the region; mixed woodland and sand forest support different assemblages (van Rensburg et al. 2000). Tembe lies in the summer rainfall region of the subcontinent and experiences relatively high humidity, especially in summer (Matthews et al. 2001). Anthropogenic threats to areas outside Tembe include frequent burning, livestock grazing and the utilization of selected plant species for traditional medicines or wood carvings. Inside the park, elephants are damaging sand forests due to the fact that their natural migration routes have been obstructed by the erection of fences around the park border, causing them to no longer exclusively select the preferred woodland areas for feeding (Matthews et al. 2001).

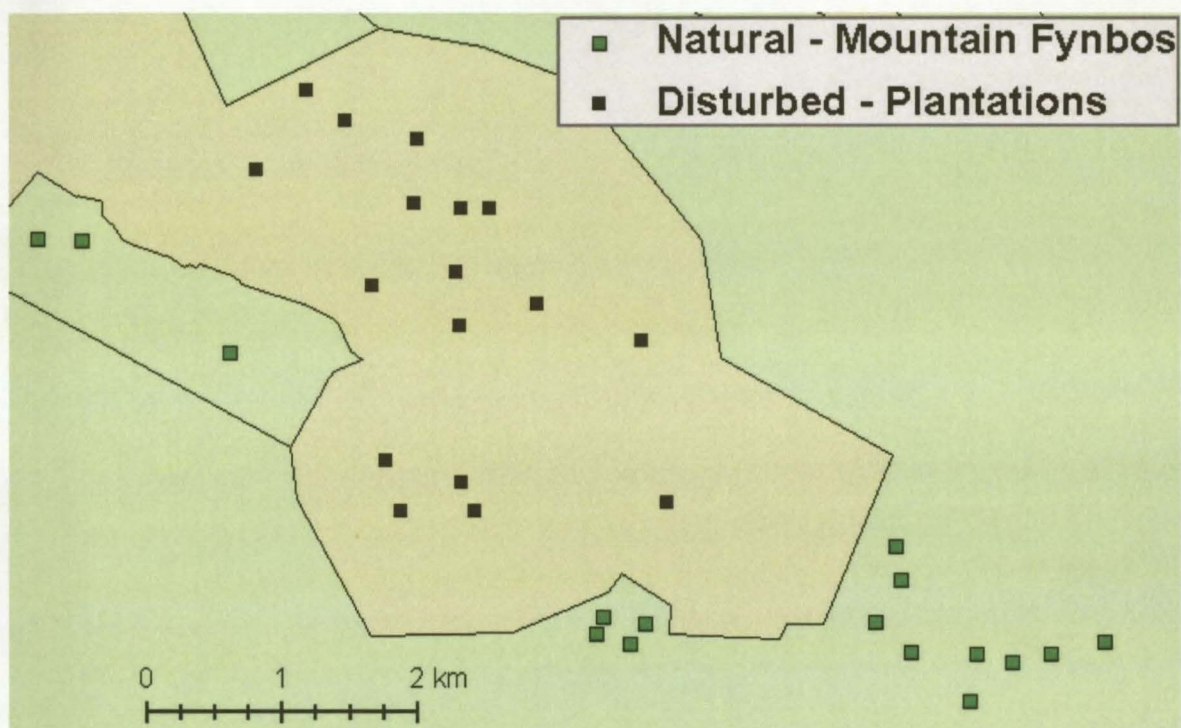
#### SAMPLING DESIGN

In each reserve, equal numbers of transects were selected in undisturbed (natural) areas inside, and in disturbed areas outside the reserve. Natural and disturbed areas are referred to as the two land-use types in the text. In Jonkershoek, a total of 32 transects (16 in natural and 16 in disturbed areas), and in Tembe and the Karoo 40 transects (20 in natural 20 in disturbed areas) were selected. In Jonkershoek and the Karoo, transects were randomly selected from the study area. Randomly selected transects which were inaccessible or far from roads were repositioned to more accessible areas. Because vegetation types and disturbed areas are patchily distributed in and around Tembe, transect-selection here was done with the assistance of the park's regional ecologist and local people of the region.

A stratified sampling design was employed. In Jonkershoek (Fig. 1), transects were selected in two vegetation types: mountain fynbos vegetation above 600 m altitude (10 transects in each land-use type) and mountain fynbos vegetation below



600 m altitude (six transects in each land-use type). Because the two vegetation types supported similar bird assemblages, data from the two vegetation types were pooled, and therefore only one vegetation type, referred to as 'mountain fynbos' here, was effectively sampled. In August/September 2005, every point was sampled on five different mornings, and in March/April on four mornings. In March, one of the transects in the plantations was harvested before sampling had been completed. For this reason, a similar point was chosen, and two counts, which were pooled with the now harvested transect's data, conducted here.



**Figure 1.** Position of point transects in Jonkershoek Nature Reserve. Areas shaded in green and brown represent protected (natural) and unprotected (disturbed) areas respectively.

In the Karoo National Park (Fig. 2), transects were only selected in areas that had been incorporated in the reserve for more than 10 years. Transects were positioned in five different vegetation types as defined by Bezuidenhout and Holness (2004). For

each land-use type, nine transects were allocated to *Stipagrostis ciliata* Dwarf Shrubland, two to both Montane Open Shrubland and *Aristida diffusa-Rhus burchelli* Grassy Shrubland, one to Montane Dwarf Shrubland and five to Karoo Slope Mosaic. Transects in *Stipagrostis ciliata* Dwarf Shrubland will henceforth be referred to as 'Lowlands' transects ( $n = 9$  in each land-use type), data from Montane Open Shrubland and Montane Dwarf Shrubland, both of which are found on the top of the escarpment, were pooled and are referred to as the 'Plateau' vegetation type ( $n = 3$ ), and *Aristida diffusa-Rhus burchelli* Grassy Shrubland, which occurs on the middle plateau, and Karoo Slope Mosaic, which occurs on the slopes of the mountains, were pooled and are referred to as 'Slopes & Middle Plateau' ( $n = 7$ ). Transects crossed riverine patches (vegetation classified as Karoo Drainage Line Complex, *sensu* Bezuidenhout and Holness 2004). In each sampling period, every transect was sampled on one morning and one afternoon. Counts were carried out in October 2005 and February/March 2006.

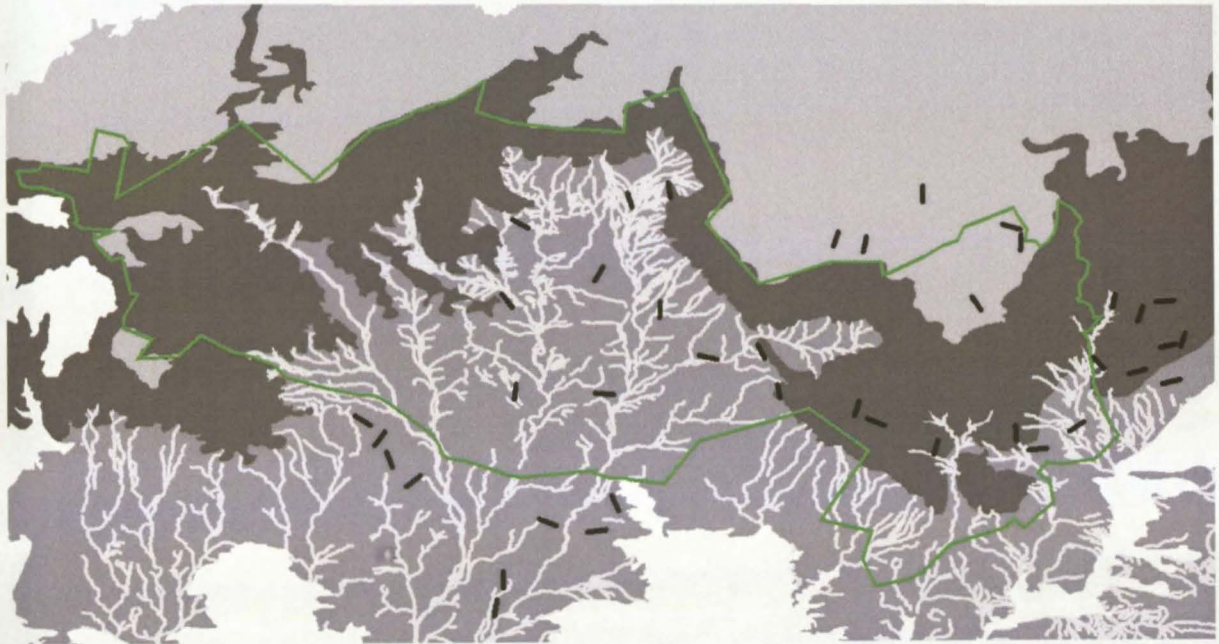
In both natural and disturbed areas in Tembe (Fig. 3), 10 transects were selected in each of two vegetation types: mixed woodland and sand forest (van Rensburg et al. 2000). According to stratified sampling theory, the proportion of transects assigned to each vegetation type should be indicative of the percentage cover of the respective vegetation type (Bibby et al. 2000). In Tembe mixed woodlands cover a larger area of the study region than sand forests (Matthews et al. 2001). However, because it has been shown that bird assemblages are more variable in sand forests than woodlands (van Rensburg et al. 2000), an equal number of transects was selected in each vegetation type. Bird counts in Tembe were done in November/December 2005 and April/May 2006. In each sampling period, every transect was visited on three mornings and two afternoons.



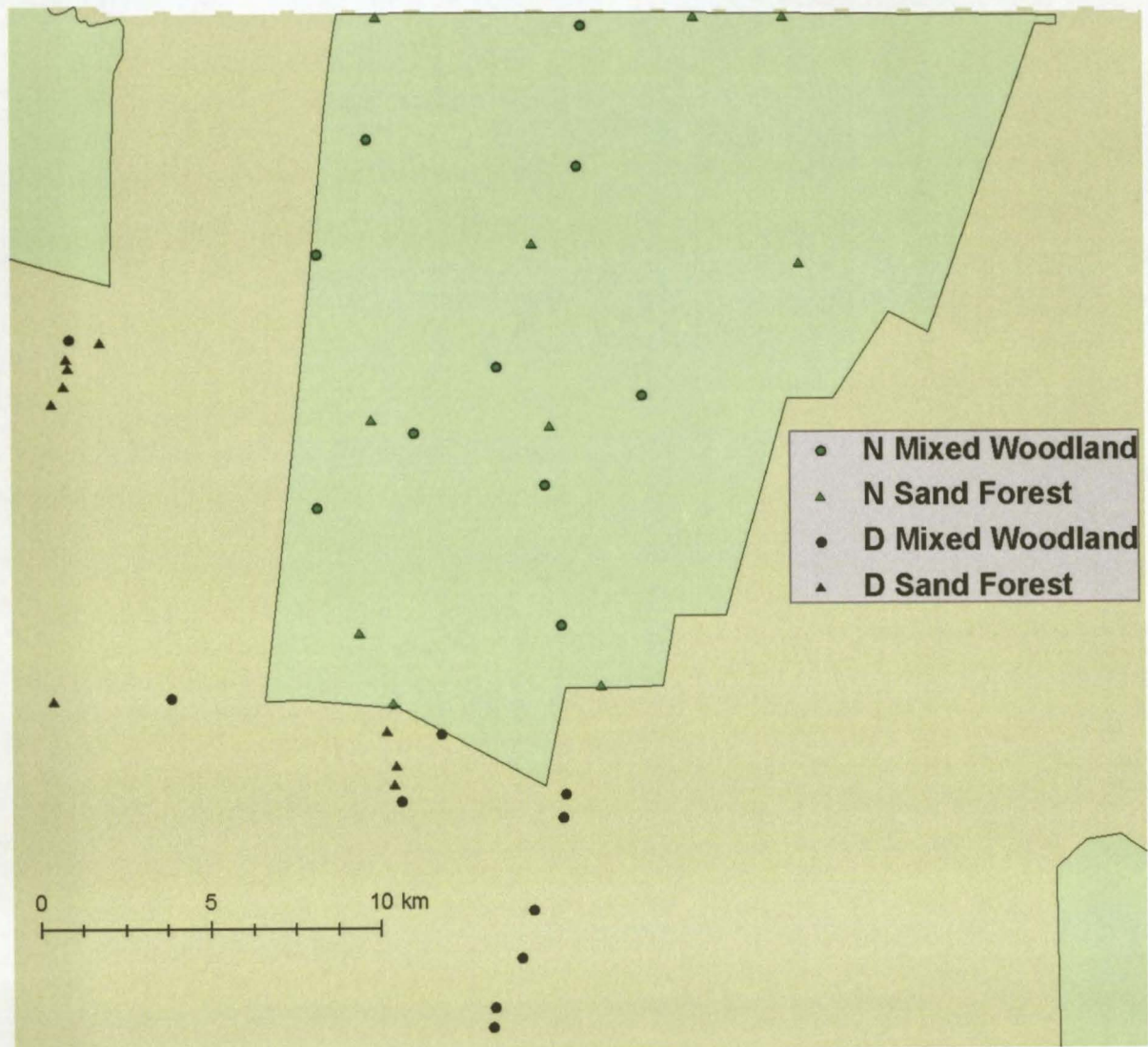
Fig. 4 is a schematic representation of the experimental set-up employed in the three regions and summarises terminology used in the text.

**Stratum**

- Lowlands
- Slopes & Middle Plateau
- Plateau
- Riverine



**Figure 2.** Position of line transects (black lines) in and around the Karoo National Park. The green line represents the park borders. Vegetation types have been mapped (data from Bezuidenhout and Holness 2004), and the position of riverine vegetation (Karoo drainage line complex vegetation type) has also been shown.

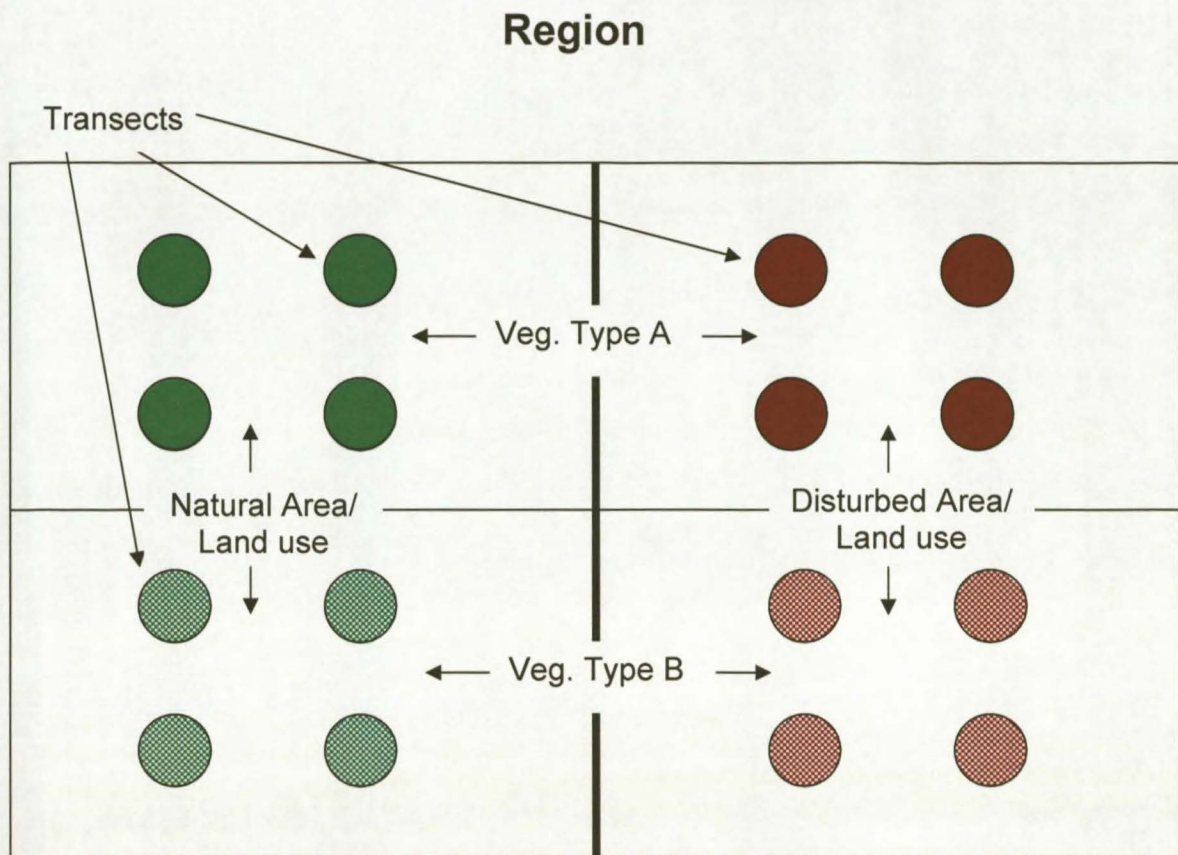


**Figure 3.** Position of point transects in Tembe. Areas shaded in green and brown represent protected (natural) areas and unprotected (disturbed) areas respectively. (N = natural, D = disturbed)

Because the three study regions possess different vegetation structure and also differ from one another in terms of their avian species richness, different sampling techniques were employed. At every transect, distance-based line transects (Karoo) or point counts (point transects – Tembe and Jonkershoek) were conducted (Buckland et al. 2001). The former involves an observer walking in a straight line for a specified distance and time, and recording the distance from the line of each bird detected (Buckland et al. 2001). In the Karoo, transects were 1 km long and



detections were recorded up to a distance of 50 m perpendicular to, and on either side of the transect line. If a bird was recorded in front of the observer, the angle of the bird from the point on the transect at which the observer was standing, and the distance of the bird from the observer were recorded. These parameters were used to calculate the perpendicular distance of the bird from the transect line. Line transects are considered the more accurate sampling method, but require that the vegetation structure is suited for walking in straight lines (Bibby et al. 2000). Because this was not practical in Jonkershoek and Tembe, birds were monitored using point transects here. For point transects, the observer stood at one point for a specified time, and recorded the birds heard or seen and their horizontal distance from the point (Buckland et al. 2001). This method is more superior in dense vegetation (Bibby et al. 2000). Swarovski 10 x 42 EL binoculars were used for bird observations, and distances were measured with a Bushnell Yardage Pro Sport laser rangefinder; if the bird was not visible or the undergrowth was very dense, distances were estimated by measuring the distance to objects thought to be in the vicinity of the bird. If birds moved within a transect, distances were recorded at the initial location they were recorded at (Buckland et al. 2001). Birds flying through transects were not counted (van Rensburg et al. 2000). The observer(s) (MG, and, in Tembe, Bongani Tembe) spent approximately two minutes at point transects before the count commenced to allow birds to become accustomed to the observers' presence and settle (Bibby et al. 2000). The duration of point counts at each point transect was seven minutes at Jonkershoek transects and ten minutes at the structurally more complex and more species-rich Tembe transects (Fuller and Langslow 1984). Count durations in the two regions were different to maximise the number of species observed in the given time, while minimising the chances of counting the same bird twice (Fuller and Langslow 1984, Bibby et al. 2000).



**Figure 4.** Schematic diagram of the experimental set-up in each of the three study regions, and terminology used throughout the text. Three regions were sampled: Jonkershoek, the Karoo and Tembe. In every region, natural areas inside a reserve and disturbed areas outside the reserve were sampled. Natural and disturbed areas are also referred to as the two land-use types. Within every land-use type, different vegetation types were identified (except in Jonkershoek, where only one vegetation type was assessed). Within every vegetation type, transects were sampled. In Jonkershoek and Tembe, point transects were used, and line transects in the Karoo. Note that the number of vegetation types per region and the number of transects within each vegetation type were not necessarily as shown.

Morning counts were conducted from dawn until three hours after sunrise, and in the afternoons from three hours before sunset until dusk. The order in which

transects were sampled was randomized so far as was possible. No counts were carried out in very windy conditions or in rain.

## ANALYSES

### *Sampling sufficiency*

Sample-based rarefaction curves were used to assess sampling adequacy (Gotelli and Colwell 2001). Rarefaction curves were calculated using a moment-based interpolation method (Mao Tau), which requires no resampling and has been shown to be as accurate as the traditional re-sampling method (Colwell et al. 2004). The rarefaction curve represents the expected shape of the corresponding sample-based accumulation curve (Gotelli and Colwell 2001). Sampling is considered to be adequate if the rarefaction curve approaches an asymptote (Longino et al. 2002). Analyses were run in EstimateS v. 7.5 (<http://viceroy.eeb.uconn.edu/estimates>, Colwell 2004).

### *Species richness and abundance*

Species richness was calculated using the Jackknife2 estimator (Burnham and Overton 1978, 1979, Smith and van Belle 1984, Palmer 1991). Unlike several other species richness estimators, Jackknife2 does not require transects to be compositionally similar, data to be normally distributed, or an independence of species (Smith and van Belle 1984, Lande et al. 2000, Chao 2004, Magurran 2004). In addition, the index has been shown to provide conservative, but accurate richness estimates (see Magurran 2004 for a synopsis of studies assessing this and other nonparametric species richness estimators). Jackknife2 is obtained by considering successively smaller samples from the observed species pool. From these, the number of undetected species occurring in the sampled area is estimated from the

number of singletons and doubletons in the subsamples (Chao 2004). EstimateS v. 7.5 (Colwell 2004) was used to obtain richness estimates.

Jackknife2 estimates were calculated for the natural or disturbed areas of each of the three regions. Two different Jackknife2 estimates are presented. The first was obtained without resampling. This produces the most accurate richness estimate (Colwell 2005). The second was obtained using 500 randomizations; sampling with replacement was used. Although sampling without replacement (which provides identical richness estimates to analyses conducted without resampling) provides more accurate estimates of richness (Colwell 2005), the generated data is dependent on the real data (Walther and Moore 2005), and no variance is provided for richness estimates (Colwell 2005). Therefore, sampling with replacement is more appropriate for the comparisons of datasets (Colwell 2005) and was therefore used to statistically compare richness between natural and disturbed sites.

Jackknife2 was also calculated for every transect using 10000 randomizations with replacement. Differences in species richness between transects in different land-use types, vegetation types (except in Jonkershoek, where only one vegetation type was sampled) and years (except for the Karoo dataset, where years were pooled due to small sample sizes) were assessed using generalized linear models (PROC GENMOD) in SAS (factorial ANOVA, Poisson distribution, log-link function, type 3 likelihood test, Quinn and Keough 2002). To account for overdispersion (Agresti 1996), standard errors were scaled using deviance as the estimate of the dispersion parameter. Where interactions were significant, post-hoc tests were conducted to determine which classes of treatments were significantly different from one another.

Bird density was calculated by dividing the mean number of birds recorded per sample by the area of the transect. Abundance (and therefore density) estimates are usually dependent on the scale at which abundance is measured (Gaston et al. 1999,



Pautasso and Gaston 2006). Comparisons of densities here were, however, made between equally-sized transects. Because the area of transects in Jonkershoek and Tembe ( $\pi \times 50 \times 50 \text{ m}^2$ ) was different to the area of transects in the Karoo ( $100 \times 1000 \text{ m}^2$ ), comparisons between reserves could, however, be confounded. Detectability was not considered for density calculations – it is therefore probable that density values given here are an underestimate, as undetected birds were not accounted for (Bibby and Buckland 1987). This effect would have been most marked in Tembe natural sand forest, where vegetation complexity was greatest. Visibility was approximately identical in natural and disturbed mixed woodland and disturbed sand forest transects. In Jonkershoek most birds in both natural and disturbed habitats were detected by their calls, while the vegetation structure between natural and disturbed areas and in different vegetation types in the Karoo was very similar. Therefore density comparisons should give representative estimates of relative increase or decreases due to land-use change.

To assess how avian density responds to disturbance, generalized linear models (PROC GENMOD in SAS: factorial ANOVA, Poisson distribution, log-link function, type 3 likelihood test) were again employed to assess the effect of disturbance, vegetation type (except in Jonkershoek, where only one vegetation type was sampled) and sampling period (except in the Karoo, where samples from 2005 and 2006 were pooled due to small sample sizes), and interactions between the three, on avian densities. Standard errors were scaled using deviance (Agresti 1996). Significant interactions were further investigated with post-hoc tests.

Rank-abundance plots are useful for visualising patterns in species richness and abundance in different communities and can be used to assess the evenness of a community (Magurran 2004). A community dominated by few species will possess a steep rank-abundance curve, while curves with a shallow slope indicate high

evenness. Rank-abundance plots were therefore plotted for the two land-use types and the different vegetation types of Jonkershoek, the Karoo and Tembe. Abundances were  $\log_{10}$  transformed to accommodate species whose abundances span several orders of magnitude on one plot (Magurran 2004).

### *$\beta$ -diversity*

$\beta$ -diversity is a measure of species turnover in space (Koleff et al. 2003). Here,  $\beta$ -diversity was assessed in two ways. Additive partitioning assesses the relative contribution of diversity at different spatial scales to the overall regional diversity (Veech et al. 2002, Crist et al. 2003). In space, diversity can be partitioned in the following manner:  $\gamma_i = \alpha_{i-1} + \beta_{i-1}$ , where  $i$  is the spatial scale (also referred to as 'level') of analysis. In other words, regional diversity ( $\gamma$ ) is the sum of local diversity ( $\alpha_i$ , the mean diversity within samples at level  $i$ ) and beta diversity (the diversity among samples, calculated as  $\alpha_{i+1} - \alpha_i$ ) (Crist et al. 2003). Additive partitioning for the reserves sampled in this study can thus be presented in the following manner:  $\gamma_{\text{region}} = \alpha_{\text{samples}} + \beta_{\text{samples}} + \beta_{\text{transects}} + \beta_{\text{vegetation types}} + \beta_{\text{land use}}$  (except in Jonkershoek, where no  $\beta_{\text{vegetation types}}$  existed because only one vegetation type was sampled). The relative contribution of diversity (species richness was used as diversity measure here) at these spatial scales to the regional diversity was calculated using the programme PARTITION developed by J.A. Veech and T.O. Crist (Crist et al. 2003, available at <http://zoology.muohio.edu/crist/>). To assess whether diversity at each level was significantly different from expected, randomization procedures were used. Two randomizations with different null expectations were employed (Crist et al. 2003): at the lowest level ( $\alpha_{\text{samples}}$  and  $\beta_{\text{samples}}$ ), randomizations were individual-based, and assessed the probability that individuals aggregate with other individuals of their species; at the other levels ( $\beta_{\text{transects}}$ ,  $\beta_{\text{vegetation types}}$  and  $\beta_{\text{land use}}$ ), samples, rather than

individuals, from one level were randomly allocated to the next higher level to test whether the samples from one level can be considered random samples from the next lowest level. Ten thousand randomizations were run, except at the third level ( $\beta_{\text{vegetation types}}$ ) in the Karoo dataset, where randomizations were only conducted 1000 times because the software could not deal with 10000 randomizations.

To obtain additional insight into how land-use changes have impacted on the composition of avian assemblages, another  $\beta$ -diversity measure,  $\beta_{sim}$  (Lennon et al. 2001), was used. The mathematical formula for  $\beta_{sim}$  is  $\frac{\min(b,c)}{\min(b,c)+a}$ , where  $a$  is the number of species shared by both transects,  $b$  is the number of species unique to one transect and  $c$  the number of species unique to the other transect. The metric is thus calculated from presence-absence data, and is therefore independent of abundance. In addition,  $\beta_{sim}$  is not biased by species richness, and was found to be one of the best  $\beta$ -diversity measures for presence-absence data (Koleff et al. 2003).  $\beta_{sim}$  was calculated for all pairs of all transects of each sampling region. Numbers of shared and unique species were calculated in EstimateS (Colwell 2004), and  $\beta_{sim}$  subsequently calculated using a spreadsheet.  $\beta_{sim}$  values were classified according to the land-use type and vegetation type of the transects from which their values were calculated. Generalized linear models (PROC GENMOD in SAS) were then used to determine how  $\beta$ -diversity is affected by disturbance, and therefore how species turnover changes as a result of disturbance. Because proportional data was used, models were run with binomial error distribution and a log-link function (Crawley 2002), and deviance was scaled to compensate for overdispersion. Post hoc tests were conducted to determine which combination of transects displayed significantly higher or lower  $\beta$ -diversity than which other combination of transects. Results are presented only for combinations of transects that are sensible in the context of this study. Comparison of  $\beta_{sim}$  between natural transects of one vegetation

type and  $\beta_{sim}$  between disturbed transects of the same vegetation type indicates within which land-use type species turnover is greater, and can indicate whether homogenization within a vegetation type has taken place. Comparisons of  $\beta_{sim}$  between two different vegetation types in natural areas and  $\beta_{sim}$  between the same two vegetation types in disturbed areas indicate whether species turnover between vegetation types of natural and disturbed areas differ, and whether homogenization has occurred between vegetation types. Finally, comparisons of  $\beta_{sim}$  between transects within either natural or disturbed transects and  $\beta_{sim}$  between disturbed and natural transects indicate whether species turnover between natural and disturbed areas is greater than within natural or within disturbed areas.

### *Ordinations*

To further assess how land-use changes affected species composition, assemblages in natural and disturbed areas were compared using multivariate analyses using the PRIMER v. 5 software (Clarke and Gorley 2001). The Bray-Curtis similarity index was used to calculate similarities between assemblages (Magurran 2004). This index considers both species identity and abundance. Data were fourth-root transformed to down-weight common species (Clarke and Warwick 1994). Non-parametric analyses of similarity (ANOSIM, Clarke 1993) were conducted to determine how treatments differed with respect to assemblage structure. Two-way crossed ANOSIMs were used to ascertain what the contribution of land use, sampling period and/or vegetation type was to the composition of bird assemblages. For Jonkershoek, where only one stratum was sampled, land use and sampling period were used as factors. For the Karoo National Park and Tembe, data from both years were pooled, and land use and vegetation type comprised the two factors. Global R values were used to determine the degree of similarity between treatments.

The closer  $R$  is to 1, the more dissimilar assemblages are. ANOSIMs were conducted between combinations of land-use type and vegetation type (where applicable) for each sampling period (except for the Karoo dataset, where results from both sampling periods were pooled due to small sample size). Species assemblages of different land-use types, vegetation types and sampling periods were plotted with multi-dimensional scaling (MDS) ordinations (Clarke and Warwick 1994). Six random restarts were used each with a different number of randomizations (10, 20, 30, 40, 50, 100) to ensure the lowest stress value (i.e. the global optimum) was obtained (Clarke 1993). The stress values presented in the results were obtained for all restarts.

### *Feeding Guilds*

Birds were assigned to one of six feeding guilds (frugivore, granivore, insectivore, mixed, nectarivore, predator, after Dean et al. 2002) based on diet descriptions in Hockey et al. (2005). The proportion of species of each guild in transects was calculated and compared between land-use types and, for the Tembe dataset, vegetation types. (Sample sizes were too small to consider vegetation types in the Karoo dataset.) Data from different sampling periods were pooled. Because proportional data was used, generalized linear models with binomial error distribution and a log-link function (Crawley 2002) were run in SAS (Proc GENMOD). The deviance of the model was scaled to compensate for overdispersion. Percentage deviance explained was calculated by dividing the difference between the deviance of an empty model (no predictors) and that of the model with predictors, by the deviance of the empty model. Post-hoc tests were conducted to determine which classes of treatments were significantly different from one another. Analyses were

not conducted for guilds that were absent/rare (Jonkershoek: predators; Karoo: predators and nectarivores; Tembe: nectarivores).

### *Indicator Species*

To determine whether any species could be considered as indicators of a land-use type, Indicator Value (*IndVal*, Dufrêne and Legendre 1997) analyses were conducted. The advantage of this method is that it is based both on the specificity and fidelity of species to a defined site group, i.e. indicator species should be unique to, and widespread and abundant within the sites in the site group (McGeoch and Chown 1998). 999 permutations of random allocations of transects among transect groups were used to assess the significance of indicator values. Analyses were conducted separately for both sampling periods, except for the Karoo dataset for which years were pooled. Comparisons were made between land-use types (i.e. natural vs. disturbed) for each vegetation type separately. Species with significant *IndVals* larger than 70% were considered to be indicator species (van Rensburg et al. 1999).

### *Body Size*

Kruskal-Wallis tests were conducted to determine whether species found in natural and disturbed areas differed from one another with respect to body mass. Species body mass values were obtained from the database used in Chapter 2. To ascertain whether land use, vegetation type (except for Jonkershoek, where only one vegetation type was sampled) and sampling period (except for the Karoo data, where data from both years was pooled) affect the mean biomass of the avifauna recorded at transects, generalized linear models (log-link function, normal distribution) were utilized.



## Results

Sample-based rarefaction curves started flattening off for all three study regions (Fig. 5), although they did not reach an asymptote, especially in the Karoo lowland (Fig. 5b) and the Tembe transects (Fig. 5c). Therefore, results should be treated with the necessary caution.

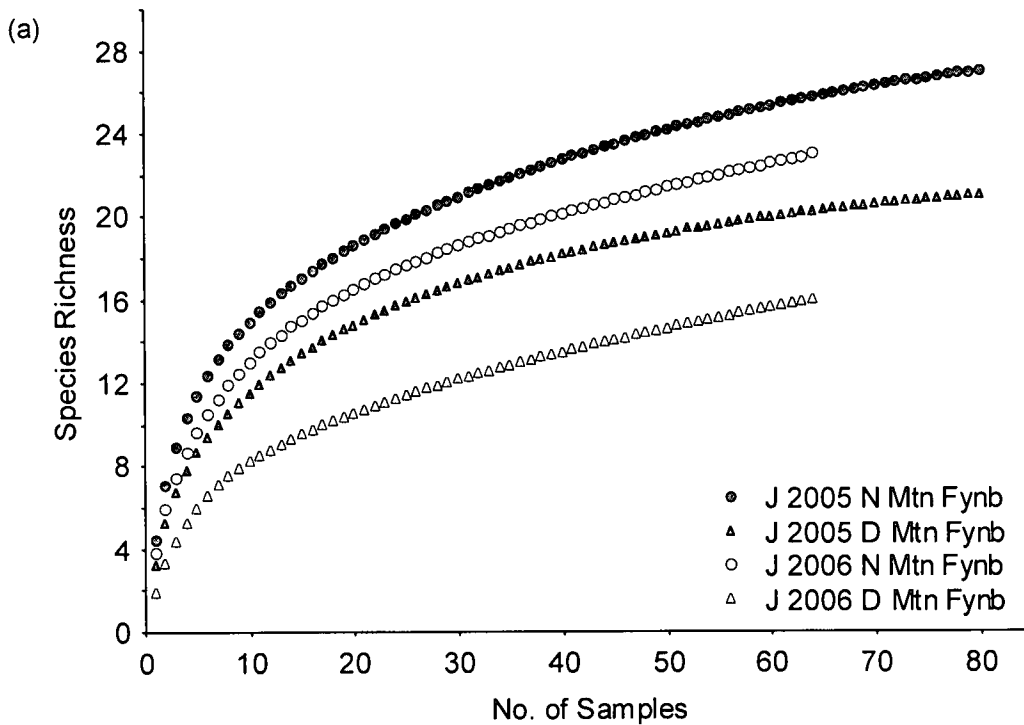
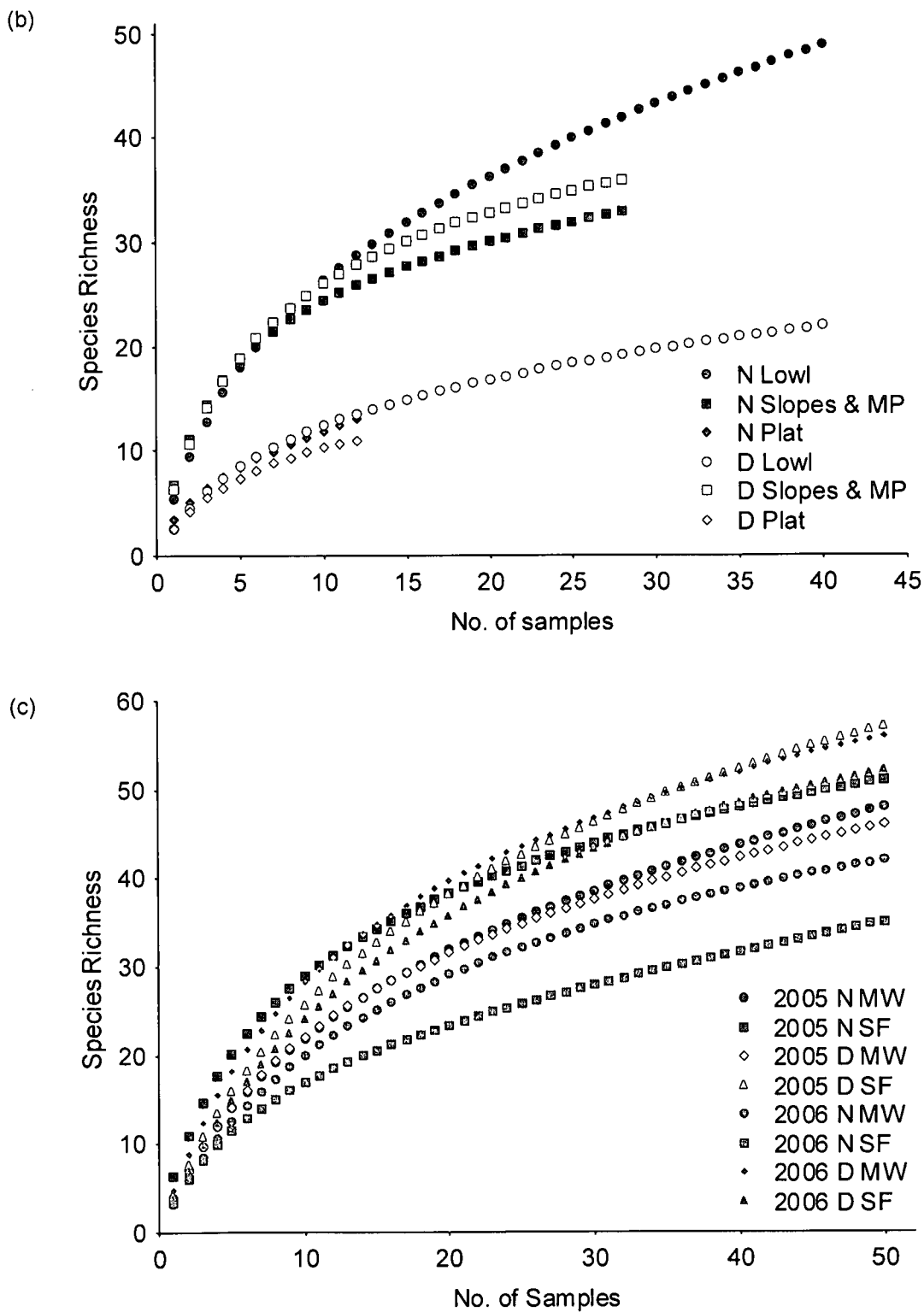


Figure 5. (see next page for figure title)



**Figure 5.** Sample-based rarefaction curves of avian assemblages in Jonkershoek (a), the Karoo (b) and Tembe (c). (N = natural, D = disturbed, Mtn Fynb = mountain fynbos, Lowl = lowlands, Slopes & MP = slopes & middle plateau, Plat = plateau, MW = mixed woodland, SF = sand forest.)

Jackknife2 species richness estimates were larger for natural areas than disturbed areas in all three regions, although they were not statistically different from one another (Table 1). The total number of individual birds recorded was also greater in natural than disturbed areas in all three regions (Table 1), although abundances have not been statistically compared, and the higher abundance in Tembe's natural area can mainly be attributed to one record of 750 barn swallows (scientific names of birds are provided in the appendix) in a natural transect. In all regions some of the species were only identified in one land-use type (Table 1).

**Table 1.** Total abundance, recorded species richness and estimated species richness (Jackknife2, obtained without resampling and with resampling with replacement) of natural (N) and disturbed (D) sites, and the number of recorded species shared between natural and disturbed sites. Jackknife2 estimates obtained without resampling provide more accurate estimates, while estimates obtained from resampling with replacement provide measures of variation (standard deviations are shown here) allowing statistical comparisons to be made (Colwell 2005, Walther and Moore 2005).

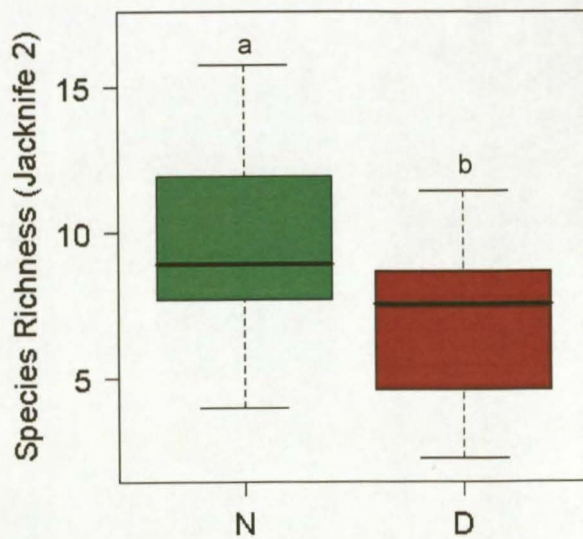
	Jonkershoek		Karoo		Tembe	
	N	D	N	D	N	D
Abundance	937	497	1220	707	2032	1827
No. of Species Recorded	33	25	57	49	95	95
Jackknife2 (no resampling)	46	32	91	62	136	119
Jackknife2 (with resampling)	35.2 ± 5.1	26.8 ± 4.5	61.8 ± 9.3	52.9 ± 7.0	83.0 ± 9.3	77.6 ± 8.8
No. of Species Shared	20		43		70	

Avian richness recorded per transect did not respond to disturbance in a consistent way. Land use had the most apparent effect on avian species richness in Jonkershoek Nature Reserve (Fig. 6). Natural transects supported more species than

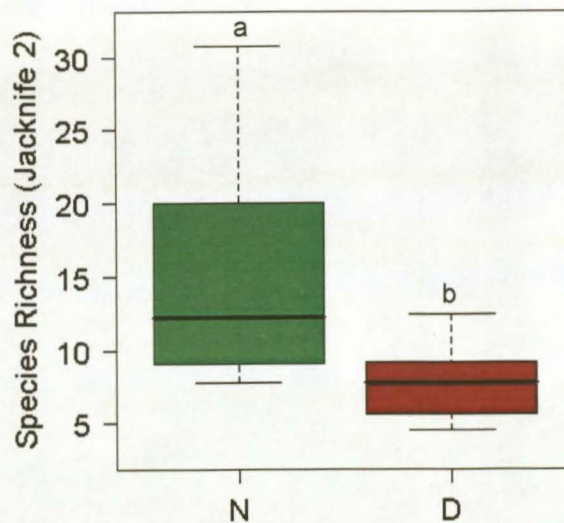
disturbed transects. More species were also recorded per transect in spring 2005 than in autumn 2006 (Appendix 2). In the Karoo, land use alone had no effect on species richness, while significant differences were observed between the different vegetation types (Appendix 2). When interactions between land use and vegetation types were considered, significant differences between different land uses of one vegetation type were only observed in the lowlands: more species were recorded in natural than disturbed lowland transects (Fig. 7). In Tembe, differences in species richness between land-use types within one sampling period were recorded in autumn 2006, when more species were recorded in disturbed than natural transects (Fig. 8, Appendix 2). In summer 2005, more species were also recorded in sand forest than in mixed woodland transects (Appendix 2).

In Jonkershoek and the Karoo, land use was a significant predictor of bird densities (Table 2): natural transects supported more dense assemblages, although sampling period (in Jonkershoek) and vegetation type (in the Karoo) also affected abundances. In Tembe, land use did not influence avian density.

Disturbance resulted in lower evenness in avian communities in Jonkershoek, especially in the autumn sampling period (Fig. 9a). In disturbed areas, communities were dominated by few species, while other species possessed low abundances, whereas abundances in natural communities were relatively evenly distributed across the species in the community. The same was true for the Karoo lowlands – evenness decreased with disturbance, although this was not the case for the other two Karoo vegetation types, where rank-abundance plots of natural and disturbed transects were similar (Fig. 9b). In Tembe, disturbance did not produce a decrease in evenness – in fact, in the autumn 2006 sampling period, evenness increased after disturbance in both mixed woodlands and sand forests (Fig. 9c & d).

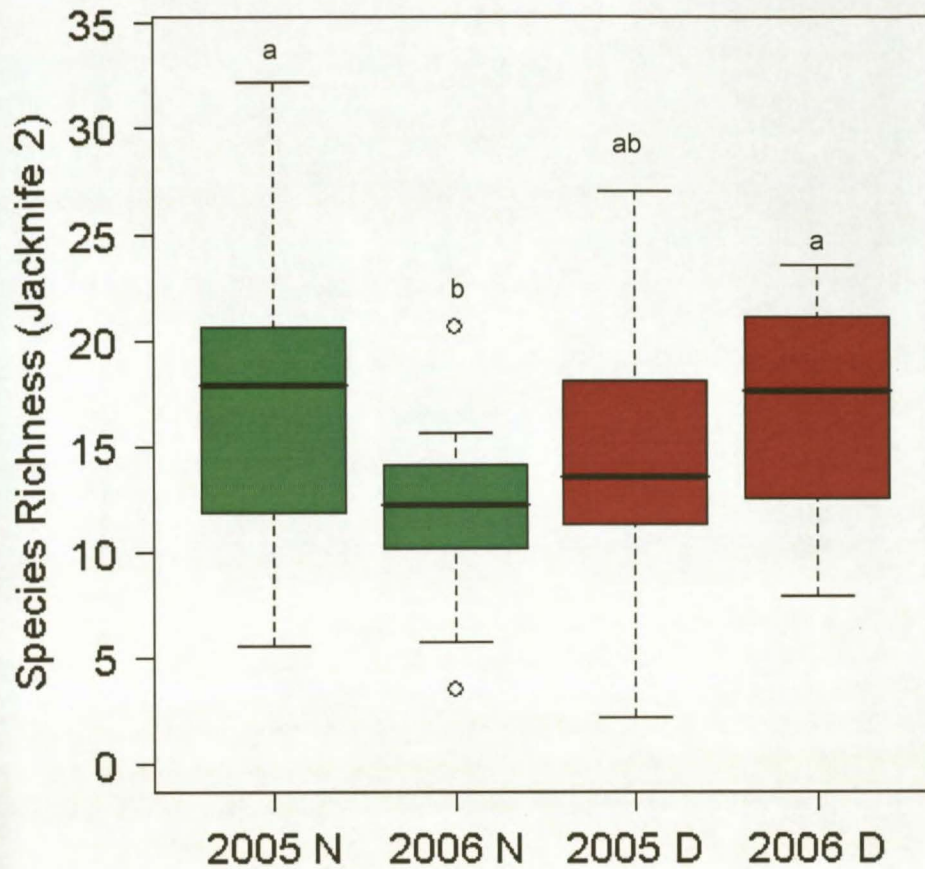


**Figure 6.** Box-and-whisker plots of mean species richness values of transects in natural (N) areas inside and disturbed (D) areas outside Jonkershoek Nature Reserve. Upper and lower bounds of the boxes represent 75% and 25% quartiles respectively, and whiskers 95% confidence intervals. Letters above the bars indicate significant differences determined by generalized linear models.



**Figure 7.** Box-and-whisker plots of mean species richness values of transects in lowland vegetation of natural (N) areas inside and disturbed (D) areas outside the Karoo National Park. Upper and lower bounds of the boxes represent 75% and 25% quartiles respectively, and whiskers 95% confidence intervals. Letters above the bars indicate significant differences determined by generalized linear models.





**Figure 8.** Box-and-whisker plots of mean species richness values of transects in different sampling periods in natural (N) areas inside and disturbed (D) areas outside Tembe Elephant Park. Upper and lower bounds of the boxes represent 75% and 25% quartiles respectively, and whiskers 95% confidence intervals. Letters above the bars indicate significant differences determined by generalized linear models.

In all three regions,  $\alpha$ -diversity within samples was lower than expected from random and never contributed more than 12 % of the overall diversity of the region (Fig. 10). Between samples within a transect,  $\beta$ -diversity was also lower than expected. This indicates that birds were not randomly distributed within samples or transects but aggregated with other individuals of their species. In contrast,  $\beta$ -diversity between transects and between vegetation types (except in Jonkershoek, where only one vegetation type was sampled) was greater than random expectation



in all three regions. Species composition between different transects and vegetation types was therefore more different than expected. At these levels,  $\beta$ -diversity also made the greatest contribution to the overall diversity: in Jonkershoek and Tembe, the greatest species turnover was between transects, while the greatest turnover in the Karoo was recorded between vegetation types. In Jonkershoek and Tembe, land use contributed more to the total diversity of the region than expected – in both cases more than 20 % of the diversity could be attributed to differences in species composition between natural and disturbed transects. In the Karoo,  $\beta$ -diversity at this level was not different from expectation.

**Table 2.** Results from generalized linear model ANOVAs and post-hoc ANOVAs comparing avian density between land-use types, vegetation types and sampling periods in Jonkershoek, the Karoo and Tembe. Italicized values in brackets represent mean density values, which may be underestimates (see Methods). Only significant differences relevant in the context of this study are shown. (N = natural, D = disturbed, SI = slopes & middle plateau, Lo = lowlands, PI = plateau)

	Scaled			X <sup>2</sup>	Effect
	Dev/df	N	df		
<b>Jonkershoek</b> (35.1)	1	64	1		
Land use				30.04***	N (42.5) > D (28.0)
Year				13.12***	2005 (39.3) > 2006 (31.1)
<b>Karoo</b> (12.33)	1	40	1		
Land use				11.68**	N (15.65) > D (9.01)
Vegetation Type				9.88**	Lo (10.19) < SI (16.21)
				4.22*	SI > PI (10.42)
<b>Tembe</b> (49.1)	1	80	1		
Land use*Year				8.14**	2005 N (78.0) > 2006 N (25.5)

When considering  $\beta_{sim}$  between different classes of land use and vegetation types (Appendix 3), species turnover between transects within disturbed areas was greater than turnover between transects within natural areas in Jonkershoek, on the slopes and middle plateau of the Karoo, and in Tembe sand forest (Fig. 11). In these areas, homogenization within vegetation types has therefore not taken place due to disturbance – the opposite has rather happened: within these vegetation types a greater turnover of species between transects has occurred as a consequence of disturbance. In the Karoo, turnover between lowland and either of the other two vegetation-type transects was greater in disturbed than in natural areas, indicating that between vegetation types, disturbance also increases the disparity between the composition of assemblages (Fig. 12a). In Tembe, however, different vegetation types supported more similar assemblages if they were disturbed, indicating a homogenization effect between vegetation types in the event of habitat disturbance (Fig. 12b). For a specific vegetation type,  $\beta$ -diversity between natural and disturbed areas was greater than  $\beta$ -diversity within either the natural or the disturbed areas in Jonkershoek and Tembe (Fig. 13a & c), which was expected due to the change in species composition in response to disturbance (see Fig. 14). However, in the Karoo, no significant differences in  $\beta$ -diversity were found between transects within one land-use type and transects between natural and disturbed areas within the same vegetation type (Fig. 13b), indicating that the identity of species in natural and disturbed areas differs little.

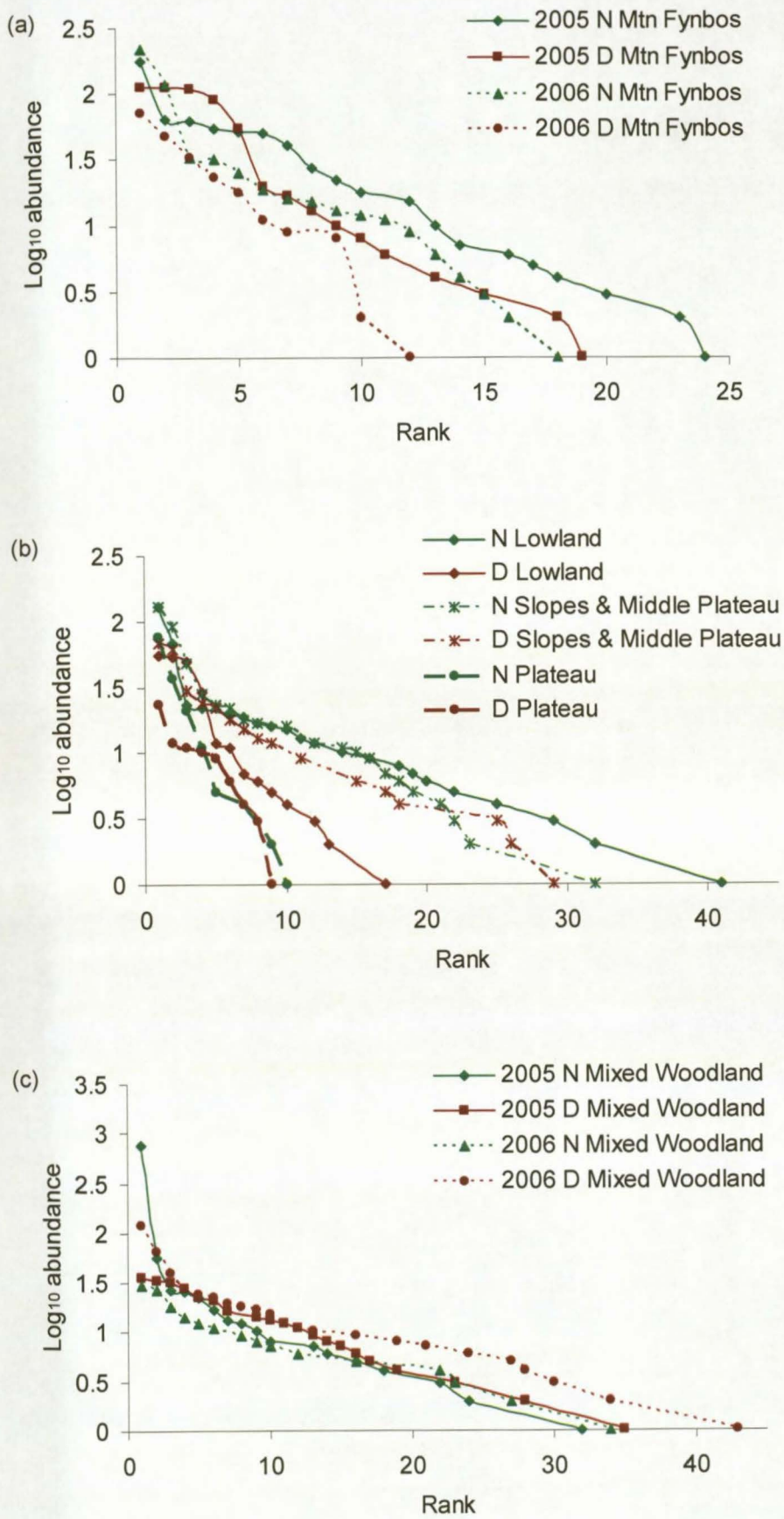
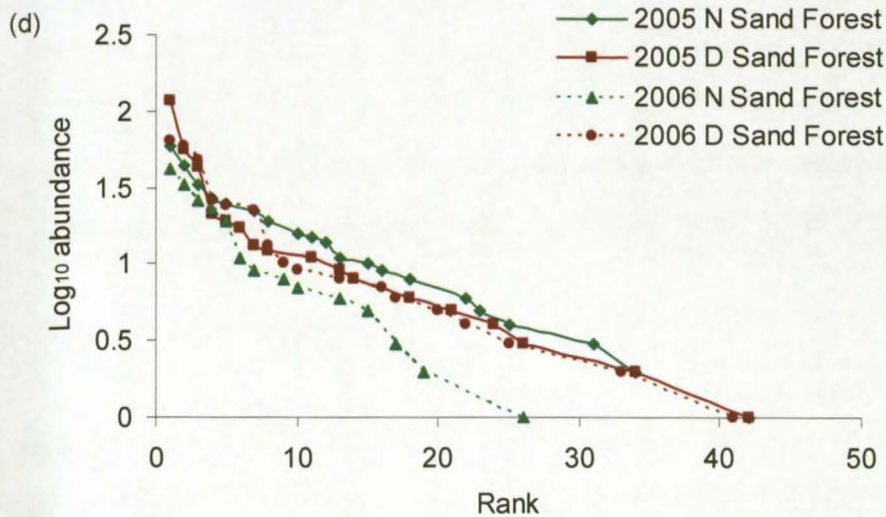


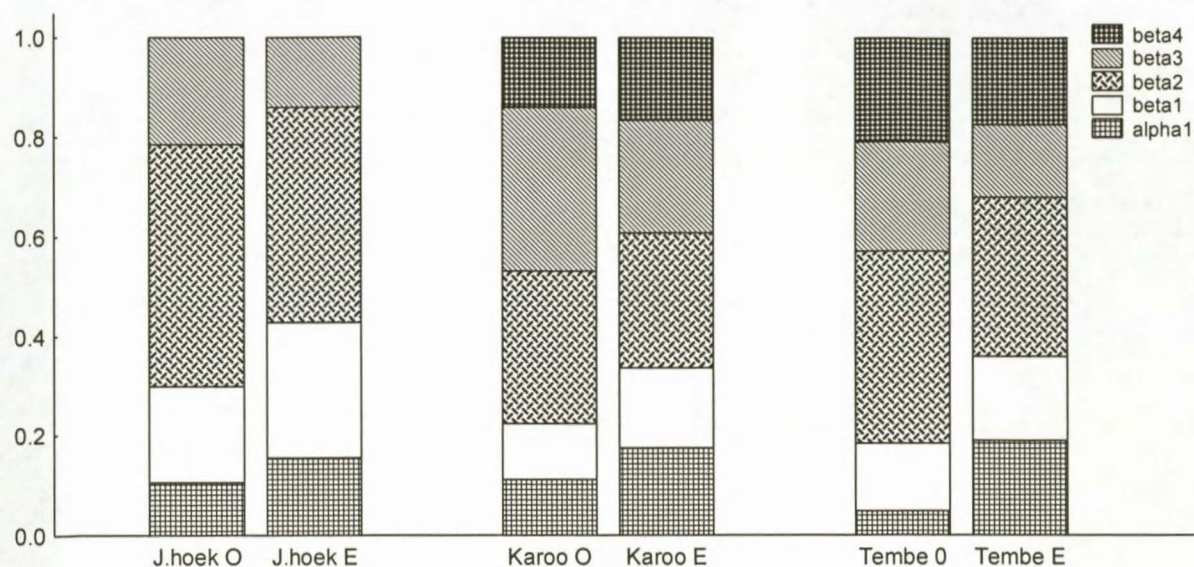
Figure 9. (see next page for figure title)





**Figure 9.** Rank-abundance curves for (a) Jonkershoek, (b) the Karoo, and Tembe mixed woodland (c) and sand forest (d). (N = natural, D = disturbed)

Assemblages differed between natural and disturbed transects in all three regions (Fig. 14). In Jonkershoek, disturbance created the greatest change in assemblage species composition, although sampling season also had a significant, though less pronounced, effect on composition. In the Karoo National Park, land use had a relatively small influence on composition (and may mainly have been driven by differences in abundance, considering the lack of significant differences in  $\beta_{sim}$  values between natural and disturbed transects [Fig. 13b]), while vegetation type comprised the more important predictor of assemblage composition in the Karoo (Fig 14b). In Tembe, bird assemblages in natural and disturbed landscapes clustered separately too. In addition, mixed woodland and sand forest assemblages separated out distinctly in the natural area, but in disturbed landscapes assemblages of the two vegetation types were more similar, providing further evidence for the homogenization of the avifauna in disturbed areas (Fig 14c).



**Figure 10.** Additive partitioning of diversity (species richness) observed (O) and expected (E) from 10000 randomizations in Jonkershoek, the Karoo and Tembe. Richness is partitioned between different spatial scales; in Jonkershoek: within samples (alpha1), between samples (beta1), between transects (beta2) and between land-use types (beta3); in the Karoo and Tembe: within samples (alpha1), between samples (beta1), between transects (beta2), between vegetation types (beta3) and between land-use types (beta4). All observed diversity values were significantly smaller or greater (as indicated in the figure) than expected from random, with the exception of beta4 (turnover between land-use types) in the Karoo.

By examining the effect of disturbance on not only species identity, but also on functional classes of organisms, an indication of the aspect of the species' biology which makes them vulnerable to disturbances may be obtained. In this study, relative proportions of different feeding guilds changed in response to land-use changes (Fig. 15, Appendix 4). (Trends and significance for absolute abundances were identical to those presented for proportions in Fig. 15, with the exception of those of Jonkershoek mixed feeders, which occurred in equal abundances in the two land-use types; data



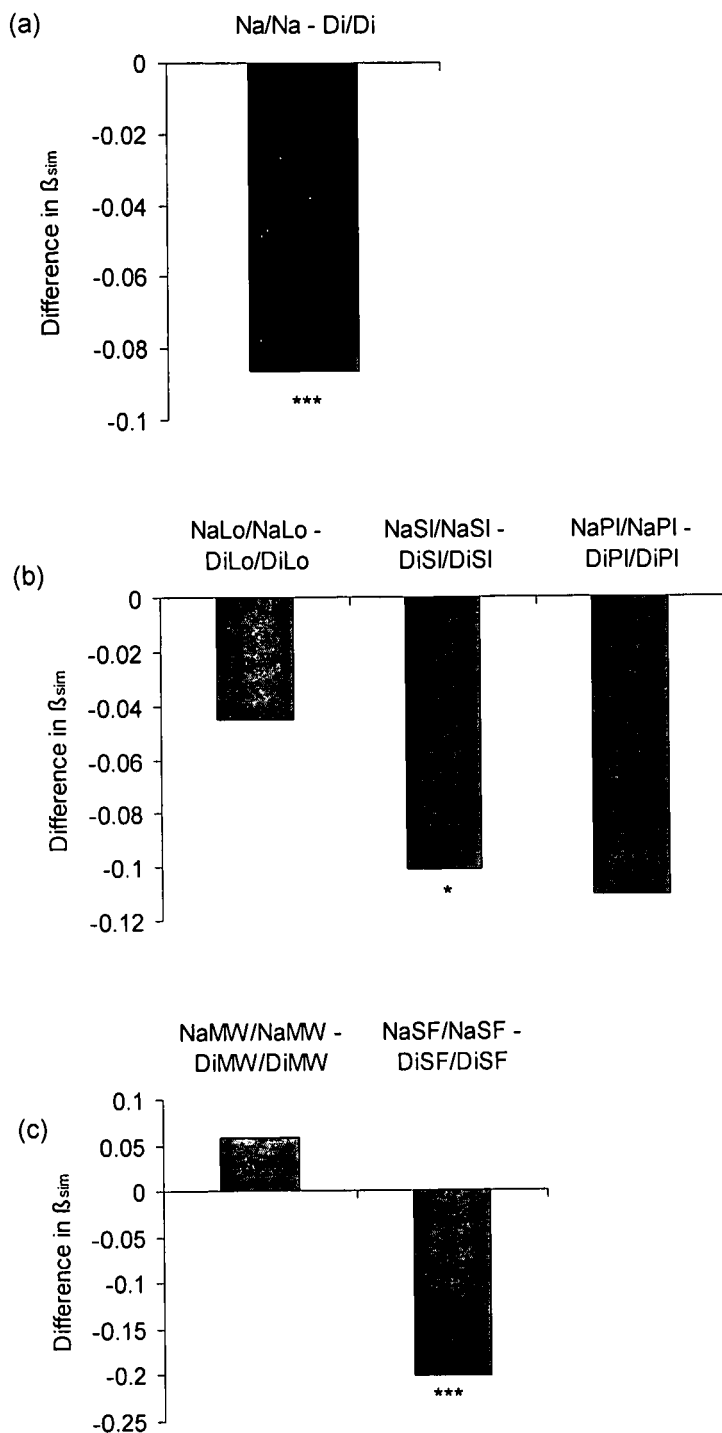
not shown.) In the Karoo, land-use changes had the least effect on feeding guilds – slightly more mixed feeders were observed in the reserve than on surrounding farms. However, in Jonkershoek and Tembe, the proportion of insectivores decreased with landscape transformation, while granivores and mixed feeders were more dominant in transformed than natural transects. The proportion of nectarivores in Jonkershoek was also lower in disturbed areas than in natural vegetation. In Tembe Elephant Park vegetation type affected the proportion of frugivores and predators – higher proportions of both guilds were recorded in sand forests than in mixed woodlands (Appendix 4).

Indicator species were identified in natural areas of all three regions (Table 3). In Jonkershoek, more species were specific to natural than disturbed areas, indicating that more species are disadvantaged by disturbance than benefit from it. Two of the indicator species (Cape sugarbird and orange-breasted sunbird) of the natural areas are endemic to the Fynbos biome (Cowling and Richardson 1995), and two other endemics (Victorin's warbler and protea seed-eater) were only recorded in natural transects (although protea seed-eaters especially were not widespread in this land-use type). Disturbance therefore poses a threat to some endemic species of the region. The Cape siskin, another endemic, however profits from the plantations – it was common here in spring (see also Armstrong and Vanhensbergen 1994). In the Karoo, few indicator species were identified, and they were all indicators of natural areas. In Tembe, indicators for natural areas were lacking in the mixed woodland, while several indicators for sand forest assemblages were identified, most of them for the spring sampling season. In the disturbed landscapes, indicator species were wide-spread generalists often associated with agriculture or human activities. In Jonkershoek and Tembe, general trends observed for the feeding guilds of all species (Fig. 15) were reflected in the indicator species: insectivores and

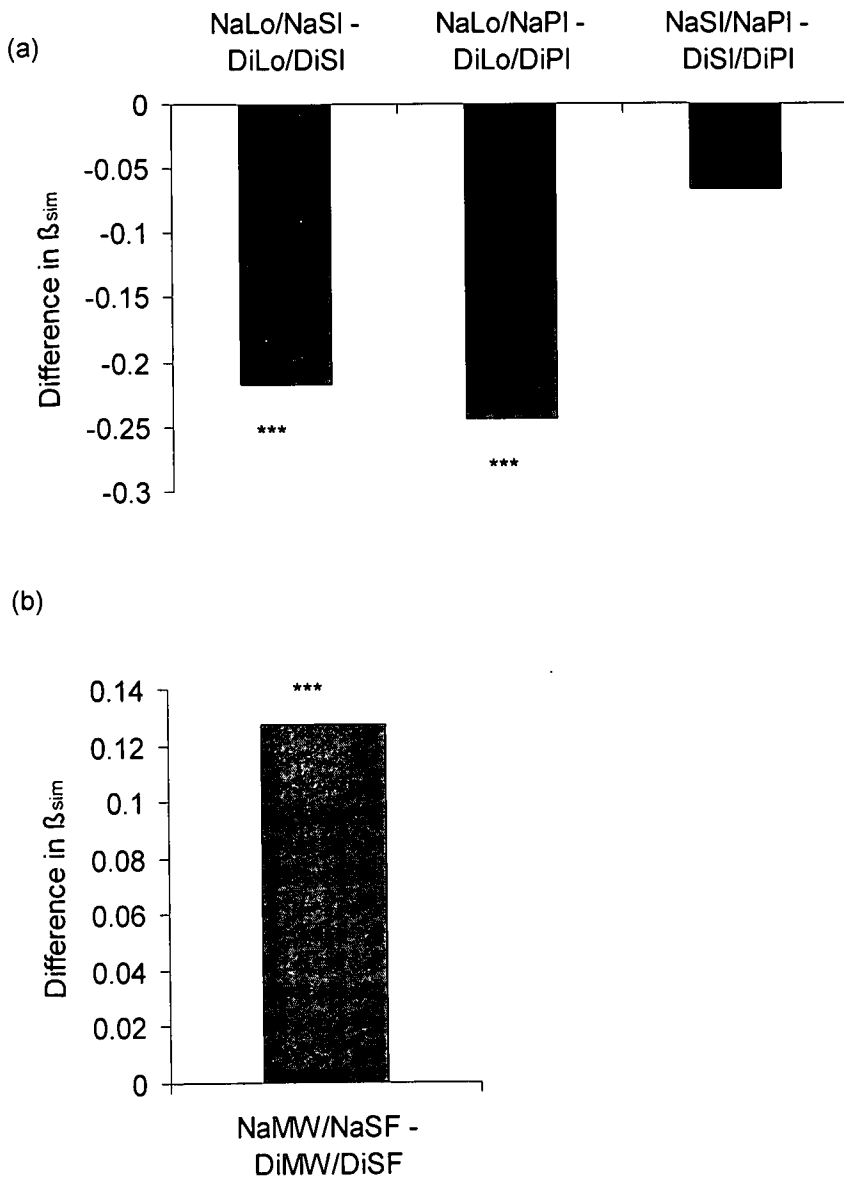


nectarivores in Jonkershoek comprised the dominant indicator species for natural transects, while granivores and mixed feeders were dominant in disturbed transects. Changes in land use therefore not only causes a decline in the abundance of insectivores (and nectarivores in Jonkershoek), but threatens individual insectivore and nectarivore species, while certain granivorous and mixed feeder species, rather than just individuals, benefit from landscape disturbance.

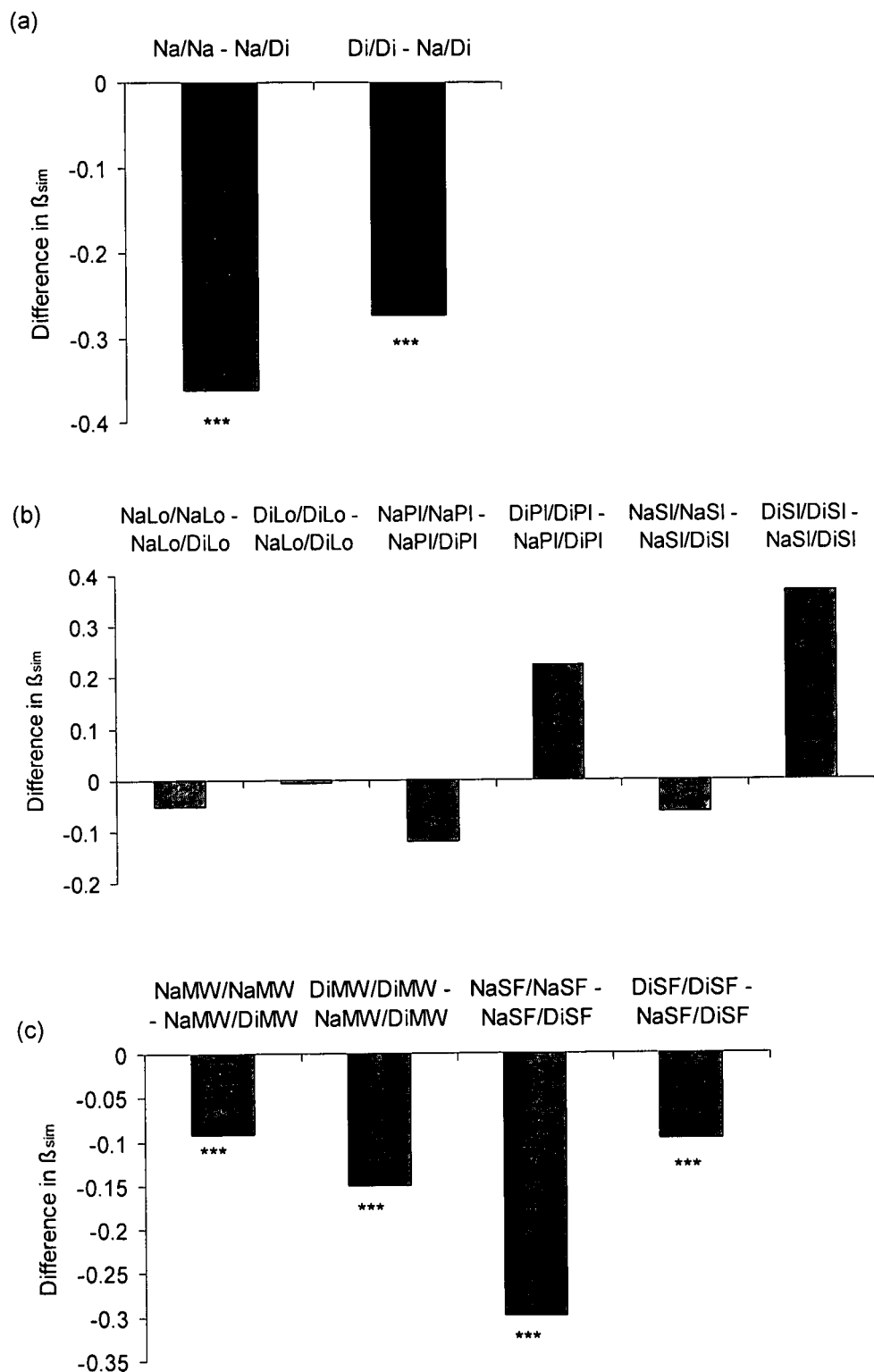
In none of the study regions did birds in natural and disturbed areas differ from one another in terms of body size (Kruskal-Wallis test, Jonkershoek:  $H = 1.351$ ,  $n = 58$ ,  $p = 0.245$ ; Karoo:  $H = 0.255$ ,  $n = 77$ ,  $p > 0.61$ ; Tembe:  $H = 0.091$ ,  $n = 191$ ,  $p = 0.763$ ). Land use had an effect on the biomass of birds in Jonkershoek and in the Karoo: in both cases biomass decreased in response to disturbance (Table 4). In Tembe, differences in biomass were only recorded between sampling periods.



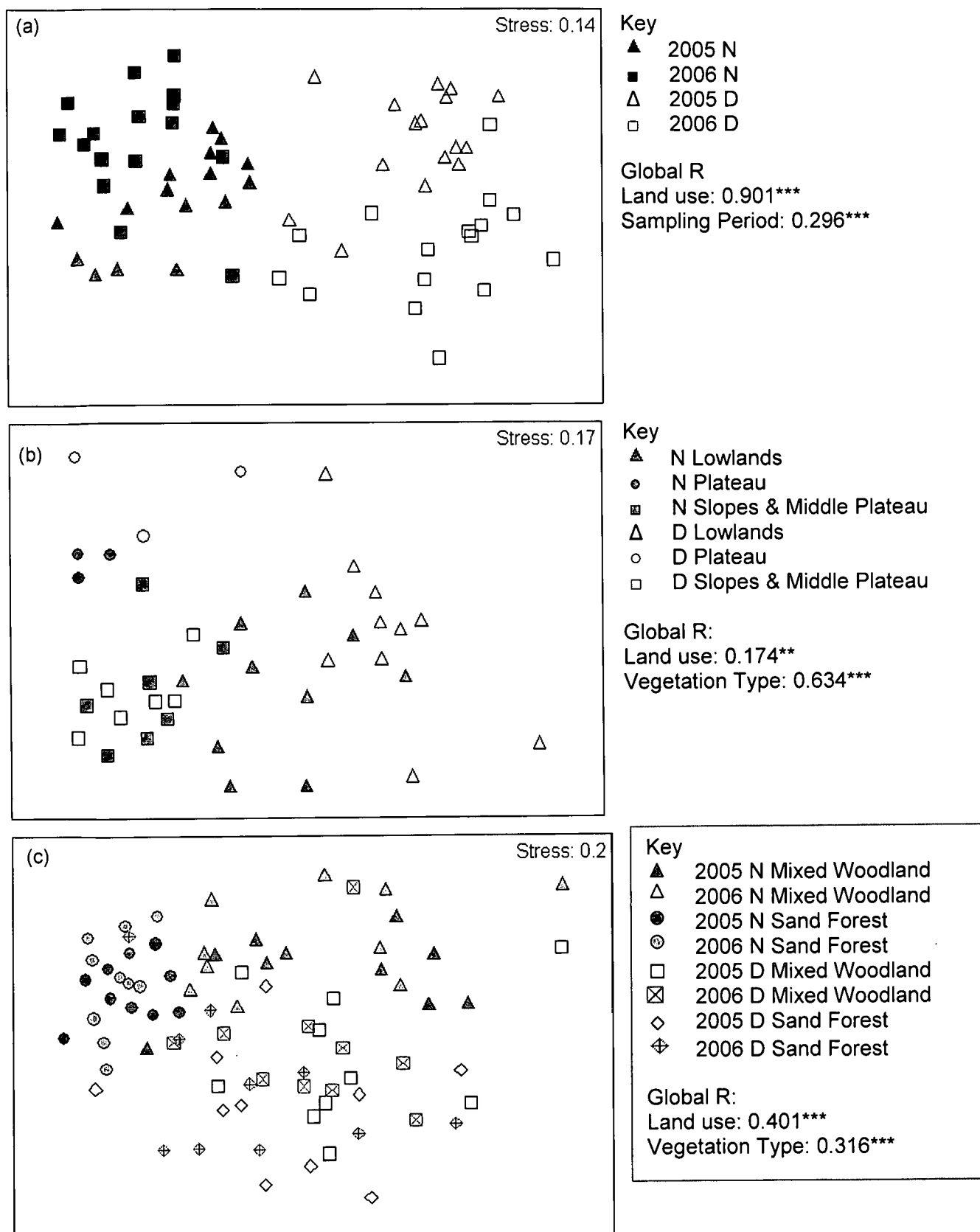
**Figure 11.** Difference between mean  $\beta_{sim}$  of transects in natural areas and mean  $\beta_{sim}$  of transects in disturbed areas for each vegetation type in (a) Jonkershoek Nature Reserve, (b) the Karoo National Park, and (c) Tembe Elephant Park. (e.g. NaLo/Natural - DiLo/Disturbed = mean  $\beta_{sim}$  between all natural lowland transects minus mean  $\beta_{sim}$  between all disturbed lowland transects.) Significant differences as determined by generalized linear models are indicated on the figures (\*\*\*  $p < 0.001$ , \*  $p < 0.05$ ). (Na = natural, Di = disturbed, Lo = lowlands, SI = slopes & middle plateau, PI = plateau, MW = mixed woodland, SF = sand forest.)



**Figure 12.** Difference between mean  $\beta_{sim}$  of transects of two vegetation types within natural areas and mean  $\beta_{sim}$  of the same two vegetation types in disturbed areas in (a) the Karoo National Park, and (b) Tembe Elephant Park. In Jonkershoek, only one vegetation type was sampled. Significant differences as determined by generalized linear models are indicated on the figures (\*\*\*)  $p < 0.001$ . (Na = natural, Di = disturbed, Lo = lowlands, SI = slopes & middle plateau, PI = plateau, MW = mixed woodland, SF = sand forest.)



**Figure 13.** Difference between mean  $\beta_{sim}$  of transects within one land-use type (either natural or disturbed) and mean  $\beta_{sim}$  of transects between both land-use types for each vegetation type in (a) Jonkershoek Nature Reserve (b) the Karoo National Park, and (c) Tembe Elephant Park. Significant differences, as determined by generalized linear models are indicated on the figures (\*\*\*)  $p < 0.001$ . (Na = natural, Di = disturbed, Lo = lowlands, SI = slopes & middle plateau, PI = plateau, MW = mixed woodland, SF = sand forest.)



**Figure 14.** Non-metric ordination plots of bird assemblages in (a) Jonkershoek Nature Reserve, (b) the Karoo National Park and (c) Tembe Elephant Park based on land-use type, sampling period and vegetation type. (N = natural, D = disturbed)

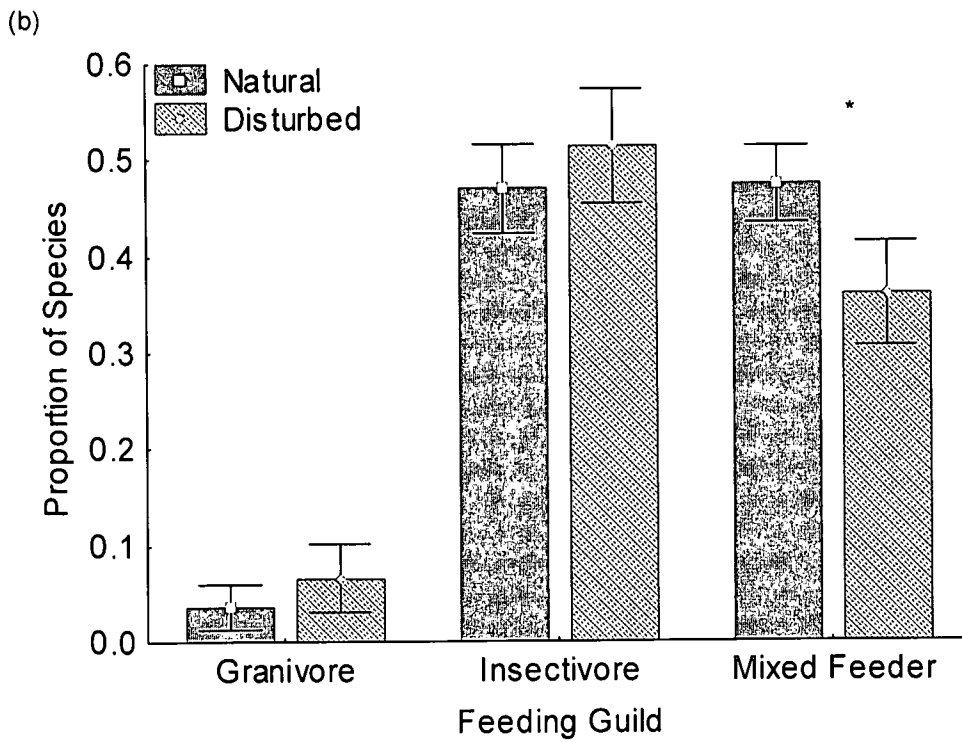
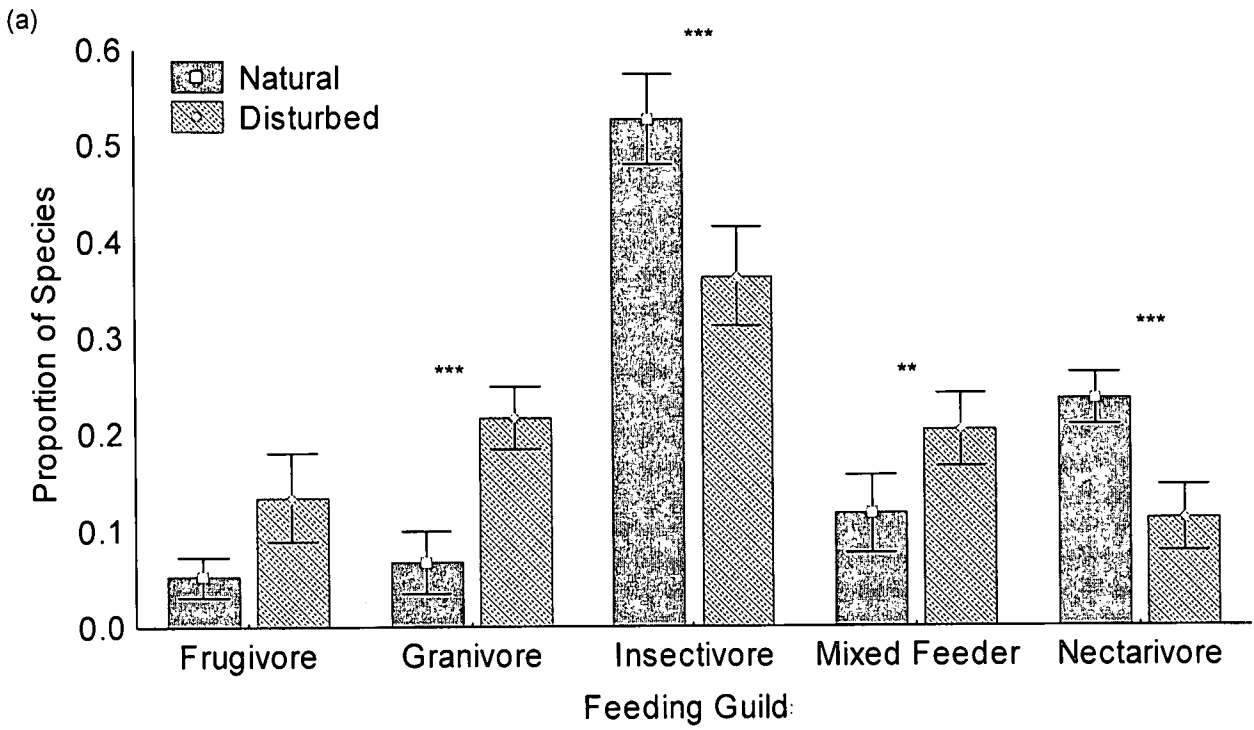
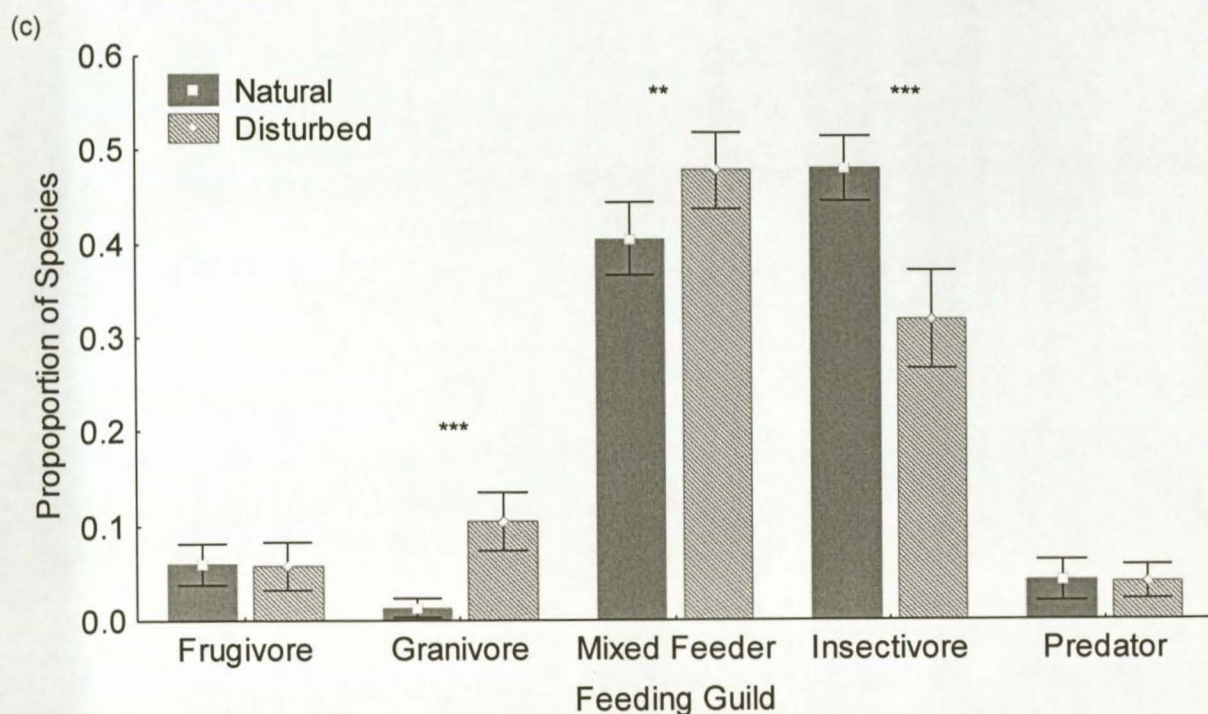


Figure 15. (see next page for figure title)





**Figure 15.** Mean proportion of abundance of birds in feeding guilds per transect in (a) Jonkershoek Nature Reserve, (b) the Karoo National Park and (c) Tembe Elephant Park. Bars represent 95 % confidence intervals, and significant differences in proportions between natural and disturbed transects as calculated from generalized linear models are indicated (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ )

**Table 3.** *IndVal* values of indicator species (*IndVal* > 70%) in natural and disturbed areas in (a) Jonkershoek, (b) the Karoo and (c) Tembe in the 2005 and 2006 sampling periods. Feeding guilds are indicated after species names in brackets (F = frugivore, G = granivore, I = insectivore, M = mixed feeder, N = nectarivore). No indicator species emerged for disturbed areas outside the Karoo National Park. Scientific names are provided in the Appendix. \*  $p < 0.05$  (MW = mixed woodland, SF = sand forest)

## (a) Jonkershoek

Natural			Disturbed		
Species	<i>IndVal</i> '05	<i>IndVal</i> '06	Species	<i>IndVal</i> '05	<i>IndVal</i> '06
Cape Grassbird (I)	73.9*	81.3*	African Dusky Flycatcher (I)	71.9*	
Cape Robin-Chat (I)		76.5*	Cape Canary (G)	74.2*	
Cape Sugarbird (N)	73.3*	93.8*	Cape Siskin (G)	79.4*	
Karoo Prinia (I)	85.1*		Cape White-eye (M)		70.5*
Neddicky (I)	74.3*				
Orange-breasted Sunbird (N)	90.6*	96.0*			

## (b) Karoo

Vegetation Type	Natural		Disturbed	
	Species	<i>IndVal</i>	Species	<i>IndVal</i>
Slopes & Middle Plateau	White-throated Canary (G)	80.7*		
Plateau	Grey-backed Cisticola (I)	76.8*		
	Karoo Prinia (I)	87.5*		

Table 3(c) Tembe

Vegetation Type	Natural			Disturbed		
	Species	<i>IndVal</i> '05	<i>IndVal</i> '06	Species	<i>IndVal</i> '05	<i>IndVal</i> '06
MW				Blue Waxbill (G)		80.0*
				Yellow-fronted Canary (G)		75.3*
SF	Bearded Scrub-Robin (I)	80.0*		Blue Waxbill (G)		70.0*
	Crested Guineafowl (M)	70.0*		Dark-capped Bulbul (F)		80.0*
	Eastern Nicator (I)	84.4*		Emerald-spotted Wood-Dove (M)		76.5*
	Green-backed Camaroptera (I)	86.2*		Red-eyed Dove (M)	70.0*	
	Square-tailed Drongo (I)	84.6*	82.5*			
	Yellow-bellied Greenbul (F)	98.3*				
	Yellow-breasted Apalis (I)	82.4*				

**Table 4.** Results from generalized linear models showing significant effects of land use (in Jonkershoek and the Karoo) and sampling period (in Tembe) on the mean biomass of birds in transects. Italicized values in brackets represent mean biomass values in grams. Only significant effects are shown. (N = natural, D = disturbed)

		Scaled				
	Factor	Dev/df	N	df	X <sup>2</sup>	Effect
Jonkershoek	Land use	1.07	64	1	19.34***	N (753) > D (168)
Karoo	Land use	1.2	80	1	4.20*	N (657) > D (287)
Tembe	Year	1.1	80	1	3.37*	2005 (655) > 2006 (239)

## Discussion

The results presented here provide only a snap-shot of the consequences of landscape transformation on birds, though human disturbance is likely to have affected assemblages at greater geographic scales and over a longer time period (Dean 2000, Willis and Birks 2006).

The effects of land-use changes on avian assemblages in three South African regions vary, but it is clear that the diversity of birds has been compromised by these changes in all three regions. The most pronounced effect of disturbance on assemblages was observed in Jonkershoek, where species richness decreased, species composition changed most drastically, changes in proportions of feeding guilds occurred and several endemic species disappeared from disturbed areas. In Tembe, avian assemblages reacted to land-use changes in a similar, though not as drastic manner. Species richness did not decrease in response to land-use change (in fact, it increased in some cases), but species composition changed considerably, as did the relative abundance of species in different feeding guilds. Karoo birds were

least affected by alterations in the land-use regime (vegetation type seemed more important in determining assemblage composition), the most significant effect being on species richness in the lowlands and bird abundances, although it has been suggested that changes in Karoo bird assemblages already occurred more than a century ago and at a greater spatial scale due to the extermination of large nomadic herds that used to roam the Karoo, which has altered ecosystem properties (Dean 2000).

In the fragmentation literature, emphasis has increasingly been placed on the importance of the landscape matrix in determining how biodiversity is affected by disturbance (Lindenmayer et al. 2001, Ricketts 2001, Watson et al. 2005, Wethered and Lawes 2005, Kupfer et al. 2006). General consensus exists that not all matrices (therefore all types of landscape transformation) bring about identical changes in the composition of indigenous species because the matrices differ in their suitability for indigenous species. For example, in a South African study of the avifauna of Afromontane forest fragments (Wethered and Lawes 2005), which highlighted how different land-use types affect avian assemblages, it was found that the composition of birds in forest patches in the natural grassland matrix was non-random, and the presence of species area-dependent. Where exotic plantations were cultivated between forest fragments, the movement of some abundant generalist species between fragments was aided, while specialists disappeared from such small fragments (Wethered and Lawes 2005). Similarly, the different extent of habitat change outside the three reserves considered here is likely to have affected the degree to, and manner in which avian assemblages were affected. In Jonkershoek, very little indigenous vegetation remained in the plantations, especially in older *Pinus* stands. Around Tembe, the extent of cultivation has risen in recent years, as there has been an influx of people to the region (W. S. Matthews, pers. comm.), but fields

are cultivated only for personal use, and transformation has not been as extensive (see also Wessels et al. 2003). Natural vegetation remains outside the reserve, although trees and smaller plants here are selectively harvested for several purposes such as traditional medicines, building material, fire wood and curios. In the disturbed areas that were sampled in the Karoo, no vegetation clearing had taken place; disturbance occurred due to grazing by non-indigenous mammals and overgrazing in some regions, though this in itself can lead to altered plant communities (du Toit and Cumming 1999) with a higher dominance of unpalatable plants which can affect the food supply of birds (Dean 2000).

Species richness of avian assemblages did not change consistently in response to land-use changes. However, in Jonkershoek and Tembe, species turnover between land-use types was greater than expected from random, and turnover between natural and disturbed areas was greater than within natural (or disturbed) areas. Therefore, while locally richness was smaller, larger, or not significantly different in disturbed than in natural areas, regional richness increased with disturbance. This supports Fairbanks' (2004) and van Rensburg et al.'s (2004) proposition that avian richness increased with landscape transformation due to increased vegetation heterogeneity, which provides habitat for a greater variety of avifauna. However, these results do not necessarily contradict Evans et al.'s (2006) findings. Although they established that percentage protected land predicted some of the variation in avian richness across South Africa, the explanatory power of this relationship became negligible when grid cells with no protected land were excluded from the analyses. Habitat heterogeneity between protected and unprotected landscapes may therefore be the principal driver of increased avian richness observed in grid cells containing protected land.



Although habitat disturbance causes an increase in regional species richness, it results in the disappearance of certain species from disturbed areas and in changes in local species composition (see Rooney et al. 2007). Beta diversity indices indicate that this effect is small in the Karoo, but quite evident in Jonkershoek and Tembe. Although in Jonkershoek and Tembe beta diversity of avian assemblages **within** vegetation types is greater in disturbed than natural areas, indicating greater heterogeneity in disturbed than natural assemblages, natural areas display greater species turnover **between** vegetation types than disturbed areas do. For Tembe, evidence for biotic homogenization (McKinney and Lockwood 1999, Olden and Poff 2004) between vegetation types is presented in Fig. 12b. In Jonkershoek only one vegetation type was sampled. However, Armstrong and Vanhensbergen (1994) found that bird assemblages in plantations (which had been mountain fynbos before afforestation) in Jonkershoek were more similar to those in riverine forests, the other vegetation type in Jonkershoek valley, than to fynbos assemblages. This suggests that disturbance is also promoting biotic homogenization in Jonkershoek.

Several of the species which emerged as indicators for the disturbed landscape in Jonkershoek and in Tembe were wide-spread generalists associated with human activities more broadly in South Africa (e.g. Cape canary, Cape white-eye, dark-capped bulbul, red-eyed dove – Hockey et al. 2005). On the other hand, some of the indicators for the natural areas were endemic or species typical to the region (e.g. orange-breasted sunbird, Cape sugarbird, Karoo prinia, bearded scrub-robin, Eastern nicator, square-tailed drongo – Cooper 1980, Cowling and Richardson 1995, Hockey et al. 2005). Because indicator species are determined not only by their fidelity, but also their specificity to a land-use type (McGeoch and Chown 1998), the indicator species of natural landscapes here were, by definition, rare or absent in disturbed areas. Therefore, some of the avifauna of Jonkershoek and Tembe that is typical of,

and unique to these regions is threatened by disturbance. Other common and widespread species associated with human activities more broadly in South Africa have benefited from land-use changes. Indeed, in South Africa, agricultural corridors have aided the spread of several such bird species to new regions (Macdonald 1986, Hockey et al. 1989, Oschadleus and Underhill 2006).

Olden et al. (2004) highlighted the fact that environmental disturbance influences not only taxonomic diversity (i.e. taxon presence or absence), but also has an effect on a genetic (e.g. through the breakdown of dispersal barriers, resulting in higher gene flow and lower genetic isolation) and functional level. If some functional characteristics of species make them more sensitive to land-use changes (see e.g. Henle et al. 2004), the distribution of functional traits in a community will change in response to land use. It is the loss of functional roles of individual species, rather than reduced species richness, which is thought to decrease ecosystem stability when species are lost (Loreau et al. 2001). In the reserves considered here, feeding habits appear to affect the sensitivity of birds to disturbance, as changes in the relative proportions of feeding guilds occurred in response to land-use change. The loss of insectivores due to land-use change, as was found here for Jonkershoek and Tembe, has been widely recorded (see Introduction). Indications are that land-use changes often greatly reduce the diversity and abundance of insects (Steenkamp and Chown 1996, Sinclair et al. 2002, Stefanescu et al. 2004, Witt and Samways 2004, Botes et al. 2006), which has knock-on effects on, amongst other, birds (Sinclair et al. 2002, Barker 2004, Newton 2004). Newton (2004) (see also McLaughlin and Mineau 1995) reviewed the proximate and ultimate causes for insectivorous (and other) farmland bird declines. The demographic mechanisms by which species decline mainly comprise lower breeding success or lower survival of adult birds due to food shortages. Ultimate causes are more varied: pesticides and

herbicides cause decreases in insect populations, either directly (pesticides) or indirectly (herbicides; by killing plants that insects feed on). Vegetation clearing results in habitat destruction, while intercropping and crop rotation are more beneficial than monocultures. Overstocking of pastures also results in changes in vegetation structure and lower insect abundance. The specific mechanisms acting on insectivore declines in this study were not considered, although dung beetle declines in human-disturbed areas outside Tembe Elephant Park were attributed to changes in vegetation structure and the abundance and quality of dung (Botes et al. 2006). However, changes in vegetation cover may be the main cause of other insect, and insectivore declines in the three sampled regions too (see also Steenkamp and Chown 1996, Cremene et al. 2005), because pesticides and herbicides are typically not used in the regions sampled (though they may be for locust outbreaks in the Karoo), while insectivore declines occur in Tembe despite the fact that disturbed areas here did not comprise monocultures.

In Jonkershoek, nectarivores also decreased in response to disturbance. This could mainly be attributed to the virtual absence of orange-breasted sunbirds and Cape sugarbirds from disturbed areas (Appendix 5). A large proportion of the food source of these two Fynbos endemics is nectar from plants endemic to Fynbos, particularly of the Proteaceae or Ericaceae (Hockey et al. 2005). The undergrowth of plantations supports few or none of these flowering plants. Nectarivores are important pollinators for several Fynbos plant species (Bond 1994), and declines in nectarivores may affect the reproduction of these plants (see Koh et al. 2004), although plants usually do not exclusively rely on the birds for pollination (Bond 1994).

Increases in granivore numbers outside Tembe Elephant Park are most likely a result of the grain crops cultivated in the area. In Jonkershoek, higher granivore

abundance could mainly be attributed to high abundances of the Cape siskin and Cape canary in the plantations, where they were foraging in the branches of the *Pinus*. Increases in mixed feeders in both reserves emphasize the fact that generalists benefit from land-use changes. In the Karoo, however, numbers of mixed feeders declined in response to land-use change.

The effect of land-use change on another functional trait, body mass, was not as pronounced as that on feeding guilds. Despite the fact that size is one of the most influential life history characteristics, (Schmidt-Nielsen 1984, Gaston and Blackburn 2000), disturbance did not influence the mean size in any of the avian assemblages (see also Watson et al. 2005). Although mean size was not affected, large birds (and mammals) at Tembe have virtually been restricted to the park because they are hunted outside the reserve (pers. obs., B. Tembe, pers. comm., see also discussions in Redford and Sanderson 2000, Scholes and Biggs 2005). In addition, in Jonkershoek and the Karoo the biomass of birds declined in disturbed areas, indicating that the carrying capacity of the land was lowered by plantations and grazing by non-native, and in some cases overstocked, species respectively.

If extinctions are dependent on functional characteristics of species, ecological repercussions and community disassembly are expected to be more pronounced as these functional traits disappear from communities (Şekercioğlu et al. 2004), and overall functional diversity (FD, describing the cumulative 'diversity' of several biological traits in a community, Petchey and Gaston 2002b) of communities may decline more than expected from random extinctions (Petchey and Gaston 2002a). Indeed, species which are extinct or have very small global populations can be considered functionally extinct, as they contribute very little (or nothing) to ecosystem processes (Şekercioğlu et al. 2004). Şekercioğlu et al. (2004) found that, for the global avifauna, species in certain feeding guilds (scavengers, frugivores, herbivores,

omnivores and piscivores) were more extinction-prone than average, while an increasing number of bird species are predicted to become extinct, functionally extinct and functionally deficient as populations continue to decline (Şekercioğlu et al. 2004). Although they established that insectivores were less threatened than average, this guild possessed the most extinction-prone species (Şekercioğlu et al. 2004). Ecosystem functioning is expected to be heavily compromised by current and predicted future land-use changes due to the loss of functional diversity.

## CONSERVATION IMPLICATIONS

Here I show what the effects are of different agricultural practices on avian assemblages in three South African regions. Species richness of transects did not respond to land-use changes in a consistent manner. However, richness estimates of natural areas were consistently greater than estimates of disturbed areas. In addition, species turnover between natural and disturbed areas in Jonkershoek and Tembe was greater than within natural areas, as natural and disturbed areas supported different avian assemblages, which contributed to elevated richness of the region. Functional diversity was also compromised by land-use changes. In Jonkershoek and Tembe, insectivores and nectarivores (in Jonkershoek only) declined, while granivores and mixed feeders benefited in disturbed landscapes. In the Karoo, only the mixed feeders declined in disturbed landscapes.

The significant contribution of protected areas as biodiversity repositories is highlighted here. In South Africa, the conflict between landscape transformation and biodiversity conservation priorities is projected to increase (Wessels et al. 2003). Indeed, Maputaland, where Tembe Elephant Park is situated, has been identified as a region of high conservation value which is currently little transformed, but where potential future agricultural activities may pose a major threat to the biodiversity of

the area (Wessels et al. 2003). The effects of land-use changes are expected to become more pronounced if land-use transformation in the regions sampled here becomes more intensive and extensive (Wessels et al. 2003), as remnants of natural vegetation outside the protected area will probably shrink (see Tilman et al. 2001, Newton 2004, Gutiérrez 2005, Watson et al. 2005 for general discussion), and the quality of the landscape matrix for indigenous biota decline (Kupfer et al. 2006). Indeed, whilst protected areas play a vital role in conserving biodiversity, they are not isolated from anthropogenic activities outside, or even inside, their borders. Edge effects (Woodroffe and Ginsberg 1998, Parks and Harcourt 2002), isolation (Carroll et al. 2004, Sigel et al. 2006, Young et al. 2006) and the area (Rivard et al. 2000, Carroll et al. 2004) of the protected landscape, the quality of the surrounding matrix (Rivard et al. 2000, Carroll et al. 2004), invasive species (Pauchard et al. 2003), and the extent of human development inside the protected area (Rivard et al. 2000) all threaten biodiversity in protected areas (Woodroffe and Ginsberg 1998, Rivard et al. 2000, Chown et al. 2003, Kupfer et al. 2006). To maintain indigenous diversity and ecological processes, management actions should therefore not be limited to the establishment of protected areas, but also to the minimization of anthropogenic disturbances inside reserves (especially considering increasing focus on ecotourism in protected areas, Krüger 2005), and to land use in surrounding landscapes.

## References

- Acocks, J. P. H. 1988. *Veld Types of South Africa*, Third edition. *Memoirs of the Botanical Survey of South Africa* No. 62.
- Agresti, A. 1996. *An Introduction to Categorical Data Analysis*. Wiley, New York.



- Armstrong, A. J., and H. J. Vanhensbergen. 1994. Comparison of avifaunas in *Pinus radiata* habitats and indigenous riparian habitat at Jonkershoek, Stellenbosch. *South African Journal of Wildlife Research* **24**:48-55.
- Balmford, A., J. L. Moore, T. Brooks, N. Burgess, L. A. Hansen, P. Williams, and C. Rahbek. 2001. Conservation conflicts across Africa. *Science* **291**:2616-2619.
- Barker, A. M. 2004. Insects as food for farmland birds - is there a problem? Pages 37-49 *in* H. F. van Emden and M. Rothschild, editors. *Insect and Bird Interactions*. Intercept Limited, Andover.
- Beecher, N. A., R. J. Johnson, J. R. Brandle, R. M. Case, and L. J. Young. 2002. Agroecology of birds in organic and nonorganic farmland. *Conservation Biology* **16**:1620-1631.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology*, Third edition. Blackwell Science Ltd, Oxford.
- Benton, T. G., D. M. Bryant, L. Cole, and H. Q. P. Crick. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* **39**:673-687.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature* **398**:330-334.
- Bezuidenhout, H., and S. D. Holness. 2004. Vegetation map of Karoo National Park and surrounds. SANParks, unpublished internal report.
- Bibby, C. J., and S. T. Buckland. 1987. Bias of bird census results due to the detectability varying with habitat. *Acta Oecologica* **8**:103-112.
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. *Bird Census Techniques*, 2nd edition. Academic Press, London.

- Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London B* **344**:83-90.
- Botes, A., M. A. McGeoch, and B. J. van Rensburg. 2006. Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biological Conservation* **130**:573-583.
- Britschgi, A., R. Spaar, and R. Arlettaz. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall Alpine meadowland management. *Biological Conservation* **130**:193-205.
- Brooks, M. 1999. Effects of protective fencing on birds, lizards, and black-tailed hares in the western Mojave Desert. *Environmental Management* **23**:387-400.
- Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. d. Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* **291**:125.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to Distance Sampling. Estimating Abundances of Biological Populations*, 1st edition. Oxford University Press, Oxford.
- Burnham, K. P., and W. S. Overton. 1978. Estimation of size of a closed population when capture probabilities vary among animals. *Biometrika* **65**:625-633.
- Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* **60**:927-936.
- Cardinale, B. J., D. S. Srivastava, E. J. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. **443**:989-992.

- Carroll, C., R. E. Noss, P. C. Paquet, and N. H. Schumaker. 2004. Extinction debt of protected areas in developing landscapes. *Conservation Biology* **18**:1110-1120.
- Chacoff, N. P., and M. A. Aizen. 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology* **43**:18-27.
- Chao, A. 2004. Species richness estimation. Pages 7907-7916 in N. Balakrishnan, C. B. Read, and B. Vidakovic, editors. *Encyclopedia of Statistical Sciences*, Vol. 12. Wiley Press, New York.
- Chown, S. L., B. J. van Rensburg, K. J. Gaston, A. S. L. Rodrigues, and A. S. van Jaarsveld. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13**:1233-1241.
- Clapperton, M. J., D. A. Kanashiro, and V. M. Behan-Pelletier. 2002. Changes in abundance and diversity of microarthropods associated with Fescue Prairie grazing regimes. *Pedobiologia* **46**:496-511.
- Clarke, K. R. 1993. Non-parametric multivariate analysis of change in community structure. *Australian Journal of Ecology* **18**:117-143.
- Clarke, K. R., and R. N. Gorley. 2001. *PRIMER*. PRIMER-E, Plymouth.
- Clarke, K. R., and R. M. Warwick. 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 1st edition. Plymouth Marine Laboratory, Plymouth.
- Cleary, D. F. R., and A. Ø. Mooers. 2006. Burning and logging differentially affect endemic vs. widely distributed butterfly species in Borneo. *Diversity and Distributions* **12**:409-416.

- Colwell, R. K. 2004. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 7.5. Available from <http://viceroy.eeb.uconn.edu/estimates>.
- Colwell, R. K. 2005. EstimateS 7.5 User's Guide. Available from <http://viceroy.eeb.uconn.edu/estimates>.
- Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**:2717-2727.
- Coomes, D. A., R. B. Allen, D. M. Forsyth, and W. G. Lee. 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology* **17**:450–459.
- Cooper, K. H. 1980. Bird ecology of Maputaland. Pages 300-306 *in* M. N. Bruton and K. H. Cooper, editors. *Studies on the Ecology of Maputaland*. Cape & Transvaal Printers (Pty) Ltd, Cape Town.
- Cowling, R. M., and C. Hilton-Taylor. 1999. Plant biogeography, endemism and diversity. Pages 42-56 *in* W. R. J. Dean and S. J. Milton, editors. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Cowling, R. M., and D. M. Richardson. 1995. *Fynbos. South Africa's Unique Floral Kingdom*, 1st edition. Fernwood Press, Vlaeberg.
- Crawley, M. J. 2002. *Statistical Computing. An Introduction to Data Analysis using S-Plus*, 1st edition. John Wiley & Sons, Ltd., Chichester.
- Cremene, C., G. Groza, L. Rakosy, A. A. Schileyko, A. Baur, A. Erhardt, and B. Baur. 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conservation Biology* **19**:1606-1618.

- Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. Partitioning species diversity across landscapes and regions: A hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* **162**:734-743.
- Dean, W. R. J. 1997. The distribution and biology of nomadic birds in the Karoo, South Africa. *Journal of Biogeography* **24**:769-779.
- Dean, W. R. J. 2000. Factors affecting bird diversity patterns in the Karoo, South Africa. *South African Journal of Science* **96**:609-616.
- Dean, W. R. J., M. D. Anderson, S. J. Milton, and T. A. Anderson. 2002. Avian assemblages in native *Acacia* and alien *Prosopis* drainage line woodland in the Kalahari, South Africa. *Journal of Arid Environments* **51**:1-19.
- Desmet, P. G., and R. M. Cowling. 1999. The climate of the Karoo - a functional approach. Pages 3-16 in W. R. J. Dean and S. Milton, editors. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmill. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* **20**:470-474.
- Driver, A., K. Maze, M. Rouget, A. T. Lombard, J. Nel, J. K. Turpie, R. M. Cowling, P. Desmet, P. Goodman, J. Harris, Z. Jonas, B. Reyers, K. Sink, and T. Strauss. 2005. National Spatial Biodiversity Assessment 2004: Priorities for Biodiversity Conservation in South Africa. *Strelitzia* 17, South African National Biodiversity Institute, Pretoria.
- du Toit, J. T., and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* **8**:1643-1661.

- Dudley, N., D. Baldock, R. Nasi, and S. Stolton. 2005. Measuring biodiversity and sustainable management in forests and agricultural landscapes. *Philosophical Transactions of the Royal Society B* **360**:457-470.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345-366.
- Evans, K. L., A. S. L. Rodrigues, S. L. Chown, and K. J. Gaston. 2006. Protected areas and regional avian species richness in South Africa. *Biology Letters* **2**:184-188.
- Fairbanks, D. H. K. 2004. Regional land-use impacts affecting avian richness patterns in Southern Africa - insights from historical avian atlas data. *Agriculture, Ecosystems and Environment* **101**:269-288.
- Fjeldså, J. 1999. The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird Conservation International* **9**:47-62.
- Fox, S.-J. C. 2006. Habitat fragmentation and Strandveld bird assemblages in an 'ecologically friendly' golf estate in the Western Cape, South Africa. MSc Thesis. University of Cape Town, Cape Town.
- Fuller, R. J., and D. R. Langslow. 1984. Estimating numbers of birds by point counts: how long should counts last? *Bird Study* **31**:195-202.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and Process in Macroecology*, 1st edition. Blackwell Science, Oxford.
- Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1999. Does variation in census area confound density comparisons? *Journal of Applied Ecology* **36**:191-204.
- Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, and W. E. Kunin. 2006. The



ecological effectiveness of protected areas: the United Kingdom. *Biological Conservation* **132**:76-87.

Gebeyehu, S., and M. J. Samways. 2002. Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa). *Biodiversity and Conservation* **11**:283-304.

Gebeyehu, S., and M. J. Samways. 2003. Responses of grasshopper assemblages to long-term grazing management in a semi-arid African savanna. *Agriculture, Ecosystems and Environment* **95**:613-622.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379-391.

Gutiérrez, D. 2005. Effectiveness of existing reserves in the long-term protection of a regionally rare butterfly. *Conservation Biology* **19**:1586-1597.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**:207-251.

Herremans, M. 1998. Conservation status of birds in Botswana in relation to land use. *Biological Conservation* **86**:139-160.

Hockey, P. A., L. G. Underhill, M. Neatherway, and P. G. Ryan. 1989. Atlas of the Birds of the Southwestern Cape, 1st edition. Cape Bird Club, Cape Town.

Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. 2005. Roberts Birds of Southern Africa, 7th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

Hoffman, M. T., B. Cousins, T. Meyer, A. Petersen, and H. Hendricks. 1999. Historical and contemporary land use and the desertification of the Karoo.

- Pages 257-273 in W. R. J. Dean and S. J. Milton, editors. The Karoo. Ecological Patterns and Processes. Cambridge University Press, Cambridge.
- Huntley, B. J., editor. 1989. Biotic Diversity in Southern Africa. Concepts and Conservation. Oxford University Press, Cape Town.
- Huyser, O., P. G. Ryan, and J. Cooper. 2000. Changes in population size, habitat use and breeding biology of lesser sheathbills *Chionis minor* at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* **92**:299-310.
- Jansen, R., R. M. Little, and T. M. Crowe. 1999. Implications of grazing and burning of grasslands on the sustainable use of francolins (*Francolinus* spp.) and on overall bird conservation in the highlands of Mpumalanga province, South Africa. *Biodiversity and Conservation* **8**:587-602.
- Kerr, J. T., and D. J. Currie. 1995. Effects of human activity on global extinction risk. *Conservation Biology* **9**:1528-1538.
- Kirkwood, D., and J. J. Midgley. 2003. Response to Matthews et al. (2001) vegetation of the Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany* **69**:220-221.
- Knight, R. L. 1999. Private lands: the neglected geography. *Conservation Biology* **13**:223-224.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. **437**:880-883.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286-293.

- Koh, L. P., R. R. Dunn, N. S. Sodhi, R. K. Colwell, H. C. Proctor, and V. S. Smith. 2004. Species coextinctions and the biodiversity crisis. *Science* **305**:1632-1634.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72**:367-382.
- Krüger, O. 2005. The role of ecotourism in conservation: panacea or Pandora's box? *Biodiversity and Conservation* **14**:579-600.
- Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* **15**:8-20.
- Lamprey, R. H., and R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *Journal of Biogeography* **31**:997-1032.
- Lande, R., P. J. DeVries, and T. R. Walla. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos* **89**:601-605.
- Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* **70**:966-979.
- Lim, H. C., and N. S. Sodhi. 2004. Responses of avian guilds to urbanisation in a tropical city. *Landscape and Urban Planning* **66**:199-215.
- Lindenmayer, D. B., R. B. Cunningham, C. MacGregor, C. Tribolet, and C. F. Donnelly. 2001. A prospective longitudinal study of landscape matrix effects on fauna in woodland remnants: experimental design and baseline data. *Biological Conservation* **101**:157-169.

- Little, I. T., R. M. Little, R. Jansen, and T. M. Crowe. 2005. Winter bird assemblages, species richness and relative abundance at a re-vegetated coal mine in the Middelburg district, Mpumalanga province, South Africa. *South African Journal of Wildlife Research* **35**:13-22.
- Little, R. M., and T. M. Crowe. 1994. Conservation implications of deciduous fruit farming on birds in the Elgin district, Western Cape Province, South Africa. *Transactions of the Royal Society of South Africa* **49**:185-198.
- Longino, J. T., J. Coddington, and R. K. Colwell. 2002. The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* **83**:689-702.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804-808.
- Macdonald, I. A. W. 1986. Range expansion in the pied barbet and the spread of alien tree species in southern Africa. *Ostrich* **57**:75-94.
- Macdonald, I. A. W. 1989. Man's role in changing the face of southern Africa. Pages 51-77 in B. J. Huntley, editor. *Biotic Diversity in Southern Africa*. Oxford University Press, Oxford.
- Magurran, A. E. 2004. *Measuring Biological Diversity*, 1st edition. Blackwell Publishing, Malden.
- Mangnall, M. J., and T. M. Crowe. 2003. The effects of agriculture on farmland bird assemblages on the Agulhas Plain, Western Cape, South Africa. *African Journal of Ecology* **41**:266-276.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-253.

- Maron, M., and A. Lill. 2005. The influence of livestock grazing and weed invasion on habitat use by birds in grassy woodland remnants. *Biological Conservation* **124**:439-450.
- Matthews, W. S., A. E. van Wyk, N. van Rooyen, and G. A. Botha. 2001. Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany* **67**:573-594.
- McDonald, D. J. 1985. The plant communities of Swartboschkloof, Jonkershoek. South African National Scientific Programmes Report No. 104.
- McGeoch, M. A., and S. L. Chown. 1998. Scaling up the value of bioindicators. *Trends in Ecology and Evolution* **13**:46-47.
- McKee, J. K., P. W. Sciulli, C. D. Foose, and T. A. Waite. 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* **115**:161-164.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**:450-453.
- McLaughlin, A., and P. Mineau. 1995. The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems and Environment* **55**:201-212.
- Midgley, G. F., and F. van der Heyden. 1999. Form and function in perennial plants. Pages 91-106 *in* W. R. J. Dean and S. J. Milton, editors. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Moll, E. J. 1980. Terrestrial plant ecology. Pages 52-68 *in* M. N. Bruton and K. H. Cooper, editors. *Studies on the Ecology of Maputaland*. Cape & Transvaal Printers (Pty) Ltd, Cape Town.

- Moll, E. J., B. M. Campbell, R. M. Cowling, L. Bossi, M. L. Jarman, and C. Boucher. 1984. A description of major vegetation categories in and adjacent to the Fynbos biome. South African National Scientific Programmes Report No. 83.
- Moreby, S. J. 2004. Birds of lowland arable farmland: the importance and identification of invertebrate diversity in the diet of chicks. Pages 21-35 in H. F. van Emden and M. Rothschild, editors. *Insect and Bird Interactions*. Intercept Limited, Andover.
- Newmark, W. D. 2006. A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. *Conservation Biology* **20**:122-134.
- Newton, I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**:579-600.
- Norton, D. A. 2000. Conservation biology and private land: shifting the focus. *Conservation Biology* **14**:1221-1223.
- Olden, J. D., and N. L. Poff. 2004. Clarifying biotic homogenization. *Trends in Ecology and Evolution* **19**:282-283.
- Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19**:18-24.
- Oschadleus, H. D., and L. G. Underhill. 2006. Range expansion of the red-billed quelea, *Quelea quelea*, into the Western Cape, South Africa. *South African Journal of Science* **102**:12-13.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* **103**:91-93.
- Palmer, M. W. 1991. Estimating species richness: the second-order jackknife reconsidered. *Ecology* **72**:1512-1513.



- Parks, S. A., and A. H. Harcourt. 2002. Reserve size, local human density, and mammalian extinctions in US protected areas. *Conservation Biology* **16**:800-808.
- Pauchard, A., P. B. Alaback, and E. G. Edlund. 2003. Plant invasions in protected areas at multiple scales: *Linaria vulgaris* (Scrophulariaceae) in the west Yellowstone area. *Western North American Naturalist* **63**:416-428.
- Pautasso, M., and K. J. Gaston. 2006. A test of the mechanisms behind avian generalized individuals-area relationships. *Global Ecology and Biogeography* **15**:303-317.
- Petchey, O. L., and K. J. Gaston. 2002a. Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London B* **269**:1721-1727.
- Petchey, O. L., and K. J. Gaston. 2002b. Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**:402-411.
- Poynton, J. C. 1961. Biogeography of south-east Africa. *Nature* **189**:801-803.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*, 1st edition. Cambridge University Press, Cambridge.
- Raman, T. R. S., and R. Sukumar. 2002. Responses of tropical rainforest birds to abandoned plantations, edges and logged forest in the Western Ghats, India. *Animal Conservation* **5**:201-216.
- Redford, K. H., and S. E. Sanderson. 2000. Extracting humans from nature. *Conservation Biology* **14**:1362-1364.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented habitats. *American Naturalist* **158**:87-99.
- Rivard, D. H., J. Poitevin, D. Plasse, M. Carleton, and D. J. Currie. 2000. Changing species richness and composition in Canadian national parks. *Conservation Biology* **14**:1099-1109.

- Rivers-Moore, N. A., and M. J. Samways. 1996. Game and cattle trampling, and impacts of human dwellings on arthropods at a game park boundary. *Biodiversity and Conservation* **5**:1545-1556.
- Rooney, T. P., J. D. Olden, M. K. Leach, and D. A. Rogers. 2007. Biotic homogenization and conservation prioritization. *Biological Conservation* **134**:447-450.
- Rosenzweig, M. L. 2001. The four questions: What does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* **3**:361-367.
- Rubin, F., A. R. Palmer, and C. Tyson. 2001. Patterns of endemism within the Karoo National Park, South Africa. *Bothalia* **31**:117-133.
- Sánchez-Azofeifa, G. A., G. C. Daily, A. S. P. Pfaff, and C. Busch. 2003. Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. *Biological Conservation* **109**:123-135.
- Sax, D. F., and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* **18**:561-566.
- Scharlemann, J. P. W., R. E. Green, and A. Balmford. 2004. Land-use trends in Endemic Bird Areas: global expansion of agriculture in areas of high conservation value. *Global Change Biology* **10**:2046-2051.
- Schmidt-Nielsen, K. 1984. *Scaling. Why is Animal Size so Important?*, 1st edition. Cambridge University Press, New York.
- Scholes, R. J., and R. Biggs. 2005. A biodiversity intactness index. *Nature* **434**:45-49.
- Schulze, R. E. 1997. *South African Atlas of Agrohydrology and -Climatology*. Report TT82/96, Water Research Commission, Pretoria.
- Schwarzenberger, A., and W. R. J. Dean. 2003. The influence of vegetation structure on bird communities in a Karoo village, South Africa. *Ostrich* **74**:209-216.

- Şekercioğlu, Ç. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America* **101**:18042-18047.
- Siegfried, W. R. 1999. Human impacts. Pages 239-241 in S. J. Milton, editor. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Sigel, B. J., T. W. Sherry, and B. E. Young. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conservation Biology* **20**:111-121.
- Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2002. Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. *Proceedings of the Royal Society of London B* **269**:2401-2405.
- Smart, R., M. J. Whiting, and W. Twine. 2005. Lizards and landscapes: integrating field surveys and interviews to assess the impact of human disturbance on lizard assemblages and selected reptiles in a savanna in South Africa. *Biological Conservation* **122**:23-31.
- Smith, E. P., and G. van Belle. 1984. Nonparametric estimation of species richness. *Biometrics* **40**:119-129.
- Söderström, B., T. Pärt, and E. Linnarsson. 2001. Grazing effects on between-year variation of farmland bird communities. *Ecological Applications* **11**:1141-1150.
- South African National Parks. 2005. Karoo National Park. Available at <http://www.sanparks.org/parks/karoo/>.
- Steenkamp, H. E., and S. L. Chown. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: Scarabaeinae) assemblage in southern Africa. *Biological Conservation* **78**:305-311.

- Stefanescu, C., S. Herrando, and F. Páramo. 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography* **31**:905-915.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* **13**:1416-1423.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281-284.
- van Rensburg, B. J., S. L. Chown, A. S. van Jaarsveld, and M. A. McGeoch. 2000. Spatial variation and biogeography of sand forest avian assemblages in South Africa. *Journal of Biogeography* **27**:1385-1401.
- van Rensburg, B. J., P. Koleff, K. J. Gaston, and S. L. Chown. 2004. Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* **31**:843-854.
- van Rensburg, B. J., M. A. McGeoch, S. L. Chown, and A. S. van Jaarsveld. 1999. Conservation of heterogeneity among dung beetles in the Maputaland Centre of Endemism, South Africa. *Biological Conservation* **88**:145-153.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* **99**:3-9.
- Vernon, C. J. 1999. Biogeography, endemism and diversity of animals. Pages 57-85 *in* W. R. J. Dean and S. J. Milton, editors. *The Karoo. Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.

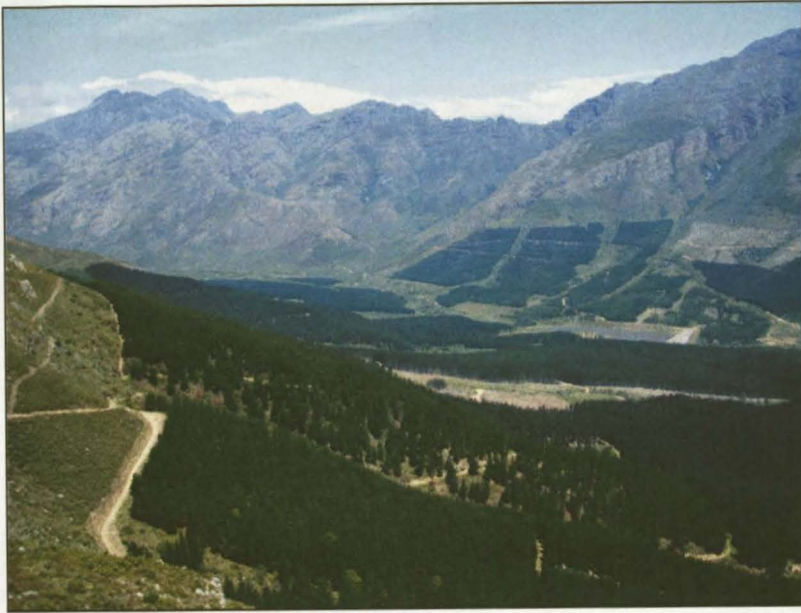
- Waltert, M., K. S. Bobo, N. M. Sainge, H. Fermon, and M. Mühlenberg. 2005. From forest to farmland: habitat effects on afrotropical forest bird diversity. *Ecological Applications* **15**:1351-1366.
- Walther, B. A., and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* **28**:815-829.
- Wardell-Johnson, G., and M. Williams. 2000. Edges and gaps in mature karri forest, south-western Australia: logging effects on bird species abundance and diversity. *Forest Ecology and Management* **131**:1-21.
- Watson, D. M. 2003. Long-term consequences of habitat fragmentation - highland birds in Oaxaca, Mexico. *Biological Conservation* **111**:283-303.
- Watson, J. E. M., R. J. Whittaker, and D. Freudenberger. 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* **32**:1353-1370.
- Werger, M. J. A. 1978. The Karoo-Namib region. Pages 231-299 in M. J. A. Werger, editor. *Biogeography and Ecology of Southern Africa*. Dr W. Junk bv Publishers, The Hague.
- Wessels, K. J., B. Reyers, and A. S. van Jaarsveld. 2000. Incorporating land cover information into regional biodiversity assessments in South Africa. *Animal Conservation* **3**:67-79.
- Wessels, K. J., B. Reyers, A. S. van Jaarsveld, and M. C. Rutherford. 2003. Identification of potential conflict areas between land transformation and biodiversity conservation in north-eastern South Africa. *Agriculture, Ecosystems and Environment* **95**:157-178.

- Wethered, R., and M. J. Lawes. 2005. Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. *Biological Conservation* **123**:125-137.
- Whitford, W. G. 1997. Desertification and animal biodiversity in the desert grasslands of North America. *Journal of Arid Environments* **37**:709-720.
- Wiles, G. J., J. Bart, R. E. J. Beck, and C. F. Aguon. 2003. Impacts of the Brown Tree Snake: patterns of decline and species persistence in Guam's avifauna. *Conservation Biology* **17**:1350-1360.
- Willis, K. J., and H. J. B. Birks. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. *Science* **314**:1261-1265.
- Witt, A. B. R., and M. J. Samways. 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology* **12**:89-95.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**:2126.
- Young, J. E., G. A. Sánchez-Azofeifa, S. J. Hannon, and R. Chapman. 2006. Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecology and Management* **230**:151-161.



## Appendix

**Appendix 1.** Photographs of vegetation types and land use in (a) Jonkershoek, (b) the Karoo and (c) Tembe.



(a-1) Plantation cover in Jonkershoek valley.



(a-2) Natural mountain fynbos

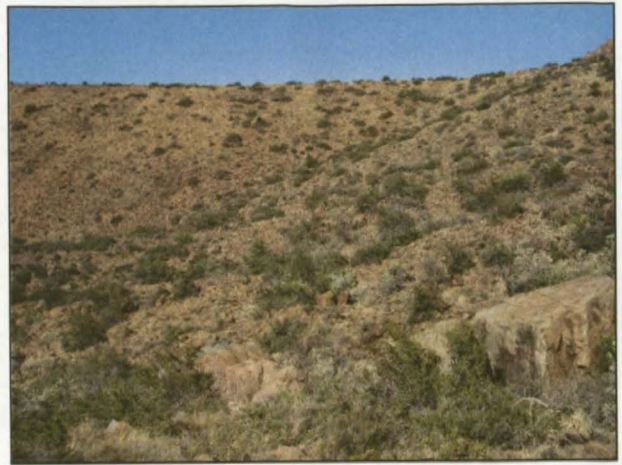


(a-3) Plantations (disturbed "mountain fynbos")

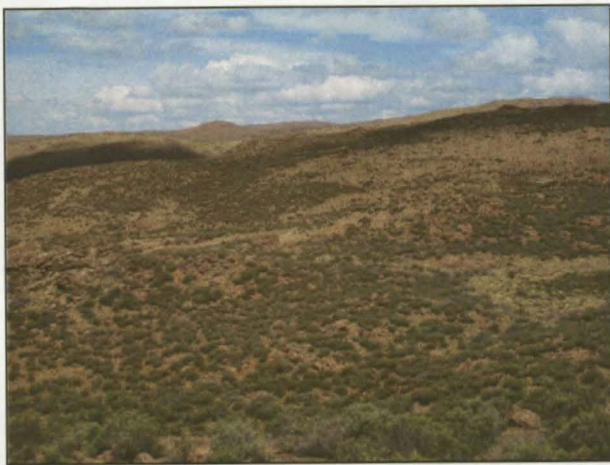




(b-1) Lowlands (in foreground)



(b-2) Slopes and middle plateau



(b-3) Plateau





(c-1) Natural mixed woodland



(c-2) Field cleared for agriculture  
(disturbed "mixed woodland")



(c-3) Natural sand forest



(c-4) Fallow field (disturbed "sand  
forest")

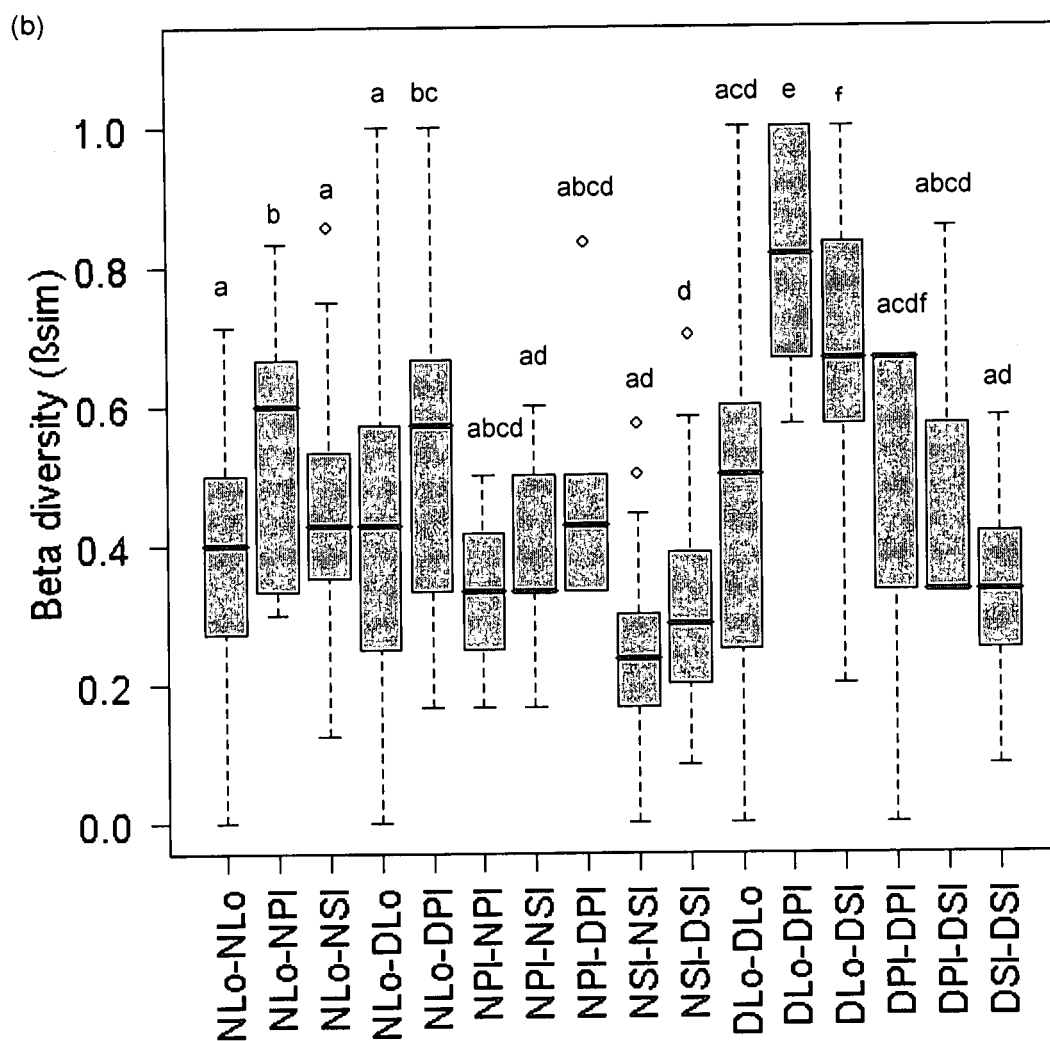
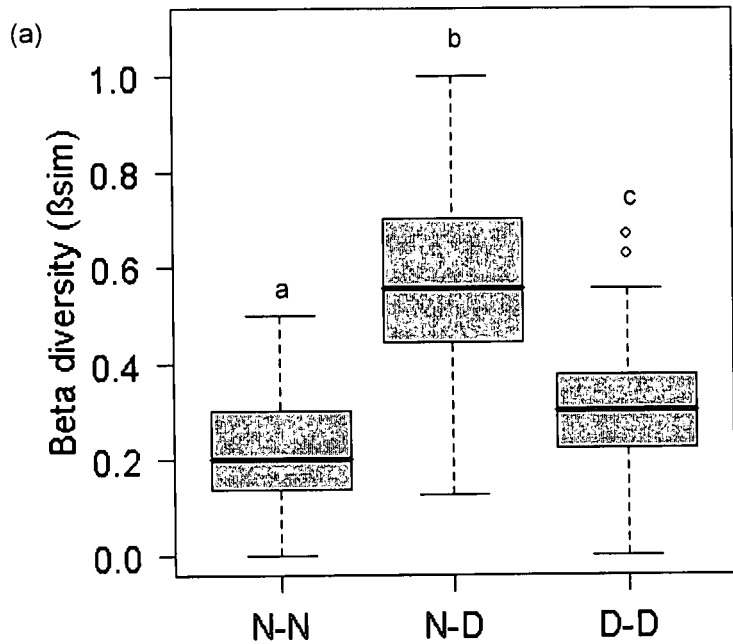
**Appendix 2.** Results from factorial generalized linear model ANOVAs and post-hoc ANOVAs comparing species richness (Jackknife2) between land-use types, vegetation types and sampling period in Jonkershoek, the Karoo and Tembe. Values in brackets are Jackknife2 values and their standard errors. Only significant results from post-hoc tests are given. Significant differences between comparable disturbed and natural transects (e.g. same land-use type/same year) have been italicized. (N = natural, D = disturbed, Slopes & MP = Slopes & Middle Plateau, MW = Mixed Woodland, SF = Sand Forest.)

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

Source	df	X <sup>2</sup>
<b>(a) Jonkershoek</b>		
Land use		
<i>N (9.69 ± 0.53) &gt; D (6.98 ± 0.43)</i>	1	20.65***
Year		
2005 (9.52 ± 0.51) > 2006 (7.16 ± 0.48)	1	16.05***
Land use*Year	1	2.36
Land use	1	3.21
<b>(b) Karoo</b>		
Land use	1	3.21
Vegetation Type	2	21.21***
Lowlands (11.82 ± 1.61) > Plateau (6.93 ± 1.02)	1	4.06*
Lowlands (11.82 ± 1.61) < Slopes & MP (17.41 ± 1.40)	1	11.3***
Plateau (6.93 ± 1.02) < Slopes & MP (17.41 ± 1.40)	1	15.26***

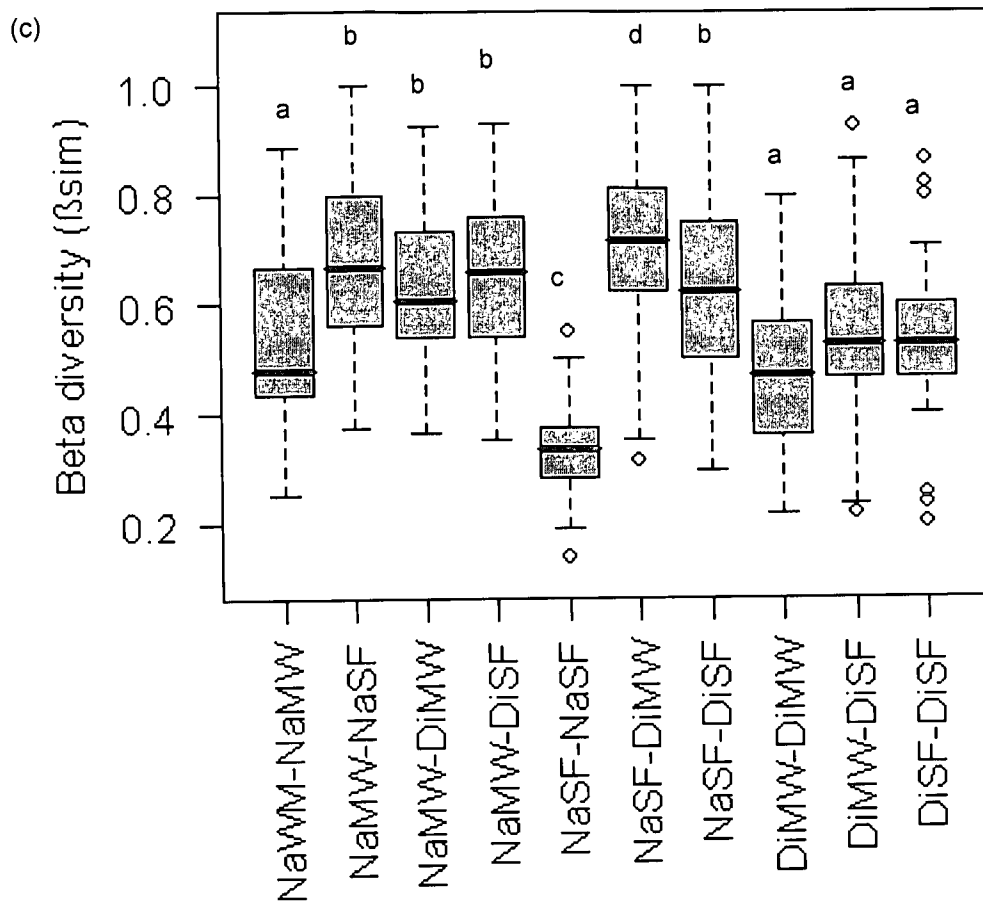
## Appendix 2 (continued)

Source	df	X <sup>2</sup>
<b>(b) Karoo (continued)</b>		
Land use*Vegetation Type	2	8.75*
N Lowlands (15.76 ± 2.64) > N Plateau (8.03 ± 1.51)	1	4.8*
N Lowlands (15.76 ± 2.64) > D Lowlands (7.87 ± 0.73)	1	12.78***
N Lowlands (15.76 ± 2.64) > D Plateau (5.84 ± 2.29)	1	7.85**
N Plateau (8.03 ± 1.51) < N Slopes & MP (16.63 ± 6.42)	1	5.35*
N Plateau (8.03 ± 1.51) < D Slopes & MP (18.19 ± 1.53)	1	6.84**
N Slopes & MP (16.63 ± 6.42) > D Lowlands (7.87 ± 0.73)	1	13.27***
N Slopes & MP (16.63 ± 6.42) > D Plateau (5.84 ± 2.29)	1	8.42**
D Lowlands (7.87 ± 0.73) < D Slopes & MP (18.19 ± 1.53)	1	17.23***
D Plateau (5.84 ± 2.29) < D Slopes & MP (18.19 ± 1.53)	1	10.04**
<b>(c) Tembe</b>		
Land use	1	1.84
Vegetation Type	1	1.7
Year	1	1.36
Land use*Vegetation Type	1	3.08
Vegetation Type*Year	1	4.9*
2005 MW (13.44 ± 1.19) < 2005 SF (18.04 ± 1.02)	1	6.5*
2005 SF (18.04 ± 1.02) > 2006 SF (13.66 ± 0.91)	1	6.03*
Land use*Year	1	8.22**
2005 N (16.85 ± 1.48) > 2006 N (11.89 ± 0.83)	1	7.65**
2006 N (11.89 ± 0.83) < 2006 D (16.80 ± 1.16)	1	8.51**
Land use*Vegetation Type*Year	1	0.02



Appendix 3 (see next page for figure title)





**Appendix 3.**  $\beta_{sim}$  values between transects of different combinations of land-use types and vegetation types in (a) Jonkershoek, (b) the Karoo and (c) Tembe. Significant differences between values as calculated from generalized linear models are indicated by letters above the bars. (N/Na = natural, D/Di = disturbed, Lo = lowlands, PI = plateau, SI = slopes and middle plateau, MW = mixed woodland, SF = sand forest). Upper and lower bounds of the boxes represent 75% and 25% quartiles respectively, and whiskers 95% confidence intervals.

**Appendix 4.** Differences between the proportion of species of feeding guilds between natural (N) and disturbed (D) areas in three South African regions. For the Tembe dataset, differences between vegetation types ([Veg Type]: mixed woodland [MW] and sand forest [SF]) were also assessed. (% DE = percentage deviance explained.) Significance values calculated from generalized linear models are indicated. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

	Scaled Dev/df	N	df	X <sup>2</sup>	Effect	% DE
<b>Jonkershoek</b>						
Frugivore	1.00	32	1	1.91		
Granivore	1.00	32	1	22.87***	N < D	45 %
Insectivore	1.00	32	1	20.43***	N > D	41 %
Mixed	1.00	32	1	7.28**	N < D	20 %
Nectarivore	1.00	32	1	21.40***	N > D	44 %
<b>Karoo</b>						
Frugivore	1.00	40	1	1.42		
Granivore	1.00	40	1	1.20		
Insectivore	1.00	40	1	0.53		
Mixed	1.00	40	1	4.40*	N > D	10 %

## Appendix 4 (continued)

	Scaled Dev/df	N	df	X <sup>2</sup>	Effect	% DE
<b>Tembe</b>						
Frugivore	1.00	40	1			17 %
Land use				0.04		
Veg Type				5.94*	MW < SF	
Land use* Veg Type				1.26		
Granivore	1.00	40	1			53 %
Land use				22.40***	N < D	
Veg Type				3.15		
Land use* Veg Type				0.83		
Insectivore	1.00	40	1			42 %
Land use				23.95***	N > D	
Veg Type				2.39		
Land use* Veg Type				0.31		
Mixed	1.00	40	1			23 %
Land use				6.89**	N < D	
Veg Type				0.00		
Land use* Veg Type				3.63		
Predator	1.00	40	1			14 %
Land use				0.03		
Veg Type				4.85*	MW < SF	
Land use* Veg Type				0.58		

**Appendix 5.** Abundance of bird species recorded in natural areas (N) in Jonkershoek Nature Reserve and in disturbed areas (D) outside the reserve.

Common Name	Scientific Name	Spring 2005		Autumn 2006	
		N	D	N	D
African Dusky Flycatcher	<i>Muscicapa adusta</i>	22	110	4	33
African Goshawk	<i>Accipiter tachiro</i>	0	2	0	0
African Olive-Pigeon	<i>Columba arquatrix</i>	0	13	1	23
Bar-throated Apalis	<i>Apalis thoracica</i>	5	0	1	0
Bokmakierie	<i>Telophorus zeylonus</i>	0	1	1	0
Cape Batis	<i>Batis capensis</i>	10	6	1	0
Cape Bulbul	<i>Pycnonotus capensis</i>	18	0	13	1
Cape Canary	<i>Serinus canicollis</i>	3	111	0	8
Cape Grassbird	<i>Sphenoeacus afer</i>	55	6	25	0
Cape Robin-Chat	<i>Cossypha caffra</i>	27	10	32	2
Cape Rock-Thrush	<i>Monticola rupestris</i>	1	0	0	0
Cape Siskin	<i>Crithagra totta</i>	3	90	1	48
Cape Spurfowl	<i>Pternistis capensis</i>	1	0	0	0
Cape Sugarbird	<i>Promerops cafer</i>	64	0	117	0
Cape Turtle-Dove	<i>Streptopelia capicola</i>	0	3	2	0
Cape White-eye	<i>Zosterops virens</i>	62	112	11	72
Cloud Cisticola	<i>Cisticola textrix</i>	1	0	0	0
Common Waxbill	<i>Estrilda astrild</i>	6	0	0	0
Fiscal Flycatcher	<i>Sigelus silens</i>	0	4	2	0
Forest Buzzard	<i>Buteo trizonatus</i>	0	0	0	1
Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	3	8	0	11
Greater Honeyguide	<i>Indicator indicator</i>	1	0	0	0
Grey-backed Cisticola	<i>Cisticola subruficapilla</i>	2	3	0	0
Karoo Prinia	<i>Prinia maculosa</i>	50	0	33	2
Lesser Swamp-Warbler	<i>Acrocephalus gracilirostris</i>	0	0	1	0
Malachite Sunbird	<i>Nectarinia famosa</i>	18	54	19	1
Neddicky	<i>Cisticola fulvicapilla</i>	51	20	15	18
Olive Thrush	<i>Turdus olivaceus</i>	0	17	0	9
Olive Woodpecker	<i>Dendropicos griseocephalus</i>	4	1	3	1

## Appendix 5 (continued)

Common Name	Scientific Name	Spring 2005		Autumn 2006	
		N	D	N	D
Orange-breasted Sunbird	<i>Anthobaphes violacea</i>	176	4	217	9
Protea Seedeater	<i>Crithagra leucopterus</i>	7	0	9	0
Red-chested Cuckoo	<i>Cuculus solitarius</i>	0	1	0	0
Southern Boubou	<i>Laniarius ferrugineus</i>	4	0	0	1
Southern Double-collared Sunbird	<i>Cinnyris chalybeus</i>	0	0	6	0
Speckled Mousebird	<i>Colius striatus</i>	7	0	0	0
Speckled Pigeon	<i>Columba guinea</i>	0	3	0	0
Victorin's Warbler	<i>Cryptillas victorini</i>	41	0	16	0
Yellow Bishop	<i>Euplectes capensis</i>	15	0	12	0
Species Richness		27	21	23	16
Total Abundance		657	579	542	240

**Appendix 6.** Abundance of bird species recorded in three vegetation types in natural areas in the Karoo National Park and in disturbed areas outside the park. (Lo = lowlands, PI = plateau, SI = slopes & middle plateau)

Common Name	Scientific Name	Natural			Disturbed		
		Lo	PI	SI	Lo	PI	SI
Acacia Pied Barbet	<i>Tricholaema leucomelas</i>	1	0	0	0	0	0
African Pipit	<i>Anthus cinnamomeus</i>	0	0	0	0	0	5
African Red-eyed Bulbul	<i>Pycnonotus nigricans</i>	2	0	2	0	0	4
African Rock Pipit	<i>Anthus crenatus</i>	0	1	11	0	0	18
Ant-eating Chat	<i>Myrmecocichla formicivora</i>	1	0	0	2	0	0
Black-headed Canary	<i>Serinus alario</i>	0	0	12	0	0	4
Bokmakierie	<i>Telophorus zeylonus</i>	6	4	5	0	1	9
Cape Bunting	<i>Emberiza capensis</i>	16	11	48	2	6	30
Cape Clapper Lark	<i>Mirafrapa apiata</i>	2	0	0	1	0	0
Cape Penduline-Tit	<i>Anthoscopus minutus</i>	0	1	0	0	0	0
Cape Sparrow	<i>Passer melanurus</i>	1	0	0	0	1	0
Cape Turtle-Dove	<i>Streptopelia capicola</i>	5	0	0	0	0	1
Chat Flycatcher	<i>Bradornis infuscatus</i>	1	0	0	0	0	0
Chestnut-vented Tit-Babbler	<i>Parisoma subcaeruleum</i>	4	0	2	1	0	0
Cinnamon-breasted Bunting	<i>Emberiza tahapisi</i>	0	0	0	0	0	1
Common Fiscal	<i>Lanius collaris</i>	2	0	2	2	0	3
Double-banded Courser	<i>Rhinoptilus africanus</i>	0	0	0	3	0	0
Dusky Sunbird	<i>Cinnyris fuscus</i>	13	0	16	0	0	4
European Bee-eater	<i>Merops apiaster</i>	2	0	0	0	0	0
Fairy Flycatcher	<i>Stenostira scita</i>	12	0	22	0	0	12
Familiar Chat	<i>Cercomela familiaris</i>	10	1	10	0	0	15
Fiscal Flycatcher	<i>Sigelus silens</i>	5	0	2	0	0	0
Grey-backed Cisticola	<i>Cisticola subruficapilla</i>	22	76	92	5	23	69
Grey-backed Sparrowlark	<i>Eremopterix verticalis</i>	22	0	0	54	0	2
Grey-winged Francolin	<i>Scleroptila africanus</i>	10	37	0	0	0	0
Ground Woodpecker	<i>Geocolaptes olivaceus</i>	0	0	5	0	0	1
Karoo Chat	<i>Cercomela schlegelii</i>	23	0	6	12	0	2
Karoo Eremomela	<i>Eremomela gregalis</i>	4	0	1	0	0	0



## Appendix 6 (continued)

Common Name	Scientific Name	Natural			Disturbed		
		Lo	PI	SI	Lo	PI	SI
Karoo Korhaan	<i>Eupodotis vigorsii</i>	5	0	0	4	0	0
Karoo Lark	<i>Calendulauda albescens</i>	4	0	0	0	0	0
Karoo Prinia	<i>Prinia maculosa</i>	8	21	12	0	3	9
Karoo Scrub-Robin	<i>Cercotrichas coryphoeus</i>	19	4	9	0	1	22
Large-billed Lark	<i>Galerida magnirostris</i>	6	0	0	4	10	0
Lark-like Bunting	<i>Emberiza impetuani</i>	131	2	129	55	0	61
Laughing Dove	<i>Streptopelia senegalensis</i>	3	0	0	0	0	0
Layard's Tit-Babbler	<i>Parisoma layardi</i>	9	0	23	0	0	24
Long-billed Crombec	<i>Sylvietta rufescens</i>	3	0	4	1	0	2
Long-billed Pipit	<i>Anthus similis</i>	0	1	0	0	4	0
Malachite Sunbird	<i>Nectarinia famosa</i>	2	0	2	0	0	4
Mountain Wheatear	<i>Oenanthe monticola</i>	2	0	28	0	0	9
Namaqua Dove	<i>Oena capensis</i>	1	0	0	0	0	0
Namaqua Sandgrouse	<i>Pterocles namaqua</i>	2	0	0	0	0	0
Pale-winged Starling	<i>Onychognathus nabouroup</i>	0	0	3	0	0	13
Plain-backed Pipit	<i>Anthus leucophrys</i>	2	0	0	0	0	4
Pirit Batis	<i>Batis pirit</i>	0	0	2	0	0	1
Red-backed Shrike	<i>Lanius collurio</i>	0	0	2	0	0	0
Red-faced Mousebird	<i>Urocolius indicus</i>	1	0	2	0	0	1
Red-winged Starling	<i>Onychognathus morio</i>	0	0	0	0	9	0
Rock Kestrel	<i>Falco rupicolus</i>	0	0	0	0	0	4
Rufous-eared Warbler	<i>Malcorus pectoralis</i>	69	0	17	50	11	6
Sabota Lark	<i>Calendulauda sabota</i>	9	0	0	1	0	0
Short-toed Rock-Thrush	<i>Monticola brevipes</i>	0	0	7	0	0	6
Sickle-winged Chat	<i>Cercomela sinuata</i>	12	5	17	11	12	9
Southern Double-collared Sunbird	<i>Cinnyris chalybeus</i>	1	0	2	0	0	4
Southern Masked-Weaver	<i>Ploceus velatus</i>	15	0	0	0	0	0
Southern Pale Chanting Goshawk	<i>Melierax canorus</i>	2	0	0	0	0	0
Speckled Pigeon	<i>Columba guinea</i>	0	0	0	0	0	1
Spike-heeled Lark	<i>Chersomanes albofasciata</i>	17	5	0	29	0	0

## Appendix 6 (continued)

Common Name	Scientific Name	Natural			Disturbed		
		Lo	PI	SI	Lo	PI	SI
Tractrac Chat	<i>Cercomela tractrac</i>	1	0	0	7	0	0
White-backed Mousebird	<i>Colius colius</i>	3	0	18	0	0	12
White-throated Canary	<i>Crithagra albogularis</i>	7	0	16	1	0	1
Yellow Canary	<i>Crithagra flaviventris</i>	4	0	0	2	0	0
Yellow-bellied Eremomela	<i>Eremomela icteropygialis</i>	20	0	0	6	0	0
Species Richness		48	13	32	21	11	35
Total Abundance		522	169	529	253	81	373

**Appendix 7.** Abundance of bird species recorded in two vegetation types in natural areas in Tembe Elephant Park and in disturbed areas outside the park. (MW = mixed woodland, SF = sand forest)

Common Name	Scientific Name	2005 Summer				2006 Autumn			
		Natural		Disturbed		Natural		Disturbed	
		MW	SF	MW	SF	MW	SF	MW	SF
African Broadbill	<i>Smithornis capensis</i>	0	1	0	0	0	1	1	0
African Dusky Flycatcher	<i>Muscicapa adusta</i>	0	1	0	3	0	0	0	0
African Goshawk	<i>Accipiter tachiro</i>	0	1	0	0	0	0	0	0
African Green-Pigeon	<i>Treron calvus</i>	0	0	0	12	2	0	0	0
African Paradise-Flycatcher	<i>Terpsiphone viridis</i>	0	0	0	0	0	0	1	1
African Yellow White-eye	<i>Zosterops senegalensis</i>	0	0	0	4	6	0	0	8
Ashy Flycatcher	<i>Muscicapa caerulescens</i>	0	0	0	0	0	3	1	3
Barn Swallow	<i>Hirundo rustica</i>	766	0	0	117	0	0	0	0
Bearded Scrub-Robin	<i>Cercotrichas quadrivirgata</i>	13	16	0	0	1	19	1	2
Bennett's Woodpecker	<i>Campethera bennettii</i>	1	0	0	0	0	0	0	0
Black Cuckooshrike	<i>Campephaga flava</i>	0	1	1	3	0	0	1	1
Black-backed Puffback	<i>Dryoscopus cubla</i>	8	9	6	12	6	8	9	6
Black-bellied Starling	<i>Lamprotomis corruscus</i>	0	33	7	13	0	5	0	1
Black-collared Barbet	<i>Lybius torquatus</i>	0	0	0	0	2	0	0	0
Black-crowned Tchagra	<i>Tchagra senegalus</i>	1	0	0	0	1	0	0	0
Blue Waxbill	<i>Uraeginthus angolensis</i>	0	0	1	11	0	0	28	59
Blue-mantled Crested-Flycatcher	<i>Trochocercus cyanomelas</i>	0	8	0	0	0	7	0	1
Brimstone Canary	<i>Crithagra sulphuratus</i>	0	0	4	0	0	0	8	0
Broad-billed Roller	<i>Eurystomus glaucurus</i>	0	0	0	5	0	0	0	0
Bronze Mannikin	<i>Spermestes cucullatus</i>	0	0	28	6	0	0	117	3
Brown Scrub-Robin	<i>Cercotrichas signata</i>	0	4	0	0	0	7	0	0
Brown-crowned Tchagra	<i>Tchagra australis</i>	0	0	3	0	0	0	6	1
Brown-hooded Kingfisher	<i>Halcyon albiventris</i>	0	0	0	0	1	0	2	9
Burchell's Coucal	<i>Centropus burchellii</i>	0	1	0	0	0	0	1	0
Cape Turtle-Dove	<i>Streptopelia capicola</i>	0	0	0	0	0	2	1	0
Cape Weaver	<i>Ploceus capensis</i>	0	0	0	0	0	0	2	1
Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	1	0	0	1	0	0	3	0

## Appendix 7 (continued)

Common Name	Scientific Name	2005 Summer				2006 Autumn			
		Natural		Disturbed		Natural		Disturbed	
		MW	SF	MW	SF	MW	SF	MW	SF
Cattle Egret	<i>Bubulcus ibis</i>	0	0	0	1	0	0	0	3
Chin-spot Batis	<i>Batis molitor</i>	17	2	0	0	8	0	4	0
Chorister Robin-Chat	<i>Cossypha dichroa</i>	0	1	0	0	0	0	0	0
Collared Sunbird	<i>Hedypna collaris</i>	2	5	1	3	9	6	10	8
Common Scimitarbill	<i>Rhinopomastus cyanomelas</i>	0	0	0	0	2	0	0	0
Crested Francolin	<i>Dendroperdix sephaena</i>	1	1	0	0	0	2	0	0
Crested Guinea-fowl	<i>Guttera edouardi</i>	4	19	0	0	0	0	0	0
Croaking Cisticola	<i>Cisticola natalensis</i>	1	0	1	0	0	0	0	0
Crowned Hornbill	<i>Tockus alboterminatus</i>	2	3	0	2	3	2	2	2
Dark-backed Weaver	<i>Ploceus bicolor</i>	0	25	0	0	2	26	1	4
Dark-capped Bulbul	<i>Pycnonotus tricolor</i>	27	22	36	43	30	0	39	24
Diderick Cuckoo	<i>Chrysococcyx caprius</i>	0	0	0	1	0	0	0	0
Eastern Nicator	<i>Nicator gularis</i>	0	15	0	1	11	9	0	1
Emerald-spotted Dove	Wood- <i>Turtur chalcospilos</i>	5	8	11	8	2	1	11	22
European Bee-eater	<i>Merops apiaster</i>	0	0	0	3	0	0	0	0
Fiscal Flycatcher	<i>Sigelus silens</i>	0	0	0	0	1	0	0	0
Flappet Lark	<i>Mirafra rufocinnamomea</i>	1	0	0	0	0	0	0	0
Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	0	1	0	1	1	0	0	0
Golden-breasted Bunting	<i>Emberiza flaviventris</i>	1	0	3	1	0	0	0	1
Golden-tailed Woodpecker	<i>Campethera abingoni</i>	0	0	0	0	0	1	1	0
Gorgeous Bush-Shrike	<i>Telophorus viridis</i>	0	9	0	0	0	1	0	0
Green Wood-Hoopoe	<i>Phoeniculus purpureus</i>	0	0	0	0	3	6	6	0
Green-backed Camaroptera	<i>Camaroptera brachyura</i>	26	25	8	4	12	7	10	10
Grey Sunbird	<i>Cyanomitra veroxii</i>	0	4	0	0	0	0	0	1
Grey Waxbill	<i>Estrilda perreini</i>	0	0	2	0	2	0	7	0
Grey-headed Bush-Shrike	<i>Malaconotus blanchoti</i>	0	5	0	0	0	1	1	2
Hadeda Ibis	<i>Bostrychia hagedash</i>	0	2	0	0	0	0	0	0
House Sparrow	<i>Passer domesticus</i>	0	0	2	0	0	0	0	9
Icterine Warbler	<i>Hippolais icterina</i>	4	0	4	0	0	0	0	0

## Appendix 7 (continued)

Common Name	Scientific Name	2005 Summer				2006 Autumn			
		Natural		Disturbed		Natural		Disturbed	
		MW	SF	MW	SF	MW	SF	MW	SF
Jameson's Firefinch	<i>Lagonosticta rhodopareia</i>	0	0	0	0	0	0	4	4
Klaas's Cuckoo	<i>Chrysococcyx klaas</i>	0	0	0	1	0	0	0	0
Kurrichane Thrush	<i>Turdus libonyanus</i>	0	4	1	12	0	0	6	4
Lesser Honeyguide	<i>Indicator minor</i>	0	0	0	0	0	1	1	0
Lilac-breasted Roller	<i>Coracias caudatus</i>	0	0	0	1	0	0	0	2
Lizard Buzzard	<i>Kaupifalco monogrammicus</i>	0	0	0	1	0	0	0	0
Long-billed Crombec	<i>Sylvietta rufescens</i>	6	0	5	0	5	0	2	2
Marico Sunbird	<i>Cinnyris mariquensis</i>	2	0	0	1	0	1	0	0
Narina Trogon	<i>Apaloderma narina</i>	0	2	0	0	0	0	0	0
Neddicky	<i>Cisticola fulvicapilla</i>	2	0	0	0	6	0	0	0
Neergaard's Sunbird	<i>Cinnyris neergaardi</i>	1	11	0	0	0	0	0	0
Olive Bush-Shrike	<i>Telophorus olivaceus</i>	0	1	0	0	0	0	0	0
Olive Sunbird	<i>Cyanomitra olivacea</i>	0	4	0	0	0	0	0	0
Orange-breasted Shrike	Bush- <i>Telophorus sulfureopectus</i>	1	0	1	2	1	0	2	2
Pale Flycatcher	<i>Bradornis pallidus</i>	3	1	14	5	5	0	18	0
Pink-throated Twinspot	<i>Hypargos margaritatus</i>	0	2	0	2	7	2	9	3
Plain-backed Sunbird	<i>Anthreptes reichenowi</i>	0	4	0	0	0	0	0	0
Purple-banded Sunbird	<i>Cinnyris bifasciatus</i>	22	2	12	9	0	0	0	0
Purple-crested Turaco	<i>Gallirex porphyreolophus</i>	2	3	2	2	0	0	0	0
Rattling Cisticola	<i>Cisticola chiniana</i>	56	0	22	3	18	0	22	2
Red-backed Mannikin	<i>Spermestes bicolor</i>	0	0	0	0	0	0	0	63
Red-backed Shrike	<i>Lanius collurio</i>	2	0	2	1	0	0	0	0
Red-billed Firefinch	<i>Lagonosticta senegala</i>	0	0	0	3	3	0	19	3
Red-capped Robin-Chat	<i>Cossypha natalensis</i>	0	4	1	2	2	1	1	0
Red-chested Cuckoo	<i>Cuculus solitarius</i>	0	8	0	1	0	0	0	0
Red-eyed Dove	<i>Streptopelia semitorquata</i>	1	0	16	11	0	5	9	13
Red-faced Mousebird	<i>Urocolius indicus</i>	0	0	1	2	0	0	0	0
Red-fronted Tinkerbird	<i>Pogoniulus pusillus</i>	0	0	2	1	0	1	0	0
Retz's Helmet-Shrike	<i>Prionops retzii</i>	0	11	4	0	0	0	0	0

## Appendix 7 (continued)

Common Name	Scientific Name	2005 Summer				2006 Autumn			
		Natural		Disturbed		Natural		Disturbed	
		MW	SF	MW	SF	MW	SF	MW	SF
Rudd's Apalis	<i>Apalis ruddi</i>	0	0	0	0	7	2	0	0
Rufous-naped Lark	<i>Mirafrwa africana</i>	4	0	0	0	0	0	0	0
Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	1	2	0	2	0	0	0	6
Sombre Greenbul	<i>Andropadus importunus</i>	6	14	13	17	14	11	2	3
Southern Black Flycatcher	<i>Melaenomis pammelaina</i>	1	0	3	8	5	0	17	5
Southern Black Tit	<i>Parus niger</i>	4	3	2	3	11	3	5	2
Southern Boubou	<i>Laniarius ferrugineus</i>	0	6	0	0	0	2	3	1
Southern Grey-headed Sparrow	<i>Passer diffusus</i>	0	0	1	21	0	0	0	24
Speckled Mousebird	<i>Colius striatus</i>	0	0	16	1	0	0	10	0
Spectacled Weaver	<i>Ploceus ocularis</i>	0	0	0	0	0	0	3	0
Spotted Flycatcher	<i>Muscicapa striata</i>	2	0	3	0	0	0	0	0
Square-tailed Drongo	<i>Dicrurus ludwigii</i>	5	44	5	8	5	33	8	7
Streaky-headed Seedeater	<i>Crithagra gularis</i>	1	0	0	0	0	0	0	0
Striped Kingfisher	<i>Halcyon chelicuti</i>	1	0	0	3	0	0	0	0
Tambourine Dove	<i>Turtur tympanistria</i>	0	8	1	0	0	0	0	0
Tawny-flanked Prinia	<i>Prinia subflava</i>	8	0	9	1	3	0	24	8
Terrestrial Brownbul	<i>Phyllastrephus terrestris</i>	0	19	0	6	1	2	7	5
Thick-billed Weaver	<i>Amblyospiza albifrons</i>	0	0	0	5	0	0	0	0
Village Indigobird	<i>Vidua chalybeata</i>	0	0	0	0	0	0	0	3
Village Weaver	<i>Ploceus cucullatus</i>	0	0	33	0	0	0	7	48
Violet-backed Starling	<i>Cinnyricinclus leucogaster</i>	0	2	4	56	0	0	0	0
White-bellied Sunbird	<i>Cinnyris talatala</i>	10	0	21	8	0	0	12	1
White-browed Scrub-Robin	<i>Cercotrichas leucophrys</i>	8	0	0	0	5	0	2	0
White-crested Helmet-Shrike	<i>Prionops plumatus</i>	0	0	0	0	6	0	0	0
White-throated Robin-Chat	<i>Cossypha humeralis</i>	0	2	0	0	0	0	3	0
Woodwards' Batis	<i>Batis fratrum</i>	1	10	0	0	0	9	0	1
Yellow Weaver	<i>Ploceus subaureus</i>	1	0	1	0	0	0	0	0
Yellow-bellied Eremomela	<i>Eremomela icteropygialis</i>	1	0	0	0	0	0	0	0



## Appendix 7 (continued)

Common Name	Scientific Name	2005 Summer				2006 Autumn			
		Natural		Disturbed		Natural		Disturbed	
		MW	SF	MW	SF	MW	SF	MW	SF
Yellow-bellied Greenbul	<i>Chlorocichla flaviventris</i>	3	59	3	1	5	23	2	6
Yellow-breasted Apalis	<i>Apalis flavida</i>	12	27	2	6	27	42	15	9
Yellow-fronted Canary	<i>Crithagra mozambicus</i>	7	0	32	19	4	1	64	26
Yellow-rumped Tinkerbird	<i>Pogoniulus bilineatus</i>	0	0	1	0	0	0	1	0
Yellow-throated Longclaw	<i>Macronyx croceus</i>	2	0	0	0	1	0	0	0
Yellow-throated Petronia	<i>Petronia supercilialis</i>	0	0	0	2	0	0	2	3
Zitting Cisticola	<i>Cisticola juncidis</i>	0	0	0	0	1	0	1	0
Species Richness		48	51	46	57	42	35	56	52
Total Abundance		1057	475	351	482	247	253	555	439

# Chapter 4

## General Conclusion

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I have here considered the response of avian assemblages to the environmental conditions acting on two different time scales. In Chapter 2 I examined the response of the body size of avian assemblages to environmental conditions over an evolutionary time scale. Because it is central to many aspects of an organism's ecology and physiology, body size is likely under selection (McKinney 1990). Indeed, most studies of large-scale variation of body size in multi-species assemblages (e.g. Zeweloff and Boyce 1988, Blackburn and Gaston 1996, Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006) have examined how size correlates with environmental predictors to examine how environmental conditions may produce existing patterns of body size variation.

In a review of the potential application of null model analyses, Gotelli (2001) suggested that null models should also be used in macroecological studies to determine probabilistic boundaries beyond which real data points cannot occur. In accordance, random draw models have been used extensively to test the mid-domain hypothesis of species ranges (see Colwell and Lees 2000, Zapata et al. 2003, Colwell et al. 2004, Zapata et al. 2005). The ability of null models to predict the size of faunal assemblages has also been assessed (Brown and Nicoletto 1991, Arita and Figueroa 1999, Marquet and Cofré 1999, Bakker and Kelt 2000, Blackburn and Gaston 2001). However, few studies have employed random draw models to assess how much geographic variation in body size measures might deviate from a random expectation (Cardillo 2002, Rodríguez et al. 2006, Ulrich 2006). Here I compared how much of variation in median body size of avian assemblages in South Africa could be explained by (a) deterministic models, which are generally used to test the

role of environmental factors in driving body size variation, and (b) random sampling from the regional body size frequency distribution. I showed that, although there was some support that large body size confers starvation resistance during seasonally unfavourable periods (Rosenzweig 1968, Lindstedt and Boyce 1985), much of the variation in body size could be explained by random draw models, especially at high richness values. The ability of null models to predict median size was weak at low richness, but increases with species richness. To my knowledge, this is the first study to empirically test how the ability of random draw models to predict size changes with richness.

I recommend that, in addition to deterministic models usually employed, the use of null models to assess body size variation becomes standard practice. By employing null models alongside traditional techniques that relate abiotic or biotic factors to life history characteristics of organisms, the manner in which both neutral (Hubbell 1997, 2001) and niche-based processes (Leibold et al. 2001, Gravel et al. 2006) operate in a system can be explored (see Alonso et al. 2006), as was done here. In a review of neutral theory, Chave (2004) stated, "Further improvements should lead to an explicit linking (of neutral theory) to niche-based processes. This research programme will depend crucially on forthcoming theoretical and empirical achievements". Several authors have tested such theoretical models that integrate niche and neutral processes with simulations (Etienne and Olf 2004, Gravel et al. 2006, Leibold and McPeck 2006, Scheffer and van Nes 2006), though empirical evidence has at times been lacking (but see Etienne and Olf 2004, Scheffer and van Nes 2006). Here I found empirical support for Gravel et al.'s (2006) continuum hypothesis uniting niche and neutral theory, which suggests that niche-based processes become less evident as species richness increases.

Although van Rensburg et al. (2004) found that landscape transformation had no effect on species turnover in South African avian assemblages, and therefore concluded that, at this scale, underlying biogeographical patterns persist for birds, it is unlikely that only evolutionary and stochastic processes act on bird assemblages. At smaller spatial scales the effects of non-evolutionary deterministic processes on assemblages may be detected. Therefore, while Chapter 2 focussed on evolutionary and stochastic processes in avian assemblages, Chapter 3 examined the response of assemblages to environmental conditions, more specifically human-induced conditions, over a significantly shorter time scale. Land-use changes are happening at an alarming rate world-wide (Vitousek et al. 1997), and the rate of change is of such a nature that many organisms cannot adapt to new conditions and are suffering population declines or local extinction as they cannot subsist in the altered environment (e.g. Kerr and Currie 1995, McKee et al. 2003, Thomas et al. 2004). Because birds comprise one of the taxa which is least sensitive to land-use changes, they provide a conservative estimate of the effects of disturbance on biodiversity (Şekercioğlu et al. 2004). However, birds fulfil important ecological functions (Şekercioğlu 2006) and changes in avian assemblages may result in effects cascading to other species and to processes in the ecosystem.

I assessed the effect of different anthropogenic land-use changes on avian assemblages in three regions of South Africa. In all regions, bird assemblages were affected by these changes, although the consequences of disturbance were not consistent across regions. Species richness of disturbed transects was greater, smaller and not significantly different to richness of natural transects, but regional richness increased due to habitat heterogeneity: natural and disturbed areas supported different assemblages. This observation allowed me to examine species richness trends previously assessed at larger spatial scale and grain (Fairbanks

2004, van Rensburg et al. 2004, Evans et al. 2006a). In addition, the carrying capacity for birds of landscapes in two of the regions decreased with disturbance. I also showed how functional diversity, particularly feeding guilds, was affected by land-use changes. One of the effects of disturbance on functional diversity was the decline of insectivores in two of the regions sampled. This indicates that disturbance is probably causing declines in insect abundance, and possibly diversity (see also Şekercioğlu et al. 2004). Indeed, bird declines have been directly linked to decreases in insect abundance (Sinclair et al. 2002, Barker 2004, Newton 2004). This suggests that the potential exists for insectivores to be used as indicators of trends in insect assemblages, both in time and over space, although it remains to be determined whether changes in insectivore abundances reflect changes in insect diversity or abundance or both.

A strength of this study is that it examines the effects of land-use change on avian assemblages for several regions in South Africa which differ in their climate, vegetation, land use and biodiversity. This allows for approximations of the effect of land-use change to be made. The study therefore makes a valuable contribution to determining the consequences of human activities on, but also the contribution of protected areas to avian assemblages, which were previously not consistently assessed in South Africa. Indeed, as the country's human population is growing (Statistics South Africa 2006, see also Evans et al. 2006b) and anthropogenic pressure on untransformed areas is expected to increase in years to come (Wessels et al. 2003), it is vital to prioritise conservation early to maximise the biodiversity conserved and to prevent the need to conduct costly remedial action when much damage has already been done (Fuller et al. 2007). Currently, approximately six percent of South Africa's terrestrial surface enjoys formal protection, although it has been recommended that this area be expanded to better represent the range of

South Africa's biodiversity (Driver et al. 2005). Here I show that the benefits of protected areas extend beyond the conservation of species to the preservation of functional diversity and therefore ecological processes – one of the priorities for biodiversity planning in South Africa (Driver et al. 2005). It is therefore essential that South Africa continues to identify and protect areas of conservation importance that are threatened by land-use changes (Wessels et al. 2000, Fairbanks et al. 2001, Wessels et al. 2003, Department: Environmental Affairs and Tourism 2005, Scholes and Biggs 2005) to prevent the local or complete extinction of indigenous biota and the loss of essential ecosystem processes in these regions.

## References

- Alonso, D., R. S. Etienne, and A. J. McKane. 2006. The merits of neutral theory. *Trends in Ecology and Evolution* **21**:451-457.
- Arita, H. T., and F. Figueroa. 1999. Geographic patterns of body-mass diversity in Mexican mammals. *Oikos* **85**:310-319.
- Bakker, V. J., and D. A. Kelt. 2000. Scale-dependent patterns in body size distributions of neotropical mammals. *Ecology* **81**:3530-3547.
- Barker, A. M. 2004. Insects as food for farmland birds - is there a problem? Pages 37-49 *in* H. F. van Emden and M. Rothschild, editors. *Insect and Bird Interactions*. Intercept Limited, Andover.
- Blackburn, T. M., and K. J. Gaston. 1996. Spatial patterns in the body sizes of bird species in the New World. *Oikos* **77**:436-446.
- Blackburn, T. M., and K. J. Gaston. 2001. Local avian assemblages as random draws from regional pools. *Ecography* **24**:50-58.
- Blackburn, T. M., and B. A. Hawkins. 2004. Bergmann's rule and the mammal fauna of northern North America. *Ecography* **27**:715-724.



- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist* **138**:1478-1512.
- Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecology and Biogeography* **11**:59-65.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* **7**:241-253.
- Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* **15**:70-76.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* **163**:E1-E23.
- Department: Environmental Affairs and Tourism. 2005. South Africa's National Biodiversity Strategy and Action Plan. Department: Environmental Affairs and Tourism, South Africa, Pretoria.
- Driver, A., K. Maze, M. Rouget, A. T. Lombard, J. Nel, J. K. Turpie, R. M. Cowling, P. Desmet, P. Goodman, J. Harris, Z. Jonas, B. Reyers, K. Sink, and T. Strauss. 2005. National Spatial Biodiversity Assessment 2004: Priorities for Biodiversity Conservation in South Africa. *Strelitzia* 17, South African National Biodiversity Institute, Pretoria.
- Etienne, R. S., and H. Olf. 2004. How dispersal limitation shapes species-body size distributions in local communities. *American Naturalist* **163**:69-83.
- Evans, K. L., A. S. L. Rodrigues, S. L. Chown, and K. J. Gaston. 2006a. Protected areas and regional avian species richness in South Africa. *Biology Letters* **2**:184-188.

- Evans, K. L., B. J. van Rensburg, K. J. Gaston, and S. L. Chown. 2006b. People, species richness and human population growth. *Global Ecology and Biogeography* **15**:625-636.
- Fairbanks, D. H. K. 2004. Regional land-use impacts affecting avian richness patterns in Southern Africa - insights from historical avian atlas data. *Agriculture, Ecosystems and Environment* **101**:269-288.
- Fairbanks, D. H. K., B. Reyers, and A. S. van Jaarsveld. 2001. Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. *Biological Conservation* **98**:365-379.
- Fuller, T., V. Sánchez-Cordero, P. Iloldi-Rangel, M. Linaje, and S. Sarkar. 2007. The cost of postponing biodiversity conservation in Mexico. *Biological Conservation* **134**:593-600.
- Gotelli, N. J. 2001. Research frontiers in null model analysis. *Global Ecology and Biogeography* **10**:337-343.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* **9**:399-409.
- Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* **16**:S9-S21.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, 1st edition. Princeton University Press, Princeton.
- Kerr, J. T., and D. J. Currie. 1995. Effects of human activity on global extinction risk. *Conservation Biology* **9**:1528-1538.
- Leibold, M.A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004.

The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**: 601-613.

Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* **87**:1399-1410.

Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. *American Naturalist* **125**:873-878.

Marquet, P. A., and H. Cofré. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos* **85**:299-309.

McKee, J. K., P. W. Sciulli, C. D. Foote, and T. A. Waite. 2003. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* **115**:161-164.

McKinney, M. L. 1990. Trends in body-size evolution. Pages 75-118 *in* K. J. McNamara, editor. *Evolutionary Trends*. The University of Arizona Press, Tucson.

Newton, I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**:579-600.

Olalla-Tárraga, M. Á., M. Á. Rodríguez, and B. A. Hawkins. 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* **33**:781-793.

Rodríguez, M. Á., I. L. López-Sañudo, and B. A. Hawkins. 2006. The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography* **15**:173-181.

Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. *The American Midland Naturalist* **80**:299-315.

- Wessels, K. J., B. Reyers, and A. S. van Jaarsveld. 2000. Incorporating land cover information into regional biodiversity assessments in South Africa. *Animal Conservation* **3**:67-79.
- Wessels, K. J., B. Reyers, A. S. van Jaarsveld, and M. C. Rutherford. 2003. Identification of potential conflict areas between land transformation and biodiversity conservation in north-eastern South Africa. *Agriculture, Ecosystems and Environment* **95**:157-178.
- Zapata, F. A., K. J. Gaston, and S. L. Chown. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology* **72**:677-690.
- Zapata, F. A., K. J. Gaston, and S. L. Chown. 2005. The mid-domain effect revisited. *American Naturalist* **166**:E144-E148.
- Zeveloff, S. I., and M. S. Boyce. 1988. Body size patterns in North American mammal faunas. Pages 123-146 *in* M. S. Boyce, editor. *Evolution of Life Histories of Mammals: Theory and Pattern*. Yale University Press, New Haven.